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EDITORIAL

Vegetation Classification and Survey is performing well

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Abstract

On the occasion of the completion of the fourth volume of Vegetation Classification and Survey (VCS), we have analysed the performance of the journal since its inception. The number of papers and pages show a moderate increase over the years. VCS has been included in the Scopus database for more than a year and received its first CiteScore of 2.0 in summer 2023 but is not yet included in the Web of Science Core Edition. We therefore used data from the Scopus database to compare the citation impact of articles in VCS with that of 29 other ecological journals. By calculating normalized citation rates per journal and publication year, we found that VCS started at the bottom of the rankings in the first two years (28th out of 30) but improved to 26th in 2022 and 14th in 2023. Together with the known time lag and the strong positive relationships between the different citation metrics, this allows a projection of the future development of the CiteScores and, after inclusion in the Web of Science, the Journal Impact Factor (JIF). Using the Field-Weighted Citation Impact (FWCI) from the Scopus database, we identified the top 12 out of 95 VCS articles published in the first four years that received more citations than expected for their age and field. We also present the four Editors' Choice papers of 2023, among which Strohbach and Strohbach (2023; Vegetation Classification and Survey 4: 241–284) received the Editors' Award in 2023. We conclude that VCS is on the right track, supported by the fact that in 2024 most authors will still be charged no or very low article processing charges (APCs).

Abbreviations: APC = article processing charge; IAVS = International Association for Vegetation Science; JIF = Journal Impact Factor; OA = open access; VCS = Vegetation Classification and Survey; WoS = Web of Science Core Edition.

Keywords

article processing charge (APC), bibliometry, CiteScore, Field-Weighted Citation Impact (FWCI), gold open access, high-impact paper, International Association for Vegetation Science (IAVS), normalized citation rate, publication trend, Scopus, vegetation classification, Web of Science

Introduction

With this editorial, we start the fifth volume of Vegetation Classification and Survey (VCS), a gold open access journal of the International Association for Vegetation Science (IAVS). The fourth volume was successfully completed due to the efforts of Subject Editors, Linguistic Editors, reviewers, publisher and, of course, the authors. On this occasion we reflect on the challenges and constraints of the "gold open access" path and how we can deal with them. We assess the performance of VCS using bibliometric analyses in the context of general developments in the publishing landscape, both in terms of published papers and of citation rates. We use this information to make projections of the widely used journal-based citation metrics for VCS in the next few years. Further, we highlight the particularly well-cited articles that have been published since the start of the journal, present the Editors' Choice papers of 2023, and provide an outlook for the new year.

The challenges of gold open access

VCS was founded as a gold open access (OA) journal, which means that authors must pay article processing charges (APCs) for the publication once a manuscript is accepted, while the content of the journal is freely available to everybody without payment. In the current publishing landscape, gold OA is essentially the only viable model for new journals as hardly any library or private person would pay for a new subscription journal because there is a strong tendency to reduce the number of existing subscriptions. We have previously argued that a diamond OA solution, where the publication is free for both authors and readers, would be advantageous (Jansen et al. 2020; Dengler 2023), but currently there are no funding models that would cover the costs of publishing in this case. While hardly anyone would object to the OA philosophy that scientific results (which were mostly generated with public money) should be freely accessible to anybody (BOAI 2002), the gold OA solution has several severe drawbacks. Most importantly, (i) it creates barriers to authors of quality studies who do not have access to OA funding and (ii) it incentivises quantity over quality (Beall 2012; Bohannon 2013; Cobo 2014; Jansen et al. 2020; Smith et al. 2021; Dengler 2023 and references therein).

For a new journal in a relatively narrow research field like VCS, authors are generally reluctant to submit papers to journals that are not yet included in the two major bibliometric databases, Web of Science and Scopus. If, in addition, they have to pay considerable APCs, while most other journals in the field (Journal of Vegetation Science, Applied Vegetation Science, Phytocoenologia, Tuexenia) are subscription journals without obligatory APCs and have a Journal Impact Factor (JIF; i.e. are included in the Web of Science Core Edition), this could diminish the willingness to submit manuscripts considerably. We are therefore very grateful that our mother organisation, the International Association for Vegetation Science (IAVS), waived the APCs for its members during the initial years. This generous support helped to attract good papers during the past four years, but it was always clear that these subsidies could not last forever, and ultimately IAVS expects VCS to generate some profit to be used for activities of the association, as do the two other IAVS journals, Journal of Vegetation Science and Applied Vegetation Science (Chytrý et al. 2023). Thus, we Chief Editors have agreed with IAVS on a solution that should make VCS financially self-sustaining latest in 2025, while at the same time we wanted to avoid the high APCs charged by most other gold OA journals, which would be particularly problematic in the research field covered by VCS, where many authors are based in the Global South or in small institutions in richer countries and do not have access to APC funding. The plan is that those authors who have access to APC funding schemes in their institutions or countries should pay a fee that is higher than the actual costs to allow all those without such opportunities to publish (almost) without impediment. So far, this solution has worked reasonably well. In 2023, thanks to APC payments from some authors in (mostly) rich countries, we could offer free publishing to all other IAVS members and at the same time we did not need as much subsidies from IAVS. Thus, we are very grateful to those IAVS members who paid the regular APCs to enable this philanthropic approach. To approach the break-even-point, in 2024 for the first time there will be obligatory, but low APCs for those IAVS members from high-income countries.

Development of VCS in the context of other ecological journals

The fourth volume of VCS is the most content-rich so far. With 25 articles it equalised the previous maximum in 2021. However, as the articles were on average longer than in the first three years, the page number reached a new maximum of 360 (+ 16% compared to the previous maximum). After four years, VCS shows a non-significant positive trend, which contrasts with most other journals in the field (Table 1). It thus confirms a pattern we already described in last year's editorial for the time until 2022 (Dengler et al. 2023a). When comparing VCS with 29 other journals relevant for vegetation ecologists, from regional journals of botanical societies, like Tuexenia or Plant Sociology, to the top journals in ecology in general, such as Global Change Biology and Nature Ecology & Evolution, the pattern strongly changed around the anomaly of the Covid-19 years 2020/2021 (see also Dengler 2023). Until 2020, these 30 journals combined showed a mean annual increment in article numbers of 12.0%, but this value dropped to only 3.2% from 2020 onwards. The patterns are more contrasting when separating the two mega-journals in the list (Diversity, Frontiers in Ecology and Evolution, which are produced by publishers of which various problematic practices are known that have often been termed “predatory” e.g. Oviedo-García 2021; Dengler 2023), from the other 28 journals (which comprise both OA and subscription journals, owned by either scholarly associations or publishers). The content of the two mega-journals on average grew by 50.5% annually from 2014 to 2020 and by 34.8% annually afterwards, while the other 28 journals grew at an annual rate of 9.8% before and shrunk by 3.9% after 2020. Looking closer at the 28 journals individually, before 2020 only 12 had a negative trend, but after 2020 this number increased to 25, with only Agriculture, Ecosystems & Environment, VCS and Nature Ecology & Evolution having a small positive trend (Table 1). While this result assures us that we are on a good path in the development of VCS, the negative to strongly negative trends in many other traditional journals raises serious concerns because the four out of 30 analysed journals with the strongest negative trend in recent years are vegetation ecological journals publishing on similar topics as we (Folia Geobotanica, Phytocoenologia, Tuexenia, Journal of Vegetation Science) (Table 1). We can only hope that most of these journals will find a way back to their old strength because without other strong journals in the field, VCS cannot be successful in the long run.

Bibliometric performance of VCS

The sheer quantity of articles, of course, does not tell anything about the relevance of the published content. If one is to compare the relative position of a journal in the field, then journal-based citation metrics are needed, in particular the Journal Impact Factor (JIF) from the Web of Science Core Edition (WoS) and the CiteScore from the Scopus database. The challenge with this approach is that new jour-

Table 1. Development of article numbers in 30 selected ecological journals over the past 10 years, including VCS (marked blue) and the two other IAVS journals (marked green). Likewise, the five years when Phytocoenologia was published in collaboration with IAVS are marked in green. The article numbers were taken from Web of Science (WoS) except for 2023 (databasing incomplete) and Tuexenia (data erroneous in several years). Data for journals or years within journals not covered by WoS were retrieved from Scopus. Data for VCS, Tuexenia and all journals in 2023 were taken from the respective journal website. Data extraction for the years until 2022 was done on 23 December 2023, that for 2023 on 8 January 2024. The change rates are based on an exponential regression model applied to all years as well as 2014–2020 and 2020–2023 separately, but considering only the years after foundation of a journal (i.e. without the NA's). The table is sorted according to decreasing growth in the recent four years.

Journal	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	Annual change full period	Annual change until 2020	Annual change since 2020
Diversity [MDPI]	NA	NA	31	54	129	246	487	684	1141	1225	74.3%	101.9%	38.8%
Frontiers in Ecology and Evolution	79	151	155	166	238	503	499	1005	1315	1131	37.5%	34.8%	31.3%
Agriculture, Ecosystems & Environment	346	303	498	360	378	286	322	457	386	420	1.5%	-2.1%	6.5%
Vegetation Classification and Survey	NA	NA	NA	NA	NA	NA	22	25	23	25	3.0%	NA	3.0%
Nature Ecology and Evolution	NA	NA	NA	354	344	308	317	278	293	326	-2.4%	-4.3%	1.4%
Global Ecology and Biogeography	137	137	134	127	126	189	178	187	167	184	4.4%	5.0%	-0.1%
Biodiversity and Conservation	211	214	179	200	219	267	211	247	193	225	1.1%	2.3%	-0.5%
Journal of Biogeography	203	219	213	257	234	275	230	203	207	224	0.0%	3.4%	-0.6%
Oikos	162	178	187	179	167	185	161	220	168	170	0.4%	-0.2%	-1.1%
Ecology and Evolution	391	497	730	981	1081	1191	1156	1325	1179	1153	12.4%	21.2%	-1.2%
NeoBiota	NA	17	24	24	19	62	84	73	56	88	23.8%	35.4%	-1.2%
Global Change Biology	322	379	323	451	516	433	548	541	497	537	5.9%	8.7%	-1.4%
Biological Conservation	332	417	371	425	434	402	449	449	325	466	1.4%	3.6%	-2.1%
Preslia	21	18	16	12	16	14	16	14	16	14	-2.6%	-4.6%	-2.6%
Basic and Applied Ecology	79	79	76	62	78	57	73	144	98	72	2.5%	-3.0%	-4.2%
Plant Sociology	23	10	11	41	10	13	15	17	13	14	-1.9%	-3.0%	-4.6%
Restoration Ecology	103	113	111	129	172	214	239	272	227	214	11.5%	16.4%	-5.0%
Forest Ecology and Management	556	455	606	611	625	736	696	1155	582	737	5.0%	6.1%	-5.0%
Hacquetia	17	17	19	11	15	23	17	26	20	15	2.0%	1.3%	-6.2%
Ecography	129	128	127	136	177	235	156	144	133	128	0.9%	7.9%	-6.5%
Plant Ecology	130	131	128	106	119	97	110	110	74	99	-4.3%	-4.1%	-6.9%
Journal of Ecology	159	157	166	167	200	284	246	245	222	183	4.4%	10.0%	-9.4%
Flora	86	85	121	157	180	210	213	245	219	157	10.6%	19.2%	-9.8%
Applied Vegetation Science	74	72	72	65	62	61	78	77	73	56	-0.9%	-1.1%	-9.9%
Alpine Botany	19	14	16	17	17	17	15	32	16	13	0.4%	-0.9%	-10.6%
Global Ecology and Conservation	46	138	87	87	146	285	589	548	397	417	29.6%	41.0%	-12.7%
Folia Geobotanica	33	36	31	36	32	24	23	21	23	12	-9.1%	-6.4%	-17.0%
Phytocoenologia	17	23	28	26	29	22	16	8	11	6	-12.8%	-0.8%	-23.1%
Tuexenia	25	21	23	26	26	20	30	23	16	14	-4.1%	2.1%	-23.3%
Journal of Vegetation Science	144	118	129	120	105	131	131	126	63	49	-8.0%	-1.0%	-30.5%
Total	**3844**	**4127**	**4612**	**5387**	**5894**	**6790**	**7327**	**8901**	**8153**	**8374**	**10.3%**	**12.0%**	**3.2%**
Mega-journals from MDPI and Frontiers	**79**	**151**	**186**	**220**	**367**	**749**	**986**	**1689**	**2456**	**2356**	**49.5%**	**50.5%**	**34.8%**
Other journals	**3765**	**3976**	**4426**	**5167**	**5527**	**6041**	**6341**	**7212**	**5697**	**6018**	**6.2%**	**9.8%**	**-3.9%**

nals get included in the relevant databases and thus receive the respective metrics only after a couple of years. The criteria for inclusion and the timeline are relatively transparent and straightforward in the case of Scopus, but not so much in the case of WoS. Before inclusion into the two main bibliometric databases, there were only the VCS profiles on Google Scholar (https://scholar.google.com/citations?hl=de&user=XsKKBm0AAAAJ) and Research Gate (https://www.researchgate.net/journal/Vegetation-Classification-and-Survey-2683-0671) that delivered a rough idea which articles were cited and how often. Fortunately, in 2022 VCS was included in the Scopus database and thus received its first CiteScore$_{2022}$ of 2.0 in summer 2023, with monthly updated CiteScoreTracker since then. However, it is unclear when the inclusion in the WoS will follow.

From communication with potential authors, we know that the lack of a JIF and the relatively low first CiteScore are major reasons not to select VCS as a publication outlet. The challenge is not only that JIF and CiteScore are not available at all in the initial years of a journal, but when they are finally published, they reflect the citation performance of articles several years back. For example, the JIF published in year x evaluates the papers published in years $x - 3$ and $x - 2$, the CiteScore refers to years $x -1$, $x - 2$, $x - 3$ and $x - 4$ and the CiteScoreTracker to the years x, $x - 1$, $x - 2$ and $x - 3$. As it is normal that with time the reputation of a journal grows and thus better articles can be attracted, the lag-phase of the usual bibliometric indices is a challenge. To overcome this, we used the Scopus database to assess the specific performance of articles of individual years, namely the initial four years of VCS, and compared them to that of the same 29 other ecological journals as above (Table 2, Suppl. material 1). Since any article accumulates more citations with time, the pure number of citations is also not informative, but it needs to be normalized by the number of citations received by an average article in the field from the same year. Thus, our approach is similar to the Source Normalized Impact per Paper (SNIP) provided by the Scopus database and the Journal Citation Indicator (JCI) of the WoS (see Suppl. material 1), but we did it individually for each year, and we used our set of 30 journals as reference instead of one of the Scopus-defined subject fields. We found that, on average, articles in this selection were cited 0.89 times in the year of publication, 3.33 times in the subsequent year, 4.79 times in the second and finally 6.03 times in the third year after publication. Our ad-hoc normalized citation rate per paper resulted from the division of the citation rate in a specific journal by the average citation rate for that year (Table 2). Thus, it is above 1 if the articles of that journal were cited more than the average of all articles from the 30 journals in that year and below 1 if they had below-average citation rates. Unlike JIFs or absolute numbers of citations, which do not have a meaning in themselves, a normalized citation rate can be directly interpreted.

We found that the normalized citation rate of VCS was around 0.2 in the first two years, i.e. articles from 2020 and 2021 received only one fifth of the citations of average ecological papers (Table 2, Suppl. material 1). However, in 2022 this value increased to 0.34 and in 2023 to 0.86. VCS' rank among the 30 journals was 28th in the first two years, 26th in 2022 and 14th in 2023 (Table 2, Figure 1, Suppl. material 1). The average articles of VCS in 2023 thus had a similar performance as those of Alpine Botany (0.86) and Biodiversity and Conservation (0.75), and the normalized citation rate was even higher than for the two other IAVS journals, Journal of Vegetation Science (0.73) and Applied Vegetation Science (0.47) (Table 2, Suppl. material 1). VCS articles of 2023 received on average about 1/3 of the citations of the journal with the highest citation rate (Global Change Biology: 2.82), but more than two times as many than Phytocoenologia (0.38) (Table 2, Figure 1, Suppl. material 1). With a mean annual increase of 0.18, VCS had the strongest positive trend in normalized citation rates among all compared journals (Table 2, Suppl. material 1). However, it must be noted that in a journal that publishes so relatively few articles per year as VCS, a single high-impact paper can have a considerable influence on the normalized citation rate (or the SNIP). There was one such paper in 2023 (Dengler et al. 2023b, see next section), which alone got 8 citations to date. However, if we would remove this paper, the normalized citation rate of 2023 papers would still be 0.45, i.e. a clear increase compared to 2022 and very similar to Applied Vegetation Science.

Projections into the future

We present the above analyses because we feel that normalized citation rates are meaningful measures by which to compare the citation impact of different journals, whether these measures be Web of Science' Journal Citation Indicator (JCI), the Scopus' Source Normalized Impact per Paper (SNIP) for multiple years, or our *ad hoc* normalized citation rate for individual years. Nonetheless, most researchers probably still rely on the "traditional" metrics, namely Web of Science' Journal Impact Factor (JIF) and Scopus' CiteScore. These metrics are all strongly correlated as they measure similar things, even though they vary in the number of citing journals considered, the years included in the calculations, and the delimitation of the subject fields. For example, the JIF$_{2022}$ can be well predicted by a linear function of the CiteScore$_{2022}$ for the 28 journals in our selection that were included in WoS (based on the numbers in Suppl. material 1):

$$(1)\ \mathrm{JIF} = -0.398 + 0.626 \cdot \mathrm{CiteScore}\ (R^2 = 0.968)$$

Taking this formula and VCS' CiteScore of 2.0 in 2022, this would result in an approximate JIF$_{2022}$ of 0.9 if VCS had been included in the WoS. As the values of the CiteScore$_{2023}$ and JIF$_{2023}$ to be released in summer 2024 are based on the citation performance of articles published 2020–2023 and 2021–2022, respectively, there is a solid basis for forecasts as the citation rates of the relevant articles are accessible. The CiteScoreTracker$_{2023}$ provides one such estimate for the CiteScore$_{2023}$ as it approaches

Table 2. Citation rates of 30 selected ecological journals in 2023 for their content in the years 2020 to 2023. The values were extracted from the Scopus database (https://www.scopus.com/) on 23 December 2023, which could mean that the latest papers and citations in various journals were likely missed. Nonetheless, the effect on the normalized citation rate should be minimal. VCS is highlighted in blue and the two other IAVS journals in green. The citation rate is the ratio of received citations to the number of articles published. The normalized citation rate results from the division of the citation rate by the average citation rate of all articles of all 30 journals in that year. The annual trend in the last column is the slope of a linear regression applied to the normalized citation rates. The table is sorted by decreasing normalized citation rate for the articles of 2023. The underlying raw data (number of papers and citations to these per publication year) as well as further common citation metrics from Scopus and Web of Science are provided in Suppl. material 1 as an editable spreadsheet.

Journal	**Citation rate 2023 for papers of...**				**Normalized citation rate 2023 for papers of...**				**Annual linear trend of normalized citation rate**
	2020	**2021**	**2022**	**2023**	**2020**	**2021**	**2022**	**2023**	
Global Change Biology	14.48	12.62	9.20	2.50	2.40	2.65	2.76	2.82	0.14
Agriculture, Ecosystems & Environment	8.27	7.49	5.54	1.72	1.37	1.57	1.66	1.94	0.18
Nature Ecology & Evolution	13.94	10.72	5.92	1.71	2.31	2.25	1.77	1.93	-0.16
Ecology Letters	11.86	8.17	7.43	1.26	1.97	1.72	2.23	1.41	-0.11
Ecography	7.65	6.79	4.98	1.13	1.27	1.43	1.49	1.27	0.01
Journal of Biogeography	4.99	3.93	3.12	1.09	0.83	0.83	0.94	1.22	0.13
Global Ecology and Biogeography	8.67	7.54	5.91	0.97	1.44	1.59	1.77	1.10	-0.08
Biological Conservation	7.11	5.77	4.02	0.96	1.18	1.21	1.20	1.09	-0.03
Journal of Ecology	7.01	6.38	4.99	0.95	1.16	1.34	1.50	1.07	-0.01
Restoration Ecology	5.35	4.26	2.91	0.93	0.89	0.90	0.87	1.04	0.04
Forest Ecology and Management	4.67	4.35	3.39	0.85	0.77	0.91	1.02	0.96	0.06
Neobiota	5.04	5.39	2.32	0.85	0.84	1.13	0.69	0.96	-0.01
Alpine Botany	2.40	4.00	1.68	0.76	0.40	0.84	0.50	0.86	0.11
Vegetation Classification and Survey	**1.27**	**0.92**	**1.14**	**0.76**	**0.21**	**0.19**	**0.34**	**0.86**	**0.21**
Biodiversity and Conservation	4.45	3.32	2.59	0.67	0.74	0.70	0.78	0.75	0.01
Basic and Applied Ecology	5.27	3.61	2.75	0.67	0.87	0.76	0.82	0.75	-0.03
Journal of Vegetation Science	**2.94**	**3.17**	**1.40**	**0.64**	**0.49**	**0.67**	**0.42**	**0.73**	**0.05**
Diversity	2.88	2.43	1.95	0.60	0.48	0.51	0.59	0.68	0.07
Hacquetia	0.53	0.62	0.68	0.60	0.09	0.13	0.21	0.68	0.18
Preslia	1.46	4.22	2.94	0.55	0.24	0.89	0.88	0.61	0.11
Global Ecology and Conservation	5.61	4.21	3.07	0.54	0.93	0.89	0.92	0.61	-0.09
Flora	2.21	1.86	1.47	0.52	0.37	0.39	0.44	0.59	0.07
Frontiers in Ecology and Evolution	4.06	3.14	1.77	0.51	0.67	0.66	0.53	0.57	-0.04
Applied Vegetation Science	**4.09**	**2.87**	**1.64**	**0.42**	**0.68**	**0.60**	**0.49**	**0.47**	**-0.07**
Ecology and Evolution	3.26	2.72	1.76	0.40	0.54	0.57	0.53	0.45	-0.03
Plant Ecology	1.95	2.07	1.98	0.37	0.32	0.43	0.59	0.42	0.04
Phytocoenologia	1.69	0.89	0.45	0.33	0.28	0.19	0.14	0.38	0.02
Plant Sociology	1.93	3.24	1.23	0.10	0.32	0.68	0.37	0.11	-0.09
Folia Geobotanica	1.44	1.80	0.81	0.00	0.24	0.38	0.24	0.00	-0.09
Tuexenia	1.07	1.17	0.14	0.00	0.18	0.25	0.04	0.00	-0.07
All	**6.03**	**4.76**	**3.33**	**0.89**	**1.00**	**1.00**	**1.00**	**1.00**	**0.00**

this value asymptotically until summer 2024. For VCS the CiteScoreTracker stands at 2.4 as of December 2023. Inserting this value into formula (1) would result in a JIF_{2023} of 1.1 if VCS is included into WoS by summer 2024.

However, as discussed above, the citation metrics released in 2024 do not reflect where a journal stands in 2024, but where it stood a couple of years ago, which can make a big difference for journals that develop dynamically like VCS (see Table 2, Figure 1). Thus, we tried to retrieve estimates for CiteScores and potential JIFs for 2024 and 2025. For the $\mathrm{CiteScore}_{2022}$ we found that it can be best predicted by the normalized citation rate for the penultimate ($R^2 = 0.922$), second best by that of the previous year ($R^2 = 0.896$), and least by that of the same year ($R^2 = 0.792$) (using the values in Suppl. material 1). This behaviour is plausible as the papers two years back get many more citations in a specific year than those in the same year (in our dataset more than five times more, see Table 1), meaning that the “quality” of the older papers from the evaluation period has a disproportionate influence on the citation metrics. The regression function of the CiteScore in year x vs. the normalized citation rate in year $x - 2$ is as follows:

$$(2)\ \mathrm{CiteScore}_x = 0.342 + 8.499 \cdot \text{normalized citation rate}_{x\text{-}2} \quad (R^2 = 0.922)$$

This means that the 2024 edition of the CiteScores/JIFs released in 2025 will be dominated by the quality of the papers published in 2022, and the 2025 edition released in 2026 by the papers from 2023. Applying our formulas (1) and (2), assuming that they are largely time-invariant, the

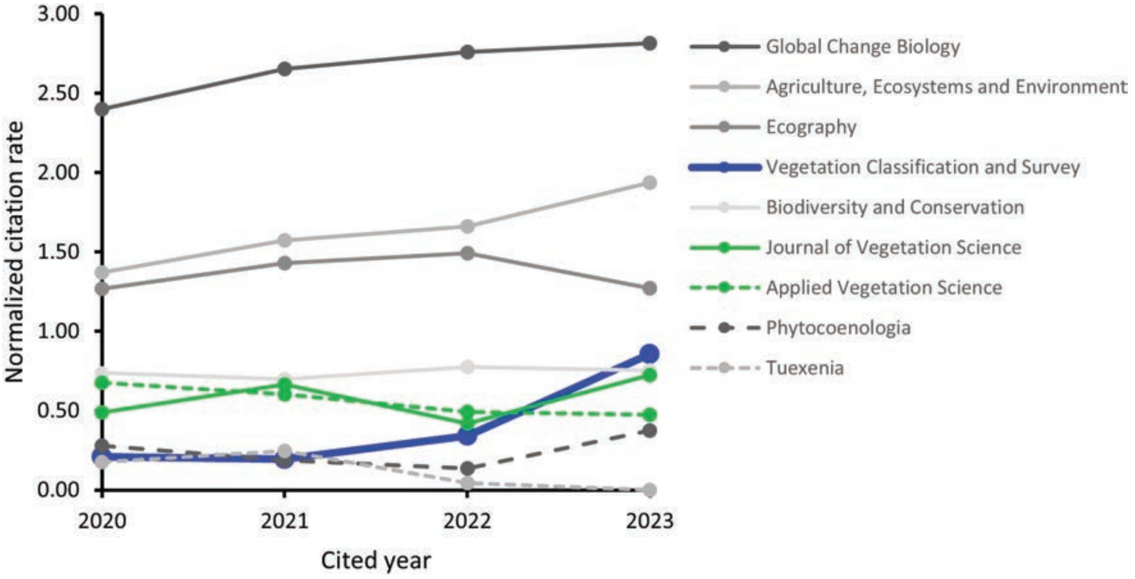

Figure 1. Development of the normalized citation rate for selected ecological journals over the past four years. Citations refer to citations in any journal included in the Scopus database in the year 2023 to articles of the year on the x-axis in the given journal. Normalization was done over all articles published in the 30 journals of Table 2 in the respective year. Accordingly, a value of 1.0 means a citation rate corresponding to the mean citation rate of all articles of the 30 journals in the respective year (averaged on a per-article base), while 1.5 means a 50% higher and 0.5 a 50% lower citation rate. For visibility reasons only 9 out of the 30 journals are shown, including the most-cited and least-cited journal, as well as VCS and the two other IAVS journals (coloured). Over the four-year period, VCS shows an accelerated increase in citation rate, Applied Vegetation Science a monotonous decrease and Journal of Vegetation Science strong interannual fluctuations without clear trend (for details see Table 2 and Suppl. material 1).

normalized citation rates of VCS in 2022 and 2023 (0.34 and 0.86), yields the following predictions:

$$\text{CiteScore}_{2024,\ \text{predicted}} = 3.2$$

$$\text{CiteScore}_{2025,\ \text{predicted}} = 7.5$$

$$\text{JIF}_{2024,\ \text{predicted}} = 1.6$$

$$\text{JIF}_{2025,\ \text{predicted}} = 4.3$$

These predictions are of course associated with some errors due to the application of one or, in the case of JIF, even two regressions, albeit both R^2 values are well above 0.9. However, being aware that the publications in the past are the sole source of the citation metrics in the future makes this whole exercise far less speculative than it might appear at first glance. We shall come back to these predictions in future editorials when we know the actual outcome.

Most-cited papers in VCS

Although it is possible to see which papers of VCS received the most citations to date in Scopus (https://www.scopus.com/sourceid/21101083451) and in Google Scholar (https://scholar.google.com/citations?hl=de&user=XsKKBm0AAAAJ) based on their respective databases, a simple ranking would ignore that every article over time collects more and more citations. To find out which papers in VCS were cited above average thus requires a standardisation like the SNIPs for journals. In Scopus such values are called Field-Weighted Citation Impact (FWCI) and are available for all papers. As in the case of SNIPs and our own normalized citation rates for journals, a FWCI value above 1 means above-average citation rate. Using this criterion, we selected the 12 out of the hitherto 95 published VCS articles that were cited more than average from the subject fields in which Scopus has placed VCS (namely “Agricultural and Biological Sciences (miscellaneous)”; “Plant Science”; “Ecology, Evolution, Behavior and Systematics”) (Table 3). Although, in absolute numbers, Zeballos et al. (2020) on the classification of dry subtropical forests in Argentina has received the highest number of citations so far (18), Dengler et al. (2023b, the presentation of the Ecological Indicator Values for Europe), has already eight citations despite it is less than one year old, which corresponds to an FWCI of 15.2. While the high-impact papers stem from different article categories, except Database Reports and Nomenclatural Proposals, it seems that methodological papers are particularly often cited as all three publications in the category “VCS Methods” made it into the high-impact list (Table 3). It is very positive that also various presentations of classification systems are among our top-12, including three from South America, two from Asia and one from Australia (Table 3). Thus, VCS here nicely complements our sister journal Applied Vegetation Science, which regularly publishes broad-scale classification systems from Europe, but only very rarely from other continents. The relatively high

Table 3. The 12 articles in VCS that had been cited above average compared to the subject fields of VCS until December 2023 (based on the Scopus database; https://www.scopus.com). The table is sorted by decreasing Field-Weighted Citation Impact (FWCI).

FWCI	Citations	VCS category	Citation	Year	Title
15.20	8	VCS Methods	Dengler et al. (2023b)	2023	Ecological Indicator Values for Europe (EIVE) 1.0
3.02	7	Research Paper	Luebert and Pliscoff (2022)	2022	The vegetation of Chile and the EcoVeg approach in the context of the International Vegetation Classification project
2.28	18	Research Paper	Zeballos et al. (2020)	2020	The lowland seasonally dry subtropical forests in central Argentina: vegetation types and a call for conservation
2.03	17	Research Paper	Nowak et al. (2020)	2020	Classification of tall-forb vegetation in the Pamir-Alai and western Tian Shan Mountains (Tajikistan and Kyrgyzstan, Middle Asia)
1.90	1	VCS Methods	Dengler and Dembicz (2023)	2023	Should we estimate plant cover in percent or on ordinal scales?
1.90	1	Research Paper	Chakkour et al. (2023)	2023	Plant diversity in traditional agroecosystems of North Morocco
1.72	4	Research Paper	Liu et al. (2022)	2022	Vegetation classification of *Stipa* steppes in China, with reference to the International Vegetation Classification
1.38	8	VCS Methods	Janišová et al. (2021)	2021	Grassland with tradition: sampling across several scientific disciplines
1.29	4	Review and Synthesis	Loidi et al. (2022)	2022	Climatic definitions of the world's terrestrial biomes
1.29	3	Research Paper	Montenegro-Hoyos et al. (2022)	2022	Plant diversity and structure in desert communities of the Andean piedmont in Ica, Peru
1.26	12	Forum Paper	Willner (2020)	2020	What is an alliance?
1.01	8	Research Paper	Hunter and Hunter (2020)	2020	Montane mire vegetation of the New England Tablelands Bioregion of Eastern Australia

citation rates for some of these studies demonstrate that there is a real need for such publications, and VCS thus fills an important niche.

Outstanding papers in 2023

As in every year, to highlight outstand papers, we selected one Editors' Choice paper per quarter and from these four papers, we selected one for the annual Editors' Award (Dengler et al. 2022). The selected articles are permanently labelled as such with a banner in the online presentation of the journal. Both are also highlighted in various media of VCS, namely the VCS Newsletter, the News section on the VCS website and the vegsciblog of IAVS. In addition, The Editors' Award comes with the right to provide the photos or other illustrations for the cover of the respective VCS volume, and the first author receives a certificate and prize from the publisher.

The Editors' Award 2023 goes to the Editors' Choice paper of the fourth quarter by Ben and Marianne Strohbach. They provided a comprehensive syntaxonomic description of the Karstelveld vegetation in Namibia (Strohbach and Strohbach 2023), a contribution to the Special Collection "African vegetation studies" (see https://vcs.pensoft.net/collection/316/). Based on 889 relevés of 1000 m^2 extracted from the Phytosociological Database of Namibia, the authors distinguished four main vegetation types by mean of TWINSPAN: wetlands and associated grasslands, transitional vegetation between Thornbush savanna and Karstveld, Kalahari type sandy vegetation and true Karstveld vegetation types. Each main vegetation type was further divided in more detailed plant communities, 17 of them being formally described as new plant associations. All associations are clearly defined by diagnostic species. The authors described the true Karstveld vegetation as a new phytosociological class *Terminalietea prunoides*, with eight associations, two new orders and three new alliances. The description of these vegetation units was completed with the comparison of their structure and diversity and intuitive visualisation of catenas representing their position along topographic gradients. A concluding remark of the authors concerns the high species richness of this region, which is seriously threatened in some areas that are not protected inside the Etosha National Park or private nature reserves and conservancies. This study is outstanding because formal syntaxonomic vegetation classification is still rare in Africa as a whole and mostly restricted to the francophone parts of North Africa. In other regions, there have been only very few such studies (e.g. Luther-Mosebach et al. 2012; Behn et al. 2022). We hope that the current paper will be a first in a series that eventually leads to a comprehensive synopsis of the plant communities of Namibia.

The Editors' Choice of the first quarter went to Elvira Casagranda and Andrea Izquierdo. This article (Casagranda and Izquierdo 2023) is part of the ongoing Special Collection "Neotropical vegetation" (see https://vcs.pensoft.net/collection/350/). The authors studied the *vegas* of Argentina, a very peculiar wetland vegetation of the high elevations of the Andes and particular the Altiplano, at elevations of 3,300–5,000 m a.s.l. The *vegas* are dominated by graminoids forming dense cushions, embedded in which various tiny forbs can live. The authors could distinguish two main types, which are dominated either by *Juncaceae* (*Oxychloe andina*, *Distichia muscoides*) or *Cyperaceae* (*Eleocharis pseudoalbibracteata*, *Zameioscirpus atacamensis*). Applying species distribution modelling (SDM) techniques, the authors were able to effectively predict the occurrence of the two main *vegas* types throughout the Argentinean Andes. This paper demonstrates the merit of transferring a statistical technique from a neighbouring field to vegetation typology.

The Editors' Choice of the second quarter went to Gonzalo Navarro and colleagues for their "Review and Synthesis" article in the same ongoing Special Collection "Neotropical vegetation" (Navarro et al. 2023). The authors provide a synthetic overview of the terrestrial vegetation of South America. They use the concept of "geocomplex biomes" of which they distinguish 33 on the continent. These units are grouped into 16 "macrobiomes" within the four macroclimates "tropical", "mediterranean", "temperate" and "boreal". Each of the "geocomplex biomes" is visualised by one or several drawings that illustrate typical sequences of vegetation types along landscape gradients (catenas). These figures provide the reader with a realistic picture of the landscape and what the driving forces are. The descriptions of the "geocomplex biomes" are very dense in information, based on extensive field studies by the authors throughout the continent and a comprehensive literature review. This contribution is prototypic for what we envisage under "Review and Synthesis" articles. They are like textbooks or textbook chapters; as authoritative as these, but more concise. Compared to normal research articles, they can be longer, as in this case (40 pp.). We hope that this contribution will contribute to a better understanding of the diverse vegetation of South America and at the same time inspire other author teams to consider VCS as outlet for comparable synthetic treatments.

The Editors' Choice of the third quarter went to Sebastián Zeballos and colleagues for another paper in the Special Collection "Neotropical Vegetation" (Zeballos et al. 2023). The authors provide a new hierarchical classification of the vegetation in the Arid Chaco in Central-Western Argentina, based on more than 600 relevés. The endemic-rich vegetation in the region mainly consists of xerophytic shrublands and forests. This contribution is particularly welcome because there have been few broad-scale plot-based vegetation syntheses in South America.

Changes in the Editorial Board

The Editorial Board of VCS consists of the Chief Editors, the Associate Editors, the Guest Editors, the Linguistic Editors and the Editorial Review Board. While the Associate and Guest Editors manage the peer review of a paper and make the editorial decisions, the members of the Editorial Review Board are those experts from around the world who serve as the primary pool of reviewers. These members know the journal and are committed to it; thus, they usually provide better and faster reviews than external reviewers. We are happy to announce that as of 2024 we have appointed two new Associate Editors with broad expertise in Asia and Africa: Alireza Naqinezhad (University of Mazandaran, Babolsar, Iran) and Gaolathe Tsheboeng (University of Botswana, Gaborone, Botswana). They previously did and are still doing an excellent job as Guest Editors in one of our Special Collections. Further we appointed four new members to the Editorial Review Board: Angie Montenegro-Hoyos (University of La Serena, Chile), Cloe Xochitl Pérez Valladares (Universidad Nacional Autónoma de México, Mexico), Jean-Paul Theurillat (University of Geneva, Switzerland) and Denys Vynokurov (M.G. Kholodny Institute of Botany, Kyiv, Ukraine). Welcome to the team!

Outlook

Starting a new OA journal within a narrow field of science remains a challenge, even after four years. However, we are doing quite well, thanks to the exciting manuscripts submitted by our authors, the great service provided by our dedicated Editorial Board, the financial support by IAVS and the technical support by our publisher Pensoft. Numbers of articles and pages show a positive trend – unlike the majority of ecological and particularly vegetation ecological journals. VCS has already been included in the Scopus bibliometric database in 2022 and received its first CiteScore in summer 2023. Projections based on annual normalized citation rates demonstrated that VCS is improving its relative position compared to other journals in the field – due to articles that attract above-average citations. We provided an overview of articles that are particularly used by other scientists, which might inspire potential authors how to write their articles if they wish to receive many citations. We hope to continue this road of success together with you and thus invite you to submit exciting manuscripts from the fields of vegetation classification and ecoinformatics – which is facilitated by the fact that during 2024, due to IAVS and our innovative APC pricing model, most authors can still publish for free or a very low fee if they are members of IAVS.

Author contributions

J.D. planned and drafted this editorial while all other authors revised and approved it.

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Appendix 1: Linguistic Editors for VCS during the last year

We thank the following colleagues for their invaluable contribution as Linguistic Editors for VCS (number of edited papers in brackets):

Stephen Bell (2)
Don Faber-Langendoen (1)
Michael Glaser (4)
Jim Martin (2)
Meghan J. McNellie (3)
Hallie Seiler (3)
Lynda Weekes (2)

Appendix 2: Reviewers for VCS during the last year

We thank the following colleagues who served during the last year (November 2022 – October 2023) as reviewers for VCS (number of reviews in brackets).

Erwin Bergmeier (2)
Idoia Biurrun (1)
Jorge Capelo (5)
Andraz Carni (2)
Victor Chepinoga (1)
Timo Conradi (3)
Romeo Di Pietro (1)
Federico Fernández-González (1)
Scott Franklin (2)
Antonio Galán de Mera (3)
François Gillet (2)
Joaquín Giménez de Azcárate (2)
Melisa A. Giorgis (1)
Riccardo Guarino (2)
Behlül Güler (1)
Rense Haveman (2)
Katarína Hegedüšová (1)
Florian Jansen (2)
Attila Lengyel (2)
Federico Luebert (1)
Isolda Luna-Vega (1)
Angie Montenegro Hoyos (1)
Alireza Naqinezhad (2)
Gonzalo Navarro-Sánchez (1)
Michael P. Nobis (1)
Jalil Noroozi (1)
Pavel Novák (1)
Bianca Ott Andrade (1)
Jens Pallas (1)
Cloe Peréz Valladares (1)
Rasmus Revermann (4)
Jan Roleček (1)
Simona Sarmati (1)
Ute Schmiedel (1)
Urban Šilc (1)
Sebastian Świerszcz (1)
Amir Talebi (2)
Jean Paul Theurillat (3)
Gaolathe Tsheboeng (3)
Kiril Vassilev (1)
Jose Alejandro Velazques Montes (1)
Denys Vynokurov (4)
Viktoria Wagner (2)
Wolfgang Willner (2)
David Zelený (1)

Supplementary material

Supplementary material 1

Publication and citation numbers, citation rates and normalized citation rates 2020–2023 as well as some current citation metrics from Scopus and Web of Science for the 30 ecological journals compared in this study (*.xlsx).

Link: https://doi.org/10.3897/VCS.118454.suppl1

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 5: 11–15
doi: 10.3897/VCS.103154

NOMENCLATURAL PROPOSAL PHYTOSOCIOLOGICAL NOMENCLATURE

Proposal (36) to conserve the name *Philonotidion seriatae* Hinterlang 1992 for the species-poor, bryophyte-dominated, non-calcareous arctic-alpine spring vegetation of Europe

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3 *Landesamt für Natur, Umwelt und Verbraucherschutz NRW, Recklinghausen, Germany*
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Abstract

According to the International Code of Phytosociological Nomenclature, a younger name of a syntaxon may be conserved against its older name to improve the stability of the nomenclature and avoid misunderstandings in scientific communication. Here, we propose conserving the name *Philonotidion seriatae* Hinterlang 1992 for arctic-alpine, bryophyte-dominated, non-calcareous spring vegetation against the names *Cardamino-Montion* Braun-Blanquet 1925, *Cardamino-Montion* Braun-Blanquet 1926, and *Montion* Maas 1959. In current vegetation classification systems, the two name-giving taxa of *Cardamino-Montion* no longer indicate the character of the vegetation corresponding to the nomenclatural type of this alliance and are instead characteristic of other currently distinguished alliances. Maintaining the oldest name *Cardamino-Montion* in strict adherence to the Code would be a source of errors. In the current vegetation classification systems, two similar but counter-intuitive names would then have to be used: *Cardamino-Montion* for arctic-alpine springs (although the name-giving taxa are more indicative of montane springs) and *Epilobio nutantis-Montion* for montane springs (although the name-giving taxon *Epilobium nutans* is indicative of arctic-alpine vegetation). Hence, there is a risk that the name *Cardamino-Montion* may gradually become ambiguous. We also propose conserving the name *Philonotidion seriatae* against *Mniobryo-Epilobion hornemannii* Nordhagen 1943 to prevent confusion in case of a merger of these alliances.

(36) *Philonotidion seriatae* Hinterlang 1992
Typus: *Cratoneuro-Philonotidetum* Geissler 1976 (holotypus)

(=) *Cardamino-Montion* Braun-Blanquet 1925
Typus: *Bryetum schleicheri* Braun-Blanquet 1925 [≡ *Montio fontanae-Bryetum schleicheri* Braun-Blanquet 1925 nom. corr. et invers. (alternative name)] (holotypus)

(=) *Cardamino-Montion* Braun-Blanquet 1926 nom. superfl. [≡ *Cardamino-Montion* Braun-Blanquet 1925]

(=) *Mniobryo-Epilobion hornemannii* Nordhagen 1943
Typus: *Mniobryo-Epilobietum hornemannii* Nordhagen 1943 (lectotypus selected by Zechmeister & Mucina 1994)

(=) *Montion* Maas 1959 nom. superfl. [≡ *Cardamino-Montion* Braun-Blanquet 1925]

Taxonomic reference: Euro+Med PlantBase (http://europlusmed.org; accessed 4 January 2024)

Keywords

Cardamino-Montion, *Montio-Cardaminetea*, *nomen conservandum*, phytosociological nomenclature, springs

The syntaxonomic classification of non-calcareous spring vegetation in Europe has evolved from the concept of a single alliance, *Cardamino-Montion*, to the concept of ecologically and floristically more homogeneous units. This may lead to the misuse of some old names.

Cardamino-Montion Braun-Blanquet 1925 is the oldest alliance name for spring vegetation in Europe. The holotype of this name is the association *Bryetum schleicheri*, published on page 128 in Braun-Blanquet (1925), which is the only element published under the alliance name in the table on page 129. In this table, the alternative name "Assoziation von *Bryum Schleicheri* und *Montia rivularis*" (recte: *Montio fontanae-Bryetum schleicheri* Braun-Blanquet 1925 nom. corr. et invers.) is used for the same association. The latter name must be corrected (Art. 44; Theurillat et al. 2021) because *Montia rivularis* is a younger synonym of *M. fontana* (see the Euro+Med PlantBase). Moreover, as *Bryum schleicheri* has a higher cover than *Montia fontana* in 6 out of 7 relevés (and equal cover in the remaining one), the name must also be inverted (Art. 42). The lectotype of the association, selected by Hinterlang (2017), is relevé 2 in Table 1 of the Braun-Blanquet article (1925).

The association *Bryetum schleicheri* Braun-Blanquet 1925 represents the vegetation of open subalpine springs on non-calcareous bedrock. Its relevés were sampled at high elevations (1350–1610 m a.s.l.) in the Massif Central, as specified in a subsequent article (Braun-Blanquet 1926). *Bryum schleicheri* (*Ptychostomum schleicheri* in the Euro+Med PlantBase), the dominant taxon in the original diagnosis (Braun-Blanquet 1925, 1926), is a circumpolar species with an arctic-alpine distribution. *Saxifraga stellaris*, another predominantly arctic-alpine species that only rarely descends to the montane belt, is the second most abundant species listed among the faithful (*treue*) character species. *Sagina linnaei* (*S. saginoides*) and *Epilobium nutans* are listed as two other faithful character species with optimum distribution in arctic-alpine areas. The arctic-alpine character of the *Bryetum schleicheri* association (Braun-Blanquet 1925, 1926) is further underlined by the firm (*feste*) character species *Philonotis seriata*, which co-dominated the moss layer. *Montia fontana*, reported as a firm (*feste*) character species, occurred in all seven relevés, but with low abundance (+ in five cases; 1 in two cases). In contrast to the other species mentioned, this taxon has its distributional optimum at lower elevations, where it often dominates, whereas it only rarely occurs in vegetation where arctic-alpine taxa prevail. Besides the type association, Braun-Blanquet (1926) included within the alliance the association *Cardaminetum amarae subatlanticum*, which was documented with only one relevé, again from the high elevations of the Massif Central (Mt Puy Mary, 1350 m a.s.l.).

As knowledge of the variability of non-calcareous spring vegetation in Europe increased, new alliances were identified. Nordhagen (1943) described the *Mniobryo-Epilobion hornemannii* alliance, another bryophyte-dominated non-calcareous vegetation with many similarities to *Bryetum schleicheri* (e.g. the dominance of *Philonotis seriata* and *Saxifraga stellaris*).

Maas (1959) divided Braun-Blanquet´s *Cardamino-Montion* into two alliances: *Cardaminion amarae* (shaded springs) and *Montion* (open springs). The latter is a superfluous name (Art. 29c), since its diagnosis contains the *Bryetum schleicheri* Braun-Blanquet "1926" (recte: 1925), which is the nomenclatural type of *Cardamino-Montion* Braun-Blanquet 1925. Shaded forest springs were then distinguished from non-forest springs at the alliance level in most subsequent vegetation surveys. Mucina et al. (2016) classified them as the *Caricion remotae* Kästner 1941 alliance (the oldest valid name).

Table 1. Literature survey showing the variable use of the name *Cardamino-Montion* with regard to shading and elevation.

(Sub)alpine non-calcareous springs	(Sub)alpine non-calcareous springs plus other types of spring vegetation	Low- and mid-elevation non-forest (unshaded) springs	Forest (shaded) springs
Braun-Blanquet (1926)	Bartsch and Bartsch (1940)	Büker (1942)	Tüxen (1937)
Zechmeister and Mucina (1994)	Oberdorfer (1957)	Lebrun et al. (1949)	Lebrun et al. (1949)
Bardat et al. (2004)	Dierßen (1996)	Maas (1959)	Soó (1949)
Tomaselli et al. (2011)	Coldea (1997)	Hadač (1983)	Raţiu et al. (1983)
Mucina et al. (2016)	Diekmann (1997)	Hinterlang (1992)	Siebum et al. (1995)
	Mertz (2000)	Siebum et al. (1995)	Laiviņš (1998)
	Rennwald et al. (2000)	Redžić (2007)	Passarge (1999)
	Oberdorfer (2001)	Ranđelović and Zlatković (2010)	Lawesson (2004)
	Rivas-Martínez et al. (2001)	Redžić et al. (2011)	Schaminée et al. (2017)
	Dierßen and Dierßen (2005)	Borhidi et al. (2012)	
	Matuszkiewicz (2007)	Schaminée et al. (2017)	
	Ellenberg and Leuschner (2010)		

The separation of spring vegetation with arctic-alpine species, dominated by mosses, from colline to montane spring vegetation, dominated by *Montia fontana* and other vascular plants, was introduced in the synthesis of Czechoslovak spring vegetation by Hadač (1983). He reported the *Cardamino-Montion* alliance from the montane zone in the westernmost part of Czechoslovakia, where the arctic-alpine character species of the type association do not occur. For the alpine zone, he described two new alliances: a productive, herb-dominated one (*Cratoneuro filicini-Calthion laetae* Hadač 1983) and a moss-rich one with low productivity, characterized by *Philonotis seriata* and *Diobelonella palustris* (syn.: *Anisothecium squarrosum*, *Dichodontium palustre*, *Dicranella palustris*). Due to obvious differences compared to the *Cardamino-Montion* (e.g., the presence of *Allium schoenoprasum*, *Bartsia alpina*, *Swertia perennis*, and *Pedicularis sudetic*a, and the absence of *Saxifraga stellaris*, *Sagina saginoides*, *Sedum villosum*, and *Montia fontana*), Hadač (1983) described this vegetation as *Swertio perennis-Anisothecion squarrosi* Hadač 1983.

Later, Hinterlang (1992) described another new alliance for bryophyte-dominated arctic-alpine spring vegetation, *Philonotidion seriatae*, which contains *Philonotis seriata*, *Bryum schleicheri* and *Saxifraga stellaris* as in Braun-Blanquet's original description of *Cardamino-Montion*. Nevertheless, he retained the name *Cardamino-Montion* for springs with *Montia fontana* s.l., including Braun-Blanquet´s subalpine association.

Consistent differentiation between bryophyte-dominated arctic-alpine spring vegetation and herb-rich montane spring vegetation with *Montia fontana* agg. began with the first Europe-wide synthesis of spring vegetation by Zechmeister and Mucina (1994). In this study, the vegetation of low-elevation (mostly colline and submontane) springs with *Montia fontana* was described as the new alliance *Epilobio nutantis-Montion* Zechmeister in Zechmeister et Mucina 1994. The same solution was adopted in many subsequent studies, and finally also in the European vegetation checklist by Mucina et al. (2016). The name *Philonotidion seriatae* Hinterlang 1992 was placed there, for unspecified reasons, as a synonym of *Swertio perennis-Anisothecion squarrosi* Hadač 1983 instead of *Cardamino-Montion*, with which it shares more diagnostic species.

Recently, Peterka et al. (2023) conducted a new pan-European synthesis of spring vegetation based on original relevé data classified using both unsupervised and supervised methods. This study identified vegetation types that consistently formed distinct clusters in numerical analyses (unsupervised classifications) and were reproducible by formal definitions (supervised classifications). In most cases, these vegetation types corresponded to each the above-mentioned alliances, with one exception: the relevés corresponding to the type associations of *Cardamino-Montion* and *Philonotidion seriatae* fell into one group in all cases, even when a fine classification with many clusters was performed. Peterka et al. (2023) selected the name *Philonotidion seriatae* Hinterlang 1992 for this vegetation, arguing that the name *Cardamino-Montion* was often used for different vegetation types in the past (herb-dominated colline to montane *Montia* springs and even shaded low-elevation springs), making it a source of misunderstanding among vegetation scientists and thus a *nomen ambiguum*.

Table 1 shows how the name *Cardamino-Montion* has been used for very different vegetation types corresponding to different currently distinguished alliances and even orders. Although it is not possible to prove that most of these uses excluded the type of this alliance, i.e. the open arctic-alpine vegetation of the *Bryo schleicheri-Montietum rivularis* association, it is obvious that different authors understand the name differently. Throughout the history of phytosociology, classification concepts evolved from a single broad alliance *Cardamino-Montion* towards smaller, ecologically and floristically more homogeneous units at the alliance level. The two name-giving taxa of *Cardamino-Montion*, both of which actually involve subordinate taxa with different ecological requirements, do not characterize the vegetation corresponding to the type and are instead characteristic of other currently distinguished alliances: *Cardamine amara* s.l. of *Caricion remotae* and *Cratoneuro-Calthion laetae*, and *Montia fontana* s.l. of *Epilobio nutantis-Montion*. Applying the rules strictly and maintaining the oldest name *Cardamino-Montion* would be a constant source of error. We would then have to use two similar, counter-intuitive names: *Cardamino-Montion* for arctic-alpine springs (although the name-giving taxa occur mainly in montane springs) and *Epilobio nutantis-Montion* for montane springs (although the name-giving taxon, *Epilobium nutans*, occurs mainly in arctic-alpine springs). Therefore, it is likely that the name *Cardamino-Montion* would gradually become ambiguous.

For these reasons, we propose conserving the name *Philonotidion seriatae* Hinterlang 1992 against the names *Cardamino-Montion* Braun-Blanquet 1925, *Cardamino-Montion* Braun-Blanquet 1926, and *Montion* Maas 1959. The latter three alliances share a nomenclatural type which is different from the type of *Philonotidion seriatae*. The type of *Philonotidion seriatae* is *Cratoneuro-Philonotidetum* Geissler 1976. The lectotype of this association, selected by Hinterlang (2017), is relevé 11 in table 10 in Geissler's article (1976).

In addition, we propose conserving the name *Philonotidion seriatae* Hinterlang 1992 against the name *Mniobryo-Epilobion hornemannii* Nordhagen 1943. This will prevent the name *Mniobryo-Epilobion hornemannii* Nordhagen 1943 from being used for a broader alliance containing the nomenclatural types of *Cardamino-Montion*, *Philonotidion seriatae*, and *Mniobryo-Epilobion hornemannii*, since *Epilobium hornemanii* does not occur in most of the distribution range of such a hypothetical alliance.

We acknowledge that classification systems combining associations to alliances differently than was done in the studies by Zechmeister and Mucina (1994), Mucina et al. (2016), and Peterka et al. (2023) may appear in the future. If our proposal is accepted, then the name *Philonotidion seriatae* Hinterlang 1992 should be used for all species-poor, bryophyte-dominated, non-calcareous spring vegetation types. The name, however, would exclude *Cratoneuro filicini-Calthion laetae* Hadač 1983, which is productive, herb-dominated, and partly transitional to *Cardamino-Chrysosplenietalia* Hinterlang 1992 or even *Mulgedio-Aconitetea*. It would also exclude *Swertio perennis-Anisothecion squarrosi* Hadač 1983, which is also rich in herbs and partly transitional to *Scheuchzerio-Caricetea nigrae*. Any hypothetical alliance comprising the latter two herb-rich alliances should therefore be named either *Cratoneuro filicini-Calthion laetae* Hadač 1983 or *Swertio perennis-Anisothecion squarrosi* Hadač 1983, depending on its content. We consider these names more suitable for such hypothetical alliances than *Philonotidion seriatae*, as they both contain taxa from the highest vegetation stratum (herb layer in this case). Finally, a hypothetical alliance combining all non-calcareous springs (regardless of shading and climate, i.e. comprising two currently recognized orders) would be named *Caricion remotae* Kästner 1941.

Should our proposal be accepted, the name *Cardamino-Montion* would remain available for a hypothetical alliance that excludes the type of *Philonotidion seriatae*; e.g. an alliance comprising non-calcareous springs regardless of elevation, but excluding vegetation extremely poor in vascular plants or without *Montia fontana*.

Author contributions

M.H. led the writing, while all authors conceived the idea and critically revised the manuscript.

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RESEARCH PAPER
CLASSIFICATION OF EUROPEAN FORESTS

How to classify forests? A case study from Central Europe

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Abstract

Aims: Inconsistent treatment of the vegetation layers is one of the main problems in the floristic classification of forests. In this study I investigate whether a classification based solely on woody species leads to units similar to the Braun-Blanquet system or to something completely different. **Study area:** Austria (Central Europe) and adjacent regions. **Methods:** 23,681 forest relevés from the Austrian Vegetation Database were classified using TWINSPAN. Spruce and pine plantations and stands with a cover of non-native woody species > 5% were excluded from the dataset. Only native tree and shrub species were used in the classification while herbs, dwarf shrubs, cryptogams and all records of woody species in the herb layer were omitted. **Results:** The TWINSPAN classification revealed elevation (i.e., climate) as the main floristic gradient in the data set. Within lowland communities, soil moisture was the dominant factor. The higher units of the Braun-Blanquet system were mostly well reproduced. **Conclusions:** The higher levels of the phytosociological forest classification (class, order, partly also alliance) can basically be defined by taking only the shrub and tree layer into account. However, all past and current classifications suffer from arbitrary exceptions to this rule. This leads to many inconsistencies and blurs the main biogeographical patterns within European forests. Here I argue that using the tree and shrub species for defining the higher levels and the understorey species for defining the lower ones is best suited to meet the properties that users would expect from a good forest classification.

Taxonomic reference: Fischer et al. (2008).

Syntaxonomic reference: Mucina et al. (2016) if not stated otherwise.

Abbreviations: EVC = EuroVegChecklist (Mucina et al. 2016).

Keywords

Braun-Blanquet approach, forest, shrub layer, tree layer, vegetation classification

Introduction

The classes of the Braun-Blanquet system correspond to major floristic, biogeographical and ecological units (Pignatti et al. 1995; Loidi 2020). For European zonal forests, these are the *Quercetea ilicis* (mediterranean evergreen), *Quercetea pubescentis* (submediterranean deciduous), *Quercetea robori-petraeae* and *Carpino-Fagetea* (temperate deciduous), *Vaccinio-Piceetea* (boreal and temperate montane–subalpine coniferous) and *Betulo-Alnetea viridis* (subarctic-subalpine deciduous) (Figure 1). Azonal forests can be arranged into two groups: *Erico-Pinetea*, *Pyrolo-Pinetea* and *Junipero-Pinetea* include coniferous forests on very dry sites, while *Salicetea purpureae*, *Alno-Populetea* and *Alnetea glutinosae* are wetland forests. Finally, the *Crataego-Prunetea*, *Franguletea* and *Robinietea* comprise seral woodland and tall-scrub (Mucina et al. 2016). These classes can be incorporated into a global formation system, enabling broad-scale comparisons among continents (Willner and Faber-Langendoen 2021).

For most of the 20th century, the correspondence between classes and formations was much weaker because some classes (*Vaccinio-Piceetea*, *Betulo-Adenostyletea*, *Epilobietea*) included both forest and non-forest vegetation (e.g., Oberdorfer 1957). Splitting these physiognomically heterogeneous classes has been identified as one of the megatrends in phytosociology during the last 50 years (Guarino et al. 2018; Willner and Faber-Langendoen 2021). However, many uncertainties and inconsistencies still linger within the classes, blurring the biogeographical and ecological correspondences outlined above. For instance, the EuroVegChecklist (EVC, Mucina et al. 2016) classifies Western Caucasian *Pinus brutia* forests (*Campanulo sibiricae-Pinion brutiae*) in the *Quercetea pubescentis* while the *Pinus brutia* forests of the Eastern Mediterranean are included in the *Quercetea ilicis* (but see Bonari et al. 2021 for a different solution). Boreal-subarctic birch woods on nutrient-poor podzolic soils (*Empetro hermaphroditi-Betulion pumilae*) are included in the *Vaccinio-Piceetea*, those on nutrient-rich soils (*Geranio sylvatici-Betulion pumilae*) in the *Betulo-Alnetea viridis*. Temperate pine forests on acidic soils (*Dicrano-Pinion sylvestris*) are classified within the *Vaccinio-Piceetea* by the EVC, whereas Willner and Grabherr (2007) assign them to the *Erico-Pinetea*. Acidophytic beech forests are placed in the *Carpino-Fagetea* by some authors, but in the *Quercetea robori-petraeae* by others (Willner 2002; see also remark *fag03* in Mucina et al. 2016, p. 35). High montane acidophytic beech forests of Central Europe (*Calamagrostio villosae-Fagetum*) were even assigned to the *Vaccinio-Piceetea* in Oberdorfer (1992). Temperate *Abies alba* forests are either considered as part of the *Carpino-Fagetea* (e.g., Chytrý 2013), or as part of the *Vaccinio-Piceetea* (e.g., Willner and Grabherr 2007; Mucina et al. 2016), whereas some authors split them between the two classes (Oberdorfer 1992).

All these examples have one question in common: Should one give higher weight to the tree layer or the herb layer composition when classifying forests? Floristic similarity is the main criterion in the Braun-Blanquet approach (Westhoff and Van der Maarel 1978). However, floristic similarity of the tree layer might suggest a different grouping than floristic similarity of the herb layer . As the European tree flora is rather poor in species compared to other continents (Leuschner and Ellenberg 2017), overall similarity is usually driven by the herb layer. Thus, following a purely floristic approach, communities dominated by the same tree species may end up in different classes, orders or alliances (Grabherr et al. 2003). Because such units are often very heterogenous in terms of physiognomy and at odds with broad-scale formations and biogeographical

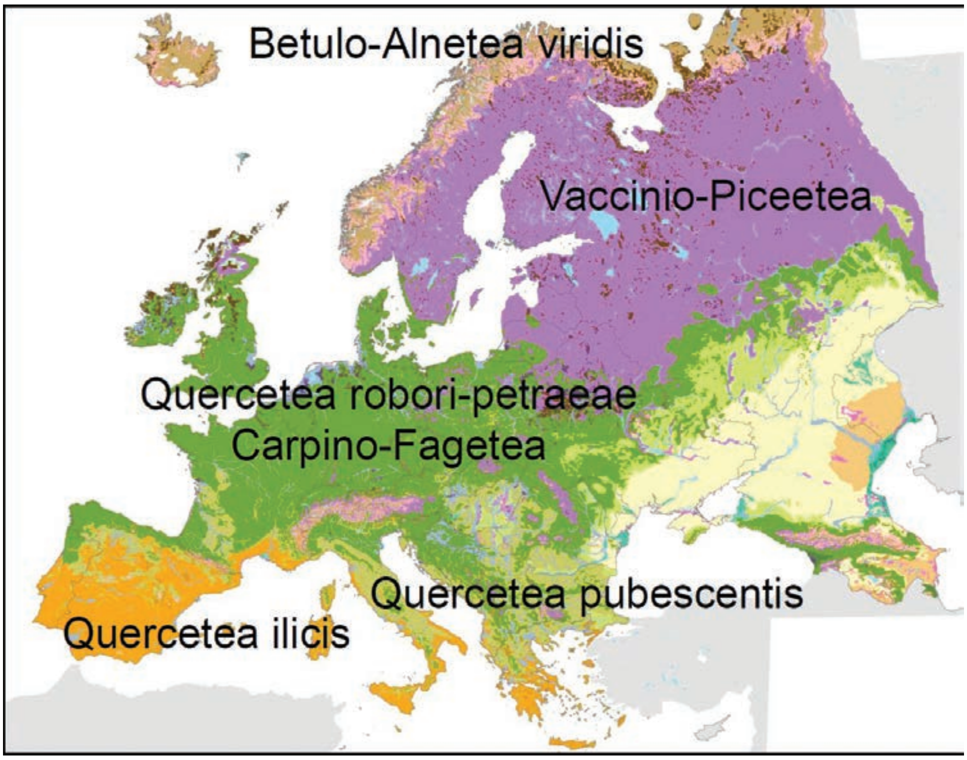

Figure 1. Main zonal formations of Europe (following Bohn et al. 2000) and corresponding EVC classes. Orange: mediterranean sclerophyllous forests and scrub (*Quercetea ilicis*); yellow-green: submediterranean deciduous broad-leaved forests (*Quercetea pubescentis*); dark green: cool-temperate deciduous broad-leaved forests (*Quercetea robori-petraeae*, *Carpino-Fagetea*); lilac: boreal, hemiboreal and temperate-montane coniferous and mixed broad-leaved-coniferous forests (*Vaccinio-Piceetea*); pale pink: subarctic and temperate-subalpine open woodland and scrub (*Betulo-Alnetea viridis*).

units, most authors consciously or unconsciously give higher weight to the tree species composition in at least some cases. However, in the absence of a general rule, these decisions are mostly subjective and arbitrary, resulting in a low stability of the forest classification in Europe.

Similar problems arise from the shrub layer, especially for communities without a tree layer. In the past, shrub communities were either joined with forests or with herb vegetation: The *Prunetalia spinosae* were part of the *Querco-Fagetea*, the *Sambucetalia racemosae* part of the *Epilobietea angustifolii*, the *Betulo-Alnetea viridis* included in the *Betulo-Adenostyletea* etc. (Oberdorfer 1992; Mucina et al. 1993). Whether shrub communities should be separated from forests on a high syntaxonomic level is still a controversial issue (e.g., Loidi 2020). Indeed, while the classes *Crataego-Prunetea* and *Betulo-Alnetea viridis* have been widely accepted in recent decades, they still include communities dominated by either shrubs or trees (see Mucina et al. 2016). The distinction between trees and tall shrubs is not always straightforward as many woody species have a rather high phenotypic plasticity. For instance, *Fagus sylvatica* often has a prostrate growth form at its upper elevational limit (Willner 2002), *Quercus pubescens* may be less than 4 m tall on dry sites with shallow soils (Jakucs 1961), while *Corylus avellana* can achieve 10 m in height despite having a shrubby branching pattern (Schütt and Lang 2014). Therefore, *a priori* separation of forests and tall scrub is inevitably at odds with the floristic principle (see also Willner and Faber-Langendoen 2021).

Interestingly, the traditional classification of tall shrub vegetation is almost exclusively based on the species composition of the shrub layer (Tüxen 1952; Weber 1997; Willner and Grabherr 2007). Herbs and grasses are often confined to the fringes and gaps of the scrub while the dense interior is almost completely devoid of a herb layer (Weber 1999). Therefore, non-woody species in relevés mainly reflect the neighbouring fringe and grassland vegetation, which belongs to a different successional stage, and their presence is strongly dependent on the delimitation of the sampling plot. Since the classification of scrub communities should reflect the ecological and biogeographical properties of the dominant shrubs rather than those of adjacent herbs and grasses, it makes sense to ignore the latter in the delimitation of higher syntaxa.

In an effort to increase the consistency of the Central European forest classification, Willner and Grabherr (2007) adopted an approach for the definition of higher forest syntaxa that was similar to that of tall shrub vegetation; that is, they suggested that the upper units of the system should be primarily based on the species composition of the tree layer, whereas the lower ones should be primarily based on the understorey composition (Willner 2017). Depending on the ecological amplitude of the dominant trees, the switch between over- and understorey was done at different hierarchical levels (e.g., between order and alliance for spruce forests, and between alliance and suballiance for most deciduous forests). However, the principle was not rigorously applied using numerical methods.

In the present study, I investigate whether a classification of Central European forests based solely on the woody species of the shrub and tree layer leads to units similar to the traditional Braun-Blanquet system or to something completely different.

Study area

The plot records (relevés) used in this study are from Austria (Central Europe) and adjacent regions in the SE Alps and NW Dinaric mountains (Figure 2). Austria covers most of the Eastern Alps and their foreland, the western part of the Pannonian Basin and the SE part of the Bohemian Massif. The elevation of the plots ranges from 120 m a.s.l. in Eastern Austria to the highest forests in the Alps at ca. 2300 m a.s.l. Annual precipitation ranges from 500 mm to 2000 mm (in the SE Alps locally up to 3000 mm). The mean annual temperature ranges from 1–2°C at the treeline to 10°C in the Pannonian lowland.

Due to the large climatic gradient Austria has a large variety of forest types, and forests cover 46% of the country (ca. 3.88 million hectares) . Lowland forests are mostly deciduous, and oaks (*Quercus* spp.), hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*) are dominant trees. The outer ranges of the Alps are occupied by mixed forests composed predominantly of beech and fir (*Abies alba*). The inner parts of the Alps, which have a strongly continental climate, and the whole subalpine belt are covered by coniferous forests with spruce (*Picea abies*), larch (*Larix decidua*), and Arolla pine (*Pinus cembra*) as dominants. The upper subalpine belt is often dominated by *Pinus mugo* krummholz (Mayer 1974).

Methods

Dataset preparation

Initially, all relevés of forest and shrub communities were selected from the Austrian Vegetation Database (GIVD-ID EU-AT-001; Willner et al. 2012). Spruce and pine plantations and stands with a cover of non-native woody species > 5% were excluded from the dataset. Also excluded were forest relevés where the cover of trees was not estimated separately for the tree and herb layer, relevés with a cover of woody species determined only at the genus level > 5%, and relevés dominated by (>25%) low shrubs [i.e., shrub species not exceeding 2 m, including all *Rubus* species]. The 2 m threshold was chosen following the definition of the forest and woodland formation class (Willner and Faber-Langendoen 2021). Finally, relevés with a total cover of trees and tall shrubs < 15% were omitted. This resulted in a dataset of 23,681 relevés, with 22,588 plots from Austria and 1,093 plots from neighbouring countries (Figure 2).

Only native tree and tall shrub species in the shrub and tree layer were used in the classification while all other taxa (including records of woody species in the herb layer and

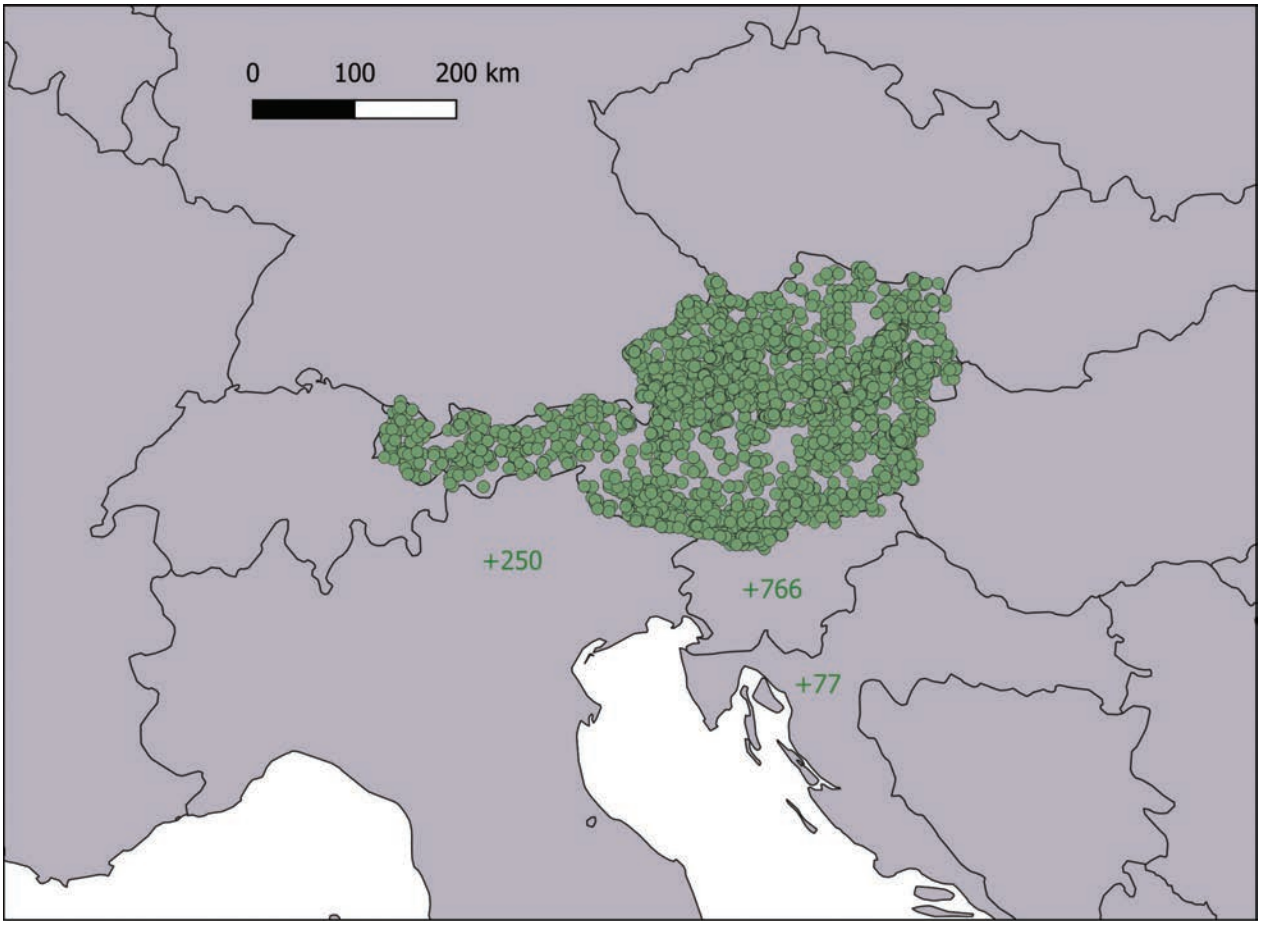

Figure 2. Plot locations in Austria (green dots) and adjacent areas (green numbers, indicating the number of plots from northern Italy, Slovenia, and Croatia, respectively).

taxa determined only at the genus level) were omitted. The omission of non-native trees and shrubs follows the consideration that the syntaxonomic system of European forest and shrub communities should be based on the native species (though syntaxa for communities dominated by non-native species might be added in a second step). Records of native tree and tall shrub species in different layers were merged using the algorithm published by Fischer (2015). Altogether, 111 taxa were kept in the final dataset. All data handling was done with JUICE 7.1 (Tichý 2002).

Numerical classification

The matrix of 23,681 relevés and 111 taxa was classified using the original TWINSPAN algorithm (Hill 1979). Parameter settings were three pseudospecies cutlevels (0%, 5%, 25%), six levels of division and a minimum group size for division of two. For species sorting and interpretation, the diagnostic value of woody species for phytosociological classes according to Mucina et al. (2016) was used. If a species was given as diagnostic for two or more classes occurring in Central Europe, the diagnostic value according to Willner and Grabherr (2007) was followed. Within each class, species were sorted by decreasing phi coefficient (Chytrý et al. 2002; Tichý and Chytrý 2006) using a threshold of 0.3. The phi coefficient was calculated assuming equal group size, and positive phi values were only accepted if the difference in species constancy between the target unit and the rest of the data set was significant according to Fisher's exact test at $p < 0.05$.

Results

The TWINSPAN classification resulted in 63 clusters (one division failed because the minimum group size was not reached). With a few exceptions, lowland forests and scrubs were separated from those at higher elevations at the first level of division. At the second division level, lowland communities were further divided along a moisture gradient, and montane communities were separated from subalpine ones (Table 1).

Specifically, the TWINSPAN clusters corresponded to the following vegetation types (numbers in brackets refer to the column number in Table 1 and Suppl. material 1, syntaxa follow the EVC system; the clusters are numbered from 1 to 64 to show the full TWINSPAN hierarchy; note that there is no cluster 48 because the corresponding level 6 division failed):

1–8 (1): nutrient-rich willow carrs with *Salix cinerea* (*Salicion cinereae* p.p.)

9–12 (2): submontane and montane alluvial willow scrub (*Salicion eleagno-daphnoidis*)
13 (3): alluvial forests with *Salix alba* (*Salicion albae* p.p.)
14 (4): alluvial forests with *Salix fragilis* (*Salicion albae* p.p.)
15–16 (5): lowland alluvial scrub with *Salix triandra* (*Salicion triandrae*)
17–20 (6): swamp forests with *Alnus glutinosa* (*Alnion glutinosae*)
21 (7): alluvial forests with *Populus alba* (*Alnion incanae* p.p.)
22 (8): alluvial forests with *Alnus incana* (*Alnion incanae* p.p.)
23 (9): alluvial forests with *Alnus glutinosa* (*Alnion incanae* p.p.)
24 (10): sycamore forests (*Tilio-Acerion*)
25 (11): moist oak-hornbeam forests with *Quercus robur* (*Carpinion betuli* p.p.)
26 (12): lime forests and mesic oak-hornbeam forests with *Fraxinus excelsior* (*Melico-Tilion platyphylli*, *Carpinion betuli* p.p.)
27 (13): mesic and dry oak-hornbeam forests with *Quercus petraea* (*Carpinion betuli* p.p.)
28 (14): acidophytic oak forests with *Quercus petraea* (*Agrostio-Quercion petraeae*)
29 (15): thermophilous oak forests on deeper soils (*Quercion petraeae*, *Quercion pubescenti-petraeae* p.p.)
30 (16): thermophilous oak forests on shallow soils with *Quercus pubescens* (*Quercion pubescenti-petraeae* p.p.)
31 (17): thermophilous seral scrub (*Berberidion vulgaris*, *Urtico-Crataegion*)
32 (18): lowland alluvial hardwood forests (*Fraxino-Quercion roboris*)
33–36 (19): beech forests (*Fagetalia sylvaticae*, *Luzulo-Fagetalia sylvaticae*)
37–38 (20): spruce forests (*Piceetalia excelsae*, *Athyrio filicis-feminae-Piceetalia*)
39–40 (21): montane elder scrub in forest clearings (*Sambuco-Salicion capreae*)
41 (22): *Pinus sylvestris* forests (*Erico carneae-Pinion*, *Dicrano-Pinion sylvestris*, *Vaccinio uliginosi-Pinion sylvestris*)
42 (23): *Pinus nigra* forests (*Erico-Fraxinion orni*)
43–44 (24): dry calcareous *Ostrya carpinifolia* forests on shallow soils (*Fraxino orni-Ostryion*)
45–47 (25): nutrient-poor willow carrs with *Salix aurita* (*Salicion cinereae* p.p.)
49–52 (26): subalpine krummholz with *Pinus mugo* (*Pinion mugo*, *Erico-Pinion mugo*)
53–54 (27): subalpine *Larix decidua* woodland (*Piceion excelsae* p.p.)
55–56 (28): subalpine *Pinus cembra* woodland (*Piceion excelsae* p.p.)
57–64 (29): subalpine green alder scrub (*Alnion viridis*)

Discussion

Syntaxonomy

The TWINSPAN classification revealed elevation (i.e., climate) as the main floristic gradient in the data set. Within lowland communities, soil moisture was the dominant factor. Interestingly, the higher units of the Braun-Blanquet system were mostly well reproduced, with clusters 1–8 corresponding to the *Franguletea*, clusters 9–16 to the *Salicetea purpureae*, clusters 17–20 to the *Alnetea glutinosae*, clusters 21–23 to the *Alno-Populetea*, clusters 24–27 to the *Carpino-Fagetea* and so on. Notable exceptions are the classes *Quercetea pubescentis*, *Quercetea robori-petraeae* and *Crataego-Prunetea*, which were all intermingled with the *Carpino-Fagetea*. This could be interpreted as support for the more traditional concept of a broadly defined class *Querco-Fagetea* (e.g., Oberdorfer 1992; Loidi 2020). However, because the *Quercetea pubescentis* and *Quercetea robori-petraeae* have their main distribution outside the study area, this question will not be further discussed in the present paper. The strange position of the *Fraxino orni-Ostryion* in the TWINSPAN table reflects the fact that *Ostrya carpinifolia* forests reach their northern distribution limit in the study area, where they are confined to dry, calcareous sites similar to those of pine forests. Indeed, Mucina et al. (1993) classified these communities within the class *Erico-Pinetea*. Alluvial hardwood forests (*Fraxino-Quercion roboris*) were widely separated from the *Alnus* and *Populus* woods of the *Alnion incanae*, which suggests keeping them in the class *Carpino-Fagetea*. Lime forests (*Melico-Tilion platyphylli*) were grouped together with oak-hornbeam forests (*Carpinion betuli*). *Abies alba* forests were not reproduced as a separate cluster, but mostly included in beech forests, supporting the concept of Chytrý (2013). The position of subalpine *Larix decidua* and *Pinus cembra* woodland seems at odds with the EVC system, but it fits well with the classification in Willner and Grabherr (2007), where both units were included in a broadly defined *Pinion mugo*.

On the whole, the traditional Braun-Blanquet system of forests seems to have given more weight to the tree species combination than is generally acknowledged in textbooks. As expected, the syntaxonomic rank of the TWINSPAN clusters varies vastly, from a single association (e.g., cluster 13: *Salicetum albae*) to a group of classes (cluster 41: *Pinus sylvestris* forests). This reflects the different ecological amplitude of the dominant species. In most cases, however, the woody species combination seems most suitable for the definition of orders and alliances. Some ecological gradients (e.g., calcareous versus acidic soils) are only visible in the herb layer (including dwarf shrubs) and are therefore not reflected in the table.

What do we expect from a good forest classification?

Loidi (2020) suggested three criteria for a “good” phytosociological class: (1) biogeographical-evolutionary criterion: common origin and evolution, (2) floristic criterion: common set of characteristic species, and (3) application criterion: coherence in the presentation. For

Table 1. Synoptic table of the TWINSPAN result. Values are percentage constancy. Bold values indicate an average cover > 14%, grey shading indicates high fidelity (i.e., phi > 0.3). Species are sorted according to their diagnostic value for classes. The vertical lines represent the division level 2. Groups 21 and 25 (with 14 and 10 relevés, respectively) and species not reaching 10% constancy in any column are omitted. The full table is provided in Suppl. material 1.

Group number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**22**	**23**	**24**	**26**	**27**	**28**	**29**
TWINSPAN level	3	4	6	6	5	4	6	6	6	6	6	6	6	6	6	6	6	6	4	5	6	6	5	4	6	6	3
Number of relevés	121	307	318	110	109	855	250	833	1087	1013	393	1847	653	397	749	546	299	96	5232	5090	1181	255	327	1000	149	133	307
Franguletea																											
Salix cinerea	**95**	1	3	3	4	14	1	3	2	1	1	.	.	.	.	.	1	.	.	1	1	.	.	1	.	.	.
Salicetea purpureae																											
Salix eleagnos	.	**57**	4	9	3	.	1	5	3	5	.	1	.	.	1	1	1	.	1	1	3	1	3	1	.	.	1
Myricaria germanica	.	17	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Salix myrsinifolia	.	21	5	.	1	1	1	6	1	1	.	.	.	.	.	.	1	.	.	1	1	.	.	1	.	.	1
Salix daphnoides	.	15	3	.	2	.	.	2	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	1
Salix fragilis	19	6	20	**91**	9	9	2	3	12	1	1	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Salix × rubens	1	1	2	24	6	2	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix triandra	1	10	14	30	**92**	1	.	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Salix viminalis	.	3	8	14	39	1	.	1	1	1	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Salix purpurea	1	**82**	31	57	33	1	2	6	6	1	1	1	.	1	1	.	1	6	.	1	1	.	.	1	.	.	.
Salix alba	5	16	**97**	32	62	2	25	8	7	1	1	1	.	1	1	.	1	2	1	.	1	.	.	.	.	.	.
Alnetea glutinosae																											
Alnus glutinosa	27	2	4	34	3	**99**	9	2	50	7	10	5	1	1	1	.	1	5	1	1	1	.	.	1	.	.	.
Frangula alnus	9	4	3	1	.	30	6	8	8	3	22	4	1	23	8	4	4	18	3	4	17	2	1	3	.	.	.
Alno-Populetea albae																											
Populus nigra	.	18	36	12	6	1	22	5	4	1	1	1	1	.	1	.	1	7	1	.	.	.	.	.	.	.	.
Populus alba	1	1	4	.	1	2	**62**	3	7	1	2	1	1	1	2	1	1	33	1	1	.	.	.	.	.	.	.
Alnus incana	2	43	39	35	4	4	46	**99**	24	26	2	1	.	1	1	.	.	.	1	6	2	.	1	1	.	3	2
Prunus padus	4	6	27	17	.	36	50	40	72	11	8	7	1	1	4	1	3	7	1	1	1	.	.	1	.	.	.
Ulmus minor	.	.	3	.	.	1	14	1	3	1	12	3	1	1	19	4	16	**70**	1	.	.	.	.	.	.	.	.
Fraxinus angustifolia	1	.	1	1	1	2	6	1	1	.	11	1	1	.	1	.	.	**32**	.	.	.	.	.	.	.	.	.
Viburnum opulus	7	4	17	9	1	17	18	15	25	7	7	6	1	2	5	1	5	8	1	1	1	1	.	.	.	.	.
Ulmus laevis	.	.	9	8	.	1	30	2	9	1	4	2	1	.	1	.	1	24	1	1	.	.	.	.	.	.	.
Crataego-Prunetea																											
Cornus sanguinea	2	5	36	18	3	7	**90**	31	48	11	22	22	4	13	51	44	44	**78**	1	1	2	2	1	.	.	.	.
Ligustrum vulgare	1	1	4	1	.	4	15	6	16	1	12	13	12	18	76	53	60	45	1	1	7	4	4	.	.	.	.
Viburnum lantana	.	1	2	1	.	1	2	6	9	7	3	14	2	2	43	53	22	2	1	1	12	5	10	1	.	.	.
Prunus spinosa	1	.	1	.	.	1	5	1	1	1	7	1	1	5	18	12	**68**	21	1	.	1	1	.	.	.	.	.
Rosa canina agg.	1	1	1	1	.	1	8	1	3	1	4	3	4	9	24	29	77	17	1	1	1	4	1	.	.	.	.
Juniperus communis	.	1	.	.	.	1	.	1	.	1	2	1	1	4	5	8	4	.	1	2	53	7	7	3	.	1	1
Amelanchier ovalis	.	.	.	.	.	.	.	.	.	1	1	2	1	.	1	33	.	.	1	1	41	70	30	6	.	.	.
Cotoneaster tomentosus	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	6	.	.	1	1	7	25	15	1	.	.	.
Crataegus monogyna	1	2	6	1	2	2	30	12	17	5	22	22	12	17	73	68	**74**	64	1	1	4	8	4	.	.	.	.
Corylus avellana	.	2	3	3	.	5	3	9	49	62	55	49	9	40	30	29	9	23	11	4	9	5	8	1	.	.	1
Berberis vulgaris	.	1	3	.	.	3	3	10	6	6	5	7	1	7	17	47	11	.	2	2	34	47	9	1	.	.	.
Euonymus europaeus	2	1	10	9	1	13	27	19	33	6	12	12	3	2	25	12	37	18	1	1	1	.	1	.	.	.	.
Rhamnus cathartica	.	.	1	1	.	9	3	1	2	1	5	5	2	3	14	35	30	19	1	1	3	3	3	.	.	.	.
Prunus mahaleb	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	13	7	.	.	.	1	1	.	.	.	.	.
Quercetea pubescentis																											
Quercus cerris	.	.	.	.	.	.	.	.	.	1	3	5	28	11	48	9	6	3	1	1	.	.	.	.	.	.	.
Quercus pubescens	.	.	.	.	.	.	.	.	.	.	1	2	1	.	26	**76**	4	1	1	.	1	6	3	.	.	.	.
Cornus mas	.	.	.	.	.	.	1	.	1	1	3	16	9	1	39	64	3	3	1	1	.	9	.	.	.	.	.

Group number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**22**	**23**	**24**	**26**	**27**	**28**	**29**
TWINSPAN level	3	4	6	6	5	4	6	6	6	6	6	6	6	6	6	6	6	6	4	5	6	6	5	4	6	6	3
Number of relevés	121	307	318	110	109	855	250	833	1087	1013	393	1847	653	397	749	546	299	96	5232	5090	1181	255	327	1000	149	133	307
Euonymus verrucosus	.	.	.	.	.	.	.	1	1	1	2	10	3	2	20	38	2	2	1	.	1	.	3	.	.	.	.
Ostrya carpinifolia	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	3	.	.	3	1	1	4	**98**	1	.	.	.
Fraxinus ornus	.	.	.	.	.	.	1	1	.	.	.	1	1	.	3	4	.	.	2	1	3	13	83	.	.	.	.
Sorbus aria agg.	.	.	.	.	.	1	.	.	1	1	2	14	7	6	9	63	1	.	11	3	30	69	55	6	1	.	.
Sorbus torminalis	.	.	.	.	.	.	.	.	1	.	2	5	16	11	27	25	2	.	2	1	.	3	.	.	.	.	.
Pyrus pyraster	.	1	.	.	.	1	.	1	1	1	5	2	4	9	15	15	1	9	1	1	1	1	1	.	.	.	.
Quercetea roboris																											
Quercus robur	1	1	1	5	.	9	10	2	23	4	**88**	22	4	11	30	7	13	63	3	1	5	.	3	.	.	.	.
Quercus petraea	.	.	.	.	.	1	.	.	.	1	9	24	**87**	**95**	**54**	11	1	.	11	1	5	1	6	.	.	.	.
Carpino-Fagetea																											
Ulmus glabra	.	3	1	5	.	1	3	3	17	60	2	34	2	1	5	5	1	1	10	1	1	1	.	.	.	.	.
Acer pseudoplatanus	.	6	2	1	.	6	2	18	49	**89**	13	59	4	2	9	9	3	4	45	10	9	7	6	12	9	.	12
Acer platanoides	.	1	1	.	.	1	.	1	4	6	1	29	3	1	5	9	1	2	3	1	1	1	1	.	.	.	.
Tilia platyphyllos	.	.	1	.	.	1	.	1	2	10	2	30	6	5	5	18	1	.	2	1	1	2	2	.	.	.	.
Acer campestre	.	.	1	.	.	1	8	1	9	3	24	34	34	4	53	34	17	58	2	1	1	.	.	.	.	.	.
Fagus sylvatica	.	1	.	.	.	2	.	1	5	39	15	**61**	46	16	5	17	.	.	**97**	21	9	25	29	5	2	.	1
Fraxinus excelsior	1	10	9	16	.	35	43	39	**91**	**88**	17	**74**	13	3	45	57	9	21	16	1	2	7	1	1	.	.	.
Carpinus betulus	.	1	1	1	.	5	1	1	16	9	**64**	**69**	**92**	54	36	18	3	16	6	1	1	.	2	.	.	.	.
Lonicera xylosteum	.	7	7	3	1	2	9	21	34	25	8	24	4	3	26	15	4	4	5	2	10	1	5	1	1	.	1
Tilia cordata	.	.	1	1	.	1	2	1	12	8	29	37	32	23	15	13	1	5	2	1	1	1	2	.	.	.	.
Prunus avium	.	1	1	1	.	1	1	2	8	5	23	24	17	17	28	9	20	5	3	1	1	.	.	.	.	.	.
Crataegus laevigata	.	.	.	.	.	1	.	1	2	1	9	12	11	4	19	14	2	14	1	1	1	.	.	.	.	.	.
Staphylea pinnata	.	.	.	.	.	.	.	.	1	3	1	13	2	.	4	14	1	.	1	.	.	.	.	.	.	.	.
Populus tremula	.	1	1	.	.	1	1	1	3	2	20	3	2	8	2	1	3	8	1	1	2	1	2	.	1	.	1
Vaccinio-Piceetea																											
Abies alba	.	.	.	.	.	1	.	1	2	8	3	7	3	2	1	1	.	.	50	26	1	1	1	5	7	.	1
Picea abies	.	11	1	1	.	23	1	28	17	51	34	21	9	14	6	4	1	.	69	**99**	62	26	38	34	60	60	43
Larix decidua	.	1	.	.	.	1	.	1	1	1	3	2	2	4	1	1	.	.	15	48	17	2	11	23	**99**	61	29
Pinus cembra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	7	1	.	.	3	51	**100**	11
Pinus uncinata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	11	.	.	2	1	.	.
Lonicera caerulea	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	.	.	.	1	1	1	.	1	6	11	3	5
Robinietea																											
Sambucus nigra	3	6	40	45	2	15	46	41	62	45	12	18	3	2	13	1	30	13	4	1	1	.	.	.	.	.	.
Erico-Pinetea																											
Pinus sylvestris	2	5	1	.	.	3	.	2	1	1	20	5	8	52	12	8	1	1	12	15	**93**	23	42	1	.	1	.
Pinus nigra	.	.	.	.	.	.	.	.	.	.	.	2	2	1	2	34	2	.	2	1	3	**98**	10	.	.	.	.
Rhamnus fallax	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	1	1	.	1	15	1	.	.	.
Roso pendulinae-Pinetea mugo																											
Sorbus chamaemespilus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	6	.	.	22	25	2	2
Pinus mugo (s. str.)	.	1	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	1	4	11	1	5	**98**	**72**	29	7
Rosa pendulina	.	.	.	.	.	1	.	1	1	2	.	1	.	.	.	1	.	.	2	2	3	2	1	16	15	.	1
Betulo-Alnetea viridis																											
Alnus alnobetula	.	.	.	1	.	1	.	1	.	1	.	1	.	.	.	.	.	.	1	3	1	.	1	9	24	13	**96**
Salix appendiculata	.	13	1	.	.	1	.	3	1	5	1	1	.	.	1	.	1	.	1	3	2	1	2	23	16	2	24
other species																											
Sorbus aucuparia	1	1	1	1	.	8	.	5	7	5	13	6	2	8	2	1	1	1	8	21	15	2	4	34	64	23	47
Betula pendula	.	7	3	6	.	2	2	4	4	2	25	6	14	25	3	1	2	2	4	7	7	1	2	1	3	3	14

the third criterion, he noted that "it is very difficult to argue, in a teaching context, that forests dominated by the same species belong to different classes". Obviously, the second and third criterion can only be simultaneously fulfilled if the class is floristically defined by the species of the dominant layer. In this way, most European tree species become character species on some hierarchical level while in many traditional systems they are only treated as companion species.

We might complement Loidi's criteria by four general properties that users might reasonably expect from a good forest classification: (a) The upper levels of the hierarchy are more easily recognizable than the lower levels. (b) The upper level units are more stable over time in terms of vegetation history. (c) The factors shaping global vegetation patters are reflected on the upper levels, while the factors responsible for regional and local patterns are reflected on the lower levels. (d) The upper levels are consistent with global formation and biome classifications.

As shown above, the higher levels of the phytosociological forest system can basically be defined by taking only the tall shrub and tree layer into account. However, this has never been formulated as a rule, and all past and current classifications suffer from arbitrary weighting of the layers, leading to inconsistencies and blurring the main biogeographical patterns within European forests. The distribution of European tree species is mainly controlled by broad climatic gradients as well as differences in soil moisture (Table 1) – the same ecological factors that are reflected in global biome and formation systems (Walter 1976; Faber-Langendoen et al. 2016; Loidi et al. 2022). Differences in calcium content, on the other hand, have a more regional significance, and are mostly visible in the herb layer composition (Leuschner and Ellenberg 2017). It is therefore advisable to reflect the latter on lower hierarchical levels, e.g., by uniting basiphytic and acidophytic beech forests in the same class or even order (Moor 1978; Oberdorfer 1992; Willner and Grabherr 2007; Willner et al. 2017), or by transferring temperate dry *Pinus sylvestris* forests on acidic bedrock (alliance *Dicrano-Pinion*) from the *Vaccinio-Piceetea* to the *Erico-Pinetea* – a solution that is also supported by numerous common understorey species (Willner and Grabherr 2007). However, given the extremely broad amplitude of *Pinus sylvestris*, it is also justified to classify the forests dominated by this species in at least two different classes, *Erico-Pinetea* (temperate dry pine forests, including the *Erico-Pinion*, *Dicrano-Pinion*, *Ononido-Pinion* and other alliances) and *Vaccinio uliginosi-Pinetea* (boreal and temperate wet pine forests, including the *Vaccinio uliginosi-Pinion* and *Cladonio stellaris-Pinion*; see Ermakov and Morozova 2011). Submediterranean pine forests dominated by *Pinus nigra* should probably be placed in a separate class.

Understorey species may have markedly different biogeographical histories than the tree species they are currently associated with (Záveská et al. 2021; Willner et al. 2023). Thus, we can assume that vegetation units defined by tree species have been more stable over time than syntaxa defined by species from different layers. In fact, vegetation units solely defined by understorey species can be completely independent of the tree layer and even exist outside the forest. A classic example is Braun-Blanquet's *Rhododendro-Vaccinion* (Braun-Blanquet et al. 1939), which comprised both coniferous forests and treeless dwarf shrub heaths. Carrying this idea to extremes, Gillet (1988) proposed to independently classify the herb, shrub and tree layers (see also Gillet and Julve 2018). While agreeing with these authors on the basic problem, I suggest a different and less radical solution: By using the tree and (tall-)shrub layer for defining the upper levels and the herb and cryptogam layer for defining the lower levels of the system, the basic units (i.e., the associations) represent the whole forest community. At the same time, over- and understorey composition are not mixed in an arbitrary and often confusing manner for the definition of the higher units as in most traditional systems. However, it must be emphasised that "upper" and "lower" level is meant in a purely relative sense here. The lowest appropriate rank to be defined by the tree and tall shrub layer depends both on the ecological amplitude of the resulting units and the floristic heterogeneity of the herb and cryptogam layer within these units; thus, it may vary from association or suballiance (though this will be uncommon) to a group of classes (see examples above).

Previous proposals have suggested separating forests and tall-scrub on the one hand and non-woody vegetation (including dwarf-shrub heaths) on the other hand as two *a-priori* structural types in syntaxonomy (Bergmeier et al. 1990; Dengler et al. 2005). If trees and tall-shrubs are used to define the classes of woody vegetation, this separation becomes a natural component of the floristic classification, without a sudden change of criteria. At the same time, phytosociological classes defined by the combination of woody species can be easily fitted into a global formation system (Willner and Faber-Langendoen 2021) as well as in most biome systems (Mucina 2019; Keith et al. 2022).

Data availability

The relevés used in this study are available upon request from the Austrian Vegetation Database (GIVD-ID EU-AT-001) managed by the author of this paper and from the European Vegetation Archive (https://euroveg.org/eva-database/).

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Supplementary material

Supplementary material 1
Full synoptic table
Link: https://doi.org/10.3897/VCS.117703.suppl1

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RESEARCH PAPER
PHYTOSOCIOLOGICAL NOMENCLATURE

Nomenclatural revision of the syntaxa of European coastal dune vegetation

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Abstract

This manuscript provides a review of the phytosociological nomenclature of the European syntaxa included in the classes *Ammophiletea arundinaceae*, *Honckenyo peploidis-Elymetea arenarii*, and *Koelerio glaucae-Corynephoretea canescentis*. The nomenclature has been refined and updated following the 4th edition of the International Code of Phytosociological Nomenclature (ICPN). In the Appendix, we submit two proposals (**37, 38**) to conserve the names *Ammophilion arundinaceae* Braun-Blanquet 1933 and *Medicagini marinae-Ammophiletum arundinaceae* Braun-Blanquet 1933.

Taxonomic reference: see references in the main text.

Syntaxonomic reference: see references in the main text.

Abbreviations: EVCC = European Vegetation Classification Committee; ICPN = 4th edition of the International Code of Phytosociological Nomenclature (Theurillat et al. 2021).

Keywords

coastal dune, Europe, nomenclature, *nomen conservandum*, plant community, syntaxonomy, vegetation

Introduction

A revision of the classification of shifting and stable coastal dune vegetation in Europe and the Mediterranean Basin was published by Marcenò et al. (2018). That study proposed several syntaxonomic changes to the classification accepted in EuroVegChecklist (Mucina et al. 2016). However, the authors maintained the same nomenclature as Mucina et al. (2016) to avoid confusion, since EuroVegChecklist is the main reference for European vegetation scientists.

In October 2019, a proposal to change the EuroVegChecklist classification of the classes *Ammophiletea*, *Helichryso-Crucianelletea maritimae* and *Koelerio-Corynephoretea canescentis* was submitted to the European Vegetation Classification Committee (EVCC), a body established by the Working Group European Vegetation Survey of the International Association for Vegetation Science (http://euroveg.org/evc-committee). The proposal was evaluated according to the EVCC procedures (http://euroveg.org/evc-committee) and eventually approved (Biurrun and Willner 2020). Before updating the new syntaxonomic treatment of coastal-dune vegetation on the European vegetation classification website (https://floraveg.eu/vegetation/), this article reviews the phytosociological nomenclature of syntaxa included in the classes *Ammophiletea arundinaceae*, *Honckenyo peploidis-Elymetea arenarii* and *Koelerio glaucae-Corynephoretea canescentis* following the 4th edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021). Two proposals for *nomina conservanda* (Art. 52) are reported in Appendix 1.

Methods

Syntaxon names were revised after reviewing the original diagnoses and descriptions in the original publications. The name-giving taxa (usually species) were checked and, where necessary, replaced with correct names (*nomina correcta*; Art. 44) or names in current use (*nomina mutata*; Art. 45), taking into account the taxonomic concepts and nomenclature of the most relevant recent floras and checklists (Castroviejo et al. 1986–2021; Tison et al. 2014; Pignatti et al. 2017–2019; Euro+Med 2023). To ensure the long-term stability of the nomenclature, we opted for the taxonomies that are most widely accepted in current floras. In particular, this applied to generic concepts of species classified in different genera. It should be noted, however, that authors are free to use either the original (and corrected if necessary) or the mutated name since *nomina mutata* are alternative forms of the name that can be used instead of the correct name (Art. 22). In contrast, *nomina correcta* are obligatory.

The information for each syntaxon contains the synonyms, the original form of the syntaxon name, the name-giving taxa for both the original and modified syntaxon names and the nomenclatural *typus*. Since the choice of the correct taxon name is based on the priority principle (Turland et al. 2018), we provide the date of publication of each taxon name to make our nomenclature solution more understandable. We have also added a brief commentary on the proposed changes when necessary. Appendix 2 contains the syntaxonomic framework in which all syntaxa considered in this paper are listed. This manuscript also contains syntaxa that have no nomenclatural issues and have been officially accepted in the EuroVegChecklist. The inclusion of these syntaxa aims to offer readers a comprehensive context and reaffirm their validity.

Results

We adopt the following names for the syntaxa of European coastal dune vegetation:

***Ammophiletea arundinaceae* Braun-Blanquet et Tüxen ex Westhoff et al. 1946**

Original form of the name (Westhoff et al. 1946: 46): "*Ammophiletea* Br.-Bl. et Tx. 1943 n. n."

Name-giving taxon: *Ammophila arenaria* subsp. *arundinacea* (Husn.) H. Lindb. 1932

Typus: *Ammophiletalia* Braun-Blanquet 1933 (*holotypus*)

Although Westhoff et al. (1946) list associations of the temperate European Atlantic coast with *Ammophila arenaria* subsp. *arenaria*, these associations are not relevant for determining the name-giving taxon of the class. The sole relevant aspect of the original diagnosis of the class is the inclusion of the single order *Ammophiletalia* Braun-Blanquet 1933 with an unambiguous reference. In the tables of Braun-Blanquet (1933), only *Ammophila arenaria* subsp. *arundinacea* is listed (see below).

***Ammophiletalia arundinaceae* Braun-Blanquet 1933**

Original form of the name (Braun-Blanquet 1933: 5): "*Ammophiletalia* Br.-Bl. (1921) 1933"

Name-giving taxon: *Ammophila arenaria* subsp. *arundinacea* (Husn.) H. Lindb. 1932 [Note: Braun-Blanquet (1933) used the incorrect author name "(Host)" for this subspecies, but this does not affect the syntaxonomic nomenclature since the subspecies had been validly published in 1932]

Typus: *Ammophilion arundinaceae* Braun-Blanquet 1933 (*holotypus*)

Mucina et al. (2016) considered *Ammophiletalia* Braun-Blanquet et Tüxen ex Westhoff et al. 1946 to be the correct name of this order. However, the order was already validly described by Braun-Blanquet (1933), who dealt with Mediterranean vegetation. The year 1921 in brackets after the order name probably refers to Braun-Blanquet (1921). However, no order is mentioned in Braun-Blanquet (1921), only the alliance "*Ammophilion*". The original diagnosis of the order contains a single valid alliance, the "*Ammophilion* Br.-Bl. (1921) 1933" [recte: *Ammophilion arundinaceae* Braun-Blanquet 1933], which is therefore the holotype of the order. There is a second alliance "*Ononidion angustissimae* Br.-Bl. prov.", but it is not validly published (Art. 3b, 8), therefore irrelevant from the nomenclatural point of view. The original diagnosis of the *Ammophilion* contains three associations that are validly described with synoptic tables. Since only *Ammophila arenaria* subsp. *arundinacea* is listed in the tables, this is the name-giving taxon of the order and the alliance.

Ammophilion arundinaceae* Braun-Blanquet 1933 *nom. cons. propos.

Original form of the name (Braun-Blanquet 1933: 5): "*Ammophilion* Br.-Bl. (1921) 1933"

Name-giving taxon: *Ammophila arenaria* subsp. *arundinacea* (Husn.) H. Lindb. 1932 [Note: Braun-Blanquet (1933) used the incorrect author name "(Host)" for this subspecies, but this has no effect on the syntaxonomic nomenclature]

Typus: *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921 *nom. invers.* (*holotypus*)

Synonym: *Ammophilion arenariae* Braun-Blanquet 1921 (correct name according to the ICPN).

The nomenclature of this alliance is discussed in Appendix 1.

Medicagini marinae-Ammophiletum arundinaceae **Braun-Blanquet 1933** ***nom. invers. et nom. cons. propos.***

Original form of the name (Braun-Blanquet 1933: 8): "Ass. à *Ammophila arundinacea* et *Medicago marina* Br.-Bl. (1921) 1933"

Name-giving taxa: *Medicago marina* L. 1753, *Ammophila arenaria* subsp. *arundinacea* (Husn.) H. Lindb. 1932 [Note: Braun-Blanquet (1933) used the incorrect author name "(Host)" for this subspecies, but this has no effect on the syntaxonomic nomenclature]

Typus: Braun-Blanquet (1921), relevé no. 2, p. 344 (Art. 18b, *lectotypus* selected by Fernández Prieto and Díaz González 1991 for the *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921)

Synonyms: *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921 *nom. invers.* (correct name according to the ICPN), *Medicagini marinae-Ammophiletum australis* Braun-Blanquet 1921 *nom. invers. et mut.* Fernández Prieto et Díaz González 1991 *nom. inept.*

The nomenclature of this association is discussed in Appendix 1.

Crucianelletalia maritimae **Sissingh 1974**

Original form of the name (Sissingh 1974: 103): "*Crucianelletalia maritimae* ordo novo [recte: ordo novus]"

Name-giving taxon: *Crucianella maritima* L. 1753

Typus: *Crucianellion maritimae* Rivas Goday et Rivas-Martínez 1958 (automatic type, Art. 20)

Ononidion ramosissimae **Pignatti 1953**

Original form of the name (Pignatti 1952: 322): "*Ononidion ramosissimae* Pign. 1953"

Name-giving taxon: *Ononis ramosissima* Desf. 1798

Typus: *Crucianelletum maritimae* Braun-Blanquet 1933: p. 9 (*lectotypus hoc loco*)

Synonym: *Crucianellion maritimae* Rivas Goday et Rivas-Martínez 1958

This syntaxon name was considered invalid by various authors. Rivas-Martínez et al. (2001, 2011) considered it a *nomen dubium* (Art. 38) without further explanation. However, Pignatti (1952, 1953) included the validly published association "*Crucianelletum maritimae* Br. Bl. (1921) 1933" [recte: *Crucianelletum maritimae* Braun-Blanquet 1933] in this alliance, providing a sufficient bibliographical reference in the last part of his work. Interestingly, the same association was reported as the holotype of the *Crucianellion maritimae* by Rivas Goday and Rivas-Martínez (1958). Mucina et al. (2016) also considered the name *Ononidion ramosissimae* as invalid (according to Art. 2b), probably because the bibliographical reference to Braun-Blanquet (1933) is not in the same part of the study as the description of the alliance (but see Art. 1, Note 2). Consequently, the *Ononidion ramosissimae* was validly described by Pignatti (1952, 1953) and it has priority over the *Crucianellion maritimae* Rivas Goday et Rivas-Martínez 1958, which is a later homotypic synonym.

Diantho attenuati-Scrophularion caninae **Baudière et Simonneau 1974** ***nom. corr. et mut.*** **Marcenò et al.** ***nom. mut. nov.***

Original form of the name (Baudière and Simonneau 1974: 39): "*Diantho-Scrofularion humifusae*"

Name-giving taxa of the original syntaxon name: *Dianthus pyrenaicus* subsp. *catalaunicus* (Willk. et Costa 1860) Tutin 1963, *Scrophularia humifusa* Timb.-Lagr. et Gaut. 1875

Name-giving taxa of the corrected and mutated syntaxon name: *Dianthus pyrenaicus* subsp. *attenuatus* (Sm. 1794) M. Bernal et al. 1988, *Scrophularia canina* L. 1753

Authoritative taxonomic treatments that use the name *Scrophularia canina*: Castroviejo et al. (1986–2021), Euro+Med (2023)

Typus: *Diantho attenuati-Corynephoretum canescentis* Baudière et Simonneau 1974 (*holotypus*)

Synonyms: *Diantho catalaunici-Scrophularion humifusae* Baudière et Simonneau ex Géhu et Bournique 1992

As noticed by Bernal (1988), Nyman (1878–1882) formally established the autonym *Dianthus attenuatus* Sm. subsp. *attenuatus* when he combined *D. attenuatus* subsp. *benearnensis* (Loret) Nyman. Hence, the epithet *attenuatus* has nomenclatural priority over *catalaunicus* at the subspecies rank. This implies a correction according to Art. 44 of the alliance name and the association name reported below.

Scrophularia humifusa Timb.-Lagr. et Gaut. is considered as a synonym of *S. canina* L. in the current taxonomic literature. Therefore, we propose a mutation of the association name. Castroviejo et al. (1986–2021) include *Scrophularia canina* var. *humifusa* (Timb.-Lagr. et Gaut.) Gaut. 1897 into the synonymy of *S. canina* subsp. *canina* and consider it as an invalid name (*nomen nudum*). However, it was published as a new combination with an indirect reference to the validly published name *S. humifusa* Timb.-Lagr. et Gaut., which renders the variety name validly published.

Diantho attenuati-Corynephoretum canescentis **Baudière et Simonneau 1974** ***nom. corr.***

Original form of the name (Baudière and Simonneau 1974): "*Diantho-Corynephoretum*"

Name-giving taxa of the original syntaxon name: *Dianthus pyrenaicus* subsp. *catalaunicus* (Willk. et Costa) Tutin 1963, *Corynephorus canescens* (L.) P. Beauv. 1812

Name-giving taxa of the corrected syntaxon name: *Dianthus pyrenaicus* subsp. *attenuatus* (Sm. 1794) M. Bernal et al. 1988, *Corynephorus canescens* (L.) P. Beauv. 1812

Typus: Baudière and Simonneau (1974), table II, relevé no. 19, p. 28 (*lectotypus hoc loco*)

Géhu and Bournique (1992) considered this syntaxon name and the corresponding alliance invalid (Art. 2b, *nom. nud.*). Baudière and Simonneau (1974) described two new associations: *Cladonio-Ephedretum*, referring to table 5: 34, 'groupements à Ephedra', and *Diantho-Corynephoretum*, referring to tables 2: 28 and 3: 30, 'groupements à *Corynephorus canescens*'. However, the *Cladonio-Ephedretum* is an invalid name because there are no *Cladonia* species in the relevés of table 5 (Art. 3f) - lichen species are only cited in the text. Therefore, the *Diantho-Corynephoretum* [recte: *Diantho attenuati-Corynephoretum canescentis*] is a valid name because both table 2 and table 3 contain relevés with *Corynephorus canescens* and *Dianthus catalaunicus*, including the name-giving taxon of the alliance *'Scrophularia canina* var. *humifusa* (Timb-Lag.) Gaut'. This suggests the validity of the two syntaxa described by Baudière and Simonneau (1974).

Helichryso barrelieri-Centaureion spinosae **Mucina et Dimopoulos in Mucina et al. 2016**

Original form of the name (Mucina et al. 2016: 142): "*Helichryso barrelieri-Centaureion spinosae* Mucina et Dimopoulos all. nov."

Name-giving taxa: *Helichrysum stoechas* subsp. *barrelieri* (Ten.) Nyman 1879, *Centaurea spinosa* L. 1753

Typus: *Thymbro capitatae-Centaureetum spinosae* Géhu 1992 *nom. illeg.* (*holotypus*)

The type chosen by Mucina and Dimopoulos is an illegitimate name (see Art. 43, Example 1). The correct name of the association is *Medicagini marinae-Centaureetum spinosae* (see below). However, this does not affect the legitimacy of the alliance name (Art. 17, Note 1).

Medicagini marinae-Centaureetum spinosae **Géhu in Géhu et al. 1988 *corr.* Marcenò et al. *nom. corr. nov.***

Original form of the name (Géhu et al. 1988: 99): "*Medicagini marinae-Stachyetum spinosae*"

Name-giving taxa of the original syntaxon name: *Medicago marina* L., *Stachys spinosa* L.

Name-giving taxa of the corrected syntaxon name: *Medicago marina* L., *Centaurea spinosa* L.

Typus: Géhu et al. (1992), table 2, relevé no. 8 (*holotypus*)

Synonym: *Thymbro capitatae-Centaureetum spinosae* Géhu 1992 *nom. illeg.* (Art. 29c)

The name *Medicagini marinae-Stachyetum spinosae* published in Géhu et al. (1988) is a *nomen ineptum* because the authors confused the name-giving taxa *Centaurea spinosa* L. and *Stachys spinosa* L. (Géhu 1992; see also ICPN, Art. 43, Example 1). Géhu (1992) published the replacement name "*Timbro capitati-Centaureetum spinosae*", but according to the ICPN, the original name must be maintained and corrected (Art. 43). The replacement name is an illegitimate *nomen superfluum* (Art. 29c).

Centaureo cuneifoliae-Verbascion pinnatifidi **Brullo in Marcenò et al. 2018**

Original form of the name (Marcenò et al. 2018): "*Centaureo cuneifoliae-Verbascion pinnatifidi* Brullo in Marcenò et al. 2018 all. nova"

Name-giving taxa: *Centaurea cuneifolia* Sm. 1813 (subsp. *cuneifolia*), *Verbascum pinnatifidum* Vahl 1791

Typus: *Sileno subconicae-Ephedretum distachyae* Oberdorfer 1952 (*holotypus*)

Helichrysion picardii **(Rivas-Martínez, Costa et Izco in Rivas-Martínez et al. 1990) Rivas-Martínez et al. 1999**

Corresponding suballiance: *Helichrysenion picardii* Rivas-Martínez, Costa et Izco in Rivas-Martínez et al. 1990

Original form of the name (Rivas-Martínez et al. 1999): "*Helichrysion picardii* (Rivas-Martínez, Costa et Izco in Rivas-Martínez, Lousa, T. E. Díaz, Fernández-González et J. C. Costa 1990) alliancia nova hoc loco"

Name-giving taxon: *Helichrysum picardii* Boiss. et Reut. 1859

Typus: *Artemisio crithmifoliae-Armerietum pungentis* Rivas Goday et Rivas-Martínez 1958 (*holotypus*)

Artemisio crithmifoliae-Armerietum pungentis **Rivas Goday et Rivas-Martínez 1958**

Original form of the name (Rivas Goday and Rivas-Martínez 1958): "*Artemisio crithmifoliae-Armerietum pungentis*"

Name-giving taxa: *Artemisia crithmifolia* L. 1753, *Armeria pungens* (Link) Hoffmanns. et Link 1813

Typus: Rivas Goday and Rivas-Martínez (1958), table 40, relevé no. 2 (*lectotypus* selected by Rivas-Martínez et al. 1990)

In Flora Iberica (Castroviejo et al. 1986–2021), *Artemisia crithmifolia* L. is accepted as a species, while in other taxonomic checklists, it is included in *A. campestris* subsp. *maritima* (DC.) Arcang. 1882 (e.g. Euro+Med 2023). However, a mutation of the name to "*Artemisio maritimae-Armerietum pungentis*" would be a source of confusion as there is also the accepted species name *A. maritima* L. 1753. Mutating the name to "*Artemisio campestris-Armerietum pungentis*" would be an option, but also a loss of information. Therefore, for the time being, we refrain from publishing a mutation of this association name.

Leymetalia racemosi **Vicherek 1971 *nom. corr. et mut.* Marcenò et al. *nom. mut. nov.***

Original form of the name (Vicherek 1971: 135): "*Elymetalia gigantei* ordo nova [recte: ordo novus]"

Correct name: *Elymetalia racemosi* Vicherek 1971 *nom. corr.*

Name-giving taxon of the original syntaxon name: *Elymus giganteus* Vahl 1794

Name-giving taxon of the corrected and mutated syntaxon name: *Leymus racemosus* (Lam.) Tzvelev 1960 (≡ *Elymus racemosus* Lam. 1792)

Authoritative taxonomic treatments that use the name *Leymus racemosus*: Mosyakin and Fedoronchuk (1999), Euro+Med (2023)

Typus: *Elymion gigantei* Morariu 1957 (*holotypus*)

Synonyms: *Elymetalia gigantei* Vicherek 1971 *nom. inept.* (Art. 44)

The name *Elymetalia gigantei* Vicherek 1971 must be corrected to *Elymetalia racemosi* Vicherek 1971 *nom. corr.* because *Elymus giganteus* Vahl is a later taxonomic synonym of *E. racemosus* Lam. In addition to this correction, we propose a mutation to match the currently prevailing taxonomic approach that assigns *E. racemosus* to the genus *Leymus*. The same reasoning is applied to the alliance and association names listed below.

Leymion racemosi **Morariu 1957 *nom. corr. et mut.* Marcenò et al. *nom. mut. nov.***

Original form of the name (Morariu 1957: 368): "*Elymion gigantei*"
Correct name: *Elymion racemosi* Morariu 1957 *nom. corr.*
Name-giving taxon of the original syntaxon name: *Elymus giganteus* Vahl 1794
Name-giving taxon of the corrected and mutated syntaxon name: *Leymus racemosus* (Lam.) Tzvelev 1960 (≡ *Elymus racemosus* Lam. 1792)
Authoritative taxonomic treatments that use the name *Leymus racemosus*: Mosyakin and Fedoronchuk (1999), Euro+Med (2023)
Typus: *Elymetum gigantei* Morariu 1957 (*holotypus*)
Synonyms: *Elymion gigantei* Morariu 1957 *nom. inept.* (Art. 44)

Leymetum racemosi **Morariu 1957 *nom. corr. et mut.* Marcenò et al. *nom. mut. nov.***

Original form of the name (Morariu 1957: 369): "*Elymetum gigantei*"
Correct name: *Elymetum racemosi* Morariu 1957 *nom. corr.*
Name-giving taxon of the original syntaxon name: *Elymus giganteus* Vahl 1794
Name-giving taxa of the corrected and mutated syntaxon name: *Leymus racemosus* (Lam.) Tzvelev 1960 (≡ *Elymus racemosus* Lam. 1792)
Authoritative taxonomic treatments that use the name *Leymus racemosus*: Mosyakin and Fedoronchuk (1999), Euro+Med (2023)
Typus: Morariu (1957), relevé no. 3, p. 369 (*lectotypus* selected by Vicherek 1971)
Synonyms: *Elymetum gigantei* Morariu 1957 *nom. inept.* (Art. 44)

Sileno thymifoliae-Jurineion kilaeae **Géhu et Uslu ex Mucina in Mucina et al. 2016**

Original form of the name (Mucina et al. 2016): "*Sileno thymifoliae-Jurineion kilaeae* Géhu et Uslu ex Mucina all. nov."
Name-giving taxa: *Silene thymifolia* Sm. 1809, *Jurinea kilaea* Azn. 1897
Typus: *Stachyo subcrenatae-Centaureetum kilaeae* Géhu et Uslu 1989 (*holotypus*)

Lomelosion ucranicae **Boscaiu 1975 *mut.* Marcenò et al. *nom. mut. nov.***

Original form of the name (Boscaiu 1975: 84): "*Scabiosion ucranicae*"
Name-giving taxon of the original syntaxon name: *Scabiosa ucranica* L. 1762
Name-giving taxon of the mutated syntaxon name: *Lomelosia ucranica* (L.) Soják 1987
Authoritative taxonomic treatments that use the name *Scabiosa ucranica*: Fedorov (1974), Czerepanov (1995), Mosyakin and Fedoronchuk (1999); for the segregate genus *Lomelosia*, see Castroviejo et al. (1986–2021), Euro+Med (2023)
Typus: *Carici colchicae-Ephedretum distachyae* Prodan ex Morariu 1959 (*holotypus*)
Synonym: *Scabiosion ucranicae* Boscaiu 1975

Although various floras and checklists (e.g., Euro+Med 2023) include the name *Scabiosa ucranica* into the synonymy of *S. argentea*, we decided to follow the taxonomic treatment used in Eastern European floras and checklists (Fedorov 1974; Czerepanov 1995; Mosyakin and Fedoronchuk 1999), where these taxa are not considered conspecific, based on morphological characters and ecology. However, for consistency, we accept the segregate genus *Lomelosia*, following the more recent taxonomic treatments of the *Dipsacaceae* family (e.g. Castroviejo et al. 1986–2021; Euro+Med 2023).

Cynodonto dactyli-Teucrion polii **Korzhenevskii et Klyukin ex Korzhenevskii et Kvitnytskaya in Ryff 2018**

Name-giving taxa: *Cynodon dactylon* (L.) Pers. 1805, *Teucrium polium* L. 1753
Typus: *Cynodonto dactyli-Ajugetum chiae* Korzhenevskii et Klyukin ex Korzhenevskii et Kvitnytskaya in Ryff 2018 (*holotypus*)
Synonym: *Cynodonto-Teucrion polii* Korzhenevskii et Klyukin 1990 (Art. 2a)

The alliance *Cynodonto-Teucrion polii* and association *Cynodonto dactyli-Ajugetum* were validated by Ryff (2018). The previous attempt by Korzhenevskii and Kvitnitskaya (2014) failed because they designated the nomenclatural type for the alliance without using the required Latin term '*holotypus*' (Art. 5). Additionally, the association was deemed invalid because it was published without being explicitly indicated as new (Art. 3i). According to Mucina et al. (2016), the "*Melico chrysolepidis-Ephedrion distachyae* Umanets et V. Solomakha 1999" [recte: Umanets et I. Solomakha 1999] would be a valid syntaxonomic synonym. This syntaxon is also listed in the recently published "Prodrome of the vegetation of Ukraine" (Dubyna et al. 2019), but it is considered a syntaxonomic synonym of the alliance *Medicagini tenderiensis-Seselion tenderiensis* Umanets et I. Solomakha 1999. This last alliance is not included in the EuroVegChecklist (Mucina et al. 2016), and its syntaxonomic status remains unresolved, possibly requiring a comprehensive, European-scale revision of the class *Festuco-Brometea*. Therefore, we opt not to consider it until further clarification emerges.

Cynodonto dactyli-Ajugetum chiae **Korzhenevskii et Klyukin ex Korzhenevskii et Kvitnytskaya in Ryff 2018**

Name-giving taxa: *Cynodon dactylon* (L.) Pers. 1805, *Ajuga chamaepitys* subsp. *chia* (Schreb.) Arcang. 1882
Typus: Korzhenevskii and Kvitnitskaya (2014), table 3, relevé 5, p. 48 (*holotypus*)
Synonym: *Cynodonto-Ajugetum chiae* Korzhenevskii et Klyukin 1990 (Art. 3i)

Honckenyo peploidis-Leymetea arenarii **Tüxen 1966 *mut.* Marcenò et al. *nom. mut. nov.***

Original form of the name (Tüxen 1966: 366): "*Honckenyo-Elymetea arenariae* class. nova"

Name-giving taxa of the original syntaxon name: *Honckenya peploides* (L.) Ehrh. 1783, *Elymus arenarius* L. 1753

Name-giving taxon of the mutated syntaxon name*: Honckenya peploides* (L.) Ehrh. 1783, *Leymus arenarius* (L.) Hochst. 1848

Authoritative taxonomic treatments that use the names *Honckenya peploides* and *Leymus arenarius*: Euro+Med PlantBase (2023), Hand and Thieme (2023)

Typus: *Honckenyo-Elymetalia arenarii* Tüxen 1966 (*holotypus*)

Leymetalia arenarii* Braun-Blanquet et Tüxen 1952 *mut.* Marcenò et al. *nom. mut. nov.

Original form of the name (Braun-Blanquet and Tüxen 1952): "*Elymetalia arenariae* Br.-Bl. et Tx. 1943"

Correct name: *Elymetalia arenarii* Braun-Blanquet et Tüxen 1952

Name-giving taxon of the original syntaxon name: *Elymus arenarius* L. 1753

Name-giving taxon of the mutated syntaxon name*: Leymus arenarius* (L.) Hochst. 1848

Authoritative taxonomic treatments that use the name *Leymus arenarius*: Euro+Med (2023), Hand and Thieme (2023)

Typus: *Agropyro-Minuartion peploidis* Tüxen in Braun-Blanquet et Tüxen 1952: 248 (*lectotypus hoc loco*)

Synonyms: *Honckenyo-Elymetalia arenarii* Tüxen 1966

The order *Elymetalia arenarii* was validly described by Braun-Blanquet and Tüxen (1952), and this name takes priority over the name *Honckenyo-Elymetalia arenarii* Tüxen 1966.

Elytrigio boreoatlanticae-Honckenyion peploidis* Tüxen in Braun-Blanquet et Tüxen 1952 *mut.* Marcenò et al. *nom. mut. nov.

Original form of the name (Braun-Blanquet and Tüxen 1952: 248): "*Agropyro-Minuartion peploidis* Tx. 1945 mskr."

Correct name: *Agropyro boreoatlantici-Minuartion peploidis* Tüxen in Braun-Blanquet et Tüxen 1952

Name-giving taxa of the original syntaxon name: *Agropyron junceum* subsp. *boreoatlanticum* Simonet et Guin. 1938, *Minuartia peploides* (L.) Hiern 1899

Name-giving taxa of the mutated syntaxon name: *Elytrigia juncea* subsp. *boreoatlantica* (Simonet et Guin.) Hyl. 1953, *Honckenya peploides* (L.) Ehrh. 1783

Authoritative taxonomic treatments that use the names *Elytrigia juncea* subsp. *boreoatlantica* and *Honckenya peploides*: Tison et al. (2014), Euro+Med (2023)

Typus: *Euphorbio-Agropyretum juncei* Tüxen in Braun-Blanquet et Tüxen 1952 (*holotypus*)

Euphorbio paraliae-Elytrigietum boreoatlanticae* Tüxen in Braun-Blanquet et Tüxen 1952 *mut.* Marcenò et al. *nom. mut. nov.

Original form of the name (Braun-Blanquet and Tüxen 1952: 248): "*Euphorbio-Agropyretum juncei* Tx. 1945 mskr."

Correct name: *Euphorbio paraliae-Agropyretum juncei* Tüxen in Braun-Blanquet et Tüxen 1952

Name-giving taxa of the original syntaxon name: *Euphorbia paralias* L. 1753, *Agropyron junceum* subsp. *boreoatlanticum* Simonet et Guin. 1938

Name-giving taxa of the mutated syntaxon name: *Euphorbia paralias* L. 1753, *Elytrigia juncea* subsp. *boreoatlantica* (Simonet et Guin.) Hyl. 1953

Authoritative taxonomic treatments that use the names *Euphorbia paralias* and *Elytrigia juncea* subsp. *boreoatlantica*: Tison et al. (2014), Euro+Med (2023)

Typus: Braun-Blanquet and Tüxen (1952), table 12, relevé no. 249 (*lectotypus hoc loco*)

In the original diagnosis of the *Euphorbio-Agropyretum juncei*, which contains relevés from Ireland, Braun-Blanquet and Tüxen (1952) used the taxon name "*Agropyron junceum* (Juslen.) P. B. ssp. *atlanticum* (Simonet)". However, a subspecies with the epithet "*atlanticum*" does not exist. Both from the author citation of Simonet and from the relevé localities, it is obvious that they meant *Agropyron junceum* subsp. *boreoatlanticum* Simonet et Guin. We use this subspecies, combined in the genus *Elytrigia*, as a name-giving taxon of the mutated name of the association and its superior alliance.

Leymion arenarii* Christiansen 1927 *mut.* Marcenò et al. *nom. mut. nov.

Original form of the name (Christiansen 1927: 55): "*Elymion*"

Name-giving taxon of the original syntaxon name: *Elymus arenarius* L. 1753

Name-giving taxon of the mutated syntaxon name*: Leymus arenarius* (L.) Hochst. 1848

Authoritative taxonomic treatments that use the name *Leymus arenarius*: Euro+Med (2023), Hand and Thieme (2023)

Typus: *Festucetum rubrae* Christiansen 1927 (*holotypus*)

Festucetum arenariae* Christiansen 1927 *mut.* Marcenò et al. *nom. mut. nov.

Original form of the name (Christiansen 1927: 55): "*Festucetum rubrae*"

Name-giving taxon of the original syntaxon name: *Festuca rubra* L. 1753

Name-giving taxon of the mutated syntaxon name: *Festuca arenaria* Osbeck 1788

Authoritative taxonomic treatments that use the name *Festuca arenaria*: Hand and Thieme (2023), Euro+Med (2023)

Typus: Christiansen (1927), table 3 (*holotypus*)

The taxon name *Festuca rubra* used by Christiansen (1927) must be replaced with *F. arenaria*, a species ecologically linked to the North Atlantic coastal dunes stretching from France to Russia, encompassing the area where Christiansen (1927) sampled the relevés to describe this association.

***Mertensio maritimae-Honckenyion diffusae* Tüxen et Géhu in Géhu 1998**

Original form of the name (Géhu 1998): "*Mertensio maritimae-Honckenyon diffusae* (R. Tüxen et Géhu 1972) inéd."

Name-giving taxa: *Mertensia maritima* (L.) Gray 1821, *Honckenya maritima* var. *diffusa* (≡ *Honckenya peploides* subsp. *diffusa* (Hornem.) Hultén 1937)

Typus: *Honckenyo diffusae-Leymetum arenarii* Tüxen 1960 (*holotypus*)

***Koelerio glaucae-Corynephoretea canescentis* Klika in Klika et Novák 1941**

Original form of the name (Klika and Novák 1941): "*Koelerio-Corynephoretales*"

Name-giving taxa: *Koeleria glauca* (Schrad.) DC. 1813; *Corynephorus canescens* (L.) P. Beauv. 1812

Typus: *Corynephoretalia* Klika 1934 (*lectotypus* selected by Moravec 1967)

Artemisio crithmifoliae-Koelerietalia albescentis* Sissingh 1974 *nom. corr.

Original form of the name (Sissingh 1974: 103): "*Artemisio-Koelerietalia albescentis* ordo novo"

Name-giving taxa of the original syntaxon name: *Artemisia lloydii* Rouy 1903, *Koeleria albescens* DC. 1813

Name-giving taxa of the corrected syntaxon name: *Artemisia crithmifolia* L. 1753, *Koeleria albescens* DC. 1813

Typus: *Euphorbio portlandicae-Helichrysion stoechadis* Géhu et Tüxen ex Sissingh 1974 (*lectotypus* selected by Dengler et al. 2003)

The correct name for "*Artemisia lloydii*" at the species level is *Artemisia crithmifolia* L. In Flora Iberica (Castroviejo et al. 1986–2021), *A. crithmifolia* L. is accepted as a species, while in other taxonomic works, it is included in *A. campestris* subsp. *maritima* (DC.) Arcang. 1882 (Euro+Med 2023). However, a mutation of the name to "*Artemisio maritimae-Koelerietalia albescentis*" would be a source of confusion as there is also the accepted species name *A. maritima* L. 1753.

***Euphorbio portlandicae-Helichrysion stoechadis* Géhu et Tüxen ex Sissingh 1974**

Original form of the name (Sissingh 1974: 103): "*Euphorbio-Helichrysion stoechadis* (Géhu et Tüxen 1972 n.n.) Sissingh"

Name-giving taxa: *Euphorbia portlandica* L. 1753, *Helichrysum stoechas* (L.) Moench 1794

Typus: *Artemisio lloydii-Ephedretum* Géhu et Sissingh in Sissingh 1974 (*lectotypus* selected by Rivas-Martínez 2011)

Artemisio crithmifoliae-Ephedretum distachyae* Géhu et Sissingh in Sissingh 1974 *nom. corr.

Original form of the name (Sissingh 1974: 101): "*Artemisio lloydii-Ephedretum* Géhu et Sissingh *ass. nov.*"

Name-giving taxa of the original syntaxon name: *Artemisia lloydii* Rouy 1903, *Ephedra distachya* L. 1753

Name-giving taxa of the corrected syntaxon name: *Artemisia crithmifolia* L. 1753, *Ephedra distachya* L. 1753

Typus: Vanden Berghen (1963), table 1, relevé 1 (*lectotypus hoc loco*)

The correct name for "*Artemisia lloydii*" at the species level is *Artemisia crithmifolia* L. In Flora Iberica (Castroviejo et al. 1986–2021), *A. crithmifolia* L. is accepted as a species, while in other taxonomic works, it is included in *A. campestris* subsp. *maritima* (DC.) Arcang. 1882 (Euro+Med 2023). However, a mutation of the name to "*Artemisio maritimae-Ephedretum distachyae*" would be a source of confusion as there is also the accepted species name *A. maritima* L. 1753.

***Koelerion arenariae* Tüxen 1937 *mut.* Gutermann et Mucina 1993**

Original form of the name (Tüxen 1937): "*Koelerion albescentis*"

Name-giving taxon of the original syntaxon name: *Koeleria albescens* DC. 1813

Name-giving taxon of the mutated syntaxon name: *Koeleria arenaria* (Dumort.) Conert 1987

Typus: *Tortulo-Phleetum* Braun-Blanquet et De Leeuw ex Tüxen 1937 *nom. illeg.* (Art. 31) (*holotypus*)

The association *Tortulo-Phleetum* was validly published by Braun-Blanquet and De Leeuw (1936). However, since there is no sufficient bibliographical reference to this work in Tüxen (1937), the type of the alliance must be considered as a later homonym.

According to Gutermann and Mucina (1993), the taxon name *Koeleria albescens* DC. used by Tüxen (1937) must be corrected to *K. arenaria* (Dumort.) Conert. *Koeleria albescens* occurs exclusively on the Atlantic coastal dunes of France and Spain, whereas *K. arenaria* has a wide range including the coastal areas of the Netherlands and Germany, where the relevés were sampled by Braun-Blanquet and De Leeuw (1936) and Tüxen (1937), respectively. Furthermore, according to the ICPN, the change of the alliance name proposed by Gutermann and Mucina (1993) is considered a mutation rather than a correction. This is because knowledge of the *Koeleria* species only came about after the description of this alliance.

Syntrichio ruraliformis-Phleetum arenarii* Braun-Blanquet et De Leeuw 1936 *mut.* Marcenò et al. *nom. mut. nov.

Original form of the name (Braun-Blanquet and De Leeuw 1936: 366): "*Tortula ruraliformis-Phleum arenarium-Assoziation*"

Name-giving taxa of the original syntaxon name: *Tortula ruraliformis* (Besch.) W. Ingham 1903, *Phleum arenarium* L. 1753

Name-giving taxa of the mutated syntaxon name: *Syntrichia ruraliformis* (Besch.) Mans 1904, *Phleum arenarium* L. 1753

Authoritative taxonomic treatments that use the name *Syntrichia ruraliformis*: Hedenäs et al. (2019), Hodgetts et al. (2020)

Typus: Braun-Blanquet and De Leeuw (1936), table 1, relevé A (*lectotypus hoc loco*)

***Syntrichio ruraliformis-Lomelosion argenteae* Biondi, Sburlino et Theurillat in Sburlino et al. 2013**

Name-giving taxa: *Syntrichia ruraliformis* (Besch.) Mans, *Lomelosia argentea* (L.) Greuter et Burdet 1985

Typus: *Tortulo-Scabiosetum* Pignatti 1952 (*holotypus*)

Syntrichio ruraliformis-Lomelosietum argenteae **Pignatti 1952 *mut.* Marcenò et al. *nom. mut. nov.***

Original form of the name (Pignatti 1952: 327): "*Tortuleto-Scabiosetum* Pign. 1952"

Name-giving taxa of the original syntaxon name: *Tortula ruralis* subsp. *ruraliformis* (Besch.) T. Barker 1900, *Scabiosa argentea* L. 1753 var. *alba*

Name-giving taxa of the mutated syntaxon name: *Syntrichia ruraliformis* (Besch.) Mans 1904, *Lomelosia argentea* (L.) Greuter et Burdet 1985

Authoritative taxonomic treatments that use the name *Syntrichia ruraliformis*: Hedenäs et al. (2019), Hodgetts et al. (2020)

Authoritative taxonomic treatments that use the name *Lomelosia argentea*: Euro+Med (2023), Pignatti et al. (2017–2019)

Typus: Pignatti (1959), table 5, relevé 141 (*neotypus* designated by Sburlino et al. 2013).

Author contributions

CM and MC planned the research, JD reviewed taxonomic and nomenclature treatment, CM, MC and WW wrote the manuscript, and all authors critically revised syntaxonomic and nomenclatural treatment.

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Appendix 1. Proposals (37, 38) to conserve the names *Ammophilion arundinaceae* Braun-Blanquet 1933 and *Medicagini marinae-Ammophiletum arundinaceae* Braun-Blanquet 1933

(37) *Ammophilion arundinaceae* Braun-Blanquet 1933 *nom. superfl.*, *nom. cons. propos.*
Typus = typus of the *Ammophilion arenariae* Braun-Blanquet 1921 (Art. 18b)
(≡) *Ammophilion arenariae* Braun-Blanquet 1921
Typus: *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921 *nom. invers.* (*holotypus*)

The alliance "*Ammophilion*" was validly published by Braun-Blanquet (1921: 347), with *Ammophila arenaria* (L.) Link 1827 as the name-giving taxon. The only association in the original diagnosis is the "*Ammophila-Medicago marina*-Assoziation" [recte: *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921 *nom. invers.*] (Braun-Blanquet 1921: 343). This association is the holotype of the alliance name. The meaning of the epithet "*littori-arenariae*" used by Braun-Blanquet in one of the two variants of the name in the original diagnosis is unclear. However, we consider this as an alternative name that has no nomenclatural relevance. Since the only *Ammophila* species mentioned in the original diagnosis is *A. arenaria*, the correct name of the alliance is *Ammophilion arenariae*.

In 1933, Braun-Blanquet changed the name of the type association to "Ass. á *Ammophila arundinacea* et *Medicago marina* Br.-Bl. (1921) 1933" (Braun-Blanquet 1933: 8), and used the taxon name *Ammophila arenaria* subsp. *arundinacea* in synoptic tables. This could be interpreted as a "correction" corresponding to a mutation according to Art. 45 §8 (the § character refers here to non-numbered paragraphs within the article). However, since Braun-Blanquet (1933) did not provide an unambiguous reference to Braun-Blanquet (1921), the mutation is invalid, and the association name must be considered as an independently published, yet superfluous name based on the same (and some additional) relevés. In the same way, the name of the alliance is a new superfluous name in 1933, which is automatically typified by the type of the earlier name (Art. 18b). The corroboration that both Braun-Blanquet's names validly published in 1933 must be considered superfluous is provided by Braun-Blanquet's (1933: 1) announcement of the future publication of the fascicles of Bibliographia Phytosociologica complementing the Prodromus. Fascicle 3, published in 1936 (Braun-Blanquet and Diemont 1936) provides an unambiguous reference to Braun-Blanquet (1921).

The formal independence of the names published by Braun-Blanquet in 1921 and 1933 leads to the paradoxical situation that a mutation of the older name *Ammophilion arenariae* Braun-Blanquet 1921 is forbidden as it would form a homonym of a name validly published before the date of the mutation (Art. 45 §7). As a solution, we propose to conserve the later name *Ammophilion arundinaceae* Braun-Blanquet 1933 against the *Ammophilion arenariae* Braun-Blanquet 1921. The adoption of this proposal does not prevent a mutation of the alliance name back to *Ammophilion arenariae* if this would be desired, because validly published mutations of a conserved name are automatically conserved in the same way as the original name (Art. 45, Note 6).

The name *Ammophilion arundinaceae* was already used by Rivas-Martínez et al. (1980) as "*Ammophilion arundinaceae* Br.-Bl. 1933 em. J.M. Géhu, Rivas-Martínez et R. Tx. inéd.".

(38) *Medicagini marinae-Ammophiletum arundinaceae* Braun-Blanquet 1933 *nom. superfl.*, *nom. invers.* et *nom. cons. propos.*
Typus = typus of the *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921 (Art. 18b)
(≡) *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921 *nom. invers.*
Typus: Braun-Blanquet (1921), relevé no. 2: 344 (*lectotypus* selected by Fernández Prieto and Díaz González 1991)

The original diagnosis of *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921 *nom. invers.* contains the species name *Ammophila arenaria*. The relevés for this original diagnosis were sampled on the French Mediterranean coast, where this species is only represented by the subspecies *A. arenaria* subsp. *arundinacea* (Husn.) H. Lindb. according to various recent taxonomic treatments (Tison et al. 2014; Euro+Med 2023). The name of the association *Medicagini marinae-Ammophiletum arenariae* Braun-Blanquet 1921 was already corrected by Fernández Prieto and Díaz González (1991) using the infraspecific taxon name *A. arenaria* subsp. *australis* (Mabille) Laínz, which is a synonym of *A. arenaria* subsp. *arundinacea*. This correction was actually a mutation, but because the authors used an incorrect subspecies name, the mutation failed (see Art. 45). A mutation using the correct name of the subspecies is blocked by the superfluous name *Medicagini marinae-Ammophiletum arundinaceae* Braun-Blanquet 1933 (see proposal 37 above). Therefore, we propose to conserve the name published in 1933, analogously to the alliance *Ammophilion arundinaceae* Braun-Blanquet 1933.

Both association names (the one from 1921 and the one from 1933) must be inverted because *Ammophila* has a higher cover in the type relevé than *Medicago marina* (3 versus 2) (Art. 42).

Appendix 2. Syntaxonomic framework of the syntaxa treated in this manuscript

- *Ammophiletea arundinaceae* Braun-Blanquet et Tüxen ex Westhoff et al. 1946
    - *Ammophiletalia arundinaceae* Braun-Blanquet 1933
        - *Ammophilion arundinaceae* Braun-Blanquet 1933 *nom. cons. propos.*
            - *Medicagini marinae-Ammophiletum arundinaceae* Braun-Blanquet 1933 *nom. invers. et cons. propos.*
    - *Crucianelletalia maritimae* Sissingh 1974
        - *Ononidion ramosissimae* Pignatti 1953
        - *Diantho attenuati-Scrophularion humifusae* Baudière et Simonneau 1974 *nom. corr. et mut.* Marcenò et al. 2024
            - *Diantho attenuati-Corynephoretum canescentis* Baudière et Simonneau 1974 *nom. corr.*
        - *Helichryso barrelieri-Centaureion spinosae* Mucina et Dimopoulos in Mucina et al. 2016
            - *Medicagini marinae-Centaureetum spinosae* Géhu in Géhu et al. 1988 *corr.* Marcenò et al. 2024
        - *Centaureo cuneifoliae-Verbascion pinnatifidi* Brullo in Marcenò et al. 2018
        - *Helichrysion picardii* (Rivas-Martínez, Costa et Izco in Rivas-Martínez et al. 1990) Rivas-Martínez et al. 1999
            - *Artemisio crithmifoliae-Armerietum pungentis* Rivas Goday and Rivas-Martínez 1958
    - *Leymetalia racemosi* Vicherek 1971 *mut.* Marcenò et al. 2024
        - *Leymion racemosi* Morariu 1957 *mut.* Marcenò et al. 2024
            - *Leymetum racemosi* Morariu 1957 *mut.* Marcenò et al. 2024
        - *Sileno thymifoliae-Jurineion kilaeae* Géhu et Uslu ex Mucina in Mucina et al. 2016
        - *Lomelosion ucranicae* Boscaiu 1975 *mut.* Marcenò et al. 2024
        - *Cynodonto dactyli-Teucrion polii* Korzhenevskii et Klyukin ex Korzhenevskii et Kvitnytskaya in Ryff 2018
            - *Cynodonto dactyli-Ajugetum chiae* Korzhenevskii et Klyukin ex Korzhenevskii et Kvitnytskaya in Ryff 2018
- *Honckenyo peploidis-Leymetea arenarii* Tüxen 1966 *mut.* Marcenò et al. 2024
    - *Leymetalia arenarii* Braun-Blanquet et Tüxen 1952 *mut.* Marcenò et al. 2024
        - *Elytrigio boreoatlanticae-Honckenyion peploidis* Tüxen in Braun-Blanquet et Tüxen 1952 *mut.* Marcenò et al. 2024
            - *Euphorbio paraliae-Elytrigietum boreoatlanticae* Tüxen in Braun-Blanquet et Tüxen 1952 *mut.* Marcenò et al. 2024
        - *Leymion arenarii Christiansen* 1927 *mut.* Marcenò et al. 2024
            - *Festucetum arenariae* Christiansen 1927 *mut.* Marcenò et al. 2024
        - *Mertensio maritimae-Honckenyion diffusae* Tüxen et Géhu in Géhu 1998
- *Koelerio glaucae-Corynephoretea canescentis* Klika in Klika et Novák 1941
    - *Artemisio crithmifoliae-Koelerietalia albescentis* Sissingh 1974 *nom. corr.*
        - *Euphorbio portlandicae-Helichrysion stoechadis* Géhu et Tüxen ex Sissingh 1974
            - *Artemisio crithmifoliae-Ephedretum distachyae* Géhu et Sissingh in Sissingh 1974 *nom. corr.*
        - *Koelerion arenariae* Tüxen 1937 *mut.* Gutermann et Mucina 1993
            - *Syntrichio ruraliformis-Phleetum arenarii* Braun-Blanquet et De Leeuw 1936 *mut.* Marcenò et al. 2024
        - *Syntrichio ruraliformis-Lomelosion argenteae* Biondi, Sburlino et Theurillat in Sburlino et al. 2013
            - *Syntrichio ruraliformis-Lomelosietum argenteae* Pignatti 1952 *mut.* Marcenò et al. 2024

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RESEARCH PAPER **GRASSLANDS OF ASIA**

Dry grasslands and thorn-cushion communities of Armenia: a first syntaxonomic classification

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Abstract

Aim: To provide the first syntaxonomic, plot-based classification of the dry grasslands and thorn-cushion communities in Armenia. **Study area:** Armenia. **Methods:** We sampled 111 vegetation plots (10 m^2) and recorded environmental and structural parameters. We collected additional 487 relevés from surrounding countries for a broad-scale comparison. We used modified TWINSPAN to derive a syntaxonomic classification system, whose units were then compared among each other regarding species composition, structure, site conditions and distribution. **Results:** The classification of Armenian vegetation plots resulted in a 12-cluster solution. Unsupervised classification of the broad-scale dataset yielded five main groups, which were used for the high-level syntaxonomic assignments of the Armenian data. We assigned about half of the plots of the Armenian dataset to the *Festuco-Brometea*, while the remaining represented a potential new class, preliminarily called "*Ziziphora tenuior-Stipa arabica* grasslands". Most of the syntaxa below class level are new to science, therefore we provide formal descriptions of three orders (*Plantagini atratae-Bromopsietalia variegatae*, *Onobrychido transcaucasicae-Stipetalia pulcherrimae*, *Cousinio brachypterae-Stipetalia arabicae*), four alliances (*Acantholimono caryophyllacei-Stipion holosericeae*, *Artemision fragrantis*, *Onobrychido michauxii-Stipion capillatae*, *Onobrychido transcaucasicae-Stipion pulcherrimae*) and six associations. We found significant differences in the topographic, climatic and soil characteristics, and structural parameters, species life forms and distribution range types between the grassland types at different syntaxonomic levels. The mean species richness was 47.3 (vascular plants: 46.8, bryophytes: 0.4, lichens: 0.1). **Conclusions:** We found remarkable differences of the Armenian dry grasslands from the previously known units and described most of the higher syntaxa and all the associations as new to science. Our study provides arguments for a potential new class of *Ziziphora tenuior-Stipa arabica* grasslands separate both from the Euro-Siberian *Festuco-Brometea* and the Anatolian *Astragalo-Brometea*. Finally, we found plot scale richness of vascular plants clearly above the Palaearctic average of dry grasslands and that of non-vascular plants clearly below, which calls for further biodiversity analyses.

Taxonomic reference: Euro+Med (2023) for vascular plants, Hodgetts et al. (2020) for bryophytes, Nimis et al. (2018) for lichens except for *Xanthoparmelia camtschadalis* (Ach.) Hale.

Abbreviations: EDGG = Eurasian Dry Grassland Group; DCA = detrended correspondence analysis; ICPN = International Code of Phytosociological Nomenclature (Theurillat et al. 2021); TWINSPAN = two-way indicator species analysis.

Keywords

Armenia, classification, dry grassland, *Festuco-Brometea*, Irano-Turanian, mountain steppe, *Onobrychido transcaucasicae-Stipetalia pulcherrimae*, *Plantagini atratae-Bromopsietalia variegatae*, species richness, syntaxonomy, thorn-cushion community, *Cousinio brachypterae-Stipetalia arabicae*

Introduction

Armenia is a land-lock country located in the southern part of the Lesser Caucasus, belonging to two global biodiversity hotspots: the Caucasian and the Irano-Anatolian (Mittermeier et al. 2004). With 3,800 vascular plant species, including 144 country endemics, it has an outstandingly rich vascular plant flora for a territory of less than 30,000 km^2 (Biodiversity and Landscape Conservation Union 2014). The specificity of the vegetation of Armenia is caused by the fact that the country is located on the border between the Euro-Siberian (or Circumboreal) and Irano-Turanian biogeographical regions (Takhtajan 1986; Manafzadeh et al. 2017; Loidi et al. 2022), which are belonging to different subkingdoms: Boreal and Ancient Mediterranean (Takhtajan 1986).

Grasslands and shrublands in the Middle East and the Caucasus areas are of great interest as they host a high biodiversity of species and habitats (Ambarlı et al. 2020), and have been shown to be the area of origin of important elements of Western Asian and European dry grasslands (e.g. *Euphorbia seguieriana*, Frajman et al. 2019; *Euphorbia nicaeensis* group, Stojilkovič et al. 2022). Grasslands are linked to human activities, so can be heavily impacted by changes in land use that are leading to the loss and disturbance of these habitats, with the consequent loss of biodiversity (Török and Dengler 2018). In this area, unregulated (unsustainable) grazing, conversion to cropland, afforestation with non-native tree species, and mining and energy production projects are the major threats (Ambarlı et al. 2020). The knowledge of these habitats in Armenia is crucial for understanding their biodiversity and actual distribution, which will make it possible to establish the necessary management measures for conservation (Ambarlı et al. 2018).

Due to the abovementioned importance of the typology of habitats and vegetation, there is a growing international consensus on the need for coherent vegetation classification systems based on the analysis of vegetation-plot data (De Cáceres et al. 2015). There are different plot-based vegetation classification approaches (De Cáceres et al. 2018), the most important globally being the phytosociological approach (Dengler et al. 2008) and the EcoVeg approach (Faber-Langendoen et al. 2014). The latter, which is applied by the International Vegetation Classification (IVC, Faber-Langendoen et al. 2020) formally incorporates two levels above the class level, which is the highest formal level in the phytosociological approach. The *formation* is based on physiognomic-structural features of the vegetation and thus it is very useful to define biomes. Recently Willner and Faber-Langendoen (2021) made a first attempt to link the European classification system, based on the phytosociological approach (EVC, Mucina et al. 2016), with the International Vegetation Classification.

Up to date, there is no formalised plot-based classification system for Armenia, which was a Soviet Socialist Republic until 1991. As the Braun-Blanquet approach to vegetation classification (Braun-Blanquet 1964; Guarino et al. 2018) developed in Central and Western Europe, it did not play a role in the USSR for political reasons (Masing 1991). Hierarchical classifications based on syntaxa were virtually non-existent in Armenia, at least not for grasslands, as vegetation scientists followed the so-called dominance approach, which categorised vegetation according to dominant and ecologically significant species (Sukachev 1928). This approach does not usually produce complete species lists with abundance data for small sample areas of defined size, i.e. it does not produce relevés or vegetation plots. As a result, the first classification attempt of grassland habitats in Armenia identified three vegetation types (Grossgeim 1928): semi-deserts, mountain-xerophilous vegetation and mountain steppes. Afterwards, different classifications were developed for dry grasslands and steppe vegetation. First, Makagian (1941) defined four types of steppes and steppe-like vegetation (stony semi-deserts, steppes, meadow-steppes and highland xerophytes). Later, Ziroyan (1989) categorised natural dry grasslands in Armenia into five vegetation types related to zonal and altitudinal distribution (deserts, semi-deserts, highland xerophytes, mountain steppes and mountain meadow steppes). Finally, Fayvush (1992) recognised four steppe subtypes (true steppes, thorny-cushion steppes, shrubby steppes and meadow steppes) with 12 classes of formations. The lack of a unified framework of grassland typology impedes acquiring knowledge about their distribution and diversity, which is harmful to their conservation.

Although the phytosociological approach has not been applied to the survey of Armenian grasslands, those of neighbouring countries of the Southern Caucasus have been at least fragmentarily studied in Transcaucasia (Azerbaijan: Peper et al. 2010; Etzold et al. 2016; Jabbarov et al. 2020; Georgia: Pyšek and Šrůtek 1989; Nakhutsrishvili et al. 2022, etc.), Eastern Anatolia in Turkey (Çetik and Tatlı 1975; Tatlı 1991; Gümüs 1992; Gümüs et al. 2003; Hamzaoğlu 2006, etc.) and North Iran (Klein 1982, 1987; Klein and Lacoste 1994; Noroozi et al. 2010, 2014, 2017, etc.).

Many of the data used for these phytosociological surveys are stored in vegetation-plot databases. In the last decades small regional and/or personal databases have been compiled in large vegetation plots databases. The European Vegetation Archive (EVA, Chytrý et al. 2016) was the pioneer, followed by the global vegetation database (sPlot, Bruelheide et al. 2019) and by GrassPlot (Dengler et al. 2018). These databases are the basis for large-scale vegetation classification studies (Novák et al. 2023b; Peterka et al. 2023), but they also permit macroecological studies to great scales leading to a broad understanding of the distribution and diversity patterns (Graco-Roza et al. 2022; Sabatini et al. 2022; Večeřa et al. 2023). Especially for grasslands, the GrassPlot database hosts high-quality data from the Palaearctic realm, sampled on precisely delimited plots, including vascular plants and cryptogam data (Dengler et al. 2018; Biurrun et al. 2019). At the regional scale, the Transcaucasian Vegetation Database, a phytosociological database of the Southern Caucasus, was recently established (Novák et al. 2023a). However, it currently lacks vegetation plots of dry grassland and thorn-cushion communities in Armenia.

It is therefore both an opportunity and a challenge to record vegetation plots and apply the Braun-Blanquet classification approach to Armenia – as its vegetation, to our knowledge, has never been studied according to this approach. Therefore, the Eurasian Dry Grassland Group (EDGG; www.edgg.org) conducted an international research expedition (called “Field Workshop”) in Armenia to collect standardised, high-quality vegetation-plot data from dry grasslands and thorn-cushion communities throughout the country. In principle the EDGG Field Workshops aim at collecting such data for regional studies on biodiversity patterns (Kuzemko et al. 2016; Dembicz et al. 2021b; Bergauer et al. 2022) and phytosociology (García-Mijangos et al. 2021; Magnes et al. 2021). Moreover, these data are provided to the GrassPlot database (Dengler et al. 2018) for biodiversity studies across all Palaearctic grasslands and other open habitats (Biurrun et al. 2021; Dembicz et al. 2021a; Zhang et al. 2021) as well as to the European Vegetation Archive (EVA; Chytrý et al. 2016) and the global vegetation-plot database sPlot (Bruelheide et al. 2019) to fill important data gaps in continental and global studies of biodiversity, global change and syntaxonomy.

In this paper, we used the plot data sampled during the Field Workshop to provide the first syntaxonomic classification scheme of the dry grasslands and thorn-cushion communities of the country, using numerical methods of unsupervised classification and determination of diagnostic species. Specifically, we asked:

(1) Which association-rank communities can be distinguished, and to which higher-rank syntaxa do they belong?
(2) How do the syntaxa in Armenia compare to those in the neighbouring countries of Western Asia?
(3) How are the syntaxa in Armenia differentiated from each other in terms of species composition, species richness, structure, site conditions and distribution?

Study area

Physiogeography, climate, soils, geology

Armenia is a South Caucasian republic, bordering Georgia, Azerbaijan, Turkey, and Iran. It is a landlocked country with a total area of 29,740 km^2, at about 145 km from the Black Sea and 175 km from the Caspian Sea. It lies between 38°50' and 41°18' northern latitude and between 43°27' and 46°37' eastern longitude, and measures 400 km along its main axis (north-west to south-east). Armenia is generally a mountainous country, having its lowest point at 375 m a.s.l. and culminating at 4,095 m a.s.l. in the Aragats, with an average elevation of 1,850 m a.s.l.

The location of Armenia at the intersection of two phytogeographical subkingdoms (Boreal and Ancient Mediterranean), together with the diversity in climatic conditions and the active geological processes, have resulted in the formation of diverse ecosystems and high biodiversity with a high level of endemism (Fayvush and Aleksanyan 2016). On the small territory of the country, there are about 3,800 species of vascular plants, 497 species of soil and water algae, 433 species of bryophytes, 4,577 species of non-lichenized fungi, 619 species of lichens, 567 species of vertebrates and about 17,000 species of invertebrates (Fayvush 2023).

A wide range of climatic zones are distinguished within Armenia, which experiences large climatic contrasts because of its intricate terrain and the big climatic gradients (Ministry of Nature Protection of the Republic of Armenia 2015). The basic climate types mainly follow the elevational gradient, from dry subtropical up to severe alpine. The average annual temperature ranges from -8°C in high-altitude mountainous regions (2,500 m a.s.l. and higher) to 12–14°C in low-traced valleys. The overall climate is best characterised as dry continental, in some areas with an annual rhythm like the Mediterranean climate regime. The average annual precipitation in Armenia is 592 mm. The most arid regions are the Ararat valley and the region of Meghri with annual precipitation of 200–250 mm. The highest annual precipitation of 800–1000 mm is observed in high-altitude mountain regions.

From the orographical and physico-geographical points of view, Armenia forms the northern edge of the system of folded-block mountains of the Armenian Highland. Unlike the Greater Caucasus, Armenia and the Lesser Caucasus are not a single, distinct watershed ridge. It is a system of coulisse-spaced ridges that merge with the mountain formations of the inner parts of the Armenian Highland and adjacent high areas (Aslanyan 1958, 1985). Four main geomorphological regions can be recognized within Armenia. (1) Mountain ridges and valleys in the north-east of the country which bear witness of extensive erosion. (2) Areas covered by lava of relatively recent (upper Pliocene) origin within Asia Minor are characterised by gentle slopes with little evidence of erosion but, in which larger rivers have carved out deep gorges and canyons. (3) A series of ridged mountains in the south of Armenia, which constitute the Lesser Caucasus system and show intense erosion. (4) The Ararat Valley represents the lowest part of the Ararat depression covered with alluvial and proluvial sediments (Aslanyan 1958; Gabrielyan 1962; Dumitrashko 1979).

In our study we tried to cover as much of the country's dry grassland diversity as possible within 11 days, with a focus on the northwestern and central parts (Figure 1). In total, we sampled in five of the 11 administrative provinces of the country (Aragatsotn, Ararat, Gegharkunik, Shirak, Vayots Dzor) and seven of the 12 floristic regions. We covered an elevational gradient from 1,338 to 2,350 m a.s.l.

National typologies of Armenian dry grasslands

So far, the syntaxonomy of grassland or thorn-cushion vegetation of Armenia hasn't been developed yet. The only existing vegetation typologies are based on the dominance approach. The first overview of the Armenian vegetation types was performed by Grossgeim (1928). He distinguished eight main types of vegetation: (1) aquatic and bog vegetation; (2) forest vegetation; (3) semi-deserts; (4) mountain-xerophilous vegetation (mountain semi-desert); (5) mountain steppes; (6) meadow-like vegetation; (7) solonetzs and solonchaks; (8) weeds. In the semi-desert type, he selected three subtypes: (a) alkaline-loamy semi-desert on the alluvium of the Aras River; (b) wormwood semi-desert on eruptive rocks; (c) sandy semi-desert.

Takhtajan (1941) explored the phytogeographic patterns of Armenia, including the division of the region into phytogeographic provinces and districts, the historical

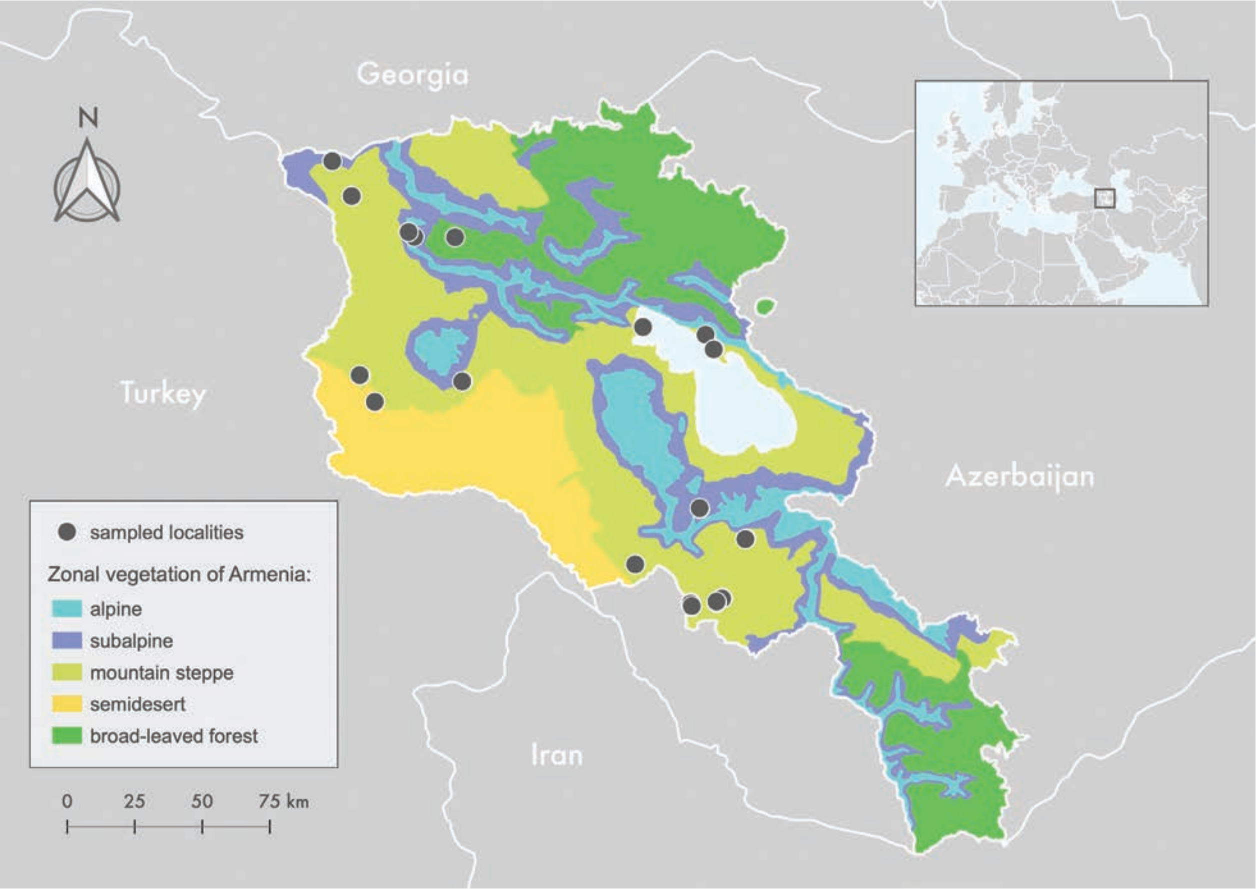

Figure 1. Map of Armenia indicating zonal vegetation types based on Grossgeim (1928). Black dots indicate the sampling localities. The light blue area refers to the Lake Sevan.

development of its vegetation, and the classification of vegetation into broad types. Among these types, subalpine vegetation, mountain-steppes, xerophilous vegetation of skeleton mountains, and wormwood semi-deserts could be considered as the scope of our study.

Makagian (1941) developed the vegetation typology of Armenia in more detail. The steppe and steppe-like vegetation included in his scheme was classified as:

- Stony semi-deserts (wormwood semi-desert, wormwood-ephemeral semi-desert, wormwood semi-desert with perennial grasses, etc.)
- Steppes (grass-forb and dry forb-grass steppe, feather-grass steppe, beardgrass steppe, fescue and fescue-junegrass steppe, mixed-grass steppe, forb and legume steppe)
- Meadow-steppes (grass meadow-steppe, forb and forb-grass meadow-steppe, legume meadow-steppe, dwarf-sedge meadow-steppe)
- Highland xerophytic vegetation (Minor-Asian thorn-cushion shrubs of *Astracantha*, *Acantholimon* etc., xeromorphic vegetation of screes and rocks)

Afterwards, the classification of natural grasslands of Armenia was done by Ziroyan (1989) on the principles of the dominant approach. The author distinguished five vegetation types of desert and steppe vegetation which have strong zonal character and mainly are characteristic to a particular altitudinal belt: **deserts** (two classes of formations, 16 formations) in the lowest elevations up to 1,000 m a.s.l.; **semi-deserts** (two classes of formations, 12 formations) at the elevations 1,000–1,300 m a.s.l.; **highland xerophytic vegetation** (one class of formations, 12 formations), 1,200–1,600 m a.s.l.; **mountain steppes** (two classes of formations, 12 formations), 1,600–2,000 m a.s.l.; **mountain meadow steppes** (two classes of formations, 12 formations), 2,000–2,400 (occasionally up to 2,800) m a.s.l.

Fayvush (1992) presents a detailed classification of the types of mountain steppes of Armenia based on the dominance approach. The author distinguishes four subtypes (true steppe, thorny-cushion steppe, shrubby steppe and meadow steppe) and 12 classes of formations within it.

Overview on the described syntaxa from the surrounding countries

In the Transcaucasus region, the first work with a description of syntaxa following the Braun-Blanquet approach was done by M. Guinochet in Azerbaijan and Georgia. Guinochet (1984) described two associations of steppe-like communities without an assignment to higher syntaxonomic units. The association *Ziziphoro serpyllaceae-Scutellarietum orientalis* Guinochet 1984 is characterized by the presence of many therophytes and is described from the lower elevations in Azerbaijan. Guinochet concludes that this vegetation type could be like the class *Thero-Brachypodietea* and emphasizes that a unique class and order should be described to include this association. The other association is described from higher elevations in the Pirqulu State Reserve (Azerbaijan), from the subalpine belt: *Onobrychieto cyri-Festucetum sulcatae* Guinochet 1984 nom. inval. (Article 2b ICPN, Theurillat et al. 2021). This association comprises mountain steppes and is similar, according to M. Guinochet, to the concept of the subalpine steppe of Gadzhiev (1962) from the national typology of Azerbaijan. Additionally, Guinochet (1984) described in Georgia another association from the alpine belt not belonging to the steppic vegetation and assigned to the class *Carici rupestris-Kobresietea bellardii*: *Alchemillo caucasicae-Festucetum supinae*, together with the new order *Campanulo-tridentatae-Caricetalia tristis* and the new alliance *Alchemillo-Festucion supinae*, all three being invalidly published due to insufficient original diagnosis (Article 2b ICPN, Theurillat et al. 2021). Lately, there was an attempt to classify the phryganoid vegetation of the Nakhchivan region of Azerbaijan (Jabbarov et al. 2020). The authors outlined several association-level units without a formal description ("*Thymeto-Acantholimonetum bracteatae*", "*Thymeto-Onobrychetum cornutae*"), and assigned them to the order *Astragalo-Brometalia* Quézel 1973 and the class *Astragalo-Brometea* Quézel 1973. Recently, a new study on the syntaxonomy of alpine and subalpine grasslands has been conducted in Georgia (Nakhutsrishvili et al. 2022). The authors proposed a new class *Bromopsio variegatae-Festucetea ovinae* to unite subalpine meso-xeric and mesic grasslands, including one new order, three alliances and seven associations. None of the suggested units were published validly due to insufficient original diagnoses.

For the Northern Caucasus, Tsepkova (1987) proposed a new class of high-mountain arid grasslands with the provisional name *Bothryochloo-Salvietea*, which according to Vynokurov et al. (2021) is a syntaxonomic synonym of the *Festuco-Brometea*. Other steppic grasslands of the Northern Caucasus have been traditionally assigned to the class *Festuco-Brometea* (Tsepkova 2005; Demina et al. 2017; Vynokurov et al. 2021).

In Turkey, several high-level syntaxonomic units have been established for dry grasslands and thorn-cushion vegetation. Zohary (1973) united semi-desert and wormwood steppe grasslands into the class "*Artemisietea fragrantis anatolica*" Zohary 1973 nom. inv. (Art. 2b ICPN), and proposed the class "*Astragaletea armeno-turcica*" Zohary 1973 nom. inv. (Art. 2b ICPN) for subalpine tragacanthic vegetation in this region. Simultaneously, Quézel (1973) described another unit for hedgehog plant communities in the subalpine zone of the Taurus Mountains in Turkey, occurring at elevations 2000–2500 m a.s.l., beyond the tree line – *Astragalo-Brometea* Quézel 1973. In the same publication, Quézel (1973) also published another class of xero-mesophytic and mesophytic subalpine grasslands, occupying higher altitudes than tragacanth vegetation communities: *Trifolio anatolici-Polygonetea arenastri* Quézel 1973. In the eastern part of Turkey, in Eastern Anatolia, there were some syntaxonomic investigations of steppe vegetation (Çetik and Tatlı 1975; Tatlı 1991; Ocakverdi 1992; Hamzaoğlu 2006; Öztürk et al. 2015). Ocakverdi (1992) surveyed the vegetation (including steppe vegetation) in the region of Turkey bordering with Armenia. He distinguished two physiognomic types of steppe vegetation (grass steppe and tragacanth steppe) and three altitudinal variants: "plain" steppe (1,675–1,725 m a.s.l., mainly grass steppe vegetation), lower mountain steppe (1,750–1,850 m a.s.l., both grass steppe and tragacanth steppe) and high-mountain steppe (1,950–2,696 m a.s.l., grass steppe). He proposed four associations, none of them published validly (Art. 1 ICPN). Later, Ocakverdi et al. (2009) described 10 new associations from the same region (Kısır Mountain). Hamzaoğlu (2006) studied steppe communities of East Anatolia. He united the studied vegetation to a new order *Festuco oreophilae-Veronicetalia orientalis* Hamzaoğlu 2006, subordinated to the class *Astragalo-Brometea* Quézel 1973.

In another bordering region, Iran, xerophilous grassland and scrub communities were first delineated by Zohary (1973), who proposed several vegetation classes: "*Artemisietea fragrantis anatolica*" Zohary 1973 nom. inv. (Art. 2b ICPN) for wormwood steppe grasslands in Northwestern Iran and Anatolia, "*Artemisietea herbae-albae iranica*" Zohary 1973 nom. inv. (Art. 2b ICPN) grouping wormwood semideserts in the Central Plateu of Iran, and "*Astragaletea iranica*" Zohary 1973 nom. inv. (Art. 2b ICPN) for tragacanth communities in Iran and Iraq. Later, the vegetation of the subalpine and alpine belts of the Alborz Mountains have been studied by Klein (1982, 1987). He described several new classes: *Onobrychidetea cornutae* Klein 1987 nom. inval. (Art. 2b ICPN) from the lower alpine belt of Alborz (3,200–3,500 m a.s.l.) and *Prangetea ulopterae* Klein 1987 nom. inval. (Art. 2b ICPN) from the subalpine belt of Alborz (2,500–3,200 m a.s.l.), aimed to unite high-mountain hedgehog communities and xeric tall-herb vegetation respectively. Also, from the subalpine belt of the northern macroslope of Alborz Mountains, Klein and Lacoste (1994) described one association subordinated to the *Festuco-Brometea*, *Alchemilletum plicatissimae* Klein et Lacoste 1994, but did not assign it to an alliance or order.

In general, the class *Astragalo-Brometea* is the most widely used name to unite the dry grasslands and thorn-cushion vegetation in the western part of the Irano-Turanian region. However, its conceptual boundaries have undergone significant changes over time, both geographically and physiognomically. Many researchers now extend its scope to include tragacanth vegetation not only from the subalpine belt but also from the lower elevations, as well as chamaephyte-dominated phryganoid vegetation, non-tragacanth dry grasslands at lower elevations, saline steppes, and gypsophilous rocky grasslands (Ketenoğlu et al. 1983; Akman et al. 1984; Aydoğdu et al. 1994; Aydoğdu et a. 2004; Hamzaoğlu et al. 2004; Kaya 2011). Additionally, xero-mesophytic and mesophytic grasslands at higher elevations, which were classified by Quézel (1973) as a separate class *Trifolio-Polygonetea*, are sometimes included within the *Astragalo-Brometea* (Eren et al. 2004; Parolly 2004). Some authors have proposed extending the concept of the class also to the northern part of Iran, synonymizing the *Onobrychidetea cornutae* and *Prangetea ulopterae* described there (Parolly 2004). Recently, the dry feather-grass steppes of Tajikistan also were provisionally included into the *Astragalo-Brometea* (Nowak et al. 2016, 2018).

Methods

Field sampling in Armenia

We sampled 111 plots of 10 m^2- size (Suppl. materials 1, 2) during the 13th Field Workshop of the Eurasian Dry Grassland Group (EDGG) in Armenia, from 26 June to 6 July 2019 (Aleksanyan et al. 2020; for distribution of sites, see Figure 1). Within each plot, we recorded vascular plants and terricolous bryophytes and lichens with the shoot presence method (Dengler 2008). Besides, we estimated their percentage cover on a continuous scale (for discussion of advantages of this method compared to ordinal scales, see Dengler and Dembicz 2023). Specimens that could not be determined in the field were dried and taken to the lab for further determination.

Other environmental and structural parameters that were recorded *in situ* following the EDGG sampling methodology (Dengler et al. 2016), included: geographical position (latitude, longitude), elevation (m), slope aspect (°), slope inclination (°), maximum microrelief (cm), soil depth (cm, mean and SD of five measurements per plot), vegetation covers (%; total vegetation, shrub layer, herb layer, cryptogam layer), cover of litter (%), covers of stones and rocks, gravel, and fine soil (all three fractions summing up to 100%), maximum height of shrubs (m), maximum height of herbs (cm), height of herb layer (cm, mean and SD of five measurements with a falling disc per plot), and land use details (grazing, mowing, burning, abandonment).

Soil was collected as mixed samples from the uppermost 15 cm of the soil in five random points inside each plot. After air drying and sieving to the fine-soil fraction, the following parameters were measured in the lab: pH (in H_2O), electrical conductivity ($\mu S\ cm^{-1}$), organic C content (%), humus content (%), N content (%), and C/N ratio. Southing was calculated from aspect as -cos (aspect).

The nomenclature of vascular plants was standardised to Euro+Med (2023) for vascular plants, Hodgetts et al. (2020) for bryophytes, Nimis et al. (2018) for lichens. For some groups of closely related species that could not always be distinguished, we defined additional species aggregates ("aggr."; see Suppl. material 3). The value distribution of all recorded and analysed numerical environmental, structural and biodiversity variables is given in Suppl. material 4. The complete data are stored in and available from the GrassPlot database (Dengler et al. 2018; Biurrun et al. 2019; https://edgg.org/databases/GrassPlot) as dataset "AM_B".

Data from external sources

Plot data from the surrounding countries

To be able to identify the high-level syntaxonomic units, we digitised from literature and used for comparison relevés from the bordering regions, focusing on the original diagnosis of the high-level units of similar vegetation types: 230 plots from Anatolia (Turkey) and 51 plots from Northern Iran. Among them, the original diagnosis of the class *Astragalo-Brometea* Quézel 1973 with the type order *Astragalo-Brometalia* Quézel 1973 and the other orders *Drabo-Androsacetalia* Quézel 1973, *Hyperico linarioidis-Thymetalia scorpilii* Akman et al. 1987, *Onobrychido armenae-Thymetalia leucostomi* Akman et al. 1985, *Festuco oreophilae-Veronicetalia orientalis* Hamzaoğlu 2006, and other lower rank units (Quézel 1973; Akman et al. 1984, 1987; Gümüs 1992; Klein and Lacoste 1994; Hamzaoğlu 2006; Ocakverdi et al. 2009). Also, 206 plots from Northern Caucasus (Russia) were taken from the Eastern European Steppe Database (Vynokurov et al. 2020). Combined with our own plots from Armenia, a dataset of 598 relevés resulted (Suppl. material 5). After the unification of the species taxonomy, removing the taxa determined to the genus level, and combining the aggregates, the final dataset contained 1,556 taxa.

Environmental data from external sources

Climatic data were extracted from the CHELSA Climate database (Karger et al. 2017, 2018). We used the following variables: BIO01 – mean annual air temperature, BIO07 – annual range of air temperature, BIO12 – annual precipitation amount, BIO17 – mean monthly precipitation amount of the driest quarter.

Maps were created using QGIS software (QGIS Development Team 2009). As basemaps, we used the map of main vegetation types of Armenia by Grossgeim (1928), and the SRTM (Shuttle Radar Topography Mission) elevation model for Armenia (EROS Center 2017).

Attributes for the Armenian species

In order to assess the distribution ranges of species, we analysed their distribution maps (according to GBIF 2023 and POWO 2023) and classified their distribution ranges into the following broad categories: European (occurring mainly in the temperate regions of Europe and Western Siberia), Mediterranean (covering the southern part of Europe in areas with Mediterranean climate), Irano-Turanian (occurring in Western and Central Asia), Transcaucasian (narrow endemics of Armenia and surrounding regions of Transcaucasia), Caucasian (broader endemics of the whole Caucasus Range, including the Northern Caucasus and adjacent parts of Eastern Anatolia in Turkey and North-Western Iran). If the species occurred predominantly in one of the mentioned regions, we assigned a value of one (1) to the corresponding category. In case that the species occurred in two regions simultaneously (European and Irano-Turanian, European and Mediterranean, or Mediterranean and Irano-Turanian), we assigned a value of 0.5 to the corresponding categories. If the species distribution covered three regions (European, Mediterranean and Irano-Turanian), we assigned a value '0.3' to each of these categories. In all other cases, when the species distribution area was greater than the mentioned categories (e.g., Palaearctic, Holarctic, etc.), we classified these species into the category 'Other'. The assigned distribution ranges of species are available in Suppl. material 6.

In addition, we classified all the species into one of the Raunkiær plant life forms: therophytes, geophytes, hemicryptophytes, chamaephytes, and phanerophytes. The data are also available in the Suppl. material 6.

Statistical analysis

Unsupervised classification

Unsupervised classification for both the West Asian and Armenian dataset was done in JUICE 7.0 (Tichý 2002) using the modified TWINSPAN method (Roleček et al. 2009) with three pseudospecies cut levels (0, 5, and 15), and Whittaker's beta-diversity index as a measure of internal cluster heterogeneity. Diagnostic species were determined based on phi values (Chytrý et al. 2002), standardised to equal plot numbers at association level (Tichý and Chytrý 2006). This was done hierarchically at the four syntaxonomic levels from association to class (García-Mijangos et al. 2021). Since this approach is not implemented in JUICE (Tichý 2002) yet, we had to do it in Microsoft Excel, which precluded the use of Fisher's exact test for significance. To avoid selecting non-significant diagnostic species, we put the thresholds for phi values rather high. For associations and alliances, we used > 0.4 for diagnostic species and > 0.6 for highly diagnostic species, while for orders and classes the thresholds were > 0.3 and > 0.5, respectively. Moreover, we also ensured that the phi values were at least 0.2 higher in the target syntaxon than the syntaxon of the same rank with the next-lower phi value (see García-Mijangos et al. 2021). If a species fulfilled the criteria to be diagnostic at several hierarchical levels, it was assigned to the level with the highest phi value. In case of monotypic syntaxa, diagnostic species were only assessed at the higher level.

Ordination

DCA-Ordination was performed with Canoco 5 (ter Braak and Šmilauer 2012) with log-transformed percent cover values of species and downweighting rare species and post hoc fitted variables (environmental, calculated or measured).

Comparison of syntaxon characteristics

Differences in variables between syntaxa were tested by univariate ANOVA using SPSS 22 (IBM, Armonk, NY, US). We tested whether the assumptions of ANOVA (normal distribution, equal variance) were sufficiently met by visually inspecting the frequency distribution of the residuals and by testing for homogeneity of variance according to Levene (Quinn and Keough 2002). Where ANOVA revealed a significant pattern, Tukey's post-hoc test at $p < 0.05$ was used to identify homogeneous groups of syntaxa. Results were presented as box-whisker plots with median and mean, and 25th/75th (boxes) and 10th/90th (whiskers) percentiles as well as outliers.

Syntaxonomic assignment

We selected a TWINSPAN resolution where the terminal clusters were floristically still well-characterised and not too small. These clusters were then assigned to the rank of association. Alliance, order and class levels were assigned to higher cut levels of the dendrogram, with the double aim to have floristically well differentiated and ecologically and chorologically interpretable units on a comparable level as these hierarchies have in Mucina et al. (2016).

After defining the hierarchical units, we carefully checked the syntaxonomic literature of the neighbouring countries to determine whether syntaxa with this content already existed. If this was the case, we took the established name. If not, we formally described new syntaxa according to the ICPN (Theurillat et al. 2021). Following Recommendation 7A of the ICPN, we refrained from establishing new associations when we had fewer than 10 relevés and instead treated the respective cluster as an informal community at association rank. Likewise, we refrained from a formal description of the new class that was supported by our analyses, suggesting that this should first be "validated" in a broader-scale analysis involving the neighbouring countries of Armenia.

Results

Unsupervised classification and ordination of the West Asian and Caucasian dataset

Modified TWINSPAN resulted into 16 clusters with five main groups of clusters: A (clusters 1–3), B (4–6), C (7), D (8–10) and E (11–16) (Figure 2). The synoptic table built with these five main groups is shown in Suppl. material 7.

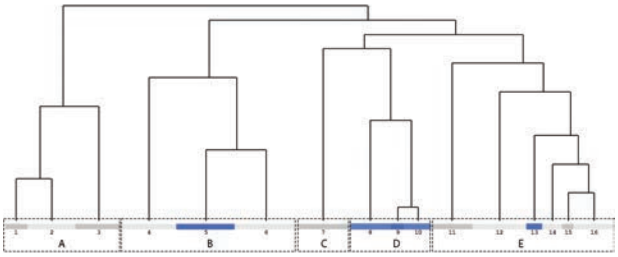

Figure 2. Results of the Modified TWINSPAN classification for the broad-scale comparison involving plots from the bordering countries (n = 598). The width of the bars is proportional to the number of included plots. The main groups (letters) and terminal clusters (numbers) are described in the text. Blue colour indicates clusters that predominantly or completely consisted of Armenian plots.

The group A (clusters 1–3) completely consisted of the relevés originally assigned to the class *Astragalo-Brometea*, including the type order *Astragalo-Brometalia* Quézel 1973 (in the cluster 2), described from the Taurus Mountains in South-Western Turkey (Quézel 1973). The plots assigned to the other orders of this class with their corresponding types were also included in this group of clusters: *Drabo-Androsacetalia* Quézel 1973 (cluster 2) from the same Taurus Mountain range; *Hyperico linarioidis-Thymetalia scorpilii* Akman et al. 1987 (cluster 1) from the Ilgaz Mountains in North-Western Turkey; *Onobrychido armenae-Thymetalia leucostomi* Akman et al. 1985 (cluster 3) described from Central Anatolia. Plots from Armenia did not fit into this group.

The second group B (clusters 4–6) comprised plots from the high-mountain steppe vegetation. Cluster 4 consisted mainly of relevés from the northern slope of the Alborz Mountains in Iran, assigned to the association *Alchemilletum plicatissimae* Klein et Lacoste 1994. Plots from the Northern Caucasus region assigned to the alliance *Artemisio chamaemelifoliae-Bromopsion variegatae* Vynokurov in Vynokurov et al. 2021 were classified into cluster 5, together with some plots from Armenia. Cluster 6 comprised plots sampled near the Kısır Mountain in Turkey, in Eastern Anatolia. They were originally assigned to several associations of the class *Astragalo-Brometea* but without placement in alliances and orders (Ocakverdi et al. 2009).

Thorn-cushion communities from Eastern Anatolia are combined in the group C (cluster 7). They were originally assigned to the order *Festuco oreophilae-Veronicetalia orientalis* Hamzaoğlu 2006 of the class *Astragalo-Brometea*, together with its type alliance *Festuco oreophilae-Veronicion orientalis* Hamzaoğlu 2006 and the respective association *Astragalo-Onobrychidetum cornutae* Gümüs 1992. Even though this cluster was not placed in the corresponding group A in the dendrogram (Figure 2), they seem closely related according to the ordination (Figure 3).

Clusters 8–10 formed group D. It consisted exclusively of plots from Armenia. Among them, cluster 8 contained the most xeric communities sampled in the driest parts of Armenia, followed by cluster 10. Cluster 9 was transitional between the groups D and E.

The group E (clusters 11–16) was formed by plots containing the more 'typical' *Festuco-Brometea* species, mostly from the region of the Northern Caucasus. Cluster 11 was comprised mainly of rocky grasslands belonging to the order *Asphodelino tauricae-Euphorbietalia petrophilae* Vynokurov in Vynokurov et al. 2021; cluster 12 contained grass steppes mostly of the *Festucetalia valesiacae*. Cluster 13 combined mountain steppes exclusively from Armenia. Clusters 14–16 comprised mostly meso-xeric communities of the order *Brachypodietalia pinnati* from the Northern Caucasus. A synoptic table with the five distinguished groups of clusters (A–E) is provided in Suppl. material 7.

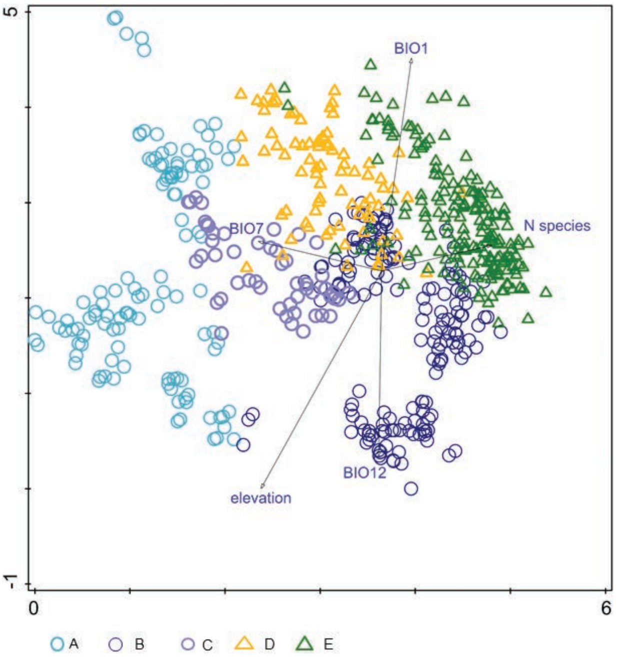

Figure 3. DCA of the West Asian dataset (DCA with supplementary variables, eigenvalues/gradient lengths/cumulative explained variation of axis 1: 0.6313/5,37/4.02, axis 2: 0.4207/4.94/6.69). Vectors (environmental variables): BIO1: annual mean temperature; BIO7: temperature annual range; BIO12: annual precipitation; elevation: elevation (m a.s.l.); N species: vascular plant richness.

General overview of the Armenian plots

In our 111 plots of 10 m^2, we recorded a total of 739 vascular plant, 40 bryophyte and 13 lichen taxa (subspecies, species, aggregates and sections, further as 'species'). The species richness per plot ranged from 21 to 85, with a mean of 47.3. On average there were 46.8 vascular plant, 0.4 bryophyte and 0.1 lichen species per plot. The most frequent vascular plant was *Galium verum* (in 72% of all plots), followed by *Thymus kotschyanus* (59%), *Teucrium capitatum* (58%), *Poa bulbosa* (55%), *Dactylis glomerata* (54%), *Scutellaria orientalis* aggr. (53%), *Koeleria macrantha* (51%), *Stachys recta* (50%) and *Potentilla recta* aggr. (50%). The most frequent bryophytes were *Syntrichia ruralis* (27%), *Ptychostomum imbricatulum* (19%) and *Syntrichia montana* (14%). Lichens were absent in most plots, with the most frequent one (*Cladonia foliacea*) reaching just 4%.

Classification of the Armenian dataset

The most meaningful modified TWINSPAN classification of the plots from Armenia resulted in the 12-cluster solution (Figure 4). The first cluster (X) had only a single relevé of scree vegetation recorded in the Vayots Dzor Province near Hermon. The rest of the clusters are interpreted at the community or association level. Clusters 1.1.1.1–1.1.3.2 consisted of the most xeric plots of the semi-desert, rocky and thorn-cushion vegetation in the lower elevations. Clusters 2.1.1.1 and 2.1.1.2 represent plots of mountain meadow steppes from the highest elevations. Clusters 2.2.1.1–2.2.1.4 consisted of plots of thorn-cushion and steppic grasslands of so-called mountain steppes.

Ordination of the Armenian dataset

Ordination of the plots with the assignment to one of these clusters revealed that the first axis of the DCA graph (Figure 5) corresponds to a gradient of moisture and temperature connected with the elevation range. The most mesic plots occupied higher altitudes (cluster 2.1.1.1), while the most xeric ones were distributed in the lower elevations (clusters 1.1.2.1–1.1.3.2). The climatic-elevation gradient and community parameters correlated with the differentiation of two higher classification units – *Ziziphora tenuior-Stipa arabica* grasslands and the class *Festuco-Brometea*.

Syntaxonomic scheme

Resulting from our analyses of the Armenian data and the comparison with the syntaxa of neighbouring territories, we propose the following syntaxonomic scheme

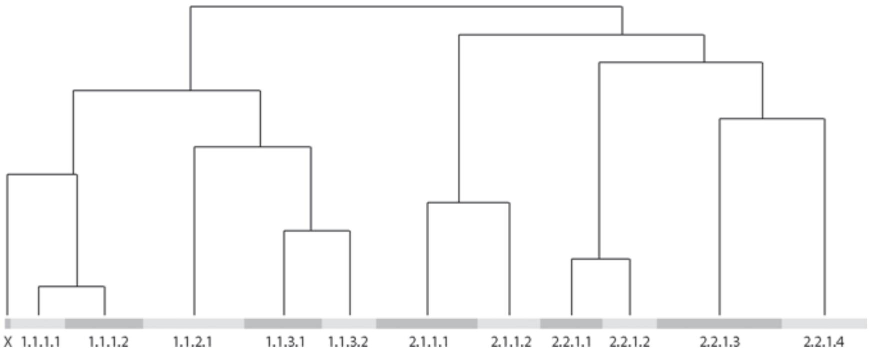

Figure 4. Results of the Modified TWINSPAN classification of the Armenian plots (n = 111). The terminal clusters were interpreted as associations or, if represented by too few plots, as informal communities at association rank. The first cluster (X) consisted only of one plot of scree vegetation. Codes at the tips of the other clusters correspond to Table 1.

for the dry grassland and thorn-cushion communities of Armenia, including a single plot with an unclear assignment (Table 1). According to our literature overview and the analysis of the West Asian and Caucasian dataset, we concluded that most of the syntaxa found are new to science. The formal descriptions of the new syntaxa ("Vynokurov et al. 2024") are provided in Appendix 1.

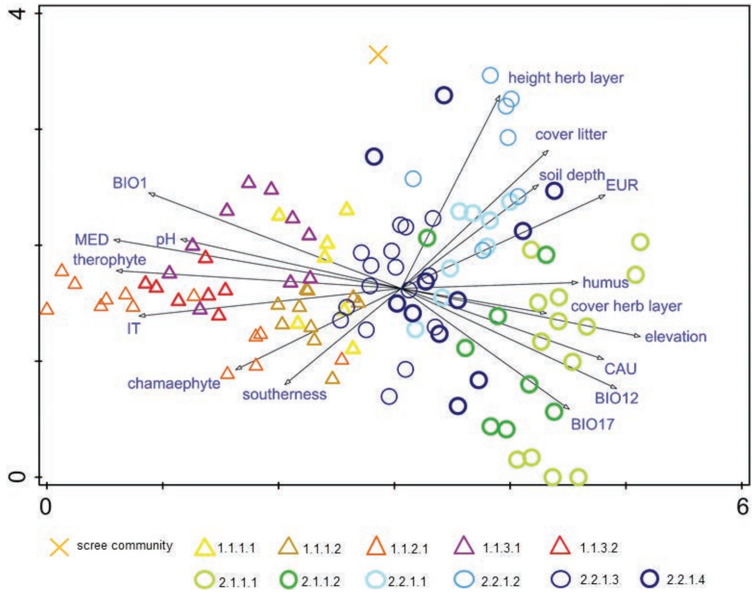

Figure 5. DCA ordination of the 111 Armenian plots with assignment to the 12 distinguished units at association level (DCA with supplementary variables, eigenvalues/gradient lengths/cumulative explained variation of axis 1: 0.5825/5.12/5.76, axis 2: 0.3160/3.64/8.89). Triangles indicate members of the class *Ziziphora tenuior-Stipa arabica* grasslands, circles members of the class *Festuco-Brometea*. Vectors: BIO1: annual mean temperature; BIO12: annual precipitation; BIO17: precipitation of driest quarter; CAU: cover of Caucasian species in %; chamaephytes: cover of chamaephytes in %; cover herb layer: cover of the herb layer in %; cover litter: cover of the litter; elevation: elevation in m a.s.l.; EUR: cover of European species in %; height herb layer: height of the herb layer; humus: soil humus content in %; IT: cover of Irano-Turanian species in %; MED: cover of Mediterranean species in %; pH: pH values of the plot soil samples; soil depth: mean soil depth of plot; southerness: -cos (aspect); therophyte: cover of therophytes in %.

Table 1. Syntaxonomic scheme for the dry grasslands and thorn-cushion communities of Armenia based on the 111 plots analysed in this paper.

Unclear class (scree communities)
      Euphorbia orientalis-Melilotus officinalis community
Potential class 1 *Ziziphora tenuior-Stipa arabica* grasslands
  Order 1.1 *Cousinio brachypterae-Stipetalia arabicae* Vynokurov et al. 2024
    Alliance 1.1.1 *Onobrychido michauxii-Stipion capillatae* Vynokurov et al. 2024
      1.1.1.1 *Stachys lavandulifolia-Astracantha condensata* community
      1.1.1.2 *Marrubio parviflorae-Stipetum capillatae* Vynokurov et al. 2024
    Alliance 1.1.2 *Artemision fragrantis* Vynokurov et al. 2024
      1.1.2.1 *Noaeo mucronatae-Artemisietum fragrantis* Vynokurov et al. 2024
    Alliance 1.1.3 *Acantholimono caryophyllacei-Stipion holosericeae* Vynokurov et al. 2024
      1.1.3.1 *Acantholimono caryophyllacei-Stipetum holosericeae* Vynokurov et al. 2024
      1.1.3.2 *Stachys inflata-Acantholimon vedicum* community
Class 2. *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947
  Order 2.1 *Plantagini atratae-Bromopsietalia variegatae* Vynokurov et al. 2024
    Alliance 2.1.1 *Artemisio chamaemelifoliae-Bromopsion variegatae* Vynokurov in Vynokurov et al. 2021
      2.1.1.1 *Ranunculo caucasici-Bromopsietum variegatae* Vynokurov et al. 2024
      2.1.1.2 *Tragopogon reticulatus-Astracantha aurea* community
  Order 2.2 *Onobrychido transcaucasicae-Stipetalia pulcherrimae* Vynokurov et al. 2024
    Alliance 2.2.1. *Onobrychido transcaucasicae-Stipion pulcherrimae* Vynokurov et al. 2024
      2.2.1.1 *Trisetum flavescens-Stachys macrostachys* community
      2.2.1.2 *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* community
      2.2.1.3 *Globulario trichosanthae-Stipetum pulcherrimae* Vynokurov et al. 2024
      2.2.1.4 *Seslerio phleoidis-Onobrychidetum cornutae* Vynokurov et al. 2024

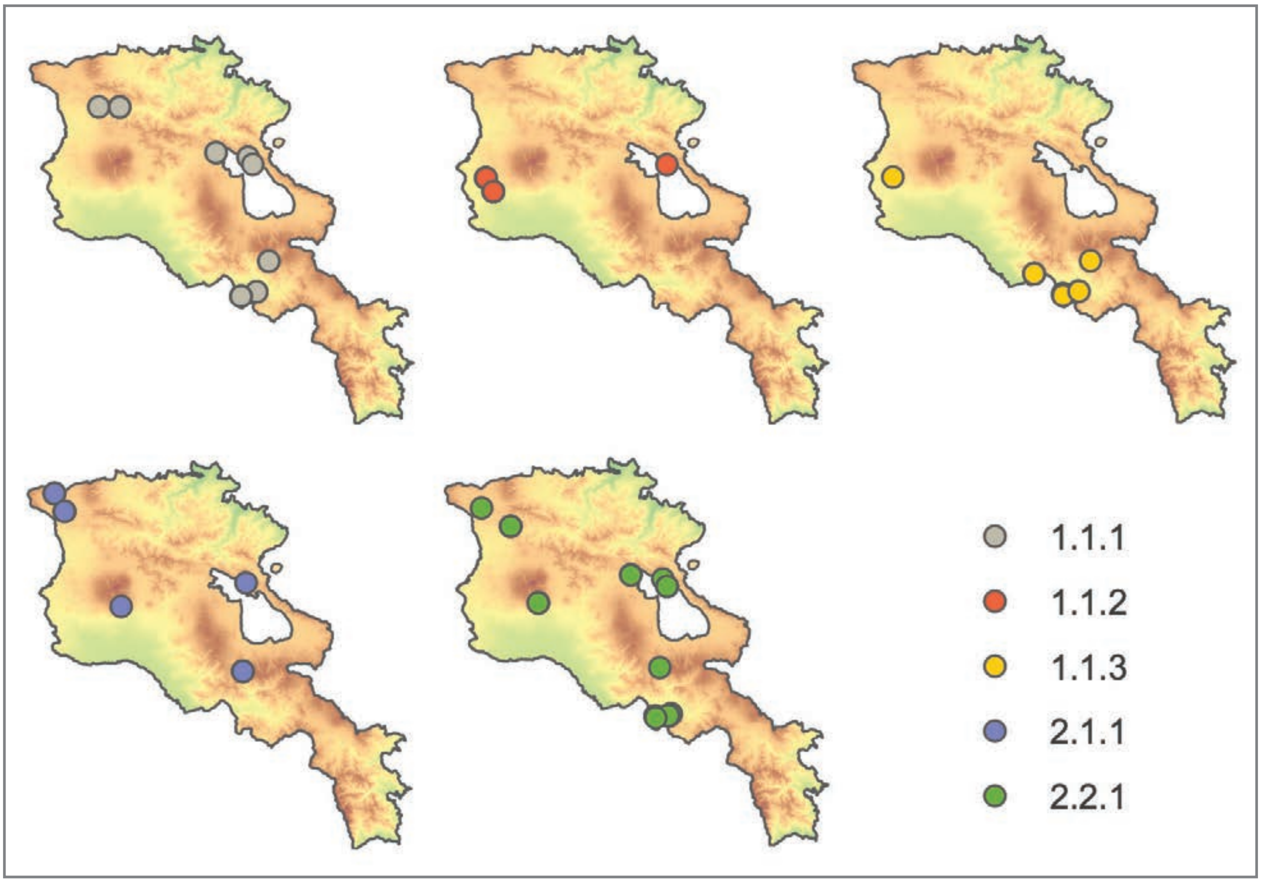

Figure 6. Distribution of five described vegetation alliances in Armenia based on sampled vegetation plots (*n* = 110). 1.1.1 – *Onobrychido michauxii-Stipion capillatae*, 1.1.2 – *Artemision fragrantis*, 1.1.3 – *Acantholimono caryophyllacei–Stipion holosericeae*, 2.1.1 – *Artemisio chamaemelifoliae–Bromopsion variegatae*, 2.2.1 – *Onobrychido transcaucasicae-Stipion pulcherrimae*. Basemap: SRTM elevation model for Armenia (obtained from Earth Resources Observation and Science (EROS) Center 2017).

Description of the syntaxa

The proposed classification of the Armenian dry grassland and thorn-cushion communities is shown in the synoptic table (abbreviated version: Table 2; full version: Suppl. material 2). The distribution of the alliances is shown in Figure 6, typical stands of the association-level units are visualised in two photo plates (Figures 7, 8), while the site conditions, structure and species richness of the syntaxa of the four hierarchical levels are compared in Figures 9–13. In the following, we provide brief descriptions of the diagnostic species and information on ecology and distribution for all syntaxonomic levels and additionally on the community structure for the association-level units. The diagnostic species are listed alphabetically, with the highly diagnostic ones highlighted in bold and bryophytes and lichens marked with B and L, respectively.

***Euphorbia orientalis-Melilotus officinalis* scree community** (Figure 7A)

One cluster in our analysis consisted of only a single relevé of scree vegetation. For this instance, we assume that a corresponding vegetation type needs to be described in the future in the rank of an order or even a class when enough relevant data is available. The aforementioned relevé was sampled in the Vayots Dzor Province, near Hermon (39.8812°N, 45.43254°E), 1,739 m a.s.l., aspect 135°, inclination 46°, 2 July 2019, total vegetation cover: 50%:

Alyssum alyssoides: 0.5, *Arenaria serpyllifolia* aggr.: 0.1, *Asperula arvensis*: 0.2, *Buglossoides arvensis*: 0.1, *Bupleurum commutatum*: 0.01, *Caucalis platycarpos*: 0.1, *Cerastium ruderale*: 3, *Chaerophyllum bulbosum*: 0.5, *Cleome ornithopodioides*: 0.01, *Convolvulus arvensis*: 0.1, *Coronilla coronata*: 2, *Crepis pulchra*: 2, *Euphorbia orientalis*: 15, *Galium spurium*: 1, *Galium tenuissimum*: 0.3, *Holosteum marginatum*: 0.1, *Lactuca viminea*: 0.5, *Lamium amplexicaule*: 0.01, *Medicago rigidula*: 0.1, *Melica taurica*: 1, *Melilotus officinalis*: 5, *Michauxia laevigata*: 0.5, *Nepeta trautvetteri*: 0.3, *Noccaea perfoliata*: 0.01, *Prangos ferulacea*: 1, *Reichardia dichotoma*: 0.3, *Salvia verticillata*: 30, *Sanguisorba minor*: 2, *Saponaria orientalis*: 0.2, *Secale vavilovii*: 2, *Stachys recta*: 0.5, *Valerianella uncinata*: 0.1, *Vicia sativa*: 0.3, *Zosima absinthiifolia*: 4.

Table 2. Abbreviated constancy table of the classes, orders, alliances and associations/communities distinguished among the Armenian dry grasslands and thorn-cushion communities. Dark grey indicates diagnostic species at the respective level, while this colour is copied to all subordinate levels. Light grey refers to transgressive diagnostic species at the higher level (only given if the sum of the phi values of the syntaxa at the lower level without the target syntaxon is > 0). Frames indicate differential species at the association level. Diagnostic species are sorted by decreasing phi values in their target unit, while companion species are sorted by decreasing total constancy. While all diagnostic species at the class level are shown, at the order, alliance and association level only the first seven plus all with a phi-value > 0.5 were kept. Additionally, all species with a total constancy of ≥ 20% were also kept. Species that did not meet any of these criteria are not shown here. The complete version of this table, including also the precise phi values and the individual relevés is available as Suppl. material 2.

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m^2 (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m^2 (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m^2 (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m^2 (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Cl. 1																						
Xeranthemum squarrosum	25	57	.	57	.	.	41	77	59	.	.	29	50	77	80	29	.	.	.	.	.	.
Teucrium capitatum	58	87	37	87	.	55	100	77	82	.	55	100	100	77	90	71	.	.	.	14	94	64
Taeniatherum caput-medusae subsp. crinitum	22	51	.	51	.	.	24	69	65	.	.	14	30	69	70	57	.	.	.	.	.	.
Holosteum umbellatum	24	51	3	51	.	5	41	54	59	.	5	14	60	54	50	71	.	.	.	.	.	18
Crupina vulgaris	18	40	2	40	.	2	6	69	53	.	2	14	.	69	40	71	.	.	.	.	6	.
Thymelaea passerina	15	34	2	34	.	2	35	38	29	.	2	14	50	38	20	43	.	.	.	.	6	.
Tanacetum aureum	23	40	10	40	.	14	47	31	41	.	14	86	20	31	10	86	.	.	.	14	6	36
Helichrysum plicatum	24	45	8	45	5	10	29	69	41	5	10	14	40	69	20	71	.	13	13	14	13	.
Marrubium parviflorum	15	32	2	32	.	2	41	23	29	.	2	.	70	23	50	.	.	.	.	.	6	.
Bromus danthoniae	10	23	.	23	.	.	18	15	35	.	.	14	20	15	30	43	.	.	.	.	.	.
Bromus squarrosus	15	30	3	30	.	5	12	38	41	.	5	14	10	38	50	29	.	.	.	.	6	9
Sideritis montana	22	40	8	40	.	12	53	69	6	.	12	71	40	69	10	.	.	.	.	14	13	18
Poa bulbosa	55	77	40	77	33	43	41	100	94	33	43	.	70	100	100	86	15	63	75	.	69	9
Achillea arabica	20	38	6	38	5	7	29	54	35	5	7	.	50	54	60	.	.	13	25	.	6	.
Anisantha tectorum	6	15	.	15	.	.	12	.	29	.	.	14	10	.	30	29	.	.	.	.	.	.
Centaurea aggregata	9	19	2	19	.	2	18	15	24	.	2	29	10	15	10	43	.	.	13	.	.	.
Dianthus orientalis	6	15	.	15	.	.	12	23	12	.	.	29	.	23	.	29	.	.	.	.	.	.
All. 1.1.1																						
Veronica multifida	23	26	21	26	19	21	65	8	.	19	21	57	70	8	.	.	31	.	13	29	25	18
Assoc. 1.1.1.1																						
Astracantha condensata	11	17	6	17	.	10	41	8	.	.	10	86	10	8	.	.	.	.	.	.	13	18
Stachys lavandulifolia	8	17	2	17	.	2	41	.	6	.	2	71	20	.	10	.	.	.	.	.	6	.
Gypsophila elegans	5	9	3	9	.	5	24	.	.	.	5	57	.	.	.	.	.	.	.	14	.	9
Onobrychis michauxii	11	17	6	17	.	10	41	8	.	.	10	71	20	8	.	.	.	.	13	.	19	.
Viola occulta	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Herniaria hirsuta	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Crepis ciliata	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Onosma setosa	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Centaurea phrygia subsp. abbreviata	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Nepeta racemosa	8	13	5	13	.	7	29	.	6	.	7	57	10	.	10	.	.	.	.	14	.	18
Asperula arvensis	31	53	14	53	.	21	65	46	47	.	21	100	40	46	60	29	.	.	13	.	44	9
Assoc. 1.1.1.2																						
Stipa capillata	23	40	10	40	.	14	47	46	29	.	14	.	80	46	50	.	.	.	.	.	31	9

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m^2 (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m^2 (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m^2 (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m^2 (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Allium cardiostemon	2	4	.	4	.	.	12	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.
Euphorbia condylocarpa	7	9	6	9	.	10	24	.	.	.	10	.	40	.	.	.	.	.	13	.	6	18
All. 1.1.2																						
Noaea mucronata	10	23	.	23	.	.	.	77	6	.	.	.	.	77	.	14	.	.	.	.	.	.
Cousinia brachyptera	8	19	.	19	.	.	6	62	.	.	.	.	10	62	.	.	.	.	.	.	.	.
Astragalus hyalolepis	13	26	3	26	5	2	12	77	.	5	2	.	20	77	.	.	8	.	.	.	6	.
Allium pseudoflavum	16	36	2	36	.	2	12	85	24	.	2	29	.	85	20	29	.	.	.	.	6	.
Minuartia hamata	24	51	3	51	.	5	29	100	35	.	5	29	30	100	20	57	.	.	13	.	6	.
B Syntrichia caninervis	6	15	.	15	.	.	.	46	6	.	.	.	.	46	.	14	.	.	.	.	.	.
Androsace albana	4	9	.	9	.	.	.	31	.	.	.	.	.	31	.	.	.	.	.	.	.	.
Polygala hohenackeriana	4	9	.	9	.	.	.	31	.	.	.	.	.	31	.	.	.	.	.	.	.	.
Meniocus linifolius	16	38	.	38	.	.	24	77	24	.	.	14	30	77	.	57	.	.	.	.	.	.
Alyssum turkestanicum	9	21	.	21	.	.	12	54	6	.	.	29	.	54	10	.	.	.	.	.	.	.
Arenaria serpyllifolia aggr.	32	57	13	57	10	14	59	100	24	10	14	86	40	100	30	14	15	.	38	.	13	9
All. 1.1.3																						
Chardinia orientalis	11	26	.	26	.	.	12	15	47	.	.	.	20	15	40	57	.	.	.	.	.	.
Crepis sancta	15	34	2	34	.	2	12	31	59	.	2	.	20	31	70	43	.	.	13	.	.	.
Stipa holosericea	11	26	.	26	.	.	18	8	47	.	.	.	30	8	50	43	.	.	.	.	.	.
Aegilops cylindrica	7	17	.	17	.	.	.	15	35	.	.	.	.	15	30	43	.	.	.	.	.	.
Roemeria hybrida	4	9	.	9	.	.	.	.	24	.	.	.	.	.	20	29	.	.	.	.	.	.
Noccaea perfoliata	26	38	17	38	14	19	35	.	71	14	19	29	40	.	60	86	23	.	.	57	6	27
Bromus japonicus	15	30	5	30	.	7	24	15	47	.	7	14	30	15	40	57	.	.	13	.	6	9
Assoc. 1.1.3.1																						
Torilis arvensis	3	6	.	6	.	.	.	.	18	.	.	.	.	.	30	.	.	.	.	.	.	.
Acantholimon caryophyllaceum	5	9	2	9	.	2	.	.	24	.	2	.	.	.	40	.	.	.	.	14	.	.
Lomelosia rotata	7	15	2	15	.	2	.	23	24	.	2	.	.	23	40	.	.	.	.	.	6	.
Carduus hamulosus	2	4	.	4	.	.	.	.	12	.	.	.	.	.	20	.	.	.	.	.	.	.
Stipa zalesskii subsp. pontica	2	4	.	4	.	.	.	.	12	.	.	.	.	.	20	.	.	.	.	.	.	.
Geranium lucidum	2	4	.	4	.	.	.	.	12	.	.	.	.	.	20	.	.	.	.	.	.	.
Aegilops triuncialis	6	15	.	15	.	.	12	.	29	.	.	.	20	.	40	14	.	.	.	.	.	.
Assoc. 1.1.3.2																						
Acantholimon vedicum	5	11	.	11	.	.	.	.	29	.	.	.	.	.	.	71	.	.	.	.	.	.
Stachys inflata	11	21	3	21	.	5	6	.	53	.	5	14	.	.	20	100	.	.	25	.	.	.
Bunium microcarpum	8	13	5	13	.	7	.	.	35	.	7	.	.	.	.	86	.	.	25	.	.	9
Petrorhagia cretica	4	9	.	9	.	.	.	.	24	.	.	.	.	.	.	57	.	.	.	.	.	.
Helianthemum ledifolium	11	26	.	26	.	.	6	23	47	.	.	.	10	23	20	86	.	.	.	.	.	.
Gaudiniopsis macra	5	11	.	11	.	.	.	8	24	.	.	.	.	8	.	57	.	.	.	.	.	.
Ephedra procera	3	6	.	6	.	.	.	.	18	.	.	.	.	.	.	43	.	.	.	.	.	.
Papaver minus	3	6	.	6	.	.	.	.	18	.	.	.	.	.	.	43	.	.	.	.	.	.
Aethionema carneum	3	6	.	6	.	.	.	.	18	.	.	.	.	.	.	43	.	.	.	.	.	.
Arabis auriculata aggr.	9	19	2	19	.	2	6	15	35	.	2	.	10	15	10	71	.	.	.	.	.	9
Lamium amplexicaule	4	6	2	6	5	.	.	.	18	5	.	.	.	.	.	43	8	.	.	.	.	.
Camelina laxa	4	9	.	9	.	.	6	.	18	.	.	.	10	.	.	43	.	.	.	.	.	.

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m^2 (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m^2 (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m^2 (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m^2 (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Galium verticillatum	7	13	3	13	.	5	6	.	29	.	5	.	10	.	10	57	.	.	.	14	6	.
Ziziphora tenuior	13	30	.	30	.	.	6	38	47	.	.	14	.	38	30	71	.	.	.	.	.	.
Aegilops biuncialis	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Cuscuta pedicellata	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Valerianella coronata	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Onobrychis atropatana	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Cousinia daralaghezica	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Astragalus ornithopodioides	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Crucianella exasperata	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Stipa arabica	14	30	2	30	.	2	18	31	41	.	2	29	10	31	20	71	.	.	.	.	6	.
Cl. 2																						
Lotus corniculatus	39	2	67	2	90	55	6	.	.	90	55	.	10	.	.	.	92	88	88	57	31	64
Achillea millefolium aggr.	47	13	73	13	95	62	29	.	6	95	62	43	20	.	10	.	92	100	75	57	63	55
Dactylis glomerata	55	26	76	26	57	86	47	.	24	57	86	43	50	.	40	.	54	63	100	86	88	73
Poa pratensis aggr.	33	11	49	11	71	38	18	15	.	71	38	.	30	15	.	.	69	75	50	86	13	36
Scabiosa bipinnata	34	6	54	6	38	62	12	8	.	38	62	29	.	8	.	.	54	13	63	43	63	73
Campanula glomerata aggr.	18	.	32	.	33	31	.	.	.	33	31	.	.	.	.	.	15	63	50	71	13	18
Potentilla recta aggr.	51	28	68	28	71	67	41	15	24	71	67	29	50	15	40	.	69	75	88	43	81	45
Galium verum	73	53	87	53	81	90	47	62	53	81	90	71	30	62	60	43	77	88	88	100	81	100
Phleum phleoides	25	6	40	6	52	33	6	.	12	52	33	14	.	.	20	.	54	50	25	71	31	18
Pimpinella saxifraga aggr.	17	.	30	.	48	21	.	.	.	48	21	.	.	.	.	.	69	13	13	.	6	64
Polygala anatolica	18	2	30	2	29	31	.	8	.	29	31	.	.	8	.	.	46	.	.	57	31	36
Leontodon hispidus	19	4	30	4	48	21	.	8	6	48	21	.	.	8	10	.	62	25	13	57	13	18
Bupleurum falcatum aggr.	13	.	22	.	19	24	.	.	.	19	24	.	.	.	.	.	31	.	.	43	19	36
Trifolium alpestre	12	.	21	.	29	17	.	.	.	29	17	.	.	.	.	.	38	13	50	.	.	27
Trisetum flavescens	13	2	21	2	29	17	.	.	6	29	17	.	.	.	10	.	8	63	63	14	.	9
Ord. 2.1																						
Trifolium ambiguum	13	.	22	.	62	2	.	.	.	62	2	.	.	.	.	.	46	88	13	.	.	.
Campanula stevenii	22	.	38	.	81	17	.	.	.	81	17	.	.	.	.	.	77	88	50	.	6	18
Plantago atrata	27	2	46	2	86	26	.	.	6	86	26	.	.	.	10	.	85	88	13	29	25	36
Trifolium trichocephalum	11	.	19	.	52	2	.	.	.	52	2	.	.	.	.	.	62	38	.	.	.	9
Bromopsis variegata	23	11	32	11	76	10	29	.	.	76	10	57	10	.	.	.	92	50	.	14	.	27
Myosotis alpestris	8	.	14	.	38	2	.	.	.	38	2	.	.	.	.	.	46	25	.	.	6	.
Koeleria albovii	12	.	21	.	43	10	.	.	.	43	10	.	.	.	.	.	38	50	.	.	25	.
[…]																						
Veronica denudata	21	9	30	9	57	17	12	8	6	57	17	.	20	8	10	.	54	63	25	14	13	18
[…]																						
Festuca ovina aggr.	20	11	27	11	52	14	.	31	6	52	14	.	.	31	10	.	54	50	13	.	19	18
[…]																						
Taraxacum sect. Taraxacum	23	6	35	6	62	21	12	.	6	62	21	14	10	.	10	.	69	50	25	43	6	27
Assoc. 2.1.1.1																						
Ranunculus caucasicus	6	.	11	.	33	.	.	.	.	33	.	.	.	.	.	.	54	.	.	.	.	.
Huynhia pulchra	5	.	10	.	29	.	.	.	.	29	.	.	.	.	.	.	46	.	.	.	.	.

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m^2 (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m^2 (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m^2 (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m^2 (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Lomelosia caucasica	5	.	10	.	29	.	.	.	.	29	.	.	.	.	.	.	46	.	.	.	.	.
Alchemilla sericea	7	.	13	.	33	2	.	.	.	33	2	.	.	.	.	.	54	.	.	.	.	9
Campanula collina	5	.	8	.	24	.	.	.	.	24	.	.	.	.	.	.	38	.	.	.	.	.
Polygonum cognatum	13	.	22	.	48	10	.	.	.	48	10	.	.	.	.	.	69	13	25	.	6	9
Phleum alpinum	6	.	11	.	29	2	.	.	.	29	2	.	.	.	.	.	46	.	13	.	.	.
Cirsium leucocephalum	15	.	27	.	52	14	.	.	.	52	14	.	.	.	.	.	77	13	13	43	.	18
Schedonorus pratensis	7	.	13	.	29	5	.	.	.	29	5	.	.	.	.	.	46	.	.	.	.	18
Stipa tirsa	8	.	14	.	29	7	.	.	.	29	7	.	.	.	.	.	46	.	.	.	19	.
B Tortula acaulon	4	.	6	.	19	.	.	.	.	19	.	.	.	.	.	.	31	.	.	.	.	.
Pedicularis condensata	4	.	6	.	19	.	.	.	.	19	.	.	.	.	.	.	31	.	.	.	.	.
Psephellus xanthocephalus	4	.	6	.	19	.	.	.	.	19	.	.	.	.	.	.	31	.	.	.	.	.
Arenaria blepharophylla aggr.	5	.	10	.	24	2	.	.	.	24	2	.	.	.	.	.	38	.	.	.	.	9
Rumex acetosella	5	.	10	.	24	2	.	.	.	24	2	.	.	.	.	.	38	.	13	.	.	.
Assoc. 2.1.1.2																						
Tragopogon reticulatus	11	4	16	4	24	12	6	8	.	24	12	.	10	8	.	.	.	63	13	.	.	36
Senecio pseudo-orientalis	4	.	6	.	14	2	.	.	.	14	2	.	.	.	.	.	.	38	13	.	.	.
Astracantha aurea	6	2	10	2	19	5	6	.	.	19	5	.	10	.	.	.	.	50	13	14	.	.
Lathyrus digitatus	5	.	8	.	19	2	.	.	.	19	2	.	.	.	.	.	8	38	.	.	6	.
Verbascum speciosum	2	.	3	.	10	.	.	.	.	10	.	.	.	.	.	.	.	25	.	.	.	.
Trifolium spadiceum	2	.	3	.	10	.	.	.	.	10	.	.	.	.	.	.	.	25	.	.	.	.
Gagea glacialis	2	.	3	.	10	.	.	.	.	10	.	.	.	.	.	.	.	25	.	.	.	.
Ord. 2.2																						
Stachys macrostachys	9	.	16	.	.	24	.	.	.	.	24	.	.	.	.	.	.	.	75	57	.	.
Stachys recta	50	32	63	32	33	79	65	8	18	33	79	57	70	8	30	.	54	.	38	100	88	82
Securigera varia	35	15	49	15	38	55	24	.	18	38	55	29	20	.	30	.	54	13	75	100	44	27
Cerinthe minor	16	6	24	6	.	36	12	.	6	.	36	.	20	.	10	.	.	.	.	57	44	36
Teucrium chamaedrys	16	4	25	4	5	36	12	.	.	5	36	14	10	.	.	.	8	.	13	43	38	45
Salvia verticillata	27	15	37	15	10	50	24	.	18	10	50	43	10	.	30	.	15	.	38	43	50	64
Stipa pulcherrima	24	15	30	15	.	45	6	8	29	.	45	.	10	8	20	43	.	.	13	57	56	45
Assoc. 2.2.1.1																						
Artemisia absinthium	12	.	21	.	19	21	.	.	.	19	21	.	.	.	.	.	23	13	75	14	.	18
Verbascum cheiranthifolium	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	25	.	.	.
Arenaria graminea	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	25	.	.	.
Chaerophyllum roseum	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	25	.	.	.
Assoc. 2.2.1.2																						
Klasea radiata	8	.	14	.	5	19	.	.	.	5	19	.	.	.	.	.	8	.	.	71	19	.
Linum nervosum	17	6	25	6	5	36	.	15	6	5	36	.	.	15	10	.	8	.	.	100	19	45
Origanum vulgare	13	.	22	.	10	29	.	.	.	10	29	.	.	.	.	.	15	.	13	86	6	36
Onobrychis transcaucasica	19	4	30	4	14	38	12	.	.	14	38	.	20	.	.	.	23	.	13	100	31	27
Thalictrum minus	9	.	16	.	14	17	.	.	.	14	17	.	.	.	.	.	15	13	25	71	.	.
B Campyliadelphus chrysophyllus	4	.	6	.	5	7	.	.	.	5	7	.	.	.	.	.	8	.	.	43	.	.
Helictochloa armeniaca	5	.	8	.	.	12	.	.	.	.	12	.	.	.	.	.	.	.	.	43	6	9
Vicia canescens subsp. variegata	18	6	27	6	14	33	6	.	12	14	33	14	.	.	20	.	23	.	25	86	13	36

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m² (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m² (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m² (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m² (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Rhinanthus subulatus	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Lathyrus latifolius	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Valeriana officinalis aggr.	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Campanula bononiensis	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Melampyrum sp.	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Seseli libanotis	8	.	14	.	14	14	.	.	.	14	14	.	.	.	.	.	15	13	13	57	6	.
Assoc. 2.2.1.4																						
Linum tenuifolium	15	.	25	.	.	38	.	.	.	.	38	.	.	.	.	.	.	.	13	.	44	73
Coronilla coronata	4	.	6	.	.	10	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	36
Asphodeline taurica	4	.	6	.	.	10	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	36
Androsace chamaejasme	4	.	6	.	.	10	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	36
B Hypnum cupressiforme	13	4	19	4	14	21	.	8	6	14	21	.	.	8	.	14	15	13	13	.	.	73
Campanula sibirica	9	6	11	6	.	17	18	.	.	.	17	43	.	.	.	.	.	.	.	.	.	64
Sesleria phleoides	6	2	10	2	5	12	.	8	.	5	12	.	.	8	.	.	8	.	.	.	.	45
Asperula affinis	5	.	8	.	.	12	.	.	.	.	12	.	.	.	.	.	.	.	.	.	6	36
Campanula rapunculoides	11	.	19	.	5	26	.	.	.	5	26	.	.	.	.	.	8	.	13	43	.	64
Pontechium maculatum	7	.	13	.	14	12	.	.	.	14	12	.	.	.	.	.	23	.	.	.	.	45
Fritillaria caucasica	3	.	5	.	.	7	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	27
Differential species in more than one association																						
Arenaria dianthoides	5	.	8	.	14	5	.	.	.	14	5	.	.	.	.	.	.	38	25	.	.	.
Gagea caroli-kochii	5	.	8	.	10	7	.	.	.	10	7	.	.	.	.	.	.	25	38	.	.	.
Silene cephalantha	5	.	8	.	10	7	.	.	.	10	7	.	.	.	.	.	.	25	38	.	.	.
Companion species																						
Thymus kotschyanus	60	66	56	66	48	60	59	69	71	48	60	43	70	69	60	86	31	75	50	71	56	64
Scutellaria orientalis aggr.	54	62	48	62	43	50	71	54	59	43	50	100	50	54	50	71	15	88	50	57	44	55
Koeleria macrantha	52	55	49	55	43	52	59	77	35	43	52	57	60	77	40	29	62	13	38	29	63	64
Elytrigia intermedia aggr.	47	49	46	49	19	60	65	46	35	19	60	71	60	46	50	14	8	38	88	57	44	64
Eryngium billardierei	38	43	35	43	5	50	24	46	59	5	50	14	30	46	60	57	.	13	50	43	69	27
Convolvulus lineatus	36	51	25	51	.	38	71	62	24	.	38	43	90	62	40	.	.	.	25	.	50	55
Medicago sativa	35	34	37	34	14	48	29	46	29	14	48	.	50	46	50	.	15	13	38	71	44	45
Alyssum alyssoides	35	43	29	43	19	33	41	38	47	19	33	43	40	38	40	57	23	13	50	.	56	9
Festuca valesiaca aggr.	35	23	43	23	48	40	41	8	18	48	40	14	60	8	20	14	54	38	75	.	38	45
Euphorbia seguieriana	32	40	25	40	10	33	24	62	41	10	33	43	10	62	50	29	8	13	13	29	56	18
Centaurea ovina aggr.	27	38	19	38	.	29	47	46	24	.	29	.	80	46	30	14	.	.	.	14	56	18
B Syntrichia ruralis	27	21	32	21	24	36	6	31	29	24	36	.	10	31	50	.	23	25	38	57	19	45
Dianthus cretaceus	26	21	30	21	52	19	29	31	6	52	19	14	40	31	.	14	54	50	13	29	6	36
Medicago x varia	26	26	27	26	29	26	41	23	12	29	26	43	40	23	20	.	8	63	13	.	44	27
Ziziphora clinopodioides	25	19	30	19	14	38	24	.	29	14	38	.	40	.	40	14	.	38	13	43	56	27
Hypericum scabrum	25	32	19	32	.	29	41	.	47	.	29	29	50	.	60	29	.	.	13	.	56	18
Leontodon asperrimus	25	13	33	13	33	33	29	.	6	33	33	14	40	.	10	.	23	50	25	14	38	45
Thesium ramosum	22	36	11	36	5	14	53	23	29	5	14	43	60	23	30	29	8	.	13	29	6	18
Plantago lanceolata	22	15	27	15	10	36	35	.	6	10	36	14	50	.	10	.	8	13	63	43	25	27
Onobrychis cornuta	21	19	22	19	.	33	29	8	18	.	33	.	50	8	20	14	.	.	.	29	44	45
Falcaria vulgaris	20	17	22	17	10	29	18	8	24	10	29	14	20	8	40	.	8	13	13	57	38	9

Potential class 1: *Ziziphora tenuior-Stipa arabica* grasslands – Western Asian dry grasslands and xeric thorn cushion communities

Diagnostic species: *Achillea arabica*, *Aegilops cylindrica*, *Agropyron cristatum*, *Allium pseudoflavum*, *Alyssum turkestanicum*, *Androsace maxima*, *Anisantha tectorum*, *Arabis auriculata* aggr., *Arenaria serpyllifolia* aggr., *Artemisia fragrans*, *Asperula arvensis*, *Bromus danthoniae*, *B. japonicus*, *B. squarrosus*, *Centaurea aggregata*, *Chardinia orientalis*, *Crepis sancta*, *Crupina vulgaris*, *Dianthus orientalis*, *Helianthemum ledifolium*, *Helichrysum plicatum*, *Holosteum marginatum*, ***H. umbellatum***, *Marrubium parviflorum*, *Meniocus linifolius*, ***Minuartia hamata***, *Noaea mucronata*, *Poa bulbosa*, *Sideritis montana*, *Stachys inflata*, *S. lavandulifolia*, *Stipa arabica*, *S. capillata*, *S. holosericea*, ***Taeniatherum caput-medusae* subsp. *crinitum***, *Tanacetum aureum*, ***Teucrium capitatum***, *Thymelaea passerina*, ***Xeranthemum squarrosum***, *Ziziphora tenuior*.

Ecology and distribution. Communities of the potential new class occur in the lower elevations in dry conditions and include semi-desert vegetation, xeric thorn-cushion communities, and xeric grasslands. Within Armenia, it is represented by one order and three alliances.

Order 1.1: *Cousinio brachypterae-Stipetalia arabicae* – Western Asian dry grasslands and xeric thorn cushion communities

Diagnostic species: Identical with those of the monotypic class.

Ecology and distribution. Communities of this order are distributed in Transcaucasia and possibly even broader within Western Asia. We expect them to occur throughout Western Asia in dry conditions (semi-deserts, dry steppe-like communities, low-elevation thorn-cushion communities). Also, according to our analysis, communities of this order may occur even in higher elevations on rocky substrates.

Alliance 1.1.1: *Onobrychido michauxii-Stipion capillatae* – Transcaucasian rocky dry grasslands

Diagnostic species: *Astracantha condensata*, *Onobrychis michauxii*, *Salvia aethiopis*, *Stachys lavandulifolia*, *Teucrium capitatum*, *Veronica multifida* (mainly negatively differentiated central alliance).

Ecology and distribution. Communities of this alliance are distributed in higher elevations than those of the other two alliances included in this order. This alliance is a transitional unit between this order and the order *Onobrychido transcaucasicae-Stipetalia pulcherrimae*, comprising Transcaucasian mountain steppes (see below).

1.1.1.1: *Stachys lavandulifolia-Astracantha condensata* community (Figure 7B)

Diagnostic species: *Asperula arvensis*, ***Astracantha condensata***, *Centaurea phrygia* subsp. *abbreviata*, *Crepis ciliata*, *Euphorbia orientalis*, ***Gypsophila elegans***, *Herniaria hirsuta*, *Leptunis trichodes*, *Melica taurica*, *Nepeta racemosa*, *Onobrychis michauxii*, *Onosma setosa*, *Salvia aethiopis*, *Sempervivum transcaucasicum*, ***Stachys lavandulifolia***, *Tanacetum aureum*, *Teucrium orientale*, *Tragopogon dubius*, *Viola occulta*, *Zosima absinthiifolia*.

Structure, ecology and distribution. We sampled this vegetation type in the Gegharkunik (vicinity of the town of Sevan, Shorja) and Vayots Dzor (Hermon, vicinity of Gnishik and Khachik) provinces. These communities were located at the most south-facing rocky slopes with shallow soil and low humus content. The herb layer was sparse and with a high representation of Irano-Turanian species, e.g. *Astracantha condensata*, *A. microcephala*, *Stachys lavandulifolia*, *Teucrium orientale*.

1.1.1.2: *Marrubio parviflorae-Stipetum capillatae* (Figure 7C)

Diagnostic species: *Allium cardiostemon*, *Centaurea ovina* aggr., *Euphorbia condylocarpa*, *Marrubium parviflorum*, *Stipa capillata*.

Structure, ecology and distribution: These communities were sampled on slopes with shallow rocky substrates in Gegharkunik (Ardanish), Lori (near Shirakamut) and Vayots Dzor (vicinity of Gnishik and Khachik) provinces. The association differed by a higher herb layer cover compared to the previous community and the highest participation of hemicryptophytes among all associations of the class. The dominant species were *Festuca valesiaca* aggr., *Onobrychis cornuta* and *Teucrium capitatum*.

Alliance 1.1.2: *Artemision fragrantis* – Transcaucasian wormwood semi-deserts

Diagnostic species: *Agropyron cristatum*, ***Allium pseudoflavum***, *Alyssum turkestanicum*, *Androsace albana*, *Arenaria serpyllifolia* aggr., *Artemisia fragrans*, ***Astragalus hyalolepis***, *Bromopsis riparia*, *Ceratocephala falcata*, ***Cousinia brachyptera***, *Crupina vulgaris*, *Cuscuta araratica*, *Consolida hispanica*, *Didymodon tophaceus* (B), *Meniocus linifolius*, *Minuartia hamata*, ***Noaea mucronata***, *Peganum harmala*, *Polygala hohenackeriana*, *Sclerocaryopsis spinocarpos*, *Syntrichia caninervis* (B).

Ecology and distribution: *Artemisia fragrans* semi-deserts in Armenia are distributed in the lowest elevations in the country. We did not sample other semi-desert types, but we can expect that Armenian loamy and sandy semi-deserts will also be probably included in this unit. In our dataset, this alliance is represented by a single association.

1.1.2.1: *Noaeo mucronatae-Artemisietum fragrantis* (Figure 7D)

Diagnostic species: identical with those of the monotypic alliance.

Structure, ecology and distribution: This association is typical for the Aragatsotn province (vicinity of Dashtadem and Tatool). The sampled plots were distributed at the lowest elevations with the highest mean annual temperature and lowest mean annual precipitation compared to the other studied associations. The communities were dominated by *Artemisia fragrans*, *Poa bulbosa*, and *Taeni-*

atherum caput-medusae subsp. *crinitum*. The herb layer is relatively sparse and with a high representation of therophytes (e.g. *Alyssum turkestanicum*, *Bromus squarrosus*, *Ceratocephala falcata*, *Crupina vulgaris*, *Sclerocaryopsis spinocarpos*) and characteristic chamaephytes (*Artemisia fragrans*, *Noaea mucronata*).

Alliance 1.1.3: *Acantholimono caryophyllacei-Stipion holosericeae* – Transcaucasian dry grasslands and xeric thorn-cushion communities

Diagnostic species: *Acantholimon vedicum*, *Aegilops cylindrica*, *Aethionema carneum*, *Arabis auriculata* aggr., *Bromus japonicus*, *Bunium microcarpum*, *Chardinia orientalis*, *Crepis sancta*, *Crupina vulgaris*, *Ephedra procera*, *Galium verticillatum*, *Gaudiniopsis macra*, *Helianthemum ledifolium*, *Noccaea perfoliata*, *Papaver minus*, *Roemeria hybrida*, ***Stachys inflata***, *Stipa arabica*, *S. holosericea*, *Taeniatherum caput-medusae* subsp. *crinitum*, *Petrorhagia cretica*, *Ziziphora tenuior*.

Ecology and distribution: This unit comprises vegetation traditionally known as 'highland xerophytic vegetation'. It includes dry grasslands and xeric tragacanth communities distributed above the semi-desert belt and below the mountain steppe altitudinal belt. We distinguish one association and one community within this alliance.

1.1.3.1: *Acantholimono caryophyllacei-Stipetum holosericeae* (Figure 7E)

Diagnostic species: *Acantholimon caryophyllaceum*, *Aegilops triuncialis*, *Carduus hamulosus*, *Crepis sancta*, *Geranium lucidum*, *Lomelosia rotata*, *Noccaea annua*, *Stipa zalesskii* subsp. *pontica*, *Torilis arvensis*, *Xeranthemum squarrosum*.

Structure, ecology and distribution: We sampled this association mainly in the Vayots Dzor province (Hermon, vicinities of Areni, Gnishik and Khachik), and also in one locality in Aragatsotn province (near Tatool). The communities were distributed on shallow soils, but with higher humus content and lower gravel cover compared to the other associations of this class. *Acantholimon caryophyllaceum*, *Stipa holosericea*, and *Taeniatherum caput-medusae* subsp. *crinitum* are the dominant species in this association. Among other species, Irano-Turanian elements often occur, such as *Achillea arabica*, *Eryngium billardierei*, *Hypericum scabrum*, and *Thymus kotschyanus*.

1.1.3.2: *Stachys inflata-Acantholimon vedicum* community (Figure 7F)

Diagnostic species: ***Acantholimon vedicum***, *Aegilops biuncialis*, *A. cylindrica*, ***Aethionema carneum***, *Androsace maxima*, ***Arabis auriculata* aggr.**, *Artemisia fragrans*, *Aspicilia hispida* (L), *Astragalus ornithopodioides*, ***Bunium microcarpum***, *Callipeltis cucullaria*, *Camelina laxa*, *Chardinia orientalis*, *Cousinia daralaghezica*, *Crossidium squamiferum* (B), *Crucianella exasperata*, *Crupina vulgaris*, *Cuscuta pedicellata*, ***Ephedra procera***, *Galium verticillatum*, ***Gaudiniopsis macra***, ***Helianthemum ledifolium***, *Holosteum marginatum*, *Lactuca tuberosa*, *Lamium amplexicaule*, *Onobrychis atropatana*, ***Papaver minus***, ***Petrorhagia cretica***, ***Stachys inflata***, *Stipa arabica*, *Tanacetum aureum*, *Trinia glauca*, *Valerianella coronata*, *Ziziphora tenuior*.

Structure, ecology and distribution: We sampled this vegetation type in Ararat (vicinity of Tigranashen) and Vayots Dzor (vicinity of Gnishik) provinces. Communities were distributed at lower elevations with high mean annual temperature and low mean annual precipitation. The substrate differed by the most alkaline soil reaction (mean pH: 8). The herb layer was sparse and with a high representation of Irano-Turanian and Mediterranean therophyte species (*Aegilops* spp., *Crupina vulgaris*, *Petrorhagia cretica*, *Ziziphora tenuior*), while the cover of hemicryptophytes was the lowest among all studied communities. These communities did not have clear dominants, but *Chardinia orientalis*, *Stachys inflata*, *Stipa arabica*, and *S. sareptana* subsp. *anisotricha* occurred with higher cover than the other species. The species richness of vascular plants, bryophytes and lichens was higher compared to the other associations of the class.

Class 2: *Festuco-Brometea* – Mesoxeric and xeric basiphilous grasslands of temperate Europe and adjacent regions

Diagnostic species: *Abietinella abietina* (B), ***Achillea millefolium* aggr.**, *Artemisia absinthium*, *Bupleurum falcatum* aggr., *Campanula glomerata* aggr., *C. rapunculoides*, *C. stevenii*, *Cirsium leucocephalum*, ***Dactylis glomerata***, *Galium verum*, *Koeleria albovii*, *Leontodon hispidus*, *Linum nervosum*, *L. tenuifolium*, ***Lotus corniculatus***, *Onobrychis transcaucasica*, *Origanum vulgare*, *Phleum phleoides*, *Pimpinella saxifraga* aggr., *Plantago atrata*, *Poa pratensis* aggr., *Polygala anatolica*, *Polygonum cognatum*, *Potentilla recta* aggr., *Scabiosa bipinnata*, *Securigera varia*, *Stachys macrostachys*, *Taraxacum* sect. *Taraxacum*, *Thalictrum minus*, *Trifolium alpestre*, *T. ambiguum*, *T. trichocephalum*, *Trisetum flavescens*.

Ecology and distribution: Within Armenia, this class comprises meso-xeric grasslands and mountain steppes at higher elevations. We distinguish two orders representing different altitudinal belts.

Order 2.1: *Plantagini atratae-Bromopsietalia variegatae* – High-mountain meso-xeric grasslands of the Caucasus

Diagnostic species: *Achillea millefolium* aggr., *Ajuga orientalis*, *Alchemilla sericea*, *Arenaria blepharophylla* aggr., *A. gypsophiloides*, *Aster alpinus*, *Brachypodium pinnatum*, ***Bromopsis variegata***, *Campanula collina*, ***C. stevenii***, *Cirsium leucocephalum*, *Festuca ovina* aggr., *Schedonorus pratensis*, *Festuca rubra* aggr., *Filipendula vulgaris*, *Gagea glacialis*, *Galium cordatum*, *Gentiana septemfida*, *Huynhia pulchra*, ***Koeleria albovii***, *Lathyrus digitatus*, *Lomelosia caucasica*, *Lotus corniculatus*, *Luzula multiflora*, *Medicago papillosa*, *Muscari armeniacum*, ***Myosotis alpestris***, *Ornithogalum sigmoideum*, *Papaver orientale*, *Pedicularis condensata*, *Phleum alpinum*, *Pilosella officinarum* aggr., *Pimpinella saxifraga* aggr., ***Plantago atrata***, *Poa pratensis* aggr., *Pohlia nutans* (B), *Polygonum cognatum*, *Potentilla argentea*, *Psephellus xanthocephalus*, *Pseudoleskella tectorum* (B), *Pulsatilla albana*, *Ranunculus caucasicus*, *Rumex acetosella*, *Senecio pseudo-orientalis*, *Stachys macrantha*, *Stipa tirsa*, *Taraxacum* sect. *Taraxacum*, *Thymus collinus*, *Tortula acaulon* (B), ***Trifolium ambiguum***, *T. spadiceum*, ***T. trichocephalum***, *Verbascum speciosum*, *Veronica denudata*, *V. gentianoides.*

Ecology and distribution: Communities of this order occupy the highest sampled elevations in Armenia: upper subalpine and lower alpine belts. They form a particular unit recognized in the dominant approach typology: mountain meadow steppes. Beyond this elevation belt, they are replaced by the alpine grasslands which possibly belong to the class *Juncetea trifidi* Hadač in Klika et Hadač 1944 (*Festucetalia woronowii* Tsepkova 1987).

Alliance 2.1.1: *Artemisio chamaemelifoliae-Bromopsion variegatae* – Caucasian subalpine and lower-alpine meso-xeric grasslands

Diagnostic species: *Achillea millefolium* aggr., *Alchemilla sericea*, *Arenaria gypsophiloides*, *Bromopsis variegata*, *Campanula collina*, ***C. stevenii***, *Festuca ovina* aggr., *F. rubra* aggr., *Huynhia pulchra*, *Koeleria albovii*, *Lathyrus digitatus*, *Lomelosia caucasica*, *Lotus corniculatus*, *Myosotis alpestris*, ***Plantago atrata***, *Polygonum cognatum*, *Potentilla argentea*, *Ranunculus caucasicus*, *Taraxacum sect. Taraxacum*, ***Trifolium ambiguum***, ***T. trichocephalum***, *Veronica denudata*, *V. gentianoides.*

Ecology and distribution: This unit was described from the Main Range of the North Caucasus (Vynokurov et al. 2021) in the elevations of 1,800–2,200 m a.s.l. In Armenia, it occurs mainly higher than 2,000 m a.s.l., and shares multiple species with the Northern Caucasus unit. Thus, we are classifying mountain meadow steppes of Armenia within the same alliance. Here we distinguish one association and one informal community within it.

2.1.1.1: *Ranunculo caucasici-Bromopsietum variegatae* (Figure 8A)

Diagnostic species: ***Alchemilla sericea***, *Arenaria blepharophylla* aggr., *Artemisia chamaemelifolia*, *Aster alpinus*, *Avenula pubescens*, *Brachypodium pinnatum*, *Bromopsis variegata*, ***Campanula collina***, *C. stevenii*, *Carex caryophyllea*, *Cirsium leucocephalum*, *Schedonorus pratensis*, *Galium cordatum*, ***Huynhia pulchra***, ***Lomelosia caucasica***, *Luzula multiflora*, *Medicago papillosa*, *Muscari armeniacum*, *Myosotis alpestris*, *Pedicularis condensata*, *Phascum cuspidatum* (B), *Phleum alpinum*, *Pilosella officinarum* aggr., *Pimpinella saxifraga* aggr., *Plantago atrata*, *Polygonum cognatum*, *Psephellus xanthocephalus*, *Pulsatilla albana*, ***Ranunculus caucasicus***, *Rumex acetosella*, *Stachys macrantha*, *Stipa tirsa*, *Tragopogon graminifolius*, *Trifolium trichocephalum*, *Veronica gentianoides.*

Structure, ecology and distribution: We sampled this vegetation type at the steep north-facing slopes at elevations around 2,100 m, mainly in the Shirak province (vicinities of Amasia and Zorakert), and also in Gegharkunik province (Ardanish). The localities were characterised by a high mean annual precipitation (around 700–900 mm). The soil reaction was slightly acidic (mean pH: 6.5). The association differed by high species richness and the highest participation of Caucasian species, e.g. *Dianthus cretaceus*, *Lomelosia caucasica*, *Stachys macrantha*, and *Trifolium trichocephalum*, among all studied communities. Graminoids were dominant, particularly *Brachypodium pinnatum*, *Bromopsis variegata*, *Carex humilis*, and *Phleum alpinum*.

2.1.1.2: *Tragopogon reticulatus-Astracantha aurea community* (Figure 8B)

Diagnostic species: *Arenaria dianthoides*, *A. gypsophiloides*, *Astracantha aurea*, *Campanula stevenii*, *Elytrigia repens*, *Gagea glacialis*, *Koeleria albovii*, *Lathyrus digitatus*, *Papaver orientale*, *Plantago atrata*, *Senecio pseudo-orientalis*, *Tragopogon reticulatus*, ***Trifolium ambiguum***, *T. spadiceum*, *Trisetum flavescens*, *Verbascum speciosum.*

Structure, ecology and distribution: We sampled this community mainly in the Gegharkunik province (Selim pass), and also in the Aragatsotn province (near the fortress of Amberd). Most of the localities were situated at 2,300–2,400 m a.s.l. and represented the highest elevations among all studied sites. The soil reaction was slightly acidic. These communities are characterised by low species richness with a high participation of Transcaucasian and Caucasian species, e.g. *Arenaria dianthoides*, *Astracantha aurea*, *Koeleria albovii*. *Festuca ovina* aggr. and *Plantago atrata* were the dominant species.

Order 2.2: *Onobrychido transcaucasicae-Stipetalia pulcherrimae* – Transcaucasian mountain steppes

Diagnostic species: *Artemisia absinthium*, *Bupleurum falcatum* aggr., *Campanula glomerata* aggr., *C. rapunculoides*, *Cerinthe minor*, *Dactylis glomerata*, *Euphrasia pectinata*, *Galium verum*, *Globularia trichosantha*, *Helictochloa armeniaca*, *Hypericum perforatum*, *Klasea radiata*, *Linum nervosum*, *L. tenuifolium*, *Lotus corniculatus*, *Nepeta nuda*, *Onobrychis transcaucasica*, *Origanum vulgare*, *Phlomis tuberosa*, *Polygala anatolica*, *Rosa spinosissima*, *Salvia verticillata*, *Scabiosa bipinnata*, *Securigera varia*, *Stachys macrostachys*, *S. recta*, *Stipa pennata*, *S. pulcherrima*, *Teucrium chamaedrys*, *Thalictrum minus*, *Vicia canescens* subsp. *variegata*, *Viola ambigua.*

Ecology and distribution: Mountain steppes in the Transcaucasus form a distinct altitudinal belt above highland xerophyte vegetation (*Cousinio brachypterae-Stipetalia arabicae*) and below mountain meadow steppes (*Plantagini atratae-Bromopsietalia variegatae*). In our dataset, the order is represented by one alliance.

Alliance 2.2.1: *Onobrychido transcaucasicae-Stipion pulcherrimae* – Transcaucasian mountain steppes

Diagnostic species: *Campanula rapunculoides*, *Cerinthe minor*, *Dactylis glomerata*, *Linum nervosum*, *L. tenuifolium*, *Onobrychis transcaucasica*, *Origanum vulgare*, *Scabiosa bipinnata*, *Securigera varia*, *Stachys macrostachys*, *S. recta.*

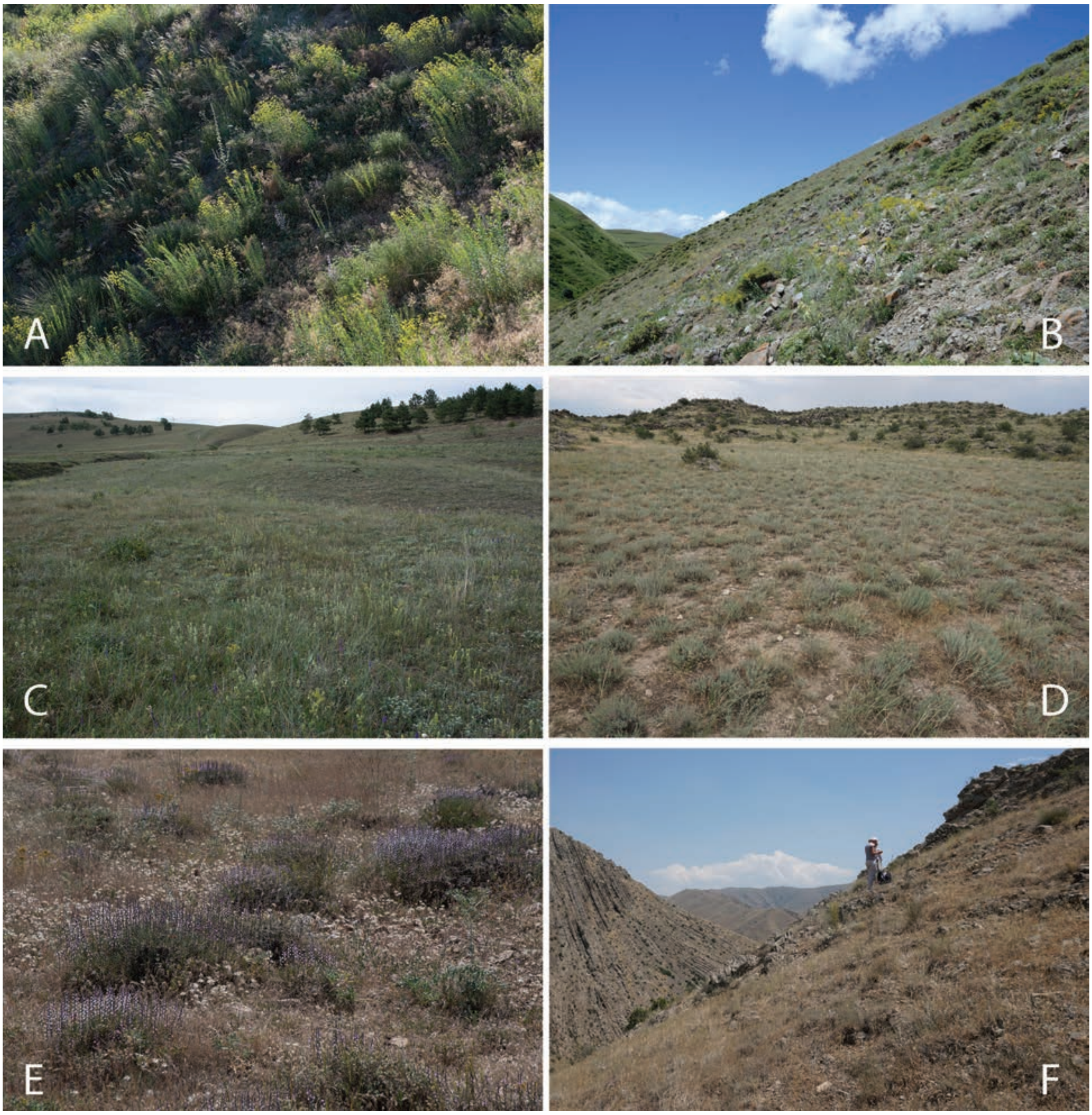

Figure 7. Dry grassland and thorn-cushion communities of Armenia that do not belong to the *Festuco-Brometea*. **A.** *Euphorbia orientalis-Melilotus officinalis* scree community near Hermon (Vayots Dzor Province); **B.** *Stachys lavandulifolia-Astracantha condensata* community (alliance 1.1.1); **C.** *Marrubio parviflorae-Stipetum capillatae* (alliance 1.1.1); **D.** Semi-deserts of the association *Noaeo mucronatae-Artemisietum fragrantis* (alliance 1.1.2); **E.** Highland xerophytic vegetation of the *Acantholimono caryophyllacei-Stipetum holosericeae* (alliance 1.1.3); **F.** *Stachys inflata-Acantholimon vedicum* community (alliance 1.1.3) (Photos: A, C, E: Jürgen Dengler; B: Thomas Becker; D: Denys Vynokurov; F: Dariia Borovyk).

Ecology and distribution: Despite its high floristic heterogeneity, we unite all mountain steppes into one alliance. We distinguish two informal communities and two associations.

2.2.1.1: *Trisetum flavescens-Stachys macrostachys* community (Figure 8C)
Diagnostic species: *Arenaria graminea*, *Artemisia absinthium*, *Chaerophyllum roseum*, *Gagea caroli-kochii*, *Silene cephalantha*, ***Stachys macrostachys***, *Trisetum flavescens*, *Verbascum cheiranthifolium.*

Structure, ecology and distribution: We sampled this vegetation type at the elevations 1,950–2,300 m a.s.l. in Aragatsotn (near Amberd fortress), Gegharkunik (Selim pass, Shorja) and Shirak (vicinity of Amasia) provinces. These communities develop on soils with high humus content. The herb layer is relatively dense with dominance of grasses (*Elytrigia intermedia* aggr., *Phleum nodosum*, *Poa pratensis* aggr., *Trisetum flavescens*) and legumes (*Securigera varia*, *Trifolium alpestre*, *Vicia tenuifolia* subsp. *variabilis*, *V. canescens* subsp. *variegata*).

2.2.1.2: *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* community (Figure 8D)

Diagnostic species: *Arabis hirsuta*, *Campanula bononiensis*, *Campyliadelphus chrysophyllus* (B), *Chaerophyllum aureum*, *Daphne oleoides* subsp. *kurdica*, *Helictochloa armeniaca*, ***Klasea radiata***, *Lathyrus latifolius*, ***Linum nervosum***, *Nepeta nuda*, ***Onobrychis transcaucasica***, ***Origanum vulgare***, *Phlomis tuberosa*, *Primula veris* subsp. *macrocalyx*, *Rhinanthus subulatus*, *Salvia nemorosa*, *Securigera varia*, *Seseli libanotis*, *Stachys macrostachys*, *Stipa zalesskii* subsp. *canescens*, ***Thalictrum minus***, *Valeriana officinalis* aggr., *Vicia canescens* subsp. *variegata*, *Viola ambigua*.

Structure, ecology and distribution: We recorded relevés of this community only in the Vayots Dzor province, at north-facing slopes (inclination 10–40°) in the vicinity of Gnishik and between Khachik and Areni. Communities differed by closed herb layer and high litter cover. The species composition is characterised by a high participation of forbs with European distribution, such as *Campanula bononiensis*, *Klasea radiata*, and *Securigera varia*. The dominant species is *Vicia canescens* subsp. *variegata*.

2.2.1.3: *Globulario trichosanthae-Stipetum pulcherrimae* (Figure 8E)

Diagnostic species: central association (no diagnostic species)

Structure, ecology and distribution: We sampled this vegetation type at elevations around 1,900–2,200 m a.s.l. in the provinces of Gegharkunik (Ardanish and vicinity of the town of Sevan), Shirak (Jajur pass) and Vayots Dzor (vicinities of Gnishik, Khachik and Areni). In the species composition, prevailing groups of species were European (*Potentilla recta* aggr., *Stachys recta*, *Stipa pulcherrima*) and Irano-Turanian (*Eryngium billardierei*, *Onobrychis michauxii*, *Thymus kotschyanus*, *Ziziphora clinopodioides*), followed by Caucasian endemics (*Astragalus cancellatus*, *Centaurea pseudoscabiosa*, *Scabiosa bipinnata*). The dominant species of the association was *Stipa pulcherrima*.

2.2.1.4: *Seslerio phleoidis-Onobrychidetum cornutae* (Figure 8F)

Diagnostic species: *Abietinella abietina* (B), *Adonis volgensis*, *Androsace chamaejasme*, *Asperula affinis*, *Asphodeline taurica*, *Briza media*, *Campanula rapunculoides*, *C. sibirica*, *Coronilla coronata*, *Euphorbia esula* aggr., *Euphrasia pectinata*, *Fritillaria caucasica*, *Homalothecium lutescens* (B), *Hypnum cupressiforme* (B), *Leucanthemum vulgare*, *Linum tenuifolium*, *Pimpinella saxifraga* aggr., *Pinus sylvestris*, *Pontechium maculatum*, *Psephellus karabaghensis*, *Sesleria phleoides*, *Spiraea crenata*, *Thalictrum foetidum*, *Viola alba*.

Structure, ecology and distribution: We sampled this association at elevations 1,940–2,070 m a.s.l. in Gegharkunik (Ardanish, Shorja, vicinity of the town of Sevan) and Shirak (Jajur pass) provinces. The association differed by the highest mean total species richness and richness of bryophytes across all studied communities. The species composition is represented by a high participation of European species of grasses and forbs, such as *Briza media*, *Campanula rapunculoides*, *Galium verum*, *Pimpinella saxifraga* aggr., and *Stachys recta*. *Carex humilis*, *Onobrychis cornuta* and *Teucrium chamaedrys* are the dominant species.

Differentiation of the syntaxa with respect to ecology, structure and biodiversity

Topography, climate and soil

Communities within the *Festuco-Brometea* predominantly thrived at higher elevations, especially those of *Plantagini atratae-Bromopsietalia variegatae*, reaching up to 2,400 m a.s.l. (Figure 9A). Generally, they occurred within the elevation range of 1,900–2,400 m a.s.l., with some exceptions, like in the case of the *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* community, which were found between 1,700 to 2,100 m a.s.l. These low elevation occurrences were compensated by local topographic preferences, particularly avoidance of drier slopes with a southerly aspect. This community exhibited the lowest southerness index among all syntaxa (Figure 9B).

In contrast, communities of the *Ziziphora tenuior-Stipa arabica* grasslands with its order *Cousinio brachypterae-Stipetalia arabicae* occurred at lower elevations, primarily below 2,000 m a.s.l. Among its three alliances, *Artemision fragrantis*, which comprises wormwood semi-deserts, thrived at the lowest altitudes, ranging from 1,300 to 1,600 m a.s.l. Additionally, the *Stachys inflata-Acantholimon vedicum* community, which belongs to the alliance *Acantholimono caryophyllacei–Stipion holosericeae*, also occupied comparably low elevations, at about 1,600 m a.s.l. Other units of this order generally occupy elevations not exceeding 2,000 m a.s.l.

The altitudinal zonation reflected the climatic preferences of the communities. The *Cousinio brachypterae-Stipetalia arabicae* communities tended to prefer warmer and drier conditions, while the class *Festuco-Brometea* thrived in more mesic and cooler environments (Figure 9C, D).

Regarding soil characteristics, most communities preferred neutral or slightly alkaline soils, except for the order *Plantagini atratae-Bromopsietalia variegatae*, which occurred in slightly acidic soil conditions with a pH around 6.5 (Figure 10A). This variation aligns with the altitudinal zonation, reflecting different soil compositions and vegetation types across elevation levels. Lower and medium elevations (montane and lower subalpine belt) were characterised by kastanozems and chernozems, which hosted semi-desert and steppe vegetation, and had neutral or slightly alkaline reaction. We classified them within the orders *Cousinio brachypterae-Stipetalia arabicae* and *Onobrychido transcaucasicae-Stipetalia pulcherrimae* respectively. Upper subalpine and lower alpine belts were home to meadow-steppe soils and mountain-meadow soils, which were characterised by slightly acidic to acidic reaction. Here, mountain meadow steppe vegetation thrived, which we summarised in the order *Plantagini atratae-Bromopsietalia variegatae*. At even higher altitudes, mountain steppes were replaced by acidophilous alpine grasslands, which were not covered in our study.

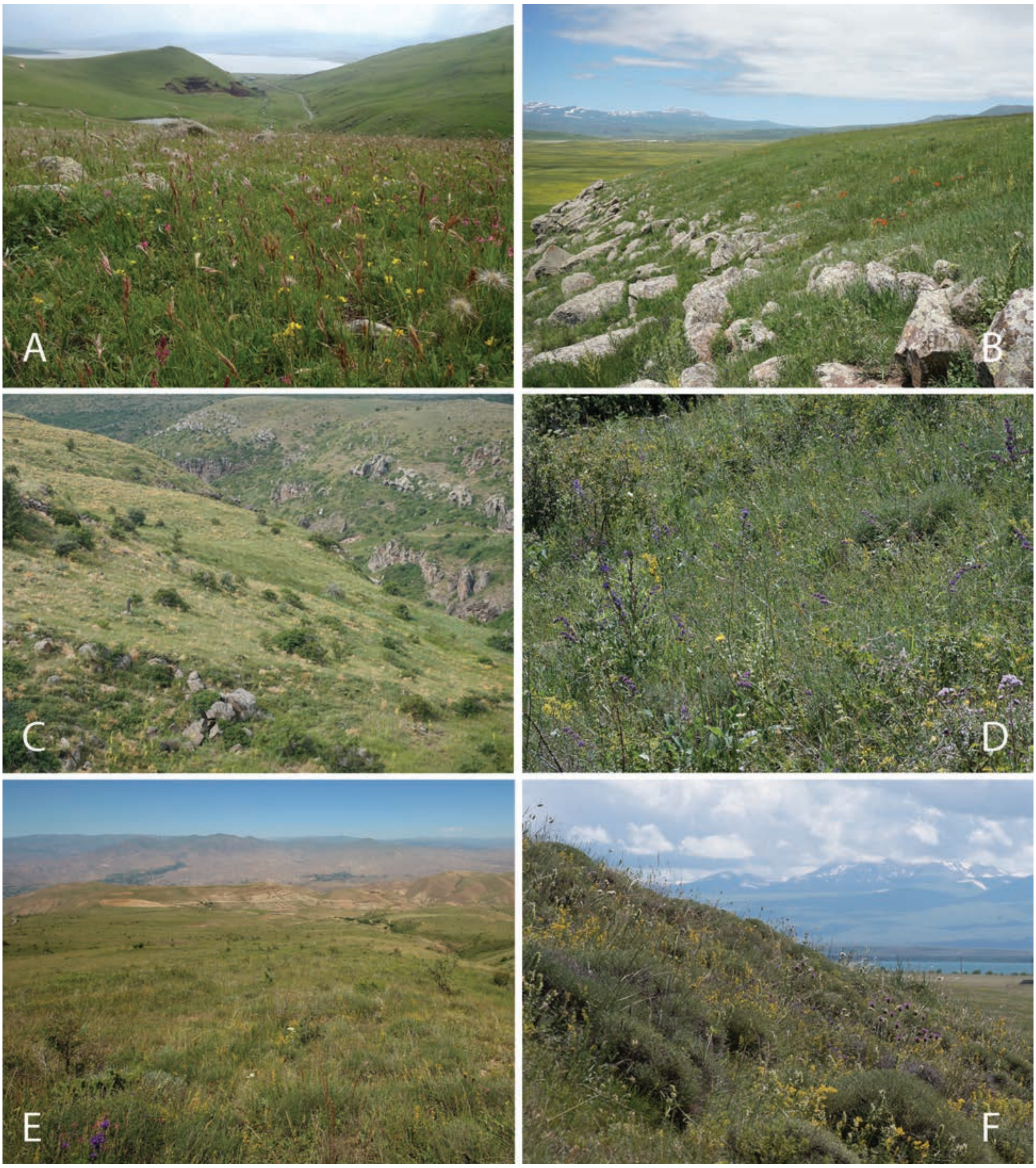

Figure 8. Dry grasslands of Armenia classified within the *Festuco-Brometea*. **A.** Mountain meadow steppes in the Lake Arpi National Park with the association *Ranunculo caucasici-Bromopsietum variegatae* (alliance 2.1.1); **B.** *Tragopogon reticulatus-Astracantha aurea* community (alliance 2.1.1); **C.** *Trisetum flavescens-Stachys macrostachys* community (alliance 2.2.1); **D.** *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* community (alliance 2.2.1); **E.** *Globulario trichosanthae-Stipetum pulcherrimae* (alliance 2.2.1); **F.** mountain steppes near the Sevan Lake with the association *Seslerio phleoidis-Onobrychidetum cornutae* (alliance 2.2.1). (Photos: A: Philipp Kirschner; B, C: Dariia Borovyk; D, F: Jürgen Dengler; E: Denys Vynokurov).

In terms of skeleton content, communities of the *Ziziphora tenuior-Stipa arabica* grasslands generally tended to occur on sites with shallower soils and higher skeleton content (Figure 10B, C). Among them, *Stachys lavandulifolia-Astracantha condensata* community and *Stachys inflata-Acantholimon vedicum* community represent rocky grasslands, and occurred on sites with the highest proportion of gravel in the upper soil level, reaching up to 80% and 90% respectively. Among the communities classified into the class *Festuco-Brometea*, we observed higher heterogeneity. Both units of the order *Plantagini atratae-Bromopsietalia variega-*

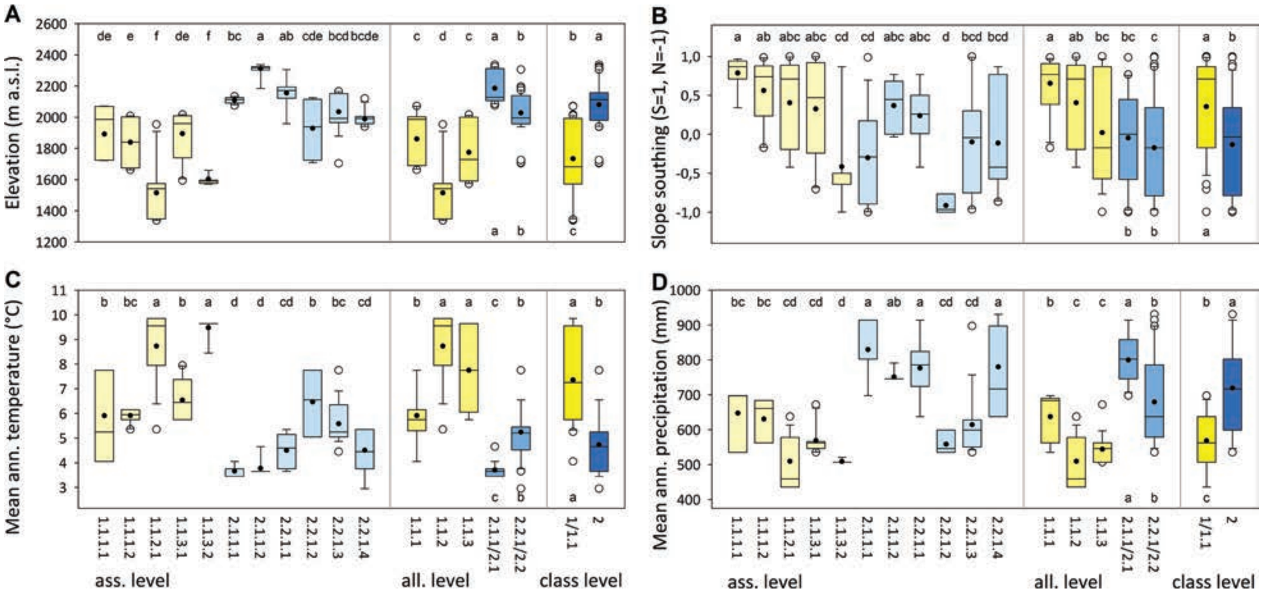

Figure 9. Site characteristics of the grassland types at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

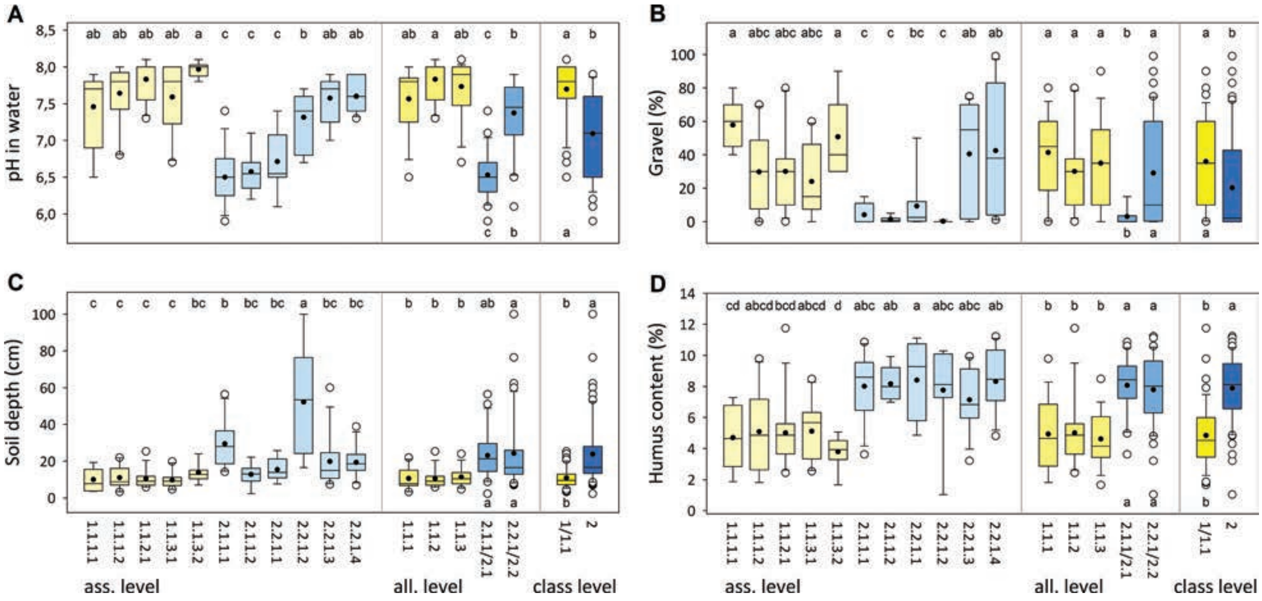

Figure 10. Soil characteristics of the grassland types at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

tae occurred on sites with low gravel content. Among them, *Ranunculo caucasici-Bromopsietum variegatae* was distributed on deeper soils. Mountain steppes of the order *Onobrychido transcaucasicae-Stipetalia pulcherrimae* seemed to occur on sites with varying skeleton proportion. While the *Trisetum flavescens-Stachys macrostachys* and *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* communities occurred on sites with low gravel proportions, the associations *Globulario trichosanthae-Stipetum pulcherrimae* and *Seslerio phleoidis-Onobrychidetum cornutae* were distributed mainly on rocky sites.

All communities of the class *Festuco-Brometea* tended to occur on sites with high humus content, with mean values within a narrow range of 7.5–8.1%. The tentative *Ziziphora tenuior-Stipa arabica* grasslands occurred on sites with significantly lower humus content, with mean values of 3.9–4.5% (Figure 10D).

Structure and species composition

Herb layer cover and litter cover, proxies for ecosystem productivity, were notably higher in the communities belonging to the class *Festuco-Brometea* (Figure 11A, B).

Regarding the dominant life forms, we observed a strong differentiation between the two classes. Communities belonging to the class *Festuco-Brometea* had a significantly higher proportion of hemicryptophytes, which was highest in the case of the *Ranunculo caucasici-Bromopsietum variegatae* association (Figure 11D). On the contrary, communities of the tentative new class '*Ziziphora tenuior-Stipa arabica* grasslands' had much lower proportions of hemicryptophytes, but a much higher proportion of therophytes (Figure 11C). The proportion of therophytes was particularly high in the case of the alliances *Artemision fragrantis* and *Acantholimono caryophyllacei-Stipion holosericeae*, which represent wormwood desert steppes and xerophytic thorn-cushions respectively. The proportion of chamaephytes was also significantly higher in the case of the latter class (not shown).

The proportion of species' range types also showed a strong differentiation between the two classes (Figure 12). The class *Festuco-Brometea* was characterised by a significantly higher proportion of species with European distribution (Figure 12A). This suggests that the class *Festuco-Brometea* comprises exclusively Euro-Siberian steppe vegetation and that its distribution range reaches a limit in Armenia. This is also well reflected by the co-occurrence of two biogeographic regions: the Euro-Siberian and the Irano-Turanian. On the contrary, the new tentative class '*Ziziphora tenuior-Stipa arabica* grasslands' represents communities with a lower presence of species with European distribution, and significantly higher proportions of species with Mediterranean and Irano-Turanian distribution (Figure 12B, E).

The presence of endemic species in the studied communities was also remarkable. While there were no significant differences detected between the two classes concerning narrow Transcaucasian endemics (Figure 12D), a distinct pattern emerged for the broader Caucasian endemics. These species, ranging across the Caucasus region, including the North Caucasus, were more prevalent in the *Festuco-Brometea* compared to the *Ziziphora tenuior-Stipa arabica* grasslands (Figure 12C). Among the two recognized orders of the *Festuco-Brometea*, the proportion of Caucasian endemics was higher in the *Plantagini atratae-Bromopsietalia variegatae*, which comprises mountain meadow steppes of higher elevations. Overall, we observed an increasing proportion of endemic species alongside elevation. Interestingly, the proportion of species with other distribution ranges, namely, broader than the listed above, was also significantly higher in the case of the *Festuco-Brometea* plant communities (Figure 12F).

Plot-scale species richness

Total species richness in 10 m^2 did not differ significantly among the higher syntaxa (Figure 13). At the association level, there was no strong differentiation either, with only the *Ranunculo caucasici-Bromopsietum variegatae* and the *Seslerio phleoidis-Onobrychidetum cornutae* being above average and *Tragopogon reticulatus-Astracantha aurea* community below. For vascular plant species richness, the pattern largely matched that of total species richness, while for lichens there were no significant differences at any level. Only bryophytes showed a weak richness pattern at the order and alliance level, with the monotypic order *Plantagini atratae-Bromopsietalia variegatae* being the richest.

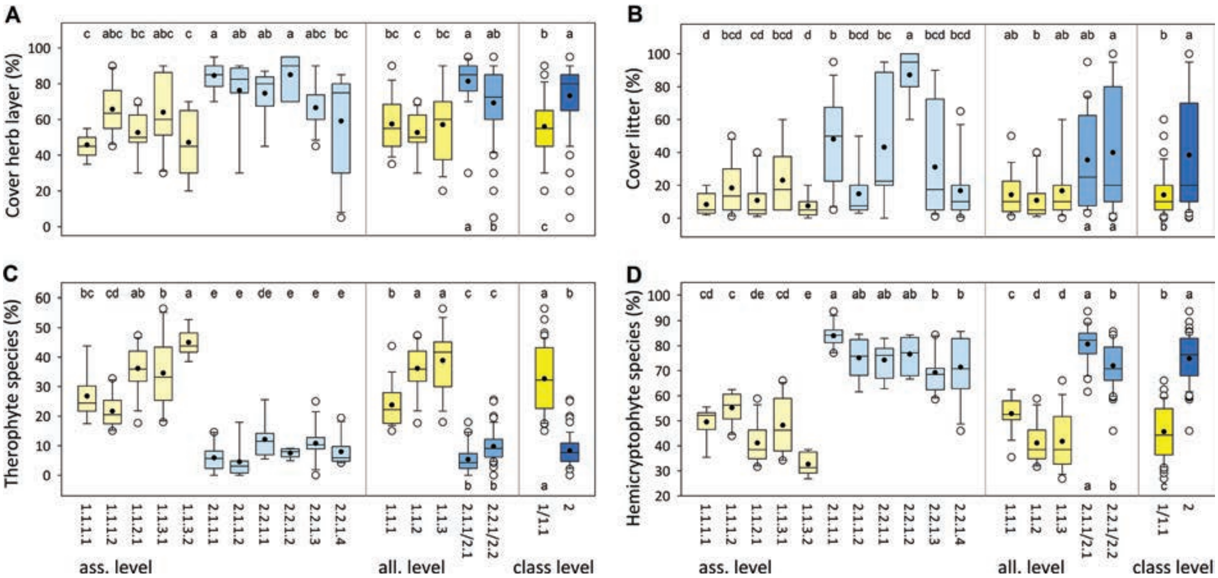

Figure 11. Structure and dominant life forms of the grassland types at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

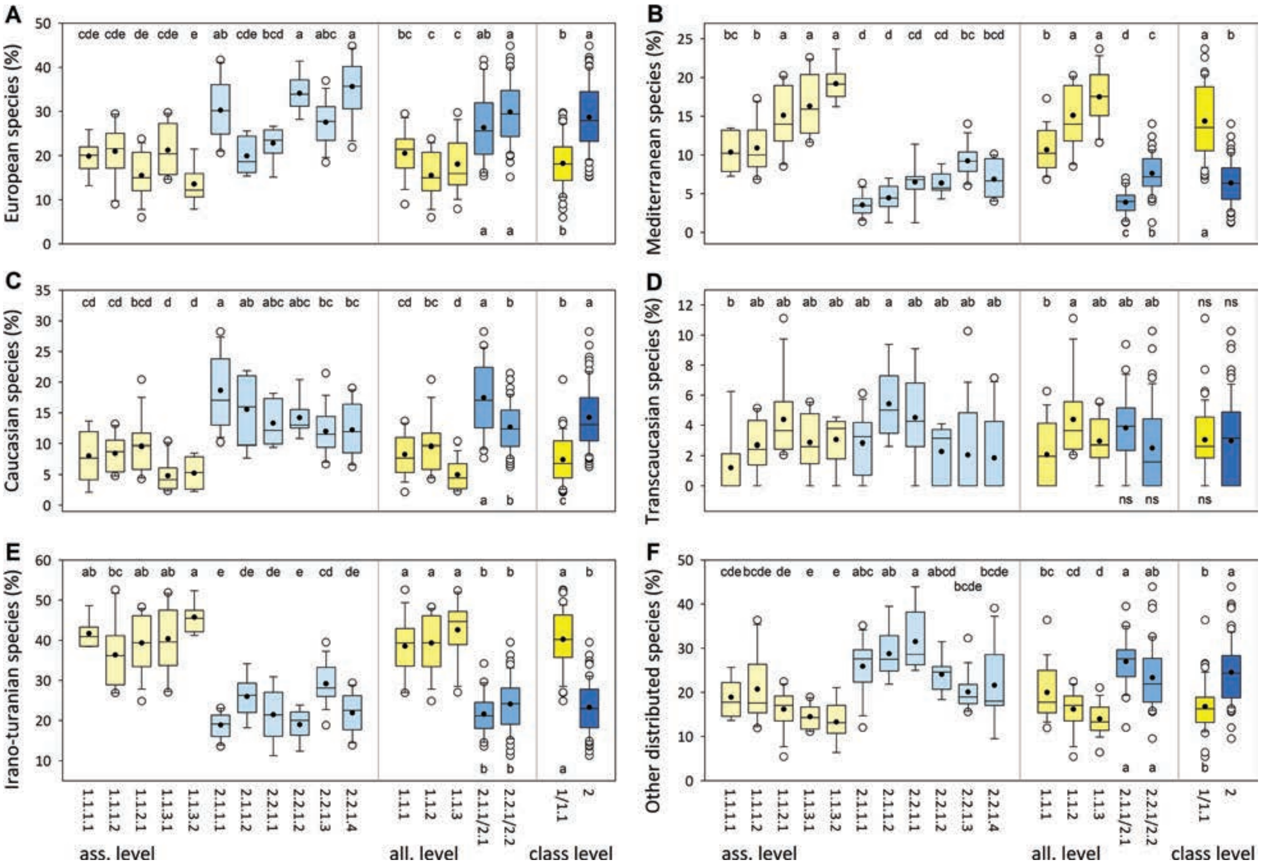

Figure 12. Proportions of range types of the grassland types at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

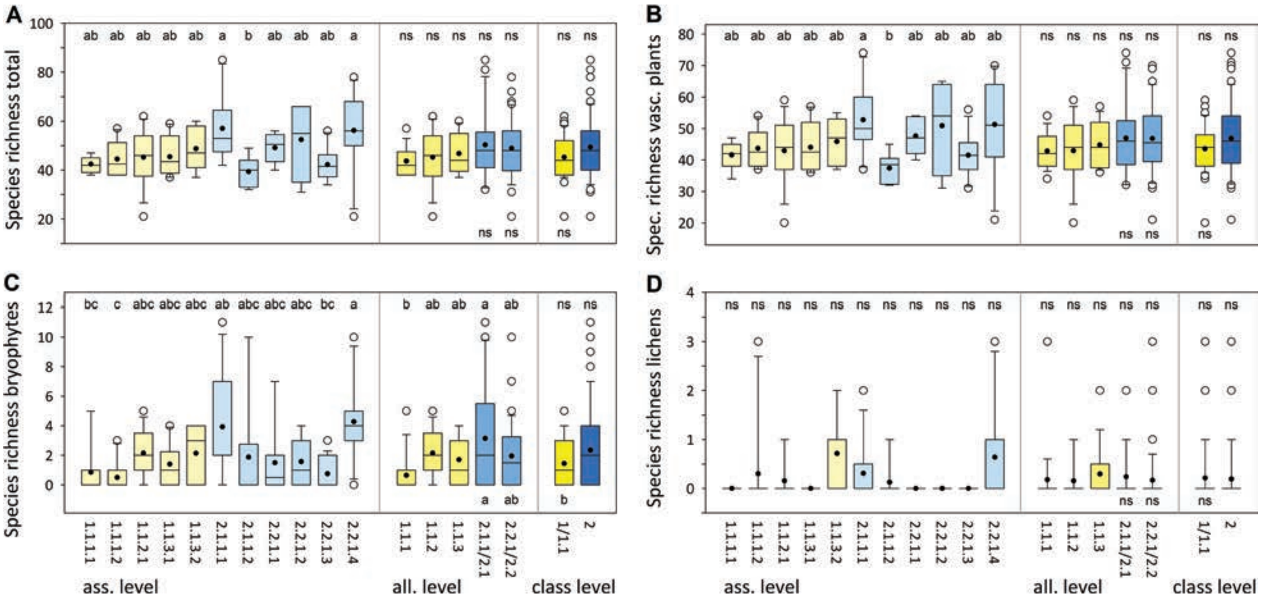

Figure 13. Species richness in 10 m^2-plots for different taxonomic groups compared at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

Discussion

Higher-level units of the dry grasslands and thorn-cushion communities of Armenia

The type of the class *Astragalo-Brometea*, namely the order *Astragalo-Brometalia*, along with other orders traditionally associated with it (*Drabo-Androsacetalia*, *Hyperico linarioidis-Thymetalia scorpilii*, *Onobrychido armenae-Thymetalia leucostomi*), were grouped together as "group A" in the Twinspan analysis (Figure 2). This suggests that these clusters collectively represent the vegetation of the class *Astragalo-Brometea*. Furthermore, although cluster 7 forms a separate group C, it is positioned closer to group A on the DCA ordination. Hence, the order *Festuco oreophilae-Veronicetalia orientalis* may also be considered part of the class *Astragalo-Brometea*, as originally described (Hamzaoğlu 2006). However, more comprehensive data analysis would be needed to clarify if *Festuco oreophilae-Veronicetalia orientalis* belongs to *Astragalo-Brometea* or should form a distinct class uniting Eastern Anatolian tragacanth communities.

Groups B and E comprised plots from meso-xeric, xeric, and rocky grasslands that can be categorised as belonging to the class *Festuco-Brometea*. Whereas plots within group E were previously assigned to order-level units (*Asphodelino tauricae-Euphorbietalia petrophilae*, *Festucetalia valesiacae*, *Brachypodietalia pinnati*), group B did not have any assignments to any syntaxonomic order. Considering the clear separation between group B and group E at the very basis of the dendrogram, and the fact that group B is, in contrast to group E, positioned above the Y-axis in the DCA ordination (Figure 3), we propose establishing a distinct order-level unit for group B. This unit would encompass high-mountain xero-mesic meadow-steppe grassland communities found in the Caucasus, Eastern Anatolia, and Northern Iran, and we suggest naming it "*Plantagini atratae-Bromopsietalia variegatae*" (see below).

Group D encompasses the driest communities sampled in Armenia, particularly cluster 8. The species present in this group are predominantly distributed in the Irano-Turanian region, such as *Artemisia fragrans*, *Eryngium billardierei*, *Noaea mucronata*, *Stipa arabica*, *S. holosericea*, and others. This species composition suggests that similar vegetation types may also exist in other regions of Western Asia. Since there is no suitable class-level unit available, we propose that in the future, a new class should be established. To do so a comprehensive comparison involving more data from the surrounding regions would be needed. For now, in this paper, we refer to this unit as "*Ziziphora tenuior-Stipa arabica* grasslands", combining the dry grassland, semi-desert and xeric thorn-cushion vegetation of Western Asia.

To summarise, we can classify all the vegetation plots of the bigger dataset into three classes: *Astragalo-Brometea* (groups A and C), *Festuco-Brometea* (groups B and E), and a tentative new class, "*Ziziphora tenuior-Stipa arabica* grasslands". This was well supported by the DCA ordination (Figure 3), in which the plots categorised as *Festuco-Brometea* were positioned to the right of the Y-axis, while *Astragalo-Brometea* was positioned on the bottom-left corner of the plot, and "*Ziziphora tenuior-Stipa arabica* grasslands" on the upper-right corner. The chorological analysis (Figure 12) suggests that the "*Ziziphora tenuior-Stipa arabica* grasslands" are an Irano-Turanian vegetation type and may be found in other parts of this region, especially in Western Asia.

Lower-level syntaxonomic units

We can identify two distinct vegetation classes in Armenia: *Festuco-Brometea* and a novel class meant to encompass drier grasslands and thorn-cushion communities found at lower elevations. This finding aligns well with the outcomes of the TWINSPAN analysis of the Armenian plots (Figure 4).

Cluster X in the TWINSPAN dendrogram corresponds to scree vegetation that currently cannot be assigned to any existing vegetation class. It appears to be similar to the *Thlaspietea rotundifolii* Br.-Bl. 1948 from temperate Europe or *Drypidetea spinosae* Quézel 1964 from the Mediterranean. In the North Caucasus, a class of high-altitude scree vegetation on siliceous outcrops, *Lamio tomentosi-Chaerophylletea humilis* Belonovskaya et al. 2014, exists. However, the latter mainly consists of subnival belt vegetation with a completely different floristic composition. Therefore, we cannot currently assign the aforementioned Armenian scree community to any existing class and leave it unassigned.

The remaining clusters in the left part of the dendrogram (clusters 1.1.1.1–1.1.3.2 in Figure 4) can be linked to the proposed new class, informally named '*Ziziphora tenuior-Stipa arabica* grasslands'. The clusters on the right side of the dendrogram (clusters 2.1.1.1–2.2.1.4) are clearly associated with the class *Festuco-Brometea*.

Further examination of the drier part of Armenian plots (clusters 1.1.1.1–1.1.3.2 on the dendrogram, Figure 4) revealed three distinct units corresponding to alliance-level syntaxa. Cluster 1.1.1.1 represented rocky grasslands, cluster 1.1.1.2 consisted of dry grasslands at higher elevations with Irano-Turanian influences, and cluster 1.1.2.1 was related to stony semi-deserts. Clusters 1.1.3.1 and 1.1.3.2 correspond to 'highland xerophytic vegetation' or Minor-Asian thorny-cushion shrubs (as per Makagian 1941). We propose interpreting these units as five associations and communities within three different alliances and one order.

Relevés from clusters 2.1.1.1–2.1.1.2 were previously categorized under group B in the earlier section (broad-scale comparison), together with plots from the North Caucasus belonging to the alliance *Artemisio chamaemelifoliae-Bromopsion variegatae*. Given their separation from the other clusters at a high level (Figure 2), we suggest uniting clusters 2.1.1.1–2.1.1.2 into a new order-level unit named *Plantagini atratae-Bromopsietalia variegatae* (see below). This new order is ecologically similar to the *Brachypodietalia pinnati* Korneck 1974 nom. cons. propos. (Willner et al. 2019; Dengler and Willner 2023). Both unite meso-xeric grasslands and share several common diagnostic species, such as *Brachypodium pinnatum*, *Filipendula vulgaris*, *Pimpinella saxifraga* aggr., *Stipa tirsa*, as well as several mesophilic species, including *Achillea millefolium* aggr., *Schedonorus pratensis*, *Festuca rubra* aggr., *Lotus corniculatus*, and *Potentilla argentea*. However, the new order is clearly distinguished by the presence of numerous Caucasian endemics and species of Irano-Turanian distribution among the diagnostic species, such as *Bromopsis variegata*, *Campanula collina*, *Gentiana septemfida*, *Huynhia pulchra*, *Koeleria albovii*, *Psephellus xanthocephalus*, *Pulsatilla albana*, *Ranunculus caucasicus*, and others. Additionally, this order is distinguished by the presence of high-mountain species of broader distribution, such as *Aster alpinus*, *Phleum alpinum*, and *Plantago atrata*.

Clusters 2.2.1.1–2.2.1.4 corresponded to the so-called mountain steppes, following the classification of Makagian (1941). These clusters are linked to the class *Festuco-Brometea* within a new order *Onobrychido transcaucasicae-Stipetalia pulcherrimae* and a new alliance *Onobrychido transcaucasicae-Stipion pulcherrimae*, which unite the Transcaucasian mountain steppes.

Biodiversity and ecology of the studied communities

With an average of 46.8 vascular plants in 10 m^2, the dry grasslands of Armenia were significantly richer than the Palaearctic average of the three relevant ecological-physiognomic vegetation types (A.3 - Xeric grasslands and steppes; B.2 - Meso-xeric grasslands; D.3 - Garrigues and thorn-cushion communities) in the high-quality database GrassPlot (v.2.10; https://edgg.org/databases/GrasslandDiversityExplorer; see Biurrun et al. 2021) with 35.8 species. By contrast, bryophytes (0.4 vs. 3.0 species) and lichens (0.1 vs. 0.9 species) were clearly poorer than in dry grasslands elsewhere. The difference is even more pronounced when comparing with the dry grasslands of the central valleys of the Alps, where Bergauer et al. (2022) reported averages of 35.1 vascular plant, 3.9 bryophyte and 1.9 lichen species in the same plot size. For the inneralpine dry grasslands of Austria, Magnes et al. (2021) reported even a slightly lower richness of vascular plants (34.2), but a slightly higher of bryophytes and lichens combined (6.1) than in Switzerland. Thus, it is astonishing why the Armenian dry grasslands deviate so strongly by higher small-scale vascular plant richness and lower bryophyte and lichen richness not only from the Palaearctic average but also from the dry grasslands in the central valleys of the Alps that should share similarities with the central valleys of the Caucasus. One explanation for the higher density of species in Armenia and also in the Italian Apennines (49.5 species in 10 m^2, Filibeck et al. 2018) could lie in the glaciations (Bergauer et al. 2022). While during the Pleistocene the valleys of the Alps were almost entirely filled by glaciers, in the case of the Caucasus and the Apennines only local glaciers on mountain tops occurred (Aseev et al. 1984), which could mean that the vascular plant flora of the Alpine valleys is simply so impoverished that no more species for higher plot-scale richness are available. By contrast, bryophytes and lichens should be much less affected by the glaciations as their spores are so much lighter than seeds of vascular plants, that they hardly suffer from dispersal limitations. One potential explanation for the very low richness of non-vascular taxa in Armenia could be that the majority of bryophyte and lichen taxa is adapted to cooler climate, while the mean annual temperature in Armenia is higher than in the Alps. However, both potential explanations are not much more than speculations at present. Moreover, while essentially in any region where EDGG studied dry grasslands before, the meso-xeric types were much richer at plot scale than the xeric types (Dengler et al. 2012; Magnes et al. 2021), we did not find a significant richness difference between our more xeric class 1 (*Ziziphora tenuior-Stipa arabica* grasslands) and the less xeric class 2 (*Festuco-Brometea*) (Figure 13). All these unexpected patterns and our *ad hoc* explanations call to be tested with a comprehensive dataset that contains standardized richness data for dry grasslands in many different situations in the Palaearctic, such as the GrassPlot database (Dengler et al. 2018).

Conclusions and outlook

Despite having compiled the available vegetation plot data, particularly the type relevés, of the relevant syntaxa described in the other countries of the Caucasus as well as Anatolia and Northern Iran, we found low correspondence of the Armenian dry grassland communities with these. It appears that only one of our five alliances had been described before, the *Artemisio chamaemelifoliae-Brompsion variegatae* from the Northern Caucasus, Russia (Vynokurov et al. 2021). We thus had to describe most of the syntaxa from associations to orders as new to science, and it will be interesting to see whether some of them will also be found in the future in neighbouring countries. To make these findings accessible in the updates of the EuroVegChecklist (Mucina et al. 2016; Preislerová et al. 2022; see https://floraveg.eu/vegetation/), we have prepared an application to the EuroVegChecklist Committee (EVCC) (Suppl. material 8) for consideration (for the procedure, see Biurrun and Willner 2020).

Even at the class level we found that the more xeric dry grassland of the lower elevations in Armenia are floristically so profoundly different from either the Euro-Siberian *Festuco-Brometea* or the Anatolian-Iranian *Astragalo-Brometea* that they might be a class of their own. However, a formal description should wait for a plot-based broad-scale classification of all the dry grasslands in the Caucasus, Anatolia and Northern Iran, similar to the studies of Eastern and Central Europe by Willner et al. (2017, 2019). Such an attempt would be facilitated in the future by the growing Iranian Vegetation Plot database (A. Naqinezhad, pers. comm.), the Turkish Non-Forest database (B. Güler, pers. comm.) and the Transcaucasian Vegetation Database (Novák et al. 2023a). If the "*Ziziphora tenuior-Stipa arabica* grasslands" should turn out to be a valid class also from the supra-national perspective, this would also impact the current European consensus vegetation classification system, which also includes the three South Caucasus countries (EuroVegChecklist; Mucina et al. 2016; with updates at https://floraveg.eu/vegetation/). It would add additional higher-rank syntaxa, but also several species currently considered as sole diagnostic species of the class *Festuco-Brometea* (Mucina et al. 2016) would not be that anymore as they are equally or even more frequent in the *Ziziphora tenuior-Stipa arabica* grasslands, for example, *Stipa capillata* or *Festuca valesiaca* aggr.

Within Armenia, the next logical step would be to compile more plot data of dry grasslands with the same methodology to ensure that the system is complete and all the determined diagnostic species can be confirmed. Then the system could be translated into an electronic expert system that enables the automatic and unequivocal classification of new dry grassland plots (see the example by Garcia-Míjangos et al. 2021). We hope that our pioneer survey will motivate Armenian researchers to apply similar approaches to other main vegetation types to allow comparable diverse analyses as well as the integration into the European habitat classification system EUNIS (Chytrý et al. 2020). While it is still a long way, ultimately a comprehensive plot-based vegetation typology as it exists in other countries of the Western Palaearctic (e.g. Schaminée et al. 1995 et seq.; Berg et al. 2001 et seq.; Chytrý 2007 et seq.) could become a powerful tool for conservation, applied and fundamental research.

Finally, our collected data of biodiversity, species composition and in situ environmental variables are also valuable for broad-scale analyses on biodiversity patterns and their drivers, global change projections and biogeographic analyses. For this purpose, we have already contributed them to the relevant international plot databases, namely EVA (Chytrý et al. 2016), sPlot (Bruelheide et al. 2019) and GrassPlot (Dengler et al. 2018).

Data availability

All original data from Armenia (species composition and header data as well as derived metrics of the plots) are provided in the Supplementary materials of this article.

Author contributions

A.A. and G.F. organised the 13th EDGG Field Workshop in Armenia, and together with A.B., A.H., D.F., D.B, D.V., I.B., I.G.-M., I.V., J.D., M.M., M.O., P.K., S.P., T.B. and U.B. collected the field data. A.A. and G.F. determined vascular plant specimens collected during the Field Workshop, I.D. critical Festuca species, D.B and D.V *Stipa* species, B.C.-M. bryophytes and H.M. lichens. A.B., D.B., D.V., I.B., I.V. and S.P. digitised the field forms and harmonised the data. D.V. performed the literature search and digitised vegetation plots from neighbouring countries. D.V. classified the relevés of the national and the supranational dataset and together with J.D. and developed the classification system for Armenia. J.D. determined the diagnostic species in the Armenian dataset and prepared the synoptic tables. T.B. assigned the life forms; D.V., T.B., and G.F. classified species distribution ranges. D.B. prepared the maps; T.B. performed the ANOVAs and prepared the boxplots and M.M. performed the ordinations. The manuscript was drafted by D.V. and J.D. with significant inputs by A.A., D.B., I.B., I.G.-M. and T.B. All authors checked, improved and approved the manuscript.

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Appendix 1

Formal descriptions of the new syntaxa according to the ICPN

For the diagnostic species we refer to the main text as well as Table 2 and Suppl. material 2.

1.1 *Cousinio brachypterae-Stipetalia arabicae* ord. nov. hoc loco

Holotypus hoc loco: *Artemision fragrantis* Vynokurov et al. 2024 (this paper)

2.1 *Plantagini atratae-Bromopsietalia variegatae* ord nov. hoc loco

Holotypus hoc loco: *Artemisio chamaemelifoliae-Bromopsion variegatae* Vynokurov in Vynokurov et al. 2021 (page 186)

2.2 *Onobrychido transcaucasicae-Stipetalia pulcherrimae* ord. nov. hoc loco

Holotypus hoc loco: *Onobrychido transcaucasicae-Stipion pulcherrimae* Vynokurov et al. 2024 (this paper)

1.1.1 *Onobrychido michauxii-Stipion capillatae* all. nov. hoc loco

Holotypus hoc loco: *Marrubio parviflorae-Stipetum capillatae* Vynokurov et al. 2024 (this paper)

1.1.2 *Artemision fragrantis* all. nov. hoc loco

Holotypus hoc loco: *Noaeo mucronatae-Artemisietum fragrantis* Vynokurov et al. 2024 (this paper)

1.1.3 *Acantholimono caryophyllacei-Stipion holosericeae* all. nov. hoc loco

Holotypus hoc loco: *Acantholimono caryophyllacei-Stipetum holosericeae* Vynokurov et al. 2024 (this paper)

2.2.1 *Onobrychido transcaucasicae-Stipion pulcherrimae* all. nov. hoc loco

Holotypus hoc loco: *Seslerio phleoidis-Onobrychidetum cornutae* Vynokurov et al. 2024 (this paper)

1.1.1.2 *Marrubio parviflorae-Stipetum capillatae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 81 in Suppl. material 2 (original code AMR008); Armenia, Lori Province, vicinity of Shirakamut, 40.85801°N, 44.19223°E, altitude: 1,662 m a.s.l., aspect: 210°, inclination: 40°, 27 June 2019, authors of the relevé: Dieter Frank, Salza Palpurina, Denys Vynokurov. Floristic composition (species sorted by their cover in percent): *Elytrigia intermedia* aggr. 10, *Marrubium parviflorum* 10, *Achillea arabica* 5, *Teucrium polium* 5, *Onobrychis michauxii* 4, *Artemisia austriaca* 3, *Thymus sipyleus* 3, *Medicago x varia* 2, *Cota melanoloma* 1, *Festuca valesiaca* aggr. 1, *Iris pumila* 1, *Isatis steveniana* 1, *Psephellus zuvandicus* 1, *Xeranthemum longepapposum* 1, *Ajuga chamaepitys* subsp. *chia* 0.5, *Asperula arvensis* 0.5, *Dactylis glomerata* 0.5, *Odontarrhena muralis* 0.5, *Stachys recta* 0.5, *Viola ambigua* 0.5, *Holosteum umbellatum* 0.3, *Nonea pulla* 0.3, *Scleranthus annuus* 0.3, *Convolvulus lineatus* 0.2, *Euphorbia condylocarpa* 0.2, *Stipa capillata* 0.2, *Zeravschania pauciradiata* 0.2, *Centaurea ovina* aggr. 0.1, *Salvia nemorosa* 0.1, *Stipa arabica* 0.1, *Thesium arvense* 0.1, *Falcaria vulgaris* 0.01, *Meniocus linifolius* 0.01, *Nepeta racemosa* 0.01, *Noccaea perfoliata* 0.01, *Reseda lutea* 0.01, *Veronica multifida* 0.01, *Viola arvensis* aggr. 0.01.

1.1.2.1 *Noaeo mucronatae-Artemisietum fragrantis* ass. nov. hoc loco

Holotypus hoc loco: plot ID 65 in Suppl. material 2 (original code AM11NE); Armenia, Aragatsotn Province, vicinity of Dashtadem, 40.32428°N, 43.85075°E, altitude: 1,357 m a.s.l., aspect: 265°, inclination: 7°, 29 June 2019, authors of the relevé: Alla Aleksanyan, Jürgen Dengler, Denys Vynokurov. Floristic composition (species sorted by their cover in percent): *Poa bulbosa* 20, *Artemisia fragrans* 17, *Peganum harmala* 10, *Taeniatherum caput-medusae* subsp. *crinitum* 10, *Stipa arabica* 1, *Androsace albana* 0.5, *Koelpinia linearis* 0.5, *Stipa x kolakovskyi* 0.5, *Allium pseudoflavum* 0.2, *Crupina vulgaris* 0.2, *Minuartia hamata* 0.2, *Noaea mucronata* 0.2, *Arenaria serpyllifolia* aggr. 0.1, *Alyssum turkestanicum* 0.1, *Astragalus hyalolepis* 0.1, *Cousinia brachyptera* 0.1, *Erysimum gelidum* 0.1, *Odontarrhena tortuosa* 0.1, *Sclerocaryopsis spinocarpos* 0.1, *Syntrichia caninervis* 0.1, *Xeranthemum squarrosum* 0.1, *Aegilops cylindrica* 0.01, *Ceratocephala falcata* 0.01, *Cota triumfettii* 0.01, *Dianthus crinitus* 0.01, *Draba verna* 0.01, *Euphorbia seguieriana* 0.01, *Helichrysum plicatum* 0.01, *Hohenackeria exscapa* 0.01, *Holosteum umbellatum* 0.01, *Linaria simplex* 0.01, *Medicago medicaginoides* 0.01, *Meniocus linifolius* 0.01, *Minuartia meyeri* 0.01, *Polygala hohenackeriana* 0.01, *Thesium szovitsii* 0.01, *Thymus collinus* 0.01.

1.1.3.1 *Acantholimono caryophyllacei-Stipetum holosericeae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 71 in Suppl. material 2 (original code AMR035); Armenia, Vayots Dzor Province, vicinity of Khachik, 39.659529°N, 45.201325°E, altitude: 2,017 m a.s.l., aspect: 315°, inclination: 9°, 4 July 2019, authors of the relevé: Alla Aleksanyan, Idoia Biurrun, Dariia Borovyk. Floristic composition (species sorted by their cover in percent): *Chardinia orientalis* 35, *Acantholimon caryophyllaceum* 25, *Taeniatherum caput-medusae* subsp. *crinitum* 20, *Poa bulbosa* 15, *Anisantha tectorum* 10, *Syntrichia ruralis* 6, *Eryngium billardierei* 5, *Onobrychis cornuta* 3, *Medicago sativa* 2, *Stipa ehrenbergiana* 0.5, *Stipa holosericea* 2, *Teucrium polium* 2, *Achillea arabica* 0.5, *Convolvulus lineatus* 0.5, *Gagea germainae* 0.5, *Xeranthemum squarrosum* 0.3, *Ziziphora capitata* 0.3, *Centaurea virgata* 0.2, *Hypericum scabrum* 0.2, *Rochelia disperma* 0.2, *Alyssum turkestanicum* 0.1, *Asperula arvensis* 0.1, *Bromus danthoniae* 0.1, *Bromus japonicus* 0.1, *Ceratocephala falcata* 0.1, *Crepis sancta* 0.1, *Euphorbia iberica* 0.1, *Hordeum bulbosum* 0.1, *Marrubium parviflorum* 0.1, *Odontarrhena tortuosa* 0.1, *Potentilla recta* aggr. 0.1, *Thymus kotschyanus* 0.1, *Alyssum alyssoides* 0.01, *Arenaria serpyllifolia* aggr. 0.01, *Caucalis platycarpos* 0.01, *Holosteum umbellatum* 0.01, *Minuartia meyeri* 0.01, *Noccaea perfoliata* 0.01, *Veronica denudata* 0.01.

2.1.1.1 *Ranunculo caucasici-Bromopsietum variegatae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 18 in Suppl. material 2 (original code AM06NW); Armenia, Shirak Province, vicinity of Zorakert, 41.10135°N, 43.66933°E, altitude: 2,114 m a.s.l., aspect: 255°, inclination: 35°, 28 June 2019, authors of the relevé: Elena Belonovskaya, Jürgen Dengler, Denys Vynokurov. Floristic composition (species sorted by their cover in percent): *Thymus sipyleus* 25, *Achillea millefolium* aggr. 15, *Phleum alpinum* 15, *Koeleria macrantha* 12, *Festuca ovina* aggr. 10, *Astragalus incertus* 8, *Carex humilis* 8, *Trifolium ambiguum* 7, *Bromopsis variegata* 5, *Hypnum cupressiforme* 5, *Lotus corniculatus* 5, *Medicago falcata* 5, *Abietinella abietina* 2, *Myosotis alpestris* 2, *Poa pratensis* aggr. 2, *Bryum caespiticium* 1, *Plantago atrata* 1, *Securigera varia* 1, *Weissia brachycarpa* 1, *Avenula pubescens* 0.5, *Streblotrichum convolutum* 0.5, *Cirsium leucocephalum* 0.5, *Gelasia rigida* 0.5, *Huynhia pulchra* 0.5, *Lomelosia caucasica* 0.5, *Rumex acetosella* 0.5, *Scabiosa bip-*

innata 0.5, *Stachys recta* 0.5, *Carex caryophyllea* 0.3, *Hypericum linarioides* 0.3, *Poa badensis* 0.3, *Potentilla argentea* 0.3, *Schedonorus pratensis* 0.3, *Taraxacum* sect. *Taraxacum* 0.3, *Teucrium orientale* 0.3, *Veronica denudata* 0.3, *Galium verum* 0.2, *Papaver monanthum* 0.2, *Pimpinella saxifraga* aggr. 0.2, *Potentilla recta* aggr. 0.2, *Ajuga orientalis* 0.1, *Alyssum alyssoides* 0.1, *Arenaria blepharophylla* aggr. 0.1, *Arenaria gypsophiloides* 0.1, *Artemisia absinthium* 0.1, *Bupleurum falcatum* aggr. 0.1, *Campanula stevenii* 0.1, *Cirsium obvallatum* 0.1, *Colchicum trigynum* 0.1, *Galium cordatum* 0.1, *Linaria schelkownikowii* 0.1, *Pedicularis condensata* 0.1, *Phascum cuspidatum* 0.1, *Ranunculus caucasicus* 0.1, *Scleranthus perennis* 0.1, *Silene bupleuroides* 0.1, *Silene chlorantha* 0.1, *Syntrichia montana* 0.1, *Bryum argenteum* 0.01, *Crepis alpina* 0.01, *Draba nemorosa* 0.01, *Encalypta vulgaris* 0.01, *Herniaria incana* 0.01, *Muscari armeniacum* 0.01, *Polygala alpicola* 0.01, *Polygonum cognatum* 0.01, *Sedum acre* 0.01.

2.2.1.3 *Globulario trichosanthae-Stipetum pulcherrimae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 93 in Suppl. material 2 (original code AM42SE); Armenia, Vayots Dzor Province, vicinity of Gnishik, 39.675269°N, 45.30616°E, altitude: 2,136 m a.s.l., aspect: 80°, inclination: 23°, 3 July 2019, authors of the relevé: Asun Berastegi, Idoia Biurrun, Denys Vynokurov. Floristic composition (species sorted by their cover in percent): *Ziziphora clinopodioides* 15, *Koeleria macrantha* 7, *Stipa capillata* 7, *Dactylis glomerata* 5, *Stipa pulcherrima* 5, *Hypericum scabrum* 4, *Onobrychis cornuta* 4, *Helichrysum graveolens* 3, *Lotus corniculatus* 2, *Odontarrhena tortuosa* 2, *Teucrium chamaedrys* 2, *Teucrium polium* 2, *Centaurea ovina* aggr. 1, *Daphne oleoides* subsp. *kurdica* 1, *Eryngium billardierei* 1, *Galium verticillatum* 1, *Galium verum* 1, *Linum tenuifolium* 1, *Medicago sativa* 1, *Stipa pennata* 1, *Cichorium intybus* 0.5, *Cruciata laevipes* 0.5, *Cuscuta epithymum* 0.5, *Euphorbia seguieriana* 0.5, *Hypericum linarioides* 0.5, *Plantago lanceolata* 0.5, *Scabiosa bipinnata* 0.5, *Securigera varia* 0.5, *Stipa tirsa* 0.5, *Tanacetum polycephalum* subsp. *argyrophyllum* 0.5, *Globularia trichosantha* 0.3, *Leontodon hispidus* 0.3, *Stachys lavandulifolia* 0.3, *Stachys recta* 0.3, *Ajuga chamaepitys* subsp. *chia* 0.2, *Cerinthe minor* 0.2, *Leontodon asperrimus* 0.2, *Linum nervosum* 0.2, *Phleum phleoides* 0.2, *Poa bulbosa* 0.2, *Tragopogon sosnowskyi* 0.2, *Verbascum chaixii* subsp. *austriacum* 0.2, *Astragalus cancellatus* 0.1, *Bupleurum falcatum* aggr. 0.1, *Carlina vulgaris* 0.1, *Sanguisorba minor* 0.1, *Silene bupleuroides* 0.1, *Thesium arvense* 0.1, *Trinia glauca* 0.1, *Veronica microcarpa* 0.1, *Achillea millefolium* aggr. 0.01, *Agrimonia eupatoria* 0.01, *Crepis pulchra* 0.01, *Euphrasia pectinata* 0.01, *Odontites aucheri* 0.01, *Polygala alpicola* 0.01.

2.2.1.4 *Seslerio phleoidis-Onobrychidetum cornutae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 13 in Suppl. material 2 (original code AMR076); Armenia, Gegharkunik Province, vicinity of Shoghakat, 40.49547°N, 45.29575°E, altitude: 1,959 m a.s.l., aspect: 305°, inclination: 30°, 1 July 2019, authors of the relevé: George Fayvush, Salza Palpurina, Iulia Vasheniak. Floristic composition (species sorted by their cover in percent): *Carex humilis* 20, *Onobrychis cornuta* 15, *Elytrigia intermedia* aggr. 8, *Primula veris* subsp. *macrocalyx* 7, *Thymus kotschyanus* 7, *Stipa pulcherrima* 6, *Onobrychis transcaucasica* 5, *Scutellaria orientalis* aggr. 5, *Galium verum* 4, *Inula aspera* 4, *Helianthemum nummularium* 2, *Sesleria phleoides* 2, *Teucrium chamaedrys* 2, *Abietinella abietina* 1, *Bromus scoparius* 1, *Campanula sibirica* 1, *Euphorbia iberica* 1, *Homalothecium lutescens* 1, *Hypnum cupressiforme* 1, *Linum tenuifolium* 1, *Lotus corniculatus* 1, *Medicago sativa* 1, *Syntrichia ruralis* 1, *Ziziphora clinopodioides* 1, *Achillea millefolium* aggr. 0.5, *Astracantha stenonychioides* 0.5, *Campanula rapunculoides* 0.5, *Dianthus cretaceus* 0.5, *Filipendula vulgaris* 0.5, *Linum nervosum* 0.5, *Plantago media* 0.5, *Polygala anatolica* 0.5, *Scabiosa bipinnata* 0.5, *Stachys recta* 0.5, *Thalictrum foetidum* 0.5, *Jurinea squarrosa* 0.3, *Viola ambigua* 0.3, *Phleum phleoides* 0.2, *Poa badensis* 0.2, *Psephellus karabaghensis* 0.2, *Tanacetum aureum* 0.2, *Convolvulus lineatus* 0.1, *Festuca valesiaca* aggr. 0.1, *Pontechium maculatum* 0.1, *Tragopogon reticulatus* 0.1, *Xanthoparmelia camtschadalis* 0.1, *Asperula prostrata* 0.01, *Carum caucasicum* 0.01, *Cetraria ericetorum* 0.01, *Euphrasia sevanensis* 0.01, *Hypericum scabrum* 0.01, *Orobanche alsatica* 0.01, *Teucrium orientale* 0.01.

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Supplementary material

Supplementary material 1
Complete header data of the Armenian plots (*.xlsx)
Link: https://doi.org/10.3897/VCS.119253.suppl1

Supplementary material 2
Complete synoptic table of 110 classified Armenian plots with percent constancies and phi values for the syntaxa of all levels as well as the individual plots (*.xlsx)
Link: https://doi.org/10.3897/VCS.119253.suppl2

Supplementary material 3
Definition of additional species aggregates (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl3

Supplementary material 4
Value distribution of all recorded and analysed numerical environmental, structural and biodiversity variables (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl4

Supplementary material 5
Data sources of the West Asian and Caucasian dataset (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl5

Supplementary material 6
List of the vascular plants from the Armenian dataset with assignment of life forms and distribution ranges (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl6

Supplementary material 7
Synoptic table of the West Asian and Caucasian dataset with the results of the broad-scale comparison with five distinguished groups of clusters (A–E) (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl7

Supplementary material 8
Planned applications to the EuroVegChecklist Committee (EVCC) (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl8

VEGETATION CLASSIFICATION AND SURVEY
International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 5: 75–84
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LONG DATABASE REPORT ECOINFORMATICS

Nordic-Baltic Grassland Vegetation Database (NBGVD) – current state and future prospects

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Abstract

This Long Database Report describes the historical background and current contents of the Nordic-Baltic Grassland Vegetation Database (NBGVD) (GIVD-code EU-00-002). NBGVD is the EDGG-associated collaborative vegetation-plot database that collects vegetation-plot data of grasslands and other open habitats (except segetal and deep aquatic vegetation) from the Nordic-Baltic region excluding Germany, namely Belarus, Denmark, Estonia, Faroe Islands, Finland, Iceland, Latvia, Lithuania, Norway, N Poland, NW Russia, Svalbard and Jan Mayen, and Sweden. Target vegetation types are lowland grasslands and heathlands, arctic-alpine communities, coastal communities, non-forested mires and other wetlands, rocky, tall-herb and ruderal communities. As of March 2024, it included 12,694 relevés recorded between 1910 and 2023. These were mainly digitised from literature sources (84%), while the remainder comes from individual unpublished sources (16%). The data quality is high, with bryophytes and lichens being treated in more than 80% of all plots and measured environmental variables such as topography and soil characteristics often available in standardised form. A peculiarity of the Nordic-Baltic region are the relatively small plot sizes compared to other regions (median: 4 m^2). The available data stem from 35 vegetation classes, with *Koelerio-Corynephoretea*, *Festuco-Brometea*, *Sedo-Scleranthetea*, *Molinio-Arrhenatheretea* and *Scheuchzerio-Caricetea* being most frequent. We conclude that NBGVD provides valuable data, allowing interesting analyses at the regional scale and fills gaps in continental to global analyses. Still, since there are many more data around, we ask interested readers to contribute their own data or help find and digitise old data from the literature.

Taxonomic reference: TURBOVEG species list “Europe”.

Syntaxonomic reference: Mucina et al. (2016).

Abbreviations: EDGG = Eurasian Dry Grassland Group, EVA = European Vegetation Archive, GIVD = Global Index of Vegetation-Plot Databases, NBGVD = Nordic-Baltic Grassland Vegetation Database

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[*] Nadiia Skobel and Łukasz Kozub shall be considered joint first authors.

Keywords

Arctic-alpine vegetation, Baltic region, coastal vegetation, ecoinformatics, European Vegetation Archive (EVA), grassland, macroecology, mire, Nordic region, plot size, relevé, vegetation-plot database

GIVD Fact Sheet: Nordic-Baltic Grassland Vegetation Database (NBGVD)

GIVD Database ID: EU-00-002 **Last update:** 2024-03-29

Nordic-Baltic Grassland Vegetation Database (NBGVD) **Web address:** https://edgg.org/databases/Regional-databases

Database manager(s): Jürgen Dengler (dr.juergen.dengler@gmail.com); Łukasz Kozub (lkozub@uw.edu.pl)

Owner: Consortium of the Nordic-Baltic Grassland Vegetation Database (NBGVD Consortium)

Scope: The former name of this database was "Database Dry Grasslands in the Nordic and Baltic Region" (with a narrower scope). Now all available relevés of grasslands and other open habitats from the study region (Iceland, Svalbard and Jan Mayen, Faroe Islands, Norway, Sweden, Finland, Denmark, N Poland, Lithuania, Latvia, Estonia, Belarus, NW Russia) are collected.

Abstract: The Nordic-Baltic Grassland Vegetation Database (NBGVD) (GIVD-code EU-00-002) is the EDGG-associated collaborative vegetation-plot database that collects vegetation-plot data of grasslands and other open habitats (except segetal and deep aquatic) from the Nordic-Baltic region, except Germany, namely Belarus, Denmark, Estonia, Faroe Islands, Finland, Iceland, Latvia, Lithuania, Norway, N Poland, NW Russia, Svalbard and Jan Mayen, Sweden. Target vegetation types are lowland grasslands and heathlands, arctic-alpine communities, coastal communities, non-forested mires and other wetlands, rocky, tall-herb and ruderal communities. As of January 2024, it included 12,694 relevés, collected between 1910 and 2023, which were mainly digitised from literature sources (79%), while the remainder comes from individual unpublished sources (21%). The data quality is high, with bryophytes and lichens being treated in 95% of all plots and measured environmental variables such as topography and soil characteristics often available in standardised form. A peculiarity of the Nordic-Baltic region are the relatively small plot sizes compared to other regions (median: 4 m2). The available data stem from 35 vegetation classes, with Koelerio-Corynephoretea, Festuco-Brometea, Sedo-Scleranthetea, Molinio-Arrhenatheretea and Scheuchzerio-Caricetea being most frequent. We conclude that NBGVD provides valuable data, allowing interesting analyses at the regional scale and filling gaps in continental to global analyses. Still, there are many more data around, and we thus ask interested readers to contribute own data or help with finding and digitising old data from the literature.

Availability: according to a specific agreement **Online upload:** no **Online search:** no

Database format(s): TURBOVEG **Export format(s):** TURBOVEG, Excel

Plot type(s): normal plots **Plot-size range (m²):** 0.04 to 600

Non-overlapping plots:	**Estimate of existing plots:**	**Completeness:**	**Status:**
12694	50000	25%	ongoing capture

Total no. of plot observations:	**Number of sources (biblioreferences, data collectors):**	**Valid taxa:**
12694	124	1750

Countries (%): BY: 12.9; DK: 1.7; EE: 10.3; FI: 1.7; LV: 2.2; LT: 1.0; NO: 10.2; PL: 24.8; RU: 1.2; SE: 24.6

Formations: Non Forest: 60% = Terrestrial: 60% (Non arctic-alpin: 60% [Semi-natural: 60%])

Guilds: all vascular plants: 100%; bryophytes (terricolous or aquatic): 86%; lichens (terricolous or aquatic): 83%

Environmental data (%): altitude: 27.9; slope aspect: 33.9; slope inclination: 29.4; microrelief: 1.9; surface cover other than plants (open soil, litter, bare rock etc.): 21.9; other soil attributes: 10.4; soil pH: 26.2; land use categories: NA; soil depth: 15.3; other attributes: Cation exchange capacity, base saturation, soil organic matter, CaCO3 content

Performance measure(s): presence/absence only: 0%; cover: 100%; number of individuals: 0%; measurements like diameter or height of trees: 0%; biomass: 0%; other: 0%

Geographic localisation: GPS coordinates (precision 25 m or less): 26.9%; point coordinates less precise than GPS, up to 1 km: 40.9%; small grid (not coarser than 10 km): 28.5%; political units or only on a coarser scale (above 10 km): 3.7%

Sampling periods: before 1920: 0.5%; 1920-1929: 6.0%; 1930-1939: 2.0%; 1940-1949: 4.9%; 1950-1959: 2.6%; 1960-1969: 7.1%; 1970-1979: 4.2%; 1980-1989: 8.4%; 1990-1999: 26.3%; 2000-2009: 21.0%; 2010-2019: 13.6%; after 2020: 3.4%; unknown: 0.0%

Information as of 2024-03-29; further details and future updates available from http://www.givd.info/ID/EU-00-002

Introduction

Vegetation-plot databases have an enormous potential for vegetation ecology, macroecology and global-change studies (Dengler et al. 2011; Wiser 2016) as they allow for generalization beyond the local or regional extent. This potential is increasingly harvested through big continental to global databases such as the European Vegetation Archive (EVA; Chytrý et al. 2016), the global database “sPlot” (Bruelheide et al. 2019) or the specialised high-quality database of Palaearctic open habitats “GrassPlot” (Dengler et al. 2018). Publications making use of data from EVA, for example, have shed light on the broad-scale classification of dry grassland types (Willner et al. 2019), the frequency and distribution of neophytes in European grasslands (Axmanová et al. 2021) and the relationship of functional vs. phylogenetic diversity in grasslands (Večeřa et al. 2023). The sPlot database, among others, was used to model how alpha-diversity patterns in grasslands and forests globally vary across grain sizes (Sabatini et al. 2022) and to test what drives stability in grasslands (Engel et al. 2023). However, such broad-scale analyses strongly depend on balanced data coverage across regions.

Within Europe, the Nordic countries (Iceland, Svalbard and Jan Mayen, Norway, Sweden, Finland), NW Russia and Belarus are generally much underrepresented (see Chytrý et al. 2016; recent update at https://euroveg.org/img/map-eva-square.png), particularly in the case of grasslands. Denmark and Poland seem to be represented quite well according to the EVA map, but this does not reflect the reality for many international studies: the main source of Danish data, the NATURDATA.DK database (GIVD ID EU-DK-002), is represented in EVA only with presence/absence data, which thus cannot be used for studies requiring cover data, while data from the Polish Vegetation Database (EUR-PL-001) contained in EVA have repeatedly not been released for specific research projects. Thus, in many international studies the models derived for the Nordic-Baltic regions have weaknesses due to sparse data from grasslands (e.g. Axmanová et al. 2021; Večeřa et al. 2021, 2023). Even for fen vegetation, one of the most typical vegetation types of the boreal zone, the current data in EVA give the false impression that these would be rare in middle and northern Sweden and Finland (see maps in Jiménez-Alfaro et al. 2023).

In addition, most of the Nordic-Baltic countries (except Germany and Poland) do not have a strong phytosociological tradition as they were in the realms of the Russian (Aleksandrova 1973) or Nordic (Trass and Malmer 1973; see also Pätsch et al. 2019) schools of vegetation ecology. Unlike the Zurich-Montpellier school (phytosociology), collecting large numbers of vegetation plot records (relevés) for broad-scale classification was never prevalent in these two schools, leading to a much lower number and density of historic relevés than in other parts of Europe (see Schaminée et al. 2009; Chytrý et al. 2016). Unlike many other European countries, most of the countries of the region (except Germany, Poland and Lithuania) still do not have national vegetation-plot databases (https://www.givd.info; see Dengler et al. 2011). This gap is partly filled for forest and mire vegetation by the Nordic Vegetation Database (EU-00-018) and the European Mire Vegetation Database (EU-00-022), but a major gap remains for grasslands and other open habitat types. The Nordic-Baltic Grassland Vegetation Database (NBGVD) aims to fill this gap. It emerged from a database focused on the dry grasslands of the region (Dengler et al. 2006b; Dengler and Rūsiņa 2012), but was later expanded to include all grasslands and other non-forest vegetation types (Dengler and Kozub 2022). Recently, the content of NBGVD has been significantly increased and its quality and consistency improved. With this Long Database Report, we would like to provide a current overview on the organisation of NBGVD, give detailed statistics on its content and outline future avenues of development as well as potential uses of its data.

Scope of NBGVD

The Nordic and Baltic region in the sense of NBGVD is defined as the combined territories of Denmark, Faroe Islands, Iceland, Svalbard and Jan Mayen, Norway, Sweden, Finland, NW Russia, Belarus, Estonia, Latvia, Lithuania and the Pleistocene lowlands of N Poland and N Germany. This region approximately corresponds to the maximum extension of the Northern European ice shield during the Pleistocene (Lang 1994). However, German plots have recently been excluded from NBGVD and transferred to our sister database GrassVeg.DE (Dengler et al. 2017, 2018a). In the future, we anticipate a similar arrangement with the Lithuanian Vegetation Database (EU-LT-001).

According to its Bylaws, NBGVD's main foci are "all natural and semi-natural grasslands s.l.". However, any vegetation types except forests, shrublands, true aquatic communities and arable fields are collected. According to Mucina et al. (2016), this means the following vegetation classes (although sources that contain a small fraction of other classes are digitised completely):

- Lowland grassland and heathland communities: *Calluno-Ulicetea*, *Festuco-Brometea*, *Koelerio-Corynephoretea canescentis*, *Molinio-Arrhenatheretea*, *Nardetea*, *Sedo-Scleranthetea*
- Arctic-alpine communities: *Carici rupestris-Kobresietea bellardii*, *Juncetea trifidi*, *Loiseleurio procumbentis-Vaccinietea*, *Salicetea herbaceae*, *Saxifrago cernuae-Cochlearietea groenlandicae*
- Coastal communities: *Ammophiletea*, *Cakiletea maritimae*, *Crithmo-Staticetea*, *Juncetea maritimi*, *Saginetea maritimae*, *Spartinetea martimae*, *Thero-Salicornietea*
- Wetland (amphibian) communities: *Isoeto-Nano-Juncetea*, *Littorelletea uniflorae*, *Montio-Cardaminetea*, *Oxycocco-Sphagnetea*, *Phragmito-Magno-Caricetea*, *Scheuchzerio palustris-Caricetea fuscae*
- Rocky communities: *Asplenietea trichomanis*, *Thlaspietea rotundifolii*
- Tall-herb communities: *Trifolio-Geranietea sanguinei*, *Mulgedio-Aconitetea*
- Ruderal communities: *Artemisietea vulgaris*, *Bidentetea*, *Epilobietea angustifolii*, *Polygono-Poetea annuae*, *Sisymbrietea*

Further, the relevés must refer to contiguous plots with a specified area in the range of 0.09 to 400 m^2. Relevés with a direct estimate of percent cover (see Dengler and Dembicz 2023) are preferred, but those with any other cover or cover-abundance measure (e.g. variants of the Braun-Blanquet or Hult-Sernander scales) are also accepted, while pure presence-absence data are not.

History and governance of NBGVD

The database originated from data collected by J. Dengler aimed at the phytosociological classification of the dry grasslands of the region, at that time managed in the software for vegetation plot handling SORT (Ackermann and Durka 1998). It was subsequently transferred to TURBOVEG 2.0 (Hennekens and Schaminée 2001) and became a collaborative project under the name "Database Dry Grasslands in the Nordic and Baltic Region" (see Dengler et al. 2006b; Dengler and Rūsiņa 2012). In 2016, the scope was widened to include all grasslands s.l., and thus, the name was changed to "Nordic-Baltic Grassland Vegetation Database" (NBGVD; Dengler and Kozub 2022). NBGVD is registered in the Global Index of Vegetation-Plot Databases (GIVD; Dengler et al. 2011) under the ID EU-00-002 (see GIVD Fact Sheet). It is one of currently five regional grassland vegetation databases associated with the Eurasian Dry Grassland Group (EDGG; https://edgg.org/), namely the Balkan Dry Grassland Database (BDGD; EU-00-013; Vassilev et al. 2012), the German Grassland Vegetation Database (GrassVeg.DE; EU-DE-020; Dengler et al. 2017, 2018), the Romanian Grassland Database (RGD; EU-RO-008; Vassilev et al. 2018) and the Ukrainian Grassland Database (UGD; EU-UA-001; Kuzemko 2012).

NBGVD is a self-governed consortium in which every data contributor becomes a member. It is regulated by a set of Bylaws (Suppl. material 1). The members elect a Custodian and a Deputy Custodian for two-year renewable terms to coordinate the database, with J. Dengler the current Custodian and Ł. Kozub the Deputy. NBGVD contributes its content at regular intervals to EVA and sPlot, allowing its members to opt-in for EVA and sPlot publications as co-authors and propose studies using the continental and global databases themselves. The NBGVD website is https://edgg.org/databases/Regional-databases.

Starting with 7,675 plots in 2012 (Dengler and Rūsiņa 2012) and 9,839 plots in 2022 (Dengler and Kozub 2022), NBGVD has now grown to 12,694 plots as of March 2024. This means a net growth of 5,019 plots over12 years. However, the number of plots that were newly made available to EVA during this period was as high as 9,143, since more than 4,000 plots have since been excluded from NBGVD. Before 2022, all plots from Germany were transferred to GrassVeg.DE (Dengler et al. 2017, 2018). Moreover, we recently excluded plots that are now included in a specialised EVA database from Latvia, the Semi-natural Grassland Vegetation Database of Latvia (EU-LV-001), to avoid duplicates in EVA. Apart from this increase in quantity, we also took great efforts to improve the quality and consistency of the plot data. This included identifying and correcting erroneous entries, filling in important header data fields (e.g. vegetation class), and improving coordinate precision (in the predecessor database under SORT, coordinates were only given with 0.1° precision).

Data management

Currently, the database is managed using the latest version of the TURBOVEG 2.0 software (Hennekens and Schaminée 2001). When we encountered cover-(abundance) scales not predefined in TURBOVEG, we added their definitions, i.e. the symbol, min, max and mean cover values of each cover class to the respective definition table of the program. The taxonomy of the database is based on the built-in "Europe" species list relying on the Flora Europaea (Tutin et al. 1964–1993) with some additions of vascular plant taxa that could not be easily attributed to any of the already existing taxonomic concepts as well as bryophytes and lichens (for these groups, TURBOVEG "Europe" does not have a clearly documented source). The header data in NBGVD consist of five groups: (1) standard TURBOVEG fields, (2) fields required by EVA (see Chytrý et al. 2016), (3) fields required by sPlot (see Bruelheide et al. 2019), (4) fields needed for NBGVD project management, and (5) structural and environmental variables provided with the data. The fields of the categories (1)–(4) are filled completely, while the fields of category (5) are created and filled upon availability and carefully curated for consistency (e.g. identical units).

Content of NBGVD

The 12,694 vegetation plots currently included in NBGVD originate from data published by consortium members (19.5%) and other authors (45.6%), while the rest are unpublished relevés from consortium members (34.9%). In total, the NBGVD currently contains data from 124 different sources (Suppl. material 2) contributed or digitised by 27 contributors, four of which contributed more than 10% each (Suppl. material 3: table S3.1).

NBGVD has data from all 13 countries or territories within its geographic scope, with the numbers being highest in the Polish lowlands (24.8%) and Sweden (24.6%), followed by Belarus (12.9%) and Estonia (10.3%) (Table 1). The plot density strongly differs between territories, with a maximum of 515 plots in 1,000 km^2 on the Faroe Islands and values below 1 plot in 1,000 km^2 in Finland and NW Russia (Table 1). The plot density also varies within territories, with maxima on Saaremaa on the Estonia West coast and on the Faroe Islands. NBGVD still contains very few plots from Russiaand the northern parts of Finland and Sweden (i.e. north of 62° latitude).

Table 1. Countries and other territories covered by NBGVD with their area and available plot number in March 2024, expressed in absolute and relative terms and density per surface area.

Country or part of country	Area included [km^2]	Number of plots	Fraction [%]	Plot density [plots/1,000 km^2]
Belarus	207,595	1,632	12.9	7.9
Denmark (mainland)	43,094	214	1.7	5.0
Estonia	45,339	1,309	10.3	28.9
Faroe Islands	1,398	720	5.7	515.0
Finland	338,145	222	1.7	0.7
Iceland	103,125	460	3.6	4.5
Latvia	64,589	280	2.2	4.3
Lithuania	65,300	127	1.0	1.9
Norway (mainland)	324,220	716	5.6	2.2
Poland (lowlands)	230,107	3,149	24.8	13.7
Russia (NW part)	956,305	158	1.2	0.2
Svalbard and Jan Mayen	62,045	587	4.6	9.5
Sweden	450,295	3,120	24.6	6.9
Total	**2,891,557**	**12,694**	**100.0**	**4.4**

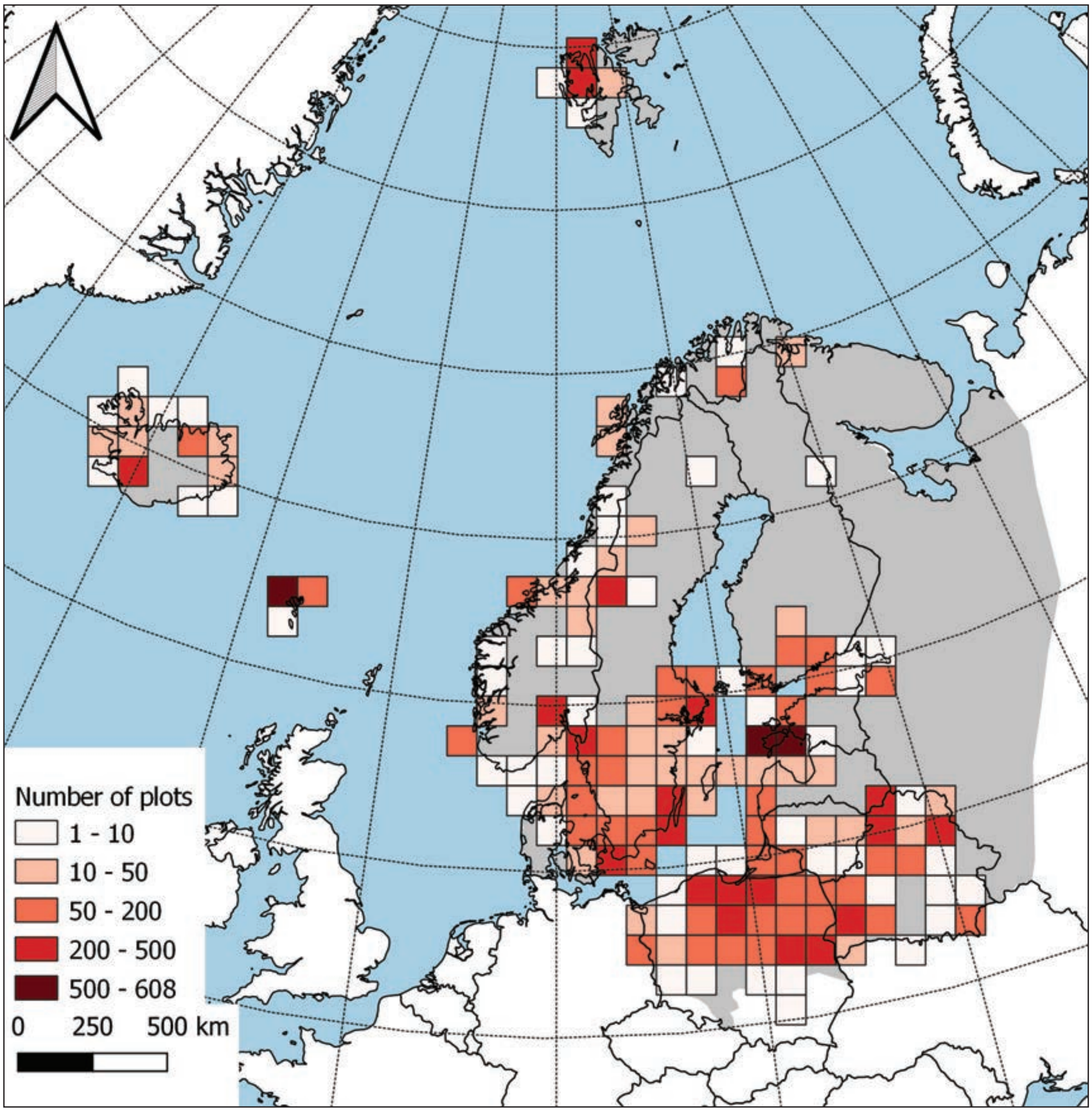

Figure 1. Spatial distribution of the 12,694 vegetation plots contained in NBGVD in March 2024. The grey shading indicates the geographic scope of NBGVD, while the colour intensity of the 100 km × 100 km grid cells represents the number of plots contained in NBGVD.

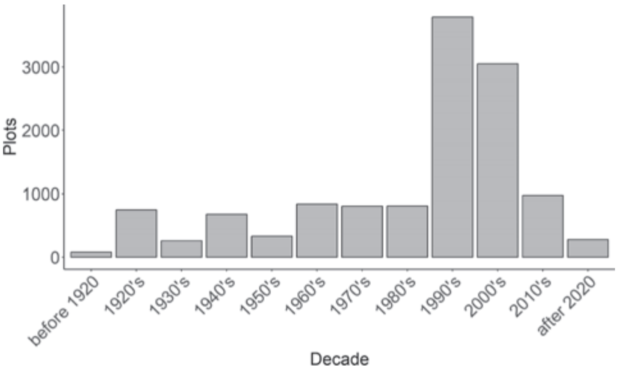

Figure 2. Temporal distribution of the 12,694 vegetation plots contained in the NBGVD in March 2024.

The data were collected from 1910 to 2023 (median: 1997), with a peak in the two decades from 1990 to 2009, but otherwise with rather uniform distribution (Figure 2). Plot sizes vary widely within the allowed range, with 1 m^2 (30.0%), 4 m^2 (17.1%), 25 m^2 (13.5%), 0.64 m^2 (7.0%), and 0.25 m^2 (4.0%) being most frequent (Figure 3, Suppl. material 3: table S3.2). Only 79 (0.6%) plots lack plot size information; these are mostly individual relevés from older literature sources (Suppl. material 3: table S3.2). The overall median of plot sizes in the database is 4 m^2, while in six territories (Belarus, Denmark, Estonia, Faroe Islands, Latvia, Norway) plot sizes of 1 m^2 and smaller prevail (Suppl. material 3: table S3.2). Plot sizes larger than 4 m^2 dominate only in Iceland (median: 6 m^2), NW Russia (median: 7.5 m^2), Poland (25 m^2), and Latvia (100 m^2) (Suppl. material 3: table S3.2). Since a large fraction of plots was digitised from older literature often including only coarse information on sampling sites, the coordinate precision in NBGVD varies widely, from GPS precision (5 m and less: 26%) to 1 km (42%) and more than 1 km (32%) (Figure 4). Currently, NBGVD contains datasets recorded with nine different cover or cover-abundance scales, dominated by the 7-step (35.0%) and 9-step variants (28.3%) of the Braun-Blanquet scale, followed by the Hult-Sernander

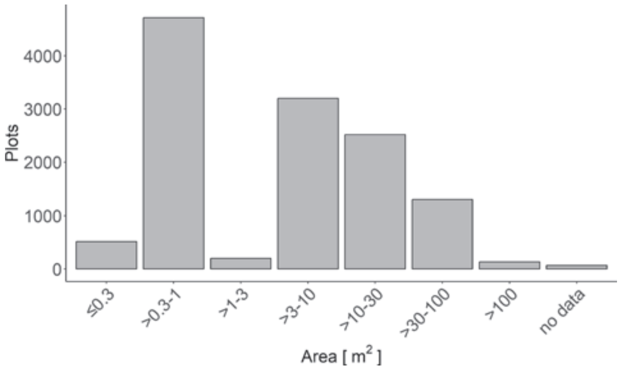

Figure 3. Distribution of the plot sizes of the 12,694 vegetation plots contained in the NBGVD in March 2024.

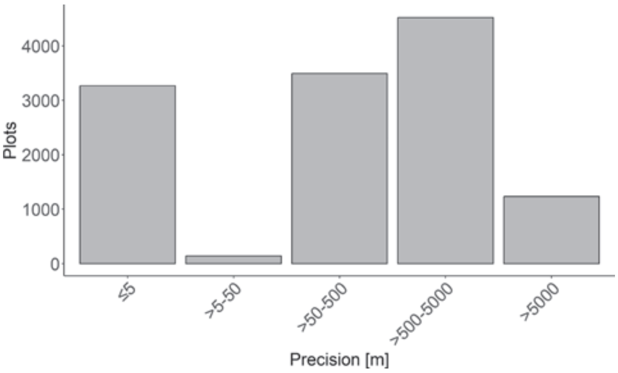

Figure 4. Distribution of coordinate precision of the 12,694 vegetation plots contained in the NBGVD in March 2024.

scale (12.9%), percent cover (2.2%) and the Londo scale (0.5%). Four datasets used idiosyncratic scales defined for specific projects (21.1% altogether).

Where this information is available, NBGVD stores the association/community, alliance, and order assignment of the vegetation plots in the source, without attempting harmonization. Moreover, more than 75% of the plots in NBGVD are currently assigned to a vegetation class according to Mucina et al. (2016), based on the original assignment in the source, expert interpretation of the species composition or the EUNIS habitat classification (Chytrý et al. 2020). For the latter, we ran the EUNIS expert system implemented in JUICE (Tichý 2002) over our relevés, and if the resulting habitat type was completely nested in one class, we assigned the relevé there. A total of 35 vegetation classes are present, with seven representing more than 2% of the plots each: *Koelerio-Corynephoretea canescentis* (1955 plots; 15.4%), *Festuco-Brometea* (1843; 14.5%), *Sedo-Scleranthetea* (1053: 8.3%), *Molinio-Arrhenatheretea* (933; 7.3%), *Scheuchzerio palustris-Caricetea fuscae* (833; 6.6%), *Trifolio-Geranietea sanguinei* (574; 4.5%), *Salicetea herbaceae* (322; 2.5%), and *Juncetea maritimi* (282; 2.2%) (for details, see Suppl. material 3: table S3.3).

NBGVD also contains various header data fields for structural and environmental variables. Apart from several environmental header data fields with free text, such as land use and soil texture class, there are currently 11 measured environmental variables referring to topography and soil characteristics (Table 2). Among these, elevation, aspect, inclination and pH (H_2O) are available for at least one quarter of the plots (Table 2).

It is worth mentioning that according to the header data, bryophytes were treated in nearly 86% of the plots and lichens in 83% of the plots in the database, meaning that NBGVD can provide real absences of non-vascular taxa. The five most frequent vascular plant taxa (after merging taxa determined at different levels across plots into some broader concepts) are *Festuca ovina* aggr. (30.6% of the plots), *Achillea millefolium* aggr. (28.9%), *Galium verum* (25.2%), *Hieracium pilosella* aggr. (23.5%), and *Festuca rubra* aggr. (23.4%) (Suppl. material 3: table S3.4). The five most frequent bryophyte taxa are *Ceratodon purpureus* (13.5% of the plots with determined bryophytes), *Polytrichum piliferum* (9.7%), *Hypnum cupressiforme* aggr. (9.7%), *Racomitrium canescens* aggr. (8.9%), and *Syntrichia ruralis* aggr. (8.50%) (Suppl. material 3: table S3.5). Among lichens, *Cetraria islandica* (10.0% of the plots with determined lichens), *Cladonia arbuscula* aggr. (9.8%), *Cladonia furcata* aggr. (7.3%), *Cetraria aculeata* (6.8%) and *Peltigera rufescens* (4.7%) are the most frequent taxa (Suppl. material 3: table S3.6).

Table 2. Measured environmental variables contained in NBGVD with their degree of availability and the distribution of values.

Variable	Unit	TURBOVEG name	Available (%)	Min	Max	Mean	Median
Elevation	m a.s.l.	ALTITUDE	27.9%	-0.5	1350	253	135
Slope aspect	°	EXPOSITION	33.9%	0	360	158	180
Slope inclination	°	INCLINATIO	29.4%	0	90	13	5
Microtopography	cm	MICROTOP	1.9%	1	30	5	4
Mean soil depth	cm	SOILDEPTH	15.3%	0	60	13	8.5
pH (H_2O)	-	PH_H20	26.2%	1.70	8.50	5.21	5.40
pH (KCl)	-	PH_KCL	8.9%	2.70	7.70	5.88	6.60
Cation exchange capacity	meq/100 g	CEC	1.8%	1.2	99	37	36.5
Base saturation	%	BASE_SAT	1.8%	67.15	100	99	100
Soil organic matter	mass %	ORG_MAT	10.4%	0	78.7	14	12.2
$CaCO_3$ content	mass %	LIME_PERC	0.5%	0.4	80	19	12.3

Resume and outlook

With the current NBGVD update, the data coverage of grasslands s.l. in the Nordic and Baltic regions has significantly improved in EVA and sPlot, thus facilitating regional, continental, and global analyses of non-forest vegetation. Aside from coming from an underrepresented region, the data in NBGVD are particularly useful for their good quality regarding the treatment of non-vascular plants (currently in more than 80% of all plots and thus high above the EVA average) and the careful curation of environmental header data. However, plot sizes could be a challenge when analysing data from the Nordic-Baltic region together with data from the rest of Europe, as the median plot sizes used in most of the NBGVD countries (4 m^2 or even 1 m^2) are well below the prevailing practice in most other European countries (Chytrý and Otýpková 2003). The data of NBGVD can be requested from NBGVD directly or via EVA and sPlot, following their respective Bylaws. In fact, they are frequently used in EVA and sPlot projects. However, in early 2024, we received the first direct data request to NBGVD, interestingly for a pan-European study where the proponent combined the European grassland data from sPlotOpen (a stratified, open access subset of an older EVA release: Sabatini et al. 2021) and GrassPlot (Dengler et al. 2018b), but wanted to achieve a data coverage in the Northern countries comparable to the rest of Europe.

Even with the release of this NBGVD update, the data coverage in the region is still poorer than in many other parts of Europe. Thus, we aim at expanding NBGVD further through the inclusion of additional data which could stem from the digitisation of older published sources from the past or from recent data (published and unpublished) in digital format from current and new consortium members. Promising avenues to retrieve further historical sources are searching for the sources underlying the few synthetic vegetation overviews of the region (e.g. Dierßen and Dierßen 1996) and systematic screening of botanical and ecological journals of the region (e.g. Acta Phytogeographica Suecica, Blyttia,…). Anyone who has data to contribute that match our scope is welcome to contact J.D. or Ł.K. However, please note that NBGVD is an all-purpose database with minimal requirements for data to be provided (see above). If you have data that meet the higher standards of our partner database GrassPlot (Dengler et al. 2018; Biurrun et al. 2019), particularly if they have been sampled on precisely delimited plots of one of the GrassPlot standard sizes (e.g. 0.1, 1, 10 or 100 m^2), we recommend contributing these to GrassPlot, not to NBGVD. In this case they would not only be available for EVA and sPlot projects, but also for GrassPlot projects (see https://edgg.org/databases/GrassPlot) (Figure 5). Likewise, data from repeatedly sampled plots (permanent or quasi-permanent plots) would likely be more beneficial if contributed to ReSurveyEurope

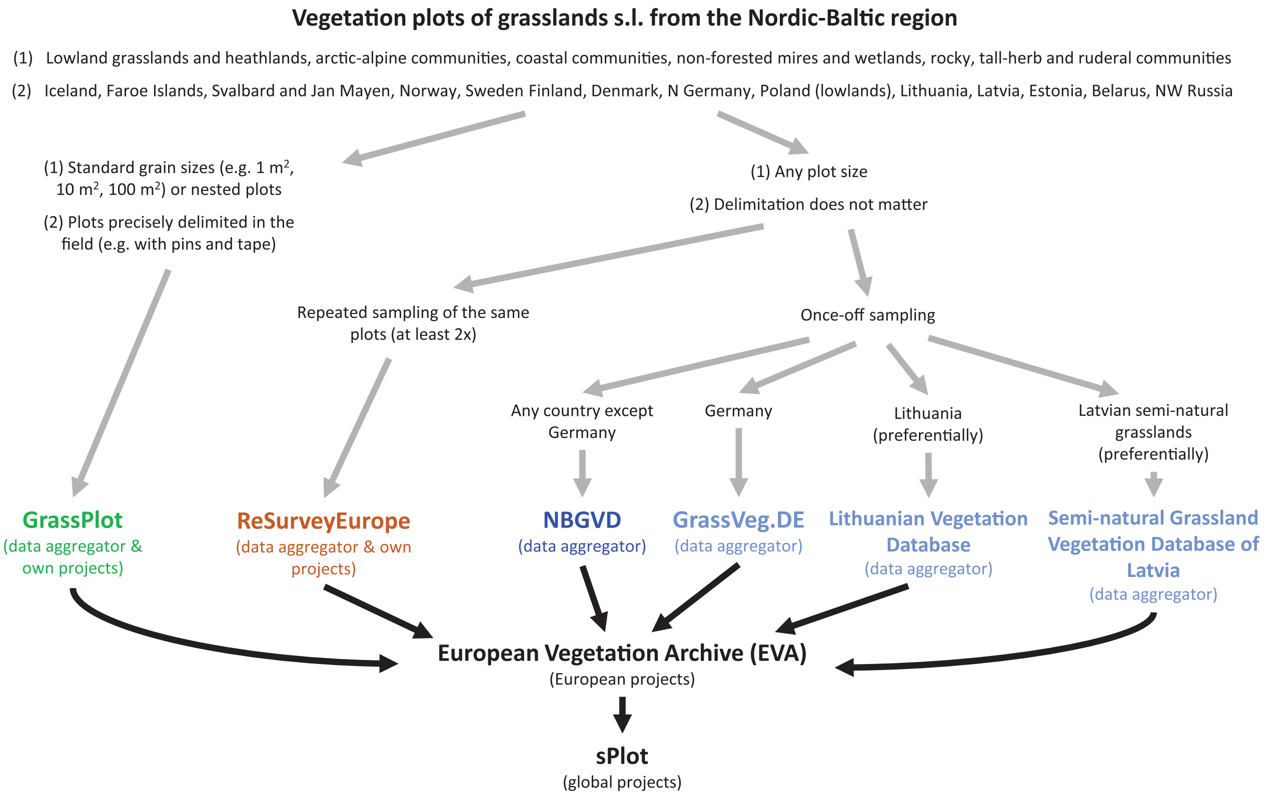
Vegetation plots of grasslands s.l. from the Nordic-Baltic region
(1) Lowland grasslands and heathlands, arctic-alpine communities, coastal communities, non-forested mires and wetlands, rocky, tall-herb and ruderal communities
(2) Iceland, Faroe Islands, Svalbard and Jan Mayen, Norway, Sweden Finland, Denmark, N Germany, Poland (lowlands), Lithuania, Latvia, Estonia, Belarus, NW Russia
(1) Standard grain sizes (e.g. 1 m², 10 m², 100 m²) or nested plots
(2) Plots precisely delimited in the field (e.g. with pins and tape)
(1) Any plot size
(2) Delimitation does not matter
Repeated sampling of the same plots (at least 2x)
Once-off sampling
Any country except Germany
Germany
Lithuania (preferentially)
Latvian semi-natural grasslands (preferentially)
GrassPlot
(data aggregator & own projects)
ReSurveyEurope
(data aggregator & own projects)
NBGVD
(data aggregator)
GrassVeg.DE
(data aggregator)
Lithuanian Vegetation Database
(data aggregator)
Semi-natural Grassland Vegetation Database of Latvia
(data aggregator)
European Vegetation Archive (EVA)
(European projects)
sPlot
(global projects)

Figure 5. Decision tree (grey) on how to contribute grassland plots s.l. from the Nordic-Baltic region to national and international vegetation-plot databases to achieve optimal benefit for data contributors and for science. The black lines indicate the flow of data to databases of higher aggregation levels.

(Knollová et al. 2024) (Figure 5). Note that despite belonging to the Nordic-Baltic region, grassland plots s.l. from Germany not meeting the GrassPlot criteria should go to GrassVeg.DE, and those from Lithuania and the semi-natural grasslands from Latvia preferentially to the respective national databases (Figure 5).

Since NBGVD has no funding, we rely on voluntary work both for digitising and georeferencing plots and for further improvement of the quality of already included plots (e.g. to increase the georeferencing precision of plots provided in the past). We also would like to adjust the taxonomic backbone to the current European standards of vascular plants, bryophytes and lichens to allow the most effective use of the data. Here, the "Euro+Med augmented" standard from Dengler et al. (2023), based on Euro+Med (2023) for vascular plants and Hodgetts et al. (2020) for bryophytes, appears particularly promising.

We anticipate that having more high-quality plot data from the Nordic-Baltic region will not only improve the validity of future macroecological and global-change studies for this region, but be particularly beneficial for the development of data-based broad-scale vegetation classification systems, of which there are only a few for the open habitats of the region so far, namely for the vegetation of fens (Peterka et al. 2017), coastal dunes (Marcenò et al. 2018), bogs (Jiroušek et al. 2022), and springs (Peterka et al. 2023) across Europe and for the rocky outcrop communities in the Nordic-Baltic region (Dengler and Löbel 2006; Dengler et al. 2006a).

Data availability

The database described here is collective property with semi-restricted access. Data can be requested from the last author following the rules defined in the NBGVD Bylaws (Suppl. material 1).

Author contributions

JD and ŁK coordinate the NBGVD Consortium as Custodian and Deputy Custodian, respectively. NS and ŁK currently manage NBGVD and have added new relevés and improved existing data in recent years. JD, ŁK, NS, and ID planned and wrote the report together, while all other authors contributed data, edited and approved the manuscript.

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Supplementary material

Supplementary material 1
Bylaws of the NBGVD (*.pdf)
Link: https://doi.org/10.3897/VCS.119968.suppl1

Supplementary material 2
List of all data sources currently contained in NBGVD (*.pdf)
Link: https://doi.org/10.3897/VCS.119968.suppl2

Supplementary material 3
Additional descriptive statistics of the current content of NBGVD (*.pdf)
Link: https://doi.org/10.3897/VCS.119968.suppl3

VEGETATION CLASSIFICATION AND SURVEY

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RESEARCH PAPER

Habitat characterization and mapping on the western slopes of Mount Hermon in Lebanon

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Abstract

Aims: Lebanon is renowned in the Levant for its distinctive vegetation types with some biodiversity hotspots as Mount Hermon, with rare and endangered endemic plant species. We aim to present the ecological characteristics and spatial distribution of habitat types present on its western slopes through the analysis of plant communities. **Study area:** Mount Hermon, Lebanon. **Methods:** We surveyed 169 plots, each spanning an area of 314 m^2, from 2020 to 2023, in the district of Rashaya, calculated compositional dissimilarity using the Bray–Curtis index, conducted hierarchical clustering analysis using the unweighted pair group method with arithmetic mean (UPGMA), applied the Nonmetric Multidimensional Scaling (NMDS) method to investigate the relationship between species frequency per site and environmental parameters, and identified significant diagnostic species for each group. **Results:** We recorded 383 taxa, including 27 narrow endemics. Ten habitat types are described; three at the oro-Mediterranean level: hedgehog-heaths of *Astragalus echinus* and *Noaea mucronata*, hedgehog-heaths of *Tanacetum densum* and *Astragalus cruentiflorus*, cliffs of *Rosularia sempervivum* subsp. *libanotica*; three at the supra-Mediterranean level: grasslands with *Eryngium glomeratum*, woodlands of *Quercus infectoria*, *Q. coccifera* and *Crataegus azarolus*, evergreen woodlands of *Q. coccifera*; four at the montane level: scree deciduous woodlands of *Prunus korshinskyi* and *Lonicera nummulariifolia*, woodlands of deciduous *P. korshinskyi* and evergreen *Q. coccifera*, shrublands of *Astragalus gummifer*, and deciduous woodlands of *Quercus look* and *Acer monspessulanum* subsp. *microphyllum*. Four environmental variables exhibited significant influences in shaping vegetation composition: elevation, mean annual temperature, slope and northness. **Conclusions:** Five habitats are novelties proposed as sub-types for the national typology. Floristic affinities with Mount Barouk are highlighted. The nature reserve on the western slopes of Mount Hermon encompasses the majority of the identified habitats. The insights from this study and the habitat map are useful for the development of a management plan and conservation measures.

Taxonomic reference: International Plant Names Index (IPNI 2023).

Abbreviations: EUNIS = European Nature Information System; NMDS = nonmetric multidimensional scaling; UPGMA = unweighted pair group method with arithmetic mean; WGS84 = World Geodetic System, 1984.

Keywords

cliffs, endemism, EUNIS, habitat type, hedgehog-heath, vegetation classification, Lebanese national typology, Levant, montane-Mediterranean, *Prunus korshinskyi*, *Quercus look*, oro-Mediterranean

Introduction

Within the eastern Mediterranean, the Levant stands as the junction point between Europe, Africa, and Asia, where three floristic regions meet: the Saharo-Sindian region, the Mediterranean region, and the Irano-Turanian region (Takhtajan 1986). In this biogeographical crossroad, complex biodiversity patterns have emerged (Krupp et al. 2009) and are distributed among the three prominent components of the Levant: the Mediterranean region, the Syro-African Rift, and the Syrian desert. Geographic and geomorphologic features allow the demarcation between the Northern and the Southern Levants. The Northern Levant, extending from the Nur Mountains northward to Galilee southward, is characterised by its distinctive mountainous topography (Abel 1933; Vaumas 1954; Suriano 2013). Mount Lebanon, Anti-Lebanon, and Mount Hermon are located in the Northern Levant, forming the highest ranges across the entire Levant (Vaumas 1954). These ranges have been recognized as regional hotspots of biodiversity within the larger Mediterranean Basin 'macro' hotspot, attributed to their remarkable floristic endemism which accounts for 12% of the total flora (Médail and Quézel 1997, 1999; Myers et al. 2000; Verlaque et al. 2001; Cañadas et al. 2014). At the Lebanese national scale, these mountain ranges are of high-priority conservation value as they have been identified as Important Plant Areas (Bou Dagher-Kharrat et al. 2018) and as Key Biodiversity Areas (El Zein et al. 2018) due to the simultaneous presence of rare and endangered endemic plant species.

Lebanon is renowned for its distinctive vegetation types in the Levant. Since ancient times, dating back to 2600 years BC, its mountains have been recognized for their remarkable and iconic conifer forests, composed of cedar (*Cedrus libani*), fir (*Abies cilicica*), and juniper (*Juniperus excelsa*) (Vaumas 1954; Beals 1965; Mikesell 1969). Nevertheless, other types of vegetation also occur in these mountains, forming unique associations of plant species (Post and Dinsmore 1932; Mouterde 1966, 1970, 1984). Several publications have described the vegetation of Lebanon. The description of the climactic series of vegetation of Lebanon and their spatial distribution constitutes one of the greatest achievements in this discipline for the country (Abi-Saleh 1982; Abi-Saleh and Safi 1988). Complementary efforts have provided detailed information about the phytosociological associations that compose some forest types on the western slopes of the Mount Lebanon range (Chouchani et al. 1975; Barghachoun 1976; de Foucault et al. 2013; Stephan et al. 2019). Recently, a typology of the natural and semi-natural terrestrial habitat types has been developed (El Zein et al. 2022) aligned to the hierarchical structure of the habitat classification of the European Nature Information System (EUNIS) (Davies et al. 2004) to facilitate efforts for conservation across the Mediterranean Basin and in neighboring countries. Moreover, the use of an international classification system improves the recognition of local diversity and natural patrimony.

However, detailed descriptions of the plant communities for each habitat type in Lebanon still require improvement and are continuously developing. The habitat types present on the western slopes of Mount Hermon in Lebanon were partly characterised through the vegetation series (Abi-Saleh and Safi 1988). Part of the area was designated as a nature reserve in December 2020, promoting the undertaking of comprehensive studies to document and conserve the natural patrimony present. The primary objective of our study was to address this knowledge gap and comprehend the ecological characteristics and spatial distribution of vegetation types. This paper consequently proposes to characterize and map the different habitats of western Mount Hermon in Lebanon based on their plant communities.

Study area

Mount Hermon, or Jabal al-Shaykh in Arabic, is administratively divided into four parts: the Lebanese western slopes, the Syrian eastern slopes, the United Nations buffer zone where the United Nations Disengagement Observer Force (UNDOF) operates, and the Israeli-occupied southern slopes that are part of the Golan Heights (Dar 1988). It stands as the second-highest mountain in the Levant, reaching an elevation of 2,814 m a.s.l., and is often considered as the southern continuation of the Anti-Lebanon mountain range. The massif extends 25 km from west to east and 45 km from north to south . The entire range spans an area of approximately 1,000 km^2, with half of it located in Lebanon (Clermont-Ganneau 1903; Abel 1933).

Most of the upper stratum of Mount Hermon is dominated by Jurassic limestone (Dubertret 1955). In the mountain's circumference, Cretaceous strata occur with occasional veins of basalt (Dubertret 1955). In most of Lebanon, the soils are young, characterized by poor consistency and shallowness, especially on sloping terrains (Clermont-Ganneau 1903; Vaumas 1954). These conditions contribute to the development of terra rossa soils (Gèze 1956). On the highest slopes, rough terrain features have been created by karstic erosion, such as crags, boulders or sinkholes. Precipitation is quickly absorbed through the porous rocky substrate and feed different watersheds. Westward and southward, the waters feed the headstreams of the Jordan River, while eastward it feeds other springs descending to the Damascus basin (Abel 1933).

Mount Hermon has a typically Mediterranean climate, with January as the coldest month, and July and August as the warmest (Abi-Saleh and Safi 1988). The annual average temperature in Rashaya, at the base of Mount Hermon at 1,200 m a.s.l., is 15.6°C (Baldy 1959). In Rachaya, the mean maximum temperature of the warmest month is 34.1°C, while the mean minimum temperature of the coldest month is 0.5°C (Baldy 1959). The mean annual rainfall in Rashaya is 675 mm (Baldy 1959), reaching around 1,500 mm at peak (YMCA Lebanon 2005; Ayalon et al. 2013). Approximately 80% of the annual rainfall takes place between November and March. The growing season spans from May to mid-September, during which the majority of plant species flower and set seed.

The western slopes of Mount Hermon, part of the Lebanese territory (Figure 1), have been recognized for their floristic diversity (Arnold et al. 2015; Baydoun and Arnold 2017) and the presence of at least 21 endangered endemic plant taxa (El Zein and Kahale 2022). The flora of the area remains relatively understudied. For instance, a species not previously reported in the flora of Lebanon was recently observed there (El Zein et al. 2023). The first checklist of the flora of western Mount Hermon (Arnold et al. 2015) highlighted the significant contribution of the region to traditional ethnobotanical knowledge held by the local communities. The prolonged historical interactions between the land and the successive communities living there have given rise to diverse traditions and cultural heritages (Dar 1993; Farra Haddad 2021). Moreover, the area constitutes a repository for wild crop relatives and a cradle for the domestication of wheat ancestors (Ghossain et al. 2023).

Methods

Vegetation sampling

This study was conducted annually from 2020 to 2023, between May and August, corresponding to the spring and summer seasons, on the Lebanese western slopes of Mount Hermon, in the district of Rachaya. The sampled area ranged between elevations of 1,000 and 2,500 meters. Geographic coordinates (WGS84) for each plot were directly recorded in the field. The coordinates and elevation of the plots are provided in Suppl. material 1. We surveyed 169 circular plots, each spanning an area of 314 m². Several studies recommend surveying plots of large size, reaching up to 400 m², across diverse habitat types, including deserts, shrublands, temperate and tropical forests (Gillison 2001; Archaux et al. 2007; Hunter and Hunter 2020; Hao et al. 2021; Montenegro-Hoyos et al. 2022, Zeballos et al. 2023). For security reasons, we had to maintain a specific distance from the country borders, limiting the accessible area of the study site. The distribution of the survey plots is mapped in Figure 2. In each plot, we documented all vascular plant species, noting their respective cover-abundance through the phytosociological method (Braun-Blanquet 1932), and subsequently transformed the data using the ordinal scale (van der Maarel 1979) as follows: r: 1; +: 2; 1: 3; 2m: 4; 2a: 5; 2b: 6; 3: 7; 4: 8; 5: 9.

Artificial habitats, such as urban areas, planted forests, and agricultural lands, were not surveyed. The flora of Syria and Lebanon (Mouterde 1966, 1970, 1984) served as the reference for species identification. Species nomenclature was based on the International Plant Names Index (IPNI 2023).

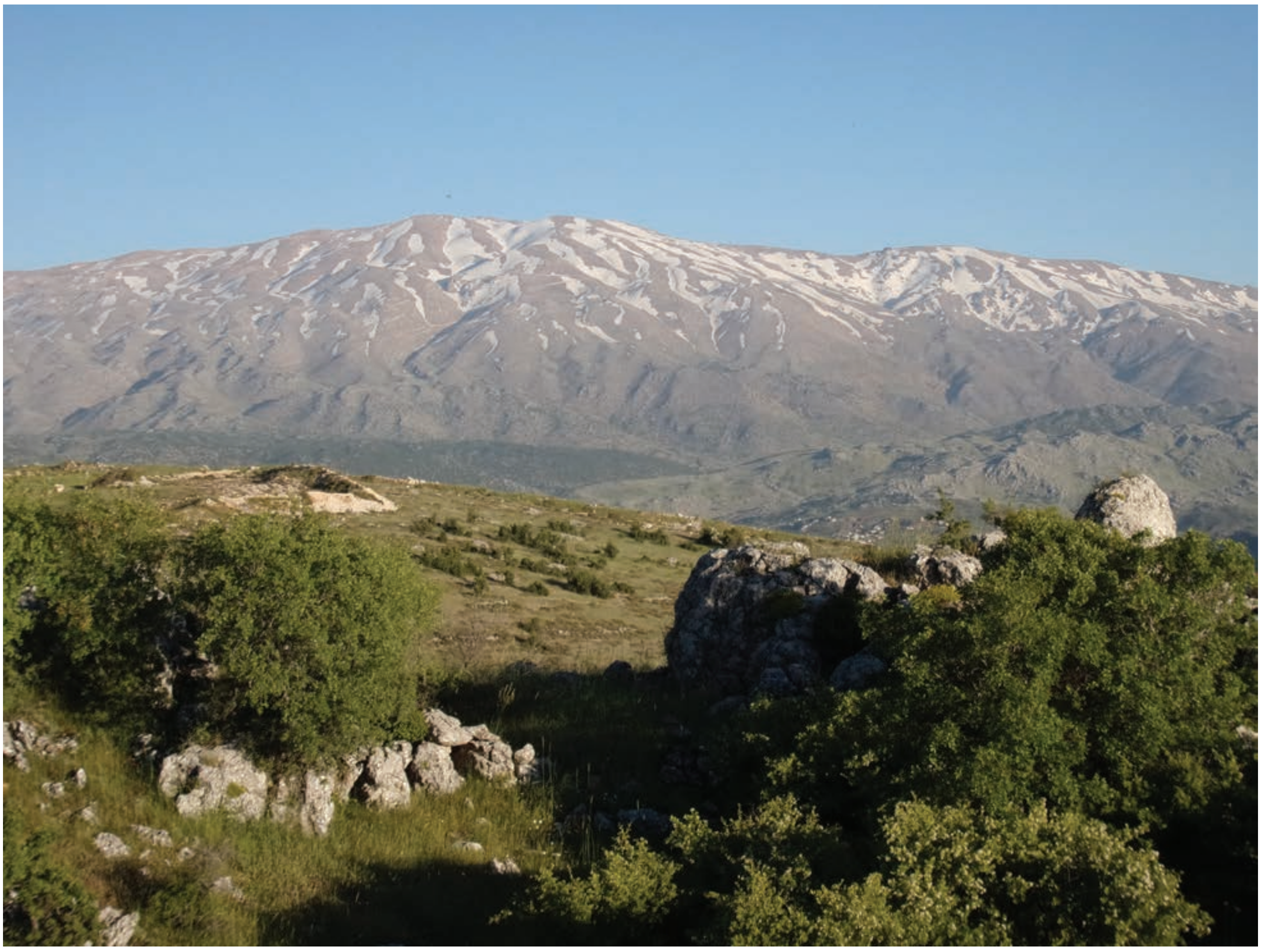

Figure 1. View on the western slopes of Mount Hermon in May 2019, Lebanon.

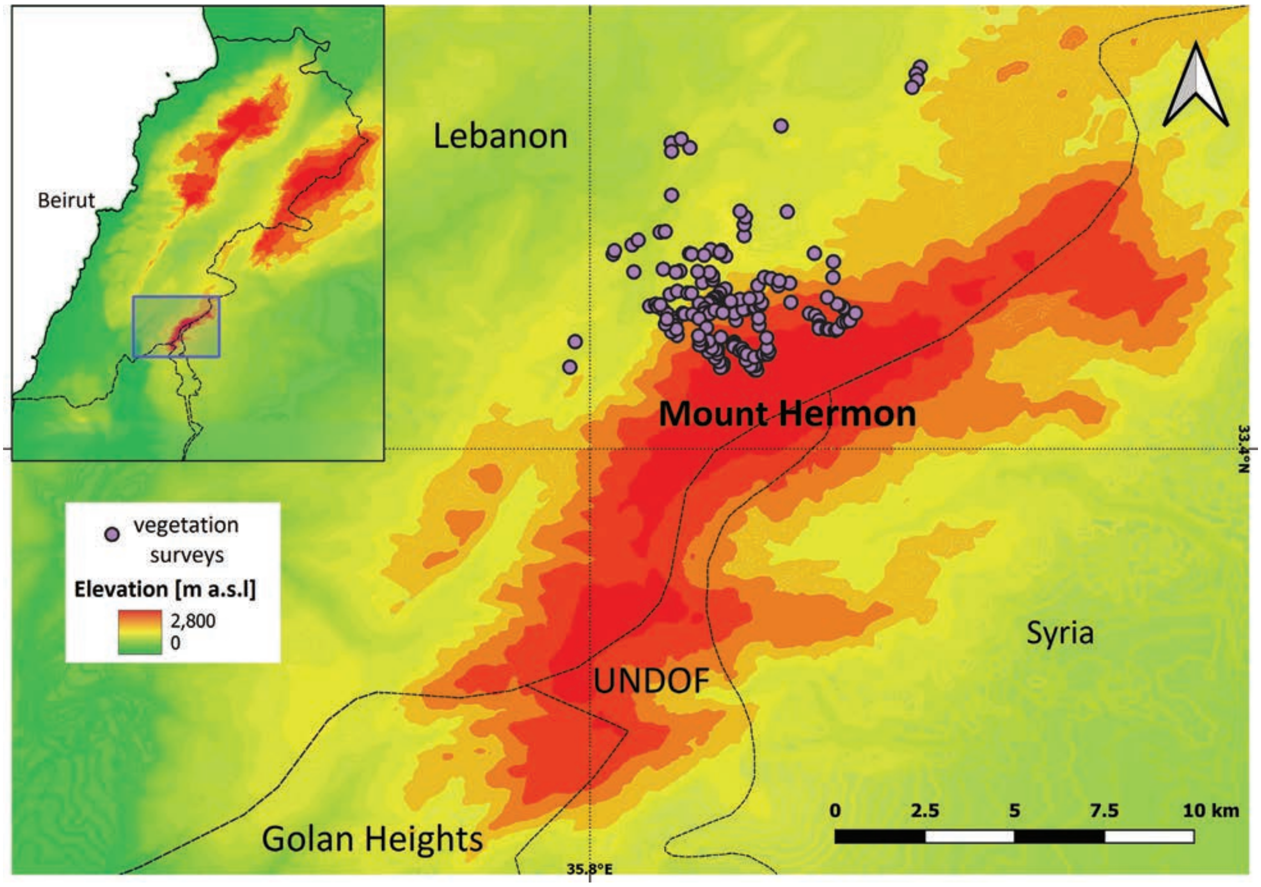

Figure 2. Map showing the geographic situation of Mount Hermon in Lebanon and vegetation plots surveyed between 2020 and 2023.

Environmental data

We extracted climatic variables, specifically the average annual precipitation and mean annual temperature calculated for the period from 1981 to 2010, from rasters provided by CHELSA database (Karger et al. 2017). The rasters have a resolution of 30 arc-seconds. Some studies demonstrated the significant role of these variables in influencing vegetation patterns and floristic composition (Dirnböck et al. 2002; Morris et al. 2016; Cabido et al. 2018; Zeballos et al. 2023). We extracted geomorphometric data, namely slope and aspect from SRTM data (Farr et al. 2007) available from the United States Geological Survey (USGS 2024), with a resolution of 1 arc-second. We transformed aspect into two components: eastness, represented by the sine, and northness, represented by the cosine. Eastness informs us about the slope orientation, ranging from west (sine = -1) to east (sine = 1). The sine value is 0 for slopes facing north or south. On the other hand, northness indicates the slope's orientation to the north (cosine = 1) or south (cosine = -1), with a cosine value of 0 for slopes facing east or west (Joly and Gillet 2017; Cheng et al. 2023). Elevation was recorded in the field. We prepared maps with the QGIS software (QGIS Development Team 2023), and downloaded the shapefiles from the DIVA-GIS website (DIVA-GIS 2023).

Data analysis

Initially, we calculated the compositional dissimilarity coefficients between sampled sites using the Bray–Curtis index, also known as the Steinhaus index (Bloom 1981; Somerfield 2008). Then, we conducted a hierarchical clustering analysis to group the sites, employing the unweighted pair group method with arithmetic mean (UPGMA; Sokal and Michener 1958; Belbin and McDonald 1993). Secondly, we applied the Nonmetric Multidimensional Scaling (NMDS) method (Kruskal 1964; Legendre and Legendre 2012) for multivariate ordination to complement the hierarchical cluster analyses. Additionally, NMDS was employed to investigate the relationship between species cover abundance per plot and environmental parameters, namely elevation, eastness, northness, slope, mean annual mean temperature and annual precipitation. The species scores were expanded based on the Wisconsin double standardization of the input data. We performed the NMDS ordination in two dimensions (Legendre and Legendre 2012). The analysis was repeated 100 times using random starting configurations to allow the algorithm to explore a larger portion of the solution space, reducing the likelihood of converging to a local minimum. For visual representation, we plotted the NMDS ordination against the environmental gradients to illustrate the ecological characteristics of the different vegetation types. We tested the overall significance of the NMDS ordination by applying a one-way Analysis of Similarities (ANOSIM; Clarke 1993; Clarke and Warwick 1994).

In a third step, we identified diagnostic species significantly associated to the different clusters. This analysis calculates the probability of having discriminating species for each group of sampled sites. We arbitrarily set the number of clusters to 10, based on the number of groups obtained from the cluster analysis. For each taxa, we calculated the percentage frequency, which indicates the constancy, and the phi-coefficient of association, which represents the fidelity (Tichý and Chytrý 2006). The phi-coefficient ranges from -1, indicating maximum negative fidelity, to 1, indicating maximum positive fidelity. We assessed the statistical significance by direct calculation of the probability of observed taxa concentrations using Fisher's exact test. Taxa with constancy ≥ 25% and significance $p \leq 0.001$ in at least one group of sites were considered constant. Taxa with a phi > 0.6 were considered highly diagnostic, those with phi > 0.4 were deemed quite diagnostic, and those with phi > 0.23 were considered relatively diagnostic.

We carried out all statistical analyses, as well as the extraction of bioclimatic variables, using the R software (R Core Team 2022) and associated packages: *BiodiversityR* (Kindt 2023), *devtools* (Wickham et al. 2022b), *dplyr* (Wickham et al. 2023b), *geoveg* (von Lampe and Schellenberg 2023), *ggfortify* (Horikoshi et al. 2023), *ggplot2* (Wickham et al. 2023c), *ggvegan* (Simpson 2023), *labdsv* (Roberts 2023), *lattice* (Sarkar et al. 2023), *memoise* (Wickham et al. 2021), metR (Campitelli 2023), *permute* (Simpson et al. 2022), *remotes* (Csárdi et al. 2021), *rlang* (Henry and Wickham 2023), *scales* (Wickham et al. 2022a), *terra* (Hijmans et al. 2023), *tibble* (Müller et al. 2023), *tidyr* (Wickham et al. 2023a), *vegan* (Oksanen et al. 2022), and *withr* (Hester et al. 2022).

We finally associated characterised habitat types to the national habitat typology of Lebanon (El Zein et al. 2022).

Results

Species richness and endemism

The fieldwork yielded a total of 3,120 observations, documenting 383 different plant taxa within the elevation range of 1,000 and 2,500 m a.s.l. The list of the species observed is provided in Suppl. material 2. The survey comprised 47 plant families, with *Fabaceae*, *Asteraceae*, *Poaceae*, *Apiaceae*, and *Lamiaceae* accounting for 56.7% of the total identified taxa (Figure 3). *Fabaceae* consisted of 67 taxa (17.5%), *Asteraceae* of 52 taxa (13.5%), *Poaceae* of 40 taxa (10.4%), *Apiaceae* of 30 taxa (7.8%), and *Lamiaceae* of 28 taxa (7.3%). The most diverse genera were *Trifolium* with 21 taxa, followed by *Astragalus* (10), *Silene* (7), *Allium* (6), *Bromus* (6), *Crepis* (6), *Galium* (6), and *Vicia* (6). In terms of life form, the taxa were distributed between 38 phanerophytes, 22 chamaephytes, 181 hemicryptophytes, 17 geophytes, and 125 therophytes. Among the phanerophytes, we found 11 tree taxa, comprising one conifer (*Juniperus excelsa*), one broadleaf evergreen tree (*Quercus coccifera*), and nine broadleaf deciduous trees (*Acer monspessulanum* subsp. *microphyllum*, *Crataegus azarolus*, *Pistacia terebinthus*, *Prunus korshinskyi*, *P. cocomilia*, *Pyrus syriaca*, *Quercus infectoria*, *Q. look* and *Styrax officinalis*). Twenty-four taxa were endemic to Mount Hermon and Mount Lebanon, including *Allium feinbergii*, *A. libani*, *Astragalus coluteoides*, *A. cruentiflorus*, *A. hermoneus*, *Bellevalia hermonis*, *Centaurea drabifolia* subsp. *libanotica*, *C. hololeuca*, *Cousinia hermonis*, *Crepis robertioides*, *Draba antilibanotica*, *D. vesicaria*, *Galium libanoticum*, *Hypericum libanoticum*, *Lophiolepis lappacea* subsp. *hermonis*, *Marrubium globosum* subsp. *libanoticum*, *Papaver libanoticum*, *Phlomis brevilabris*, *Quercus look*, *Salvia rubifolia*, *Scilla libanotica*, *Scutellaria utriculata*, *Silene libanotica*, and *S. makmeliana*; two taxa endemic to Mount Hermon and Anti-Lebanon, namely *Centaurea iberica* subsp. *hermonis* and *Euphorbia erinacea*; and one taxon endemic exclusively to Mount Hermon, *Erysimum verrucosum*.

Classification results

The classification is illustrated in Figure 4, revealing three main branches. The first branch, highlighted in red on the left, encompasses all sites surveyed above 2,000 m a.s.l. in elevation at the oro-Mediterranean belt. The second branch, colored in green, unites sites surveyed between 1,000 and 1,600 m a.s.l. in elevation at the supra-Mediterranean level. The last branch, boxed in yellow, includes sites sampled between 1,600 and 2,000 m a.s.l. in elevation at the montane-Mediterranean level. In total, ten clusters were formed from the 169 plots. Within the oro-Mediterranean branch, we identified two clusters of thorny hedgehog-heaths and one cluster of plots surveyed in cliffs. Within the supra-Mediterranean branch, one cluster comprises plots surveyed in grasslands, along with two additional clusters of plots surveyed in woodlands, one at the meso-Mediterranean level and another at the supra-Mediterranean level. Within the montane-Mediterranean branch, we observed one cluster representing plots surveyed in shrublands, and three clusters of plots surveyed in woodlands. These included scree deciduous woodlands, partially evergreen and deciduous woodlands and deciduous woodlands.

An abbreviated synoptic table, containing only diagnostic and constant species, is provided with each cluster (Table 1). It also includes the number of plots per cluster. The entire synoptic table is presented in Suppl. materials 3, 4.

Ordination and environmental gradients

The arrangement of the sites in a two-dimensional NMDS ordination space (Figure 5) closely resemble the grouping obtained from the classification (K = 2; stress = 0.1541).

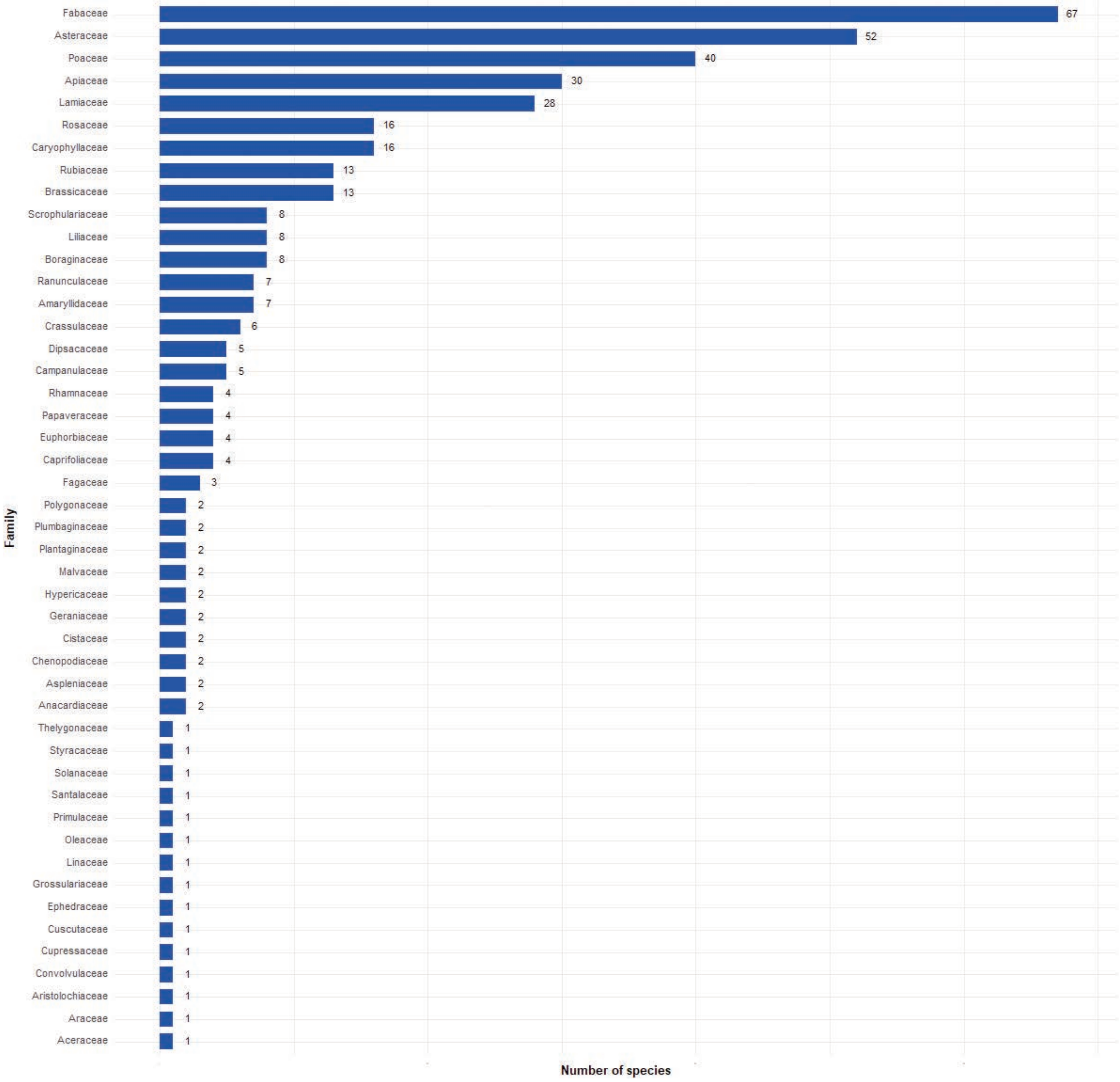

Figure 3. Number of taxa per family surveyed in Mount Hermon**.**

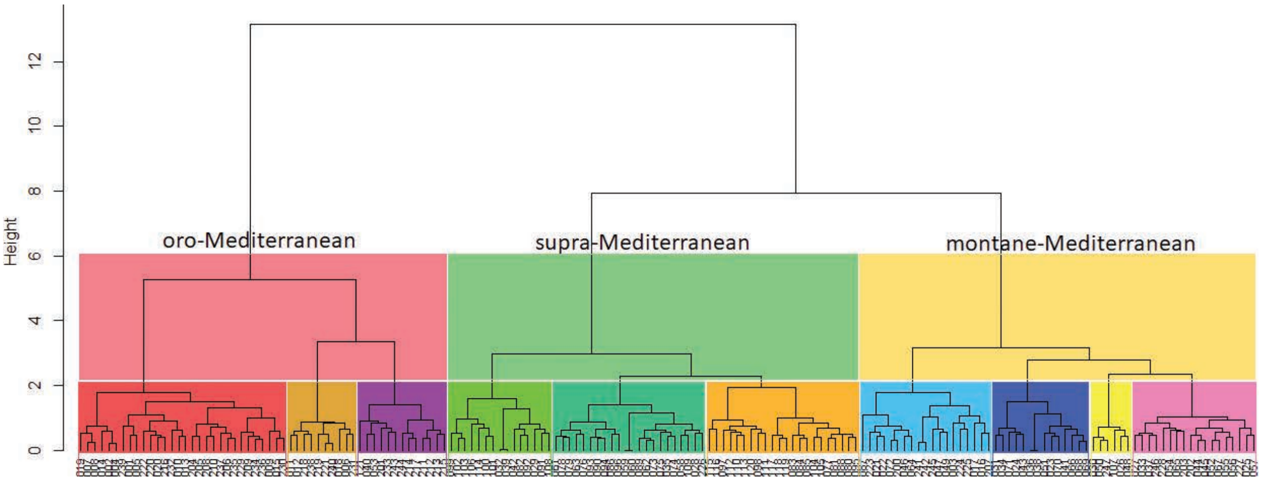

Figure 4. Cluster dendrogram built using UPGMA from the dissimilarity matrix among plots of western slopes of Mount Hermon in Lebanon.

Table 1. Abbreviated synoptic table of the ten groups obtained from the classification of 169 plots surveyed in the western slopes of Mount Hermon in Lebanon. The frequency (%) of occurrence and phi coefficient of all diagnostic and constant plant species in each group is shown. The species are sorted by decreasing fidelity (phi) within each group. phi > 0.6: dark grey; phi > 0.4: grey; phi > 0.23: light grey. Only species with constancy (Freq) ≥ 25% and significance p ≤ 0.001 in at least one group were included in the table. Vegetation types are: 1, Oro-Med. hedgehog-heaths of *Astragalus echinus* and *Noaea mucronata*; 2, Oro-Med. hedgehog-heaths of *Tanacetum densum* and *Astragalus cruentiflorus*; 3, Oro-Med. montane cliffs of *Rosularia sempervivum* subsp. *libanotica*; 4, Supra-Med. grasslands with *Eryngium glomeratum*; 5, Upper supra-Med. woodlands of *Quercus infectoria*, *Q. coccifera* and *Crataegus azarolus*; 6, Lower supra-Med. woodlands of *Quercus coccifera*; 7, Scree montane woodlands of *Prunus korshinskyi* and *Lonicera nummulariifolia*; 8, Montane woodlands of *Prunus korshinskyi* and *Quercus coccifera*; 9, Montane thickets of *Astragalus gummifer*; 10, Montane woodlands of *Quercus look* and *Acer monspessulanum* subsp. *microphyllum*. Med = Mediterranean.

Group number	**1**		**2**		**3**		**4**		**5**		**6**		**7**		**8**		**9**		**10**	
Number of sites per group	30		10		13		15		22		22		19		14		6		18	
Species	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***
Prunus prostrata	93	0.46	80	0.36	62	0.23														
Noaea mucronata	70	0.65																		
Astragalus echinus	60	0.63																		
Onobrychis cornuta	57	0.49																		
Cousinia hermonis	53	0.37																		
Eryngium heldreichii	50	0.65																		
Astragalus coluteoides	40	0.53																		
Acantholimon libanoticum	33	0.51																		
Verbascum cedreti	33	0.41																		
Veronica polifolia	30	0.39																		
Marrubium globosum subsp. *libanoticum*	43	0.34																		
Tanacetum densum			90	0.62	54	0.31														
Bromus tomentellus	57	0.30	90	0.58																
Alkanna orientalis			80	0.75																
Acantholimon ulicinum			70	0.71																
Astragalus cruentiflorus			60	0.63																
Sabulina juniperina			50	0.49	31	0.26														
Odontarrhena condensata subsp. *flexibilis*			30	0.53																
Rosularia sempervivum subsp. *libanotica*					92	0.70														
Ferulago trachycarpa					85	0.67														
Arabis caucasica					77	0.79														
Silene odontopetala					62	0.70														
Scrophularia libanotica var. *australis*					46	0.61														
Nepeta cilicica					46	0.41														
Rhamnus libanotica					38	0.52														
Lamium garganicum subsp. *striatum*					38	0.44														
Arenaria deflexa					31	0.53														
Campanula cymbalaria					31	0.53														
Heracleum humile					31	0.53														
Brunnera orientalis					31	0.50														
Avena sterilis							87	0.52			82	0.48								
Eryngium glomeratum							73	0.40							71	0.38				
Echinops spinosissimus subsp. *macrolepis*							67	0.48												
Trifolium boissieri							60	0.38	55	0.33	50	0.29								
Picnomon acarna							47	0.46												
Rhamnus punctata							33	0.37												
Bituminaria bituminosa							27	0.50												
Carthamus glaucus							27	0.45												
Ononis spinosa subsp. *leiosperma*							27	0.41												
Crataegus azarolus									100	0.59	59	0.27								
Salvia rubifolia									68	0.34										
Trifolium clusii									50	0.38	45	0.34								
Chrysojasminum fruticans									27	0.33										
Quercus coccifera									86	0.38	95	0.44			79	0.32				
Hordeum bulbosum							93	0.28	91	0.27							100	0.33		
Erysimum verrucosum									77	0.27							83	0.31		

Group number	1		2		3		4		5		6		7		8		9		10	
Number of sites per group	30		10		13		15		22		22		19		14		6		18	
Species	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***	**Freq**	***phi***
Dactylis glomerata									82	0.25	95	0.34							89	0.29
Trifolium stellatum											77	0.65								
Quercus infectoria									64	0.44	77	0.57								
Euphorbia hierosolymitana var. hierosolymitana											68	0.64								
Galium libanoticum											64	0.32								
Lathyrus aphaca											59	0.63								
Trifolium purpureum											59	0.57								
Trifolium grandiflorum											55	0.61								
Bromus sterilis											55	0.37								
Crepis reuteriana											50	0.58								
Lagoecia cuminoides											50	0.45								
Eryngium creticum											50	0.41								
Rhagadiolus edulis									36	0.24	50	0.38								
Poa bulbosa											50	0.38								
Campanula rapunculus subsp. *lambertiana*											41	0.52								
Lolium perenne											41	0.47								
Achnatherum bromoides											41	0.41								
Coronilla scorpioides											36	0.58								
Poa pratensis											36	0.50								
Klasea cerinthifolia											36	0.46								
Pistacia terebinthus											36	0.43								
Lapsana communis subsp. *pisidica*											36	0.42								
Scutellaria brevibracteata											36	0.34							33	0.30
Trifolium scabrum											36	0.31								
Hordeum spontaneum											32	0.54								
Ononis natrix											32	0.54								
Trifolium dasyurum											32	0.50								
Vicia tenuifolia											32	0.46								
Scabiosa palaestina											32	0.45								
Fibigia clypeata subsp. *clypeata*											32	0.40								
Trifolium plebeium											32	0.36								
Melica inaequiglumis											27	0.45								
Johrenia dichotoma											27	0.43								
Salvia multicaulis											27	0.41								
Scorzonera phaeopappa											27	0.39								
Orlaya platycarpos											27	0.39								
Allium stamineum											27	0.35								
Trifolium pilulare											27	0.33								
Galium incanum													42	0.41						
Phlomis chrysophylla									59	0.30	64	0.34			86	0.51				
Lonicera nummulariifolia													53	0.29			67	0.41		
Prunus korshinskyi													47	0.28	57	0.37				
Pseudoroegneria libanotica													47	0.28						
Euphorbia erinacea															36	0.39				
Phleum montanum															29	0.42				
Astragalus gummifer																	100	0.85		
Rubia tenuifolia									82	0.25									100	0.37
Cephalaria stellipilis													84	0.38	71	0.29			89	0.41
Quercus look															43	0.24			83	0.61
Acer monspessulanum subsp. *microphyllum*																			67	0.33
Eryngium billardierei																	33	0.26	44	0.38

Retaining the numbering and colors of the groups from the classification aids in an easy comparison with Figure 4. The degree of separation between groups, indicating differences in vegetation composition, was significant (ANOSIM $R = 0.80$; $p < 0.0001$). Community composition patterns per plot correlate with environmental gradients. The arrows in the ordination space represent the principal direction of variation and the strength of correlation for the environmental variables. Four environmental variables exhibited significant correlations with the NMDS axes, signifying their crucial influences in shaping vegetation composition: elevation ($r^2 = 0.889$; $p < 0.001$), mean annual temperature (temp; $r^2 = 0.858$; $p < 0.001$), slope ($r^2 = 0.227$; $p < 0.001$) and northness ($r^2 = 0.082$; $p < 0.01$). The two other environmental variables didn’t show a significant correlation ($p > 0.3$): annual precipitation (precip; $r^2 = 0.012$) and eastness ($r^2 = 0.007$). Axis 1 distinctly delineates the supra-, montane- and oro-Mediterranean levels. Elevation and

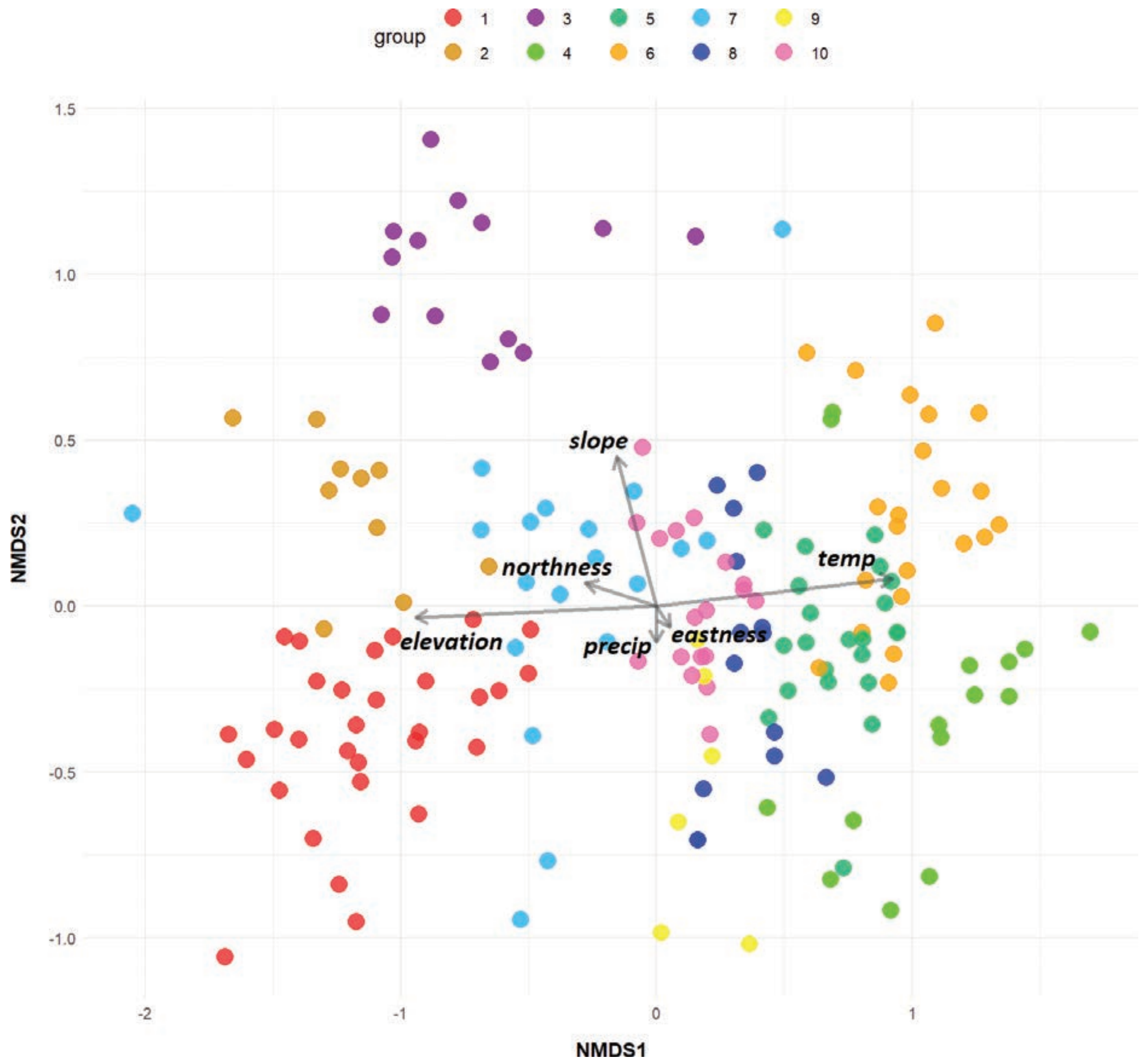

Figure 5. NMDS Ordination of 169 plots sampled in western Mount Hermon in Lebanon. Colors indicate the 10 groups obtained from the UPGMA clustering. Arrows indicate the environmental variables. temp = mean annual temperature; precip = annual precipitation.

temperature run almost parallel to the first axis, indicating a direct relationship between these two environmental variables. Therefore, Axis 1 can be interpreted as an altitudinal gradient where temperature increases in the opposite direction. Axis 2 separates clusters within each altitudinal level, with slope being the variable most correlated to this axis. The fourth significant variable, northness, displays a diagonal orientation in the ordination space, suggesting a combined correlation with variations along both NMDS axes.

Characterisation of habitat types

The habitat types are described based on the grouping obtained from the classification, the correlation with environmental variables, as displayed in the NMDS ordination, and their constant and diagnostic plant species. The code of habitat type according to the Lebanese national typology is also provided. The habitats are presented in the same order of grouping of the classification.

Oro-Mediterranean belt (2,000–2,800 m a.s.l.)

In Mount Hermon, the oro-Mediterranean belt features a complex succession of low thorny-cushion shrublands, rocky grasslands, limestone rock pavements, cliffs and screes. The environment of this altitudinal belt is characterised by bare mineral substrate with limited soil presence and scarce vegetation cover owing to harsh climatic conditions, including abundant precipitation, snow cover in winter, prolonged summer drought, and the intense wind.

1. Oro-Mediterranean hedgehog-heaths of *Astragalus echinus* and *Noaea mucronata* in thalweg and slopes – S759_LB1

This habitat is composed of low thorny-cushion shrublands known as hedgehog-heaths (Figure 6). This vegetation is characterised by the diagnostic species *Prunus prostrata*, *Noaea mucronata*, *Astragalus echinus*, *Onobrychis cornuta*, *Cousinia hermonis*, *Eryngium heldreichii*, *Astragalus coluteoides*, *Acantholimon libanoticum*, *Verbascum cedreti*, and *Veronica polifolia* in decreasing diagnostic

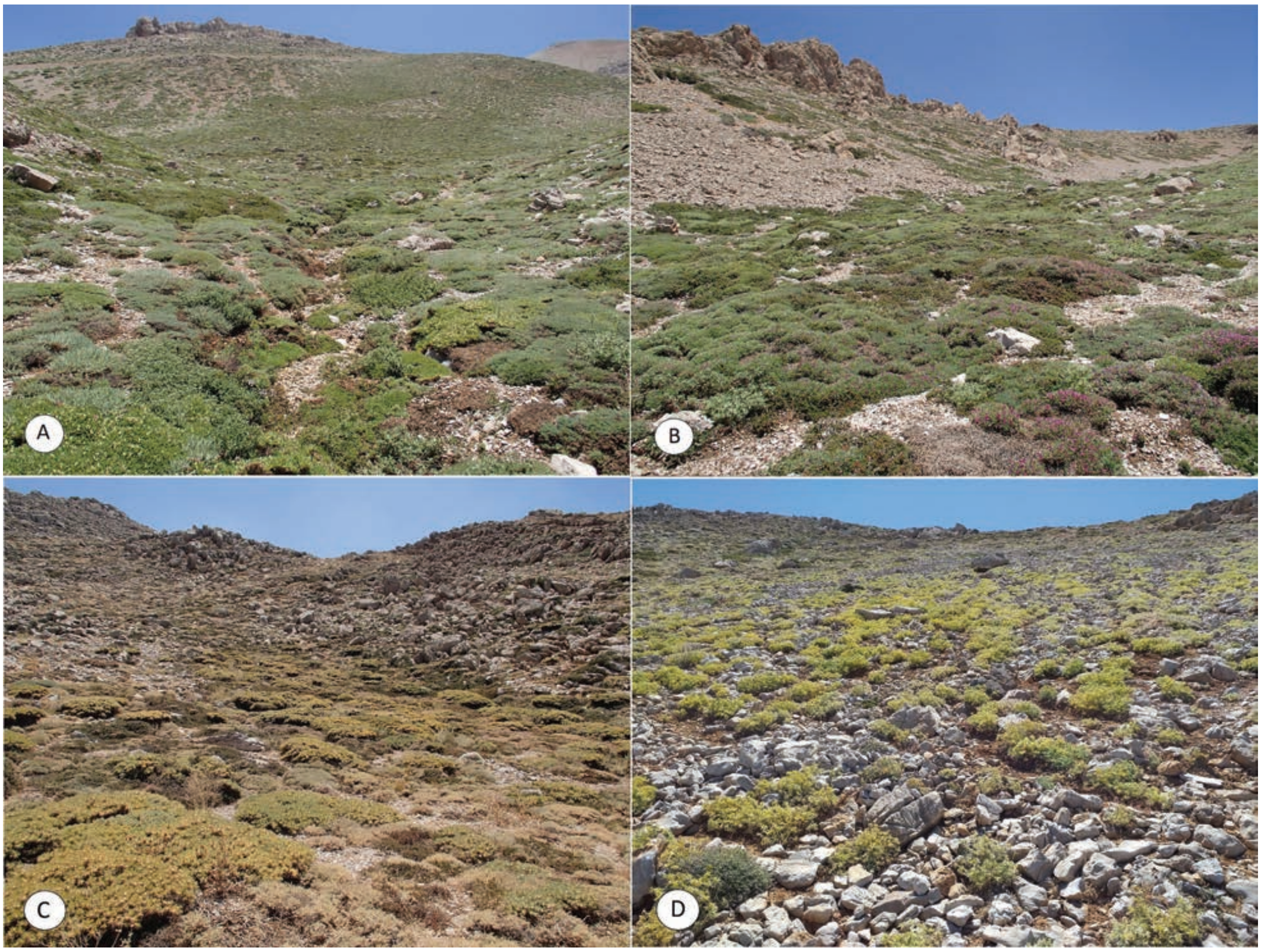

Figure 6. Oro-Mediterranean hedgehog-heaths of *Astragalus echinus* and *Noaea mucronata* in thalweg and slopes in the western slopes of Mount Hermon in Lebanon in 2020 **A.** Dominated by *Astragalus hermoneus* and *A. coluteoides*; **B.** Dominated by *Onobrychis cornuta* and *Prunus prostrata*; **C.** Dominated by *A. echinus* and *Noaea mucronata*; **D.** Dominated by *Eryngium heldreichii*.

value. This type of hedgehog-heaths is found in slopes and thalweg where the soil is relatively deeper. Other taxa are commonly found without being diagnostic or constant, namely *Astragalus hermoneus*, *A. nummularius* subsp. *trichopterus*, *Campanula stricta* var. *libanotica*, *Cruciata taurica*, *Dichoropetalum alpinum* and *Teucrium orientale*. Twelve of the twenty-six endemic taxa, such as *Astragalus hermoneus*, *Lophiolepis lappacea* subsp. *hermonis*, *Marrubium globosum* subsp. *libanoticum*, and *Phlomis brevilabris*, were observed in this habitat type.

2. Oro-Mediterranean hedgehog-heaths of *Tanacetum densum* and *Astragalus cruentiflorus* – S759_LB1

This habitat represents another type of hedgehog-heath, distinguished by the diagnostic taxa *Tanacetum densum*, *Bromus tomentellus*, *Alkanna orientalis*, *Acantholimon ulicinum*, *Astragalus cruentiflorus*, *Sabulina juniperina*, and *Odontarrhena condensata* subsp. *flexibilis* in decreasing diagnostic value (Figure 7). The surveyed sites exhibited pronounced xerophytic conditions, attributed to their exposure to wind and sun, along with the scarcity of soil, typical of sites located on the hilltops or south-oriented slopes. Three endemic taxa, namely *Cousinia hermonis*, *Draba antilibanotica*, and *D. vesicaria*, were observed in this habitat type.

3. Oro-Mediterranean and montane limestone cliffs of *Rosularia sempervivum* subsp. *libanotica* – U38

Limestone cliffs are present in both montane and oro-Mediterranean levels (Figure 8). The diagnostic taxa are *Rosularia sempervivum* subsp. *libanotica*, *Ferulago trachycarpa*, *Arabis caucasica*, *Silene odontopetala*, *Scrophularia libanotica* var. *australis*, *Rhamnus libanotica*, *Lamium garganicum* subsp. *striatum*, *Arenaria deflexa*, and *Campanula cymbalaria* in decreasing diagnostic value. Some diagnostic species are always located at the bottom of the cliffs, namely *Nepeta cilicica*, *Heracleum humile*, and *Brunnera orientalis*. Four endemic taxa, namely *Bellevalia hermonis*, *Centaurea drabifolia* subsp. *libanotica*, *Scutellaria utriculata*, and *Silene makmeliana*, were observed in this habitat type.

Supra-Mediterranean belt (1,000–1,600 m a.s.l.)

The supra-Mediterranean altitudinal level is characterised by the presence of sclerophyllous forests of *Quercus coccifera* and deciduous broadleaf woodland of *Q. infectoria*, primarily found in the hills at the base of Mount Hermon. This altitudinal belt exhibits a predilection for human activities. The general landscape consisted of rocky

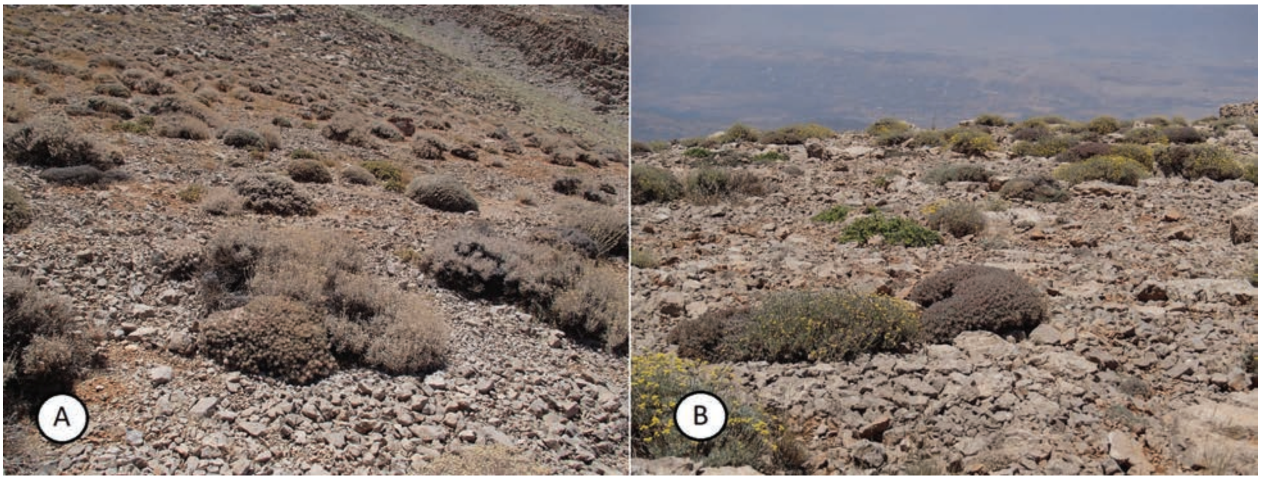

Figure 7. Oro-Mediterranean hedgehog-heaths of *Tanacetum densum* and *Astragalus cruentiflorus* in the western slopes of Mount Hermon in Lebanon in 2022.

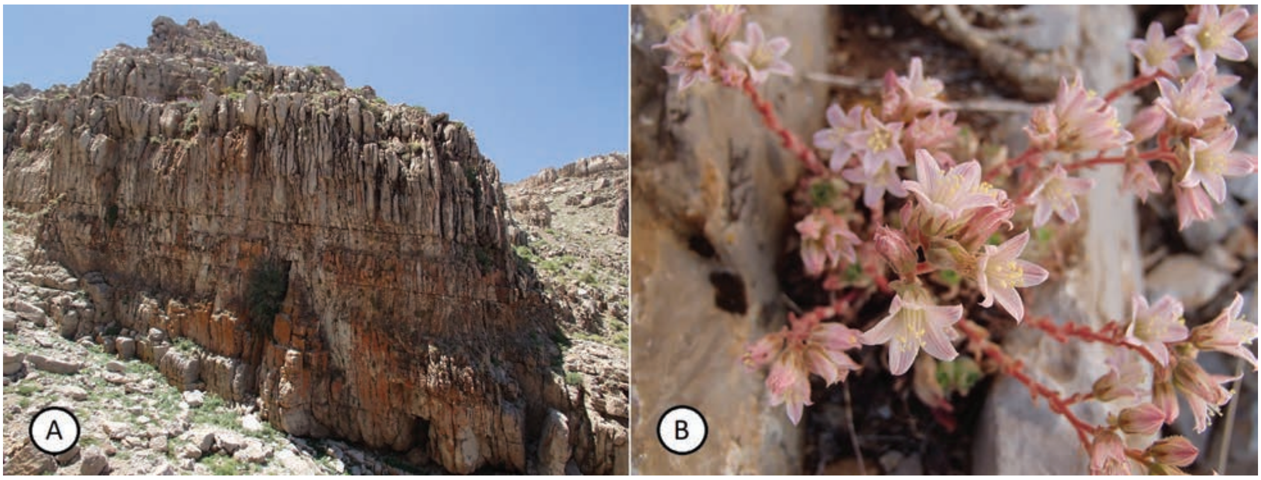

Figure 8. A. Limestone cliffs at the oro-Mediterranean level in the western slopes of Mount Hermon in Lebanon in 2022; **B.** *Rosularia sempervivum* subsp. *libanotica* in flower.

grasslands and shrublands used as pastures, interspersed with patches of woodlands, agricultural fields, and human settlements.

4. Supra-Mediterranean grasslands with *Eryngium glomeratum* – R1E_LB1

These grasslands are the results of the degradation of the supra-Mediterranean evergreen woodlands of *Quercus coccifera* and evergreen-deciduous woodlands of *Q. infectoria* (Figure 9). They are maintained as grasslands by intensive grazing which prevent the recolonisation by trees. The diagnostic taxa are *Avena sterilis*, *Eryngium glomeratum*, *Echinops spinosissimus* subsp. *macrolepis*, *Hordeum bulbosum*, *Trifolium boissieri*, *Picnomon acarna*, *Rhamnus punctata*, *Bituminaria bituminosa*, *Carthamus glaucus*, and *Ononis spinosa* subsp. *leiosperma* in decreasing diagnostic value. Sometimes very sparse shrubs or low trees of *Q. coccifera*, dwarfed by overgrazing, occur in the rocky grasslands. Two endemic taxa, *Astragalus oleifolius* and *Centaurea iberica* subsp. *hermonis*, were observed in this habitat type.

5. Upper supra-Mediterranean deciduous woodlands of *Quercus infectoria*, *Q. coccifera*, and thickets of *Crataegus azarolus* – T1953_LB1

This group includes two distinct types of vegetation that share a similar floristic composition. One of them, the thickets of *Crataegus azarolus*, represents the degraded form of the deciduous woodlands of *Q. infectoria*, and *Quercus coccifera* (Figure 10). The prevalence of *Quercus infectoria*, either dominantly or in conjunction with *Quercus coccifera*, is a defining characteristic of this woodland type, referred to as sub-Mediterranean thermophilous deciduous oak forest. The diagnostic species are *Crataegus azarolus*, *Salvia rubifolia*, *Trifolium clusii*, *Chrysojasminum fruticans*, *Q. coccifera* and *Q. infectoria*. Thickets are dense stands of shrubs or low trees, typically not exceeding 2 m in height. The thickets of *C. azarolus* are widespread at the upper supra-Mediterranean level, resulting from the degradation of woodlands. These formations act as pioneer habitats, colonising abandoned agricultural terraces and paving the way for the subsequent establishment of oak

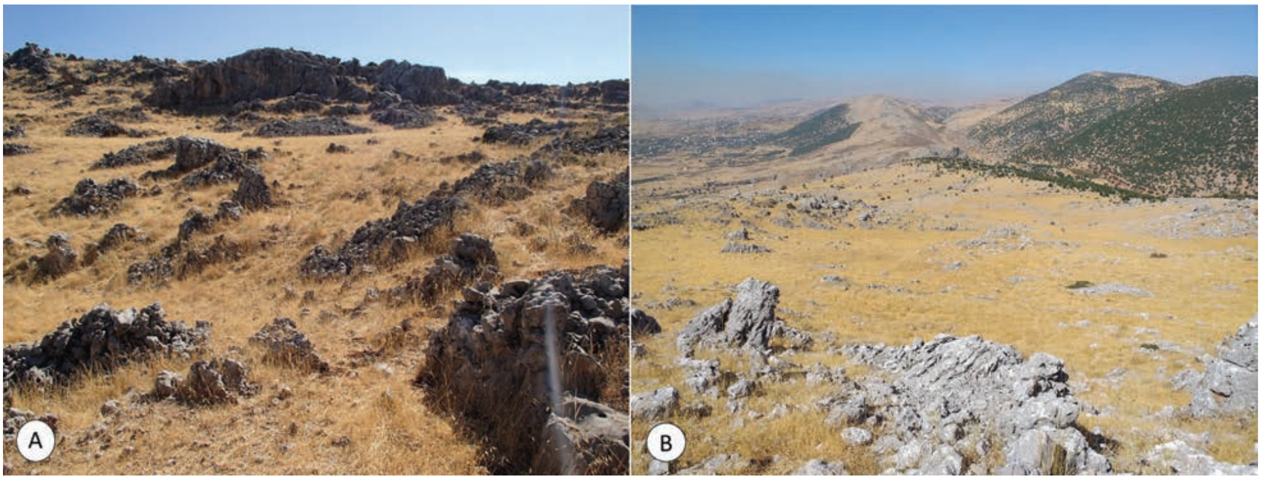

Figure 9. Supra-Mediterranean grasslands in the western slopes of Mount Hermon in Lebanon in 2020 **A.** above Qsar el-Jabal, next to Ain Hircha in summer; **B.** above Berket el-Yebse in spring.

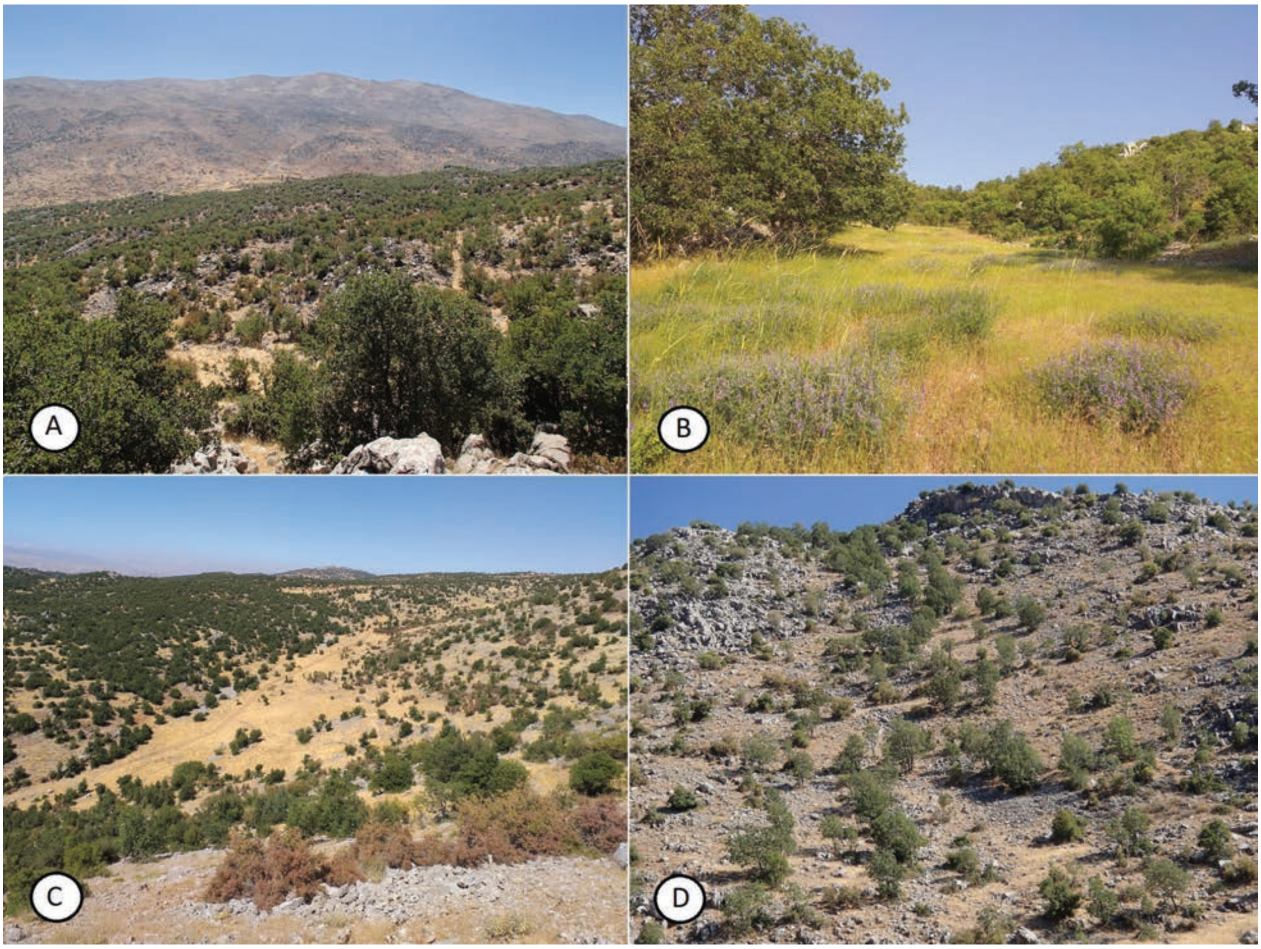

Figure 10. Upper supra-Mediterranean woodlands of *Quercus infectoria*, *Q. coccifera* with thickets of *Crataegus azarolus* in 2020 **A.** In Hima Hassan, in July; **B.** A thalweg with grassland within the woodland above Kfar Qouq in May; **C.** Contrast between preserved woodlands above Hima el-Kadarin on the left and degraded woodland with thickets of *C. azarolus* characterized by their reddish color in August; **D.** Degraded slope with remaining *Q. infectoria* in July.

forests. The thickets are scattered intermittently, alternating with extensive patches of grasslands, where *Phlomis chrysophylla*, *Hordeum bulbosum*, *Rubia tenuifolia*, and *Erysimum verrucosum* are also considered diagnostic species, albeit with a low fidelity coefficient as they are also found in other vegetation groups. *Erysimum verrucosum* is endemic to Mount Hermon, and *Salvia rubifolia* is endemic to Mount Lebanon, Anti-Lebanon ranges, and Mount Hermon. In total, four endemic taxa were observed in these habitat types.

The dominance of the evergreen *Q. coccifera* and deciduous *Q. infectoria* in woodlands alternates according to geomomorphology and soil depth. Small hills with rocky and shallow soils host woodlands of *Q. coccifera*. In contrast, thalwegs, characterised by the presence of soil, greater protection from the wind, and lower sun exposition, support woodlands with tall trees, particularly *Q. infectoria*. However, in the past, some parts of Mount Hermon's thalwegs were preferred for wood exploitation and agriculture, leading to tree removal. Areas with soils are distributed between the rocky hills, giving them this linear shape. Presently, some of these thalwegs face intensive grazing, hindering the regeneration of the deciduous woodlands. This has resulted in a composite landscape featuring alternating successions of linear thalwegs grasslands with tall *Q. infectoria* trees inserted among rocky hills with evergreen shorter *Q. coccifera* trees, creating a characteristic mosaic of vegetation types.

6. Lower supra-Mediterranean evergreen *Quercus coccifera* woodlands – T213_LB2

Climactic forests of the lower supra-Mediterranean in western Mount Hermon are characterised by the dominance of *Quercus coccifera*, reaching up to 70% of the proportion of trees in some sites (Figure 11). Stands are dense but often low, not exceeding 4 m in height, and display a coppice physiognomy believed to be a result of a long history of exploitation and forest fires. Some of the most significant diagnostic tree species of this habitat are *Q. coccifera*, *Q. infectoria* and *Pistacia terebinthus*. Some of the most significant diagnostic herbaceous taxa are *Dactylis glomerata*, *Trifolium stellatum*, *T. purpureum*, *T. grandiflorum*, *Euphorbia hierosolymitana* var. *hierosolymitana*, *Galium libanoticum*, *Lathyrus aphaca*, *Bromus sterilis*, *Crepis reuteriana*, *Lagoecia cuminoides*, *Eryngium creticum*, *Rhagadiolus edulis*, *Poa bulbosa*, *P. pratensis*, *Campanula rapunculus*, *Lolium perenne*, *Achnatherum bromoides* and *Klasea cerinthifolia*. Four endemic taxa, namely *Centaurea iberica* subsp. *hermonis*, *Galium libanoticum*, *Salvia rubifolia*, and *Silene makmeliana*, were observed in these habitat types.

Montane-Mediterranean belt (1,600–2,000 m a.s.l.)

Mount Hermon is distinctive for hosting sparse deciduous woodlands, primarily composed of the endemic thermophilous oak *Quercus look*. The specific topography, slope aspect, and steepness play crucial roles in determining the type of woodlands present. Additionally, historical tree exploitation has significantly impacted the physiognomy of these woodlands, often resulting in a succession of sparse woodlands and degraded habitats, such as rocky shrublands, rocky grasslands, and screes.

7. Scree deciduous montane woodlands of *Prunus korshinskyi* and *Lonicera nummulariifolia* – T19B9_LB1

Steep slopes of unstable limestone screes in the montane-Mediterranean belt are predominantly covered with sparse woodlands, primarily dominated by *Prunus korshinskyi* or *Lonicera nummulariifolia* (Figure 12). These formations, rarely exceeding 3 m in height, feature *P. korshinskyi* and *L. nummulariifolia* along with diagnostic herbaceous species well-adapted to screes and unstable rocky substrate, such as *Galium incanum*, *Cephalaria stellipilis* and *Pseudoroegneria libanotica*. Other taxa commonly found on rocky outcrops and scress were frequently observed, though not considered diagnostic, including the sub-shrub *Atraphaxis billardierei* and other forbs, such as *Allium libani*, *Arrhenatherum kotschyi*, *Cousinia hermonis*, *Hypericum libanoticum*, *Nepeta glomerata* and *Scrophularia peyronii*. Six endemic taxa, namely *Allium libani*, *Cousinia hermonis*, *Erysimum verrucosum*, *Euphorbia erinacea*, *Hypericum libanoticum* and *Scutellaria utriculata* were observed in these habitat types.

8. Montane woodlands of deciduous *Prunus korshinskyi* and evergreen *Quercus coccifera* – T19B9_LB1 X T213_LB2

These montane woodlands typically develop on stable rocky slopes, often at hilltops or on west-oriented slopes (Figure 13). They form sparse woodlands alternating with low garrigues of *Phlomis*. The diagnostic species include deciduous *Prunus korshinskyi*, *Phlomis chrysophylla*,

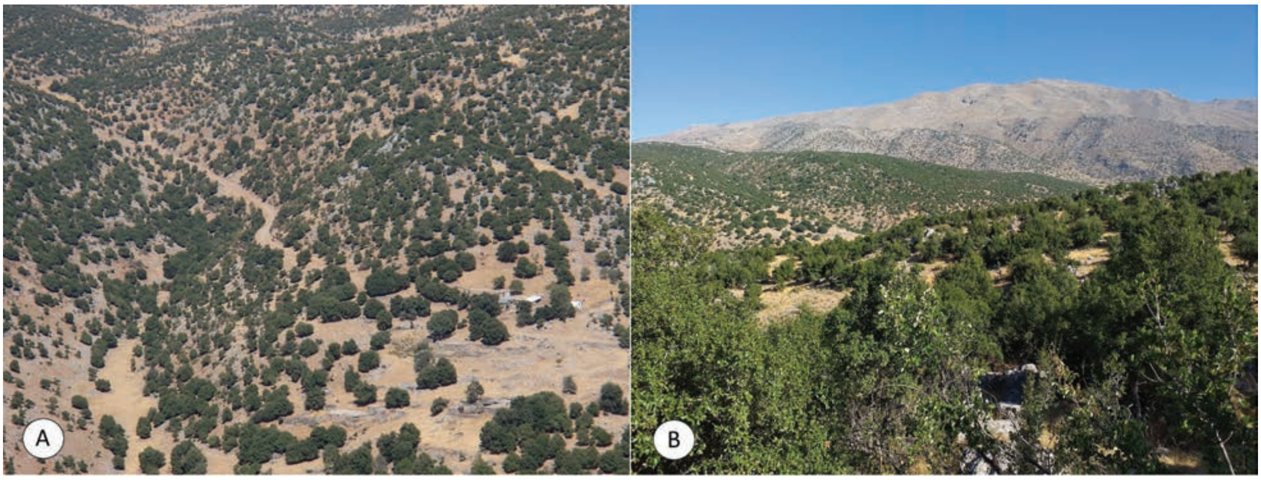

Figure 11. *Quercus coccifera* woodlands. **A.** In Wadi el-Feqaa; **B.** In Hima el-Kadarin.

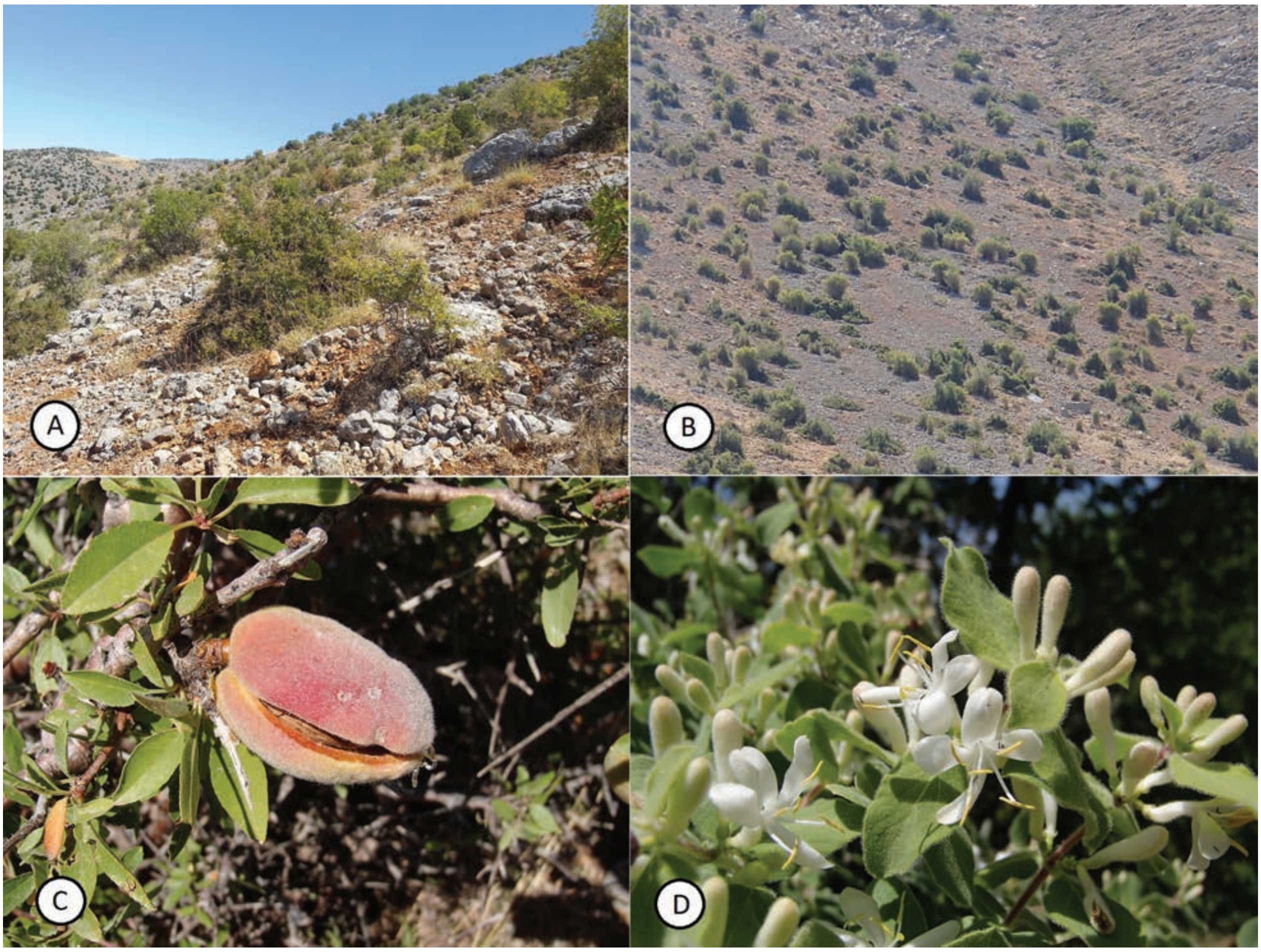

Figure 12. Montane deciduous woodlands on screes on the western slopes of Mount Hermon in Lebanon in 2020: **A.** with *Prunus korshinskyi*; **B.** with *Lonicera nummulariifolia*; **C.** Fruit of *Prunus korshinskyi*; **D.** Flowers of *Lonicera nummulariifolia*.

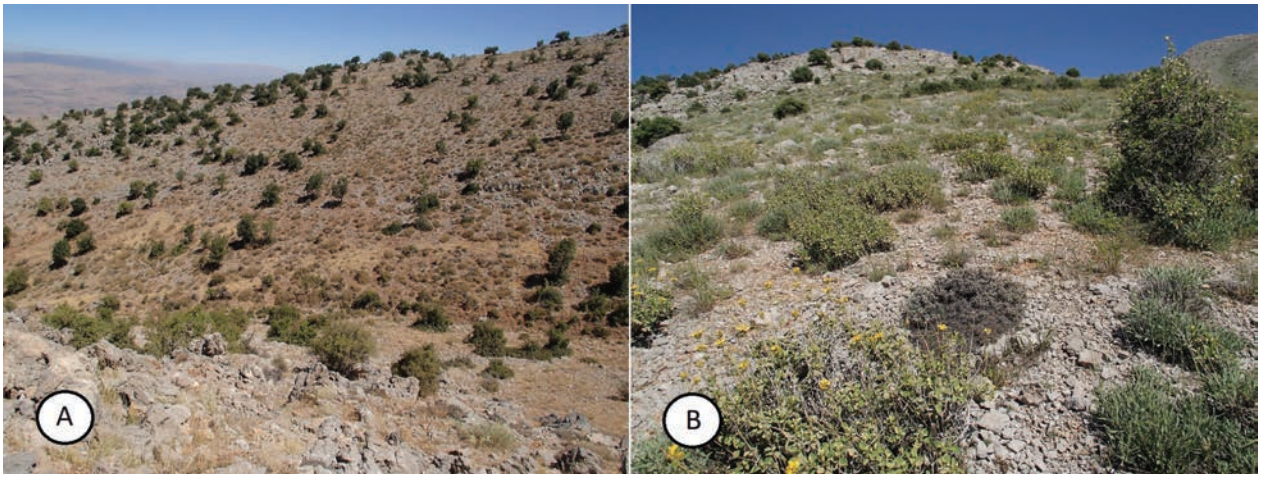

Figure 13. A. Montane woodlands of deciduous *Prunus korshinskyi* and evergreen *Quercus coccifera* on the western slopes of Mount Hermon in Lebanon in 2020; **B.** With garrigues of *Phlomis chrysophylla*.

Phleum montanum, and *Euphorbia erinacea*. While evergreen *Quercus coccifera* was a constant species, it was not considered diagnostic. In some areas with more intense grazing, the trees are reduced to low, compact and rounded shrubs, transforming the appearance of woodlands into garrigues. *Q. coccifera* is particularly susceptible to these effects. During the surveys in these woodlands, at around 1,600 m elevation, few isolated individuals of *Juniperus excelsa* were found. Apart from *Quercus look* and *Euphorbia erinacea*, two other endemic taxa were observed in this habitat type, namely *Hypericum libanoticum* and *Scutellaria utriculata*.

9. Montane-Mediterranean thalweg deciduous thickets of *Astragalus gummifer* –S3575_LB3

This type comprises montane deciduous thickets in thalwegs formed by *Astragalus gummifer*, a spiny shrub that can reach up to 1 m height and occupy up to 90% of the surface, restricting the establishment of other species (Figure 14). In areas with scree substrate, *Lonicera nummulariifolia* woodlands were observed in the contact zone around the thickets. Other taxa were commonly found without being diagnostic, such as the herbaceous *Eryngium billardierei*, *Erysimum verrucosum*, *Ferula biverticellata*, *Hordeum bulbosum*, *Marrubium globosum* subsp. *libanoticum*, and *Phlomis brevilabris*. Five endemic taxa were observed in this habitat type, namely *Centaurea iberica* subsp. *hermonis*, *Erysimum verrucosum*, *Galium libanoticum*, *Marrubium globosum* subsp. *libanoticum*, and *Phlomis brevilabris*.

10. Montane-Mediterranean deciduous *Quercus look* and *Acer monspessulanum* subsp. *microphyllum* woodlands – T1953_LB3

Quercus look, a thermophilous deciduous oak, forms small relictual clumps of trees or sparse woodlands in the montane-Mediterranean belt (Figure 15). The substrate is predominantly rocky, with soil poorly developed on limestone bedrock. Individuals of *Q. look* can reach up to 5 m height but are sometimes reduced to branched shrubs due to logging and overgrazing. Other diagnostic taxa were *Rubia tenuifolia*, *Cephalaria stellipilis*, *Acer monspessulanum* subsp. *microphyllum*, and *Eryngium billardierei* in decreasing diagnostic value. *A. monspessulanum* subsp. *microphyllum* is a tree often not exceeding 3 m height and, at times, reduced to low, compact, and rounded shrubs. The vine *Rubia tenuifolia* was prevalent in this habitat, observed growing without support, creeping at ground level, although it is typically widespread in Levantine woodlands at lower altitudes. Although not considered diagnostic, other taxa were relatively common in this habitat, such as the grass species *Dactylis glomerata*, *Elymus panormitanus*, and *Hordeum bulbosum*, as well as some forbs, such as *Anthemis pauciloba*, *Bupleurum exaltatum*, *Erysimum verrucosum*, *Nepeta cilicica*, *N. italica*, *Salvia rubifolia*, *Scutellaria brevibracteata*, and *Silene libanotica*. Ten endemic taxa were present in this habitat type, namely *Astragalus nummularius* subsp. *trichopterus*, *Centaurea iberica* subsp. *hermonis*, *Erysimum verrucosum*, *Euphorbia erinacea*, *Galium libanoticum*, *Hypericum libanoticum*, *Q. look*, *Salvia rubifolia*, *Scutellaria utriculata*, and *Silene libanotica*.

Habitat mapping

The mapping of habitat types of the western slopes of Mount Hermon encompassed areas characterised by their floristic composition (Figure 16), as well as agricultural fields, urbanised areas and planted forests.

Phryganas of *Sarcopoterium spinosum* (S7242) were sampled only once and grouped with supra-Mediterranean grasslands (cluster 4). However, they were mapped separately. These were confined to a small area in the foothills of Mount Hermon, typically occurring below 1,250 m of elevation. A single survey proved inadequate to fully characterise the floristic particularities of this habitat.

The last remaining population of *Juniperus excelsa* (T3D71) on the western slopes of Mount Hermon was located during fieldwork and consequently included in the mapping. Due to access restrictions, this habitat could not be physically reached and sampled.

Given the intricate and interwoven mosaics formed by related habitats sharing similar flora, the oro-Mediterranean habitats of hedgehog-heaths of *Astragalus echinus* and *Noaea mucronata* in thalweg and slopes, hedgehog-heaths of *Tanacetum densum* and *Astragalus cruentiflorus*, and cliffs of *Rosularia sempervivum* subsp. *libanotica*, were treated as a unified polygon. A similar approach was applied to the montane-Mediterranean woodlands of *Prunus korshinskyi* associated with *Lonicera nummulariifolia* or with *Quercus coccifera* in combination with *Phlomis chrysophylla* garrigues.

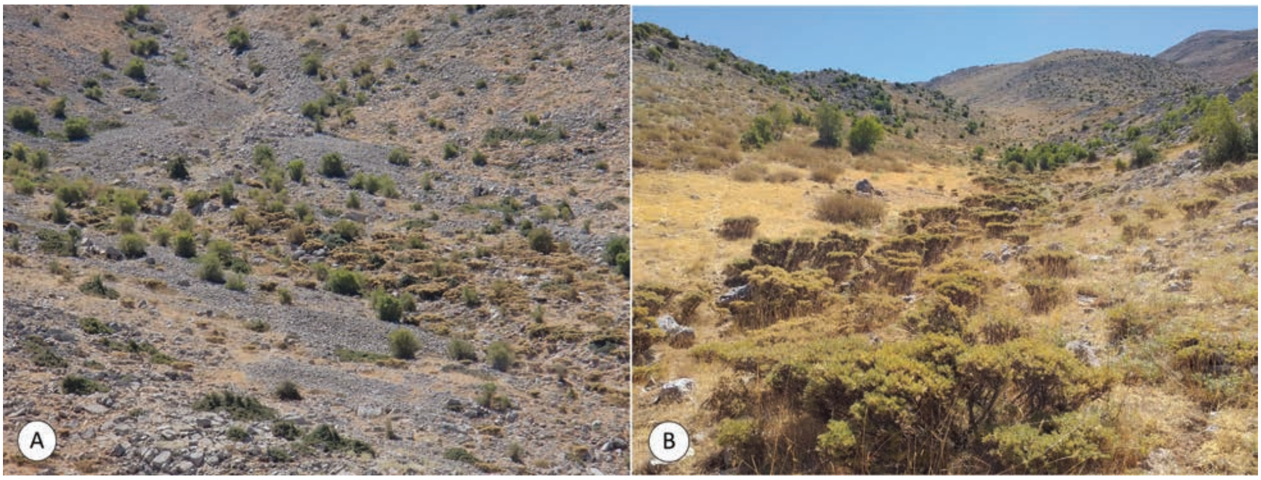

Figure 14. *Astragalus gummifer* thickets in thalwegs in the western slopes of Mount Hermon in Lebanon. **A.** View from a distance; **B.** Close-up.

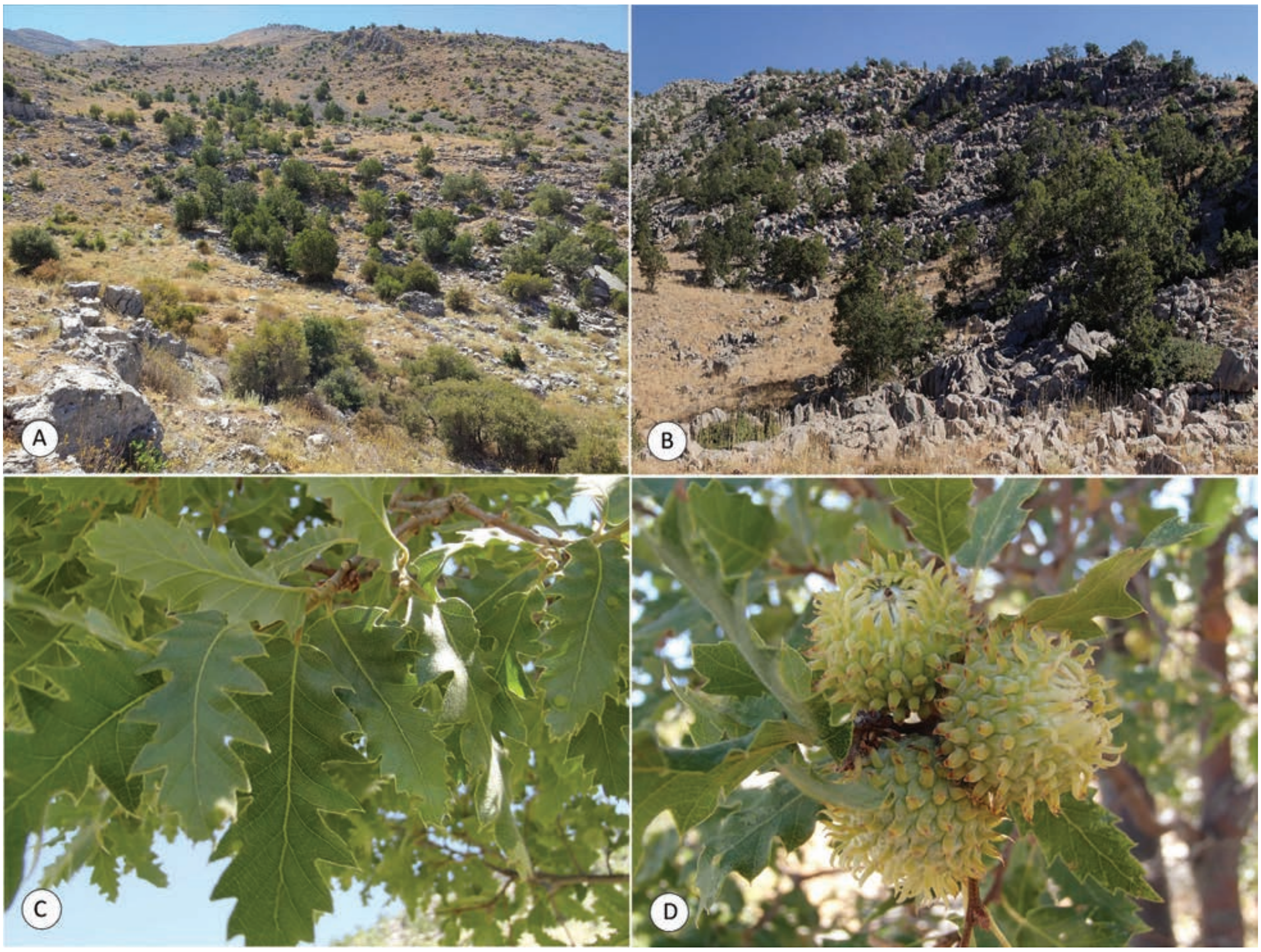

Figure 15. Montane woodlands of *Quercus look* and *Acer monspessulanum* subsp. *microphyllum* in the western slopes of Mount Hermon in Lebanon in 2020: **A. B.** Patches of woodlands; **C.** Leaves of Q. *look*; **D.** Immature acorns.

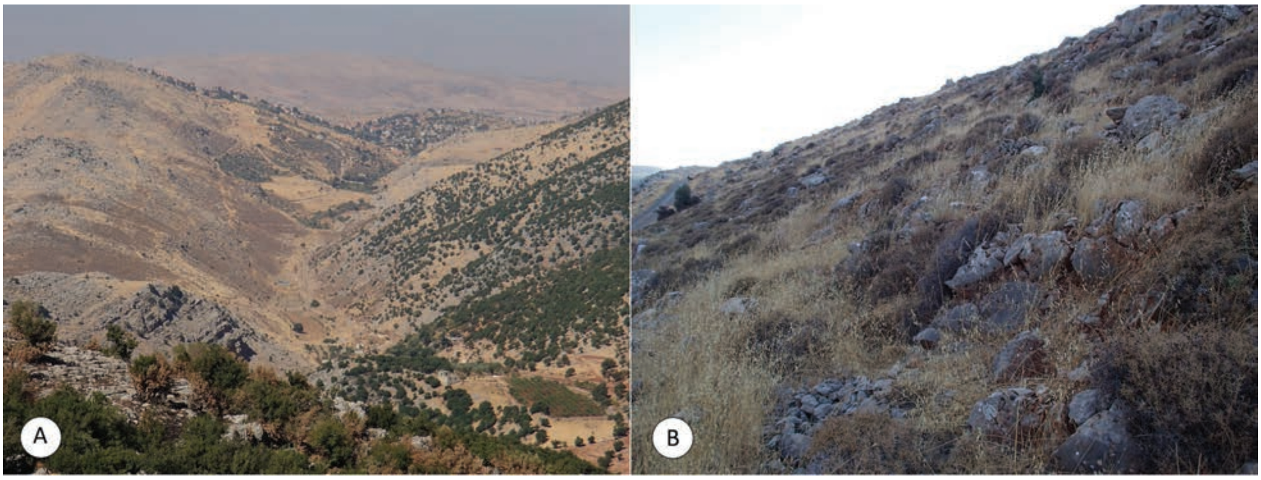

Figure 16. A. Contrast between the slope of phrygana on the left and the slope with evergreen oak woodlands in Wadi el-Feqaa; **B.** Close-up on phrygana of *Sarcopoterium spinosum*.

Patches of cultivated lands are dispersed at lower altitudes, encircling villages or situated on plateaus up to an elevation of 1,550 meters (Figure 17). These cultivated areas are mostly concentrated in thalwegs, where the soil is deeper and more level compared to the surrounding hilly, rocky slopes. This phenomenon accounts for the linear layout of numerous agricultural lands in the region. Rain-fed fields cultivating cereals (barley, wheat) and legumes (chickpeas, lentils) are prevalent. Terraced cultivation includes grapevines and fruit trees such as almonds, cherries and walnuts.

During the study, two planted forest sites were explored, although their flora was not surveyed. Comprising a mix of three conifers non-native to Mount Hermon, namely *Cupressus sempervirens*, *Pinus brutia*, and *Cedrus libani*,

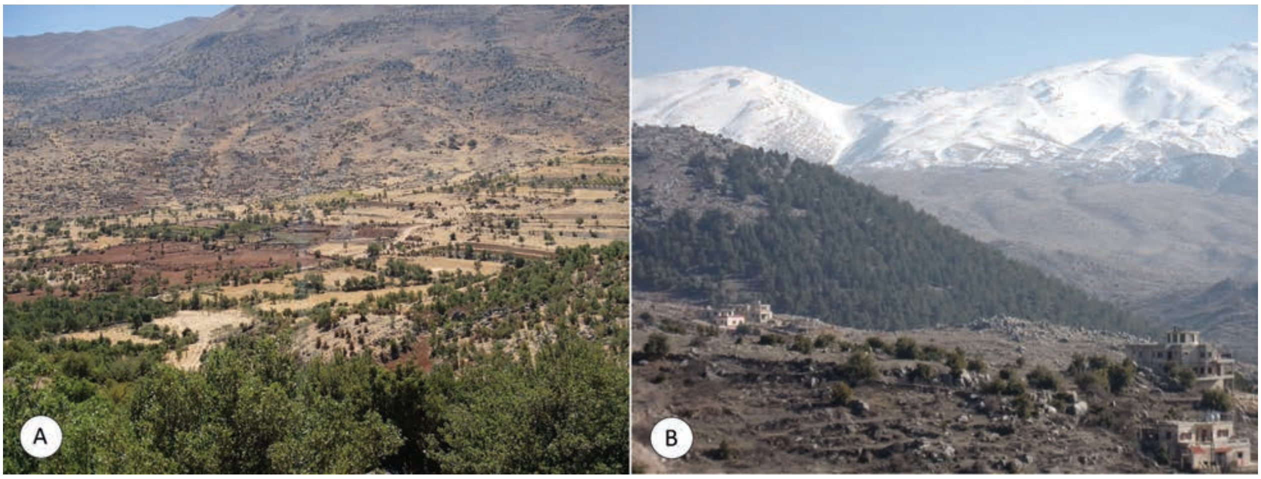

Figure 17. A. Agricultural lands in Berke el-Yebse ; **B.** Planted forest viewed from Rachaya.

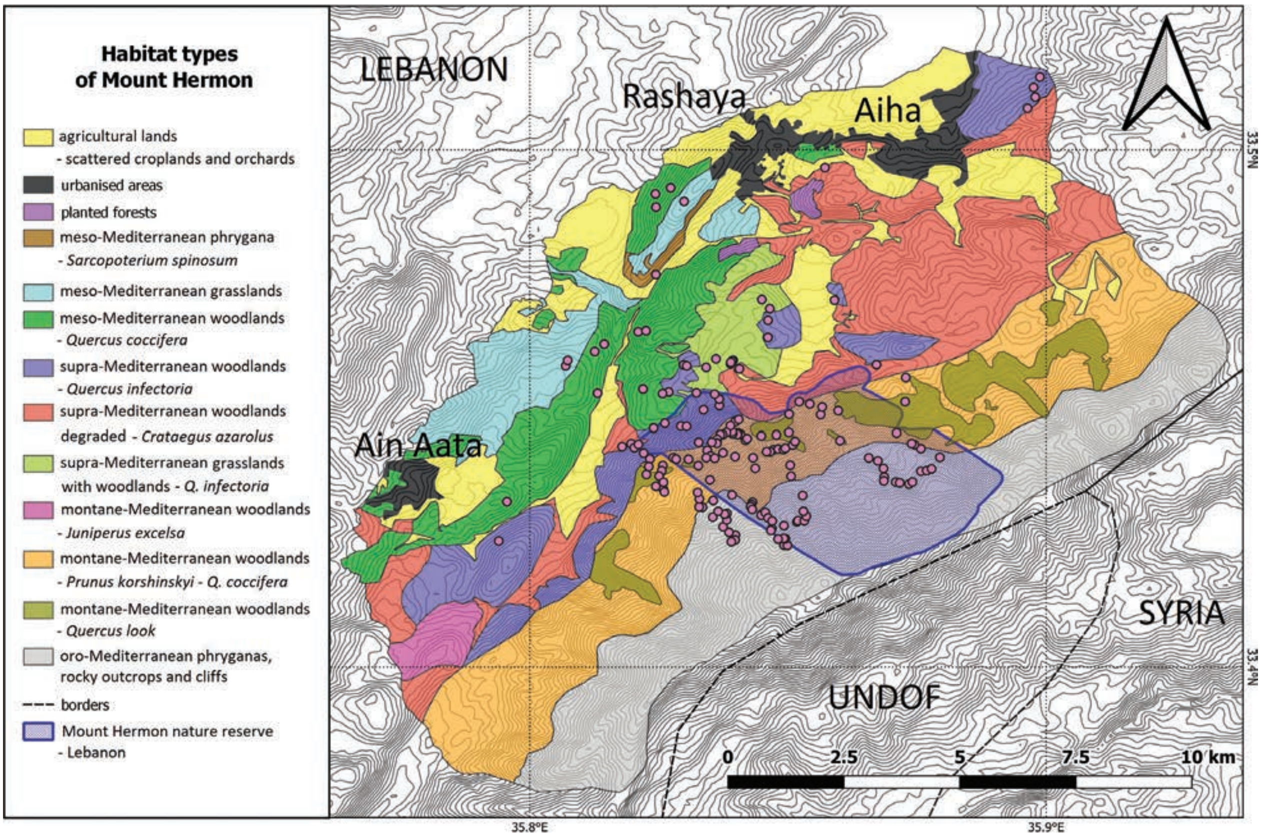
Habitat types of Mount Hermon
agricultural lands - scattered croplands and orchards
urbanised areas
planted forests
meso-Mediterranean phrygana - Sarcopoterium spinosum
meso-Mediterranean grasslands
meso-Mediterranean woodlands - Quercus coccifera
supra-Mediterranean woodlands - Quercus infectoria
supra-Mediterranean woodlands degraded - Crataegus azarolus
supra-Mediterranean grasslands with woodlands - Q. infectoria
montane-Mediterranean woodlands - Juniperus excelsa
montane-Mediterranean woodlands - Prunus korshinskyi - Q. coccifera
montane-Mediterranean woodlands - Quercus look
oro-Mediterranean phryganas, rocky outcrops and cliffs
borders
Mount Hermon nature reserve - Lebanon
LEBANON
Rashaya
Aiha
Ain Aata
SYRIA
UNDOF
0
2.5
5
7.5
10 km
33.5°N
33.4°N
35.8°E
35.9°E

Figure 18. Map of the habitat types identified on the western slopes of Mount Hermon in Lebanon.

these forests were planted in the 1960s by the Ministry of Agriculture. The trees in these planted forests exceed 5 m height. Undoubtedly, these forests play a crucial ecological role in the area, serving as a refuge for numerous wild animals, including birds and mammals.

Finally, the surveys and the boundaries of the nature reserve were mapped to illustrate the range of the habitat types included within the 12.89 km² of protected area (Figure 18). The nature reserve of the western slopes of Mount Hermon comprehensively represents oro- and montane-Mediterranean habitats, as well as upper supra-Mediterranean woodlands and their degraded form of *Crataegus azarolus* thickets.

Discussion

The floristic study conducted on the western slopes of Mount Hermon enabled the characterisation of ten habitat types, based on species differences and the influence of four significant environmental variables. Elevation and mean annual temperature emerged as the most influential factors shaping floristic composition. Although mean annual temperature and elevation exhibit a direct relationship, it is prudent to consider them separately due to the varied influences associated with them. Slope ranked as the third most significant environment variable, notably influencing floristic variation among the habitat groups of the oro-Mediterranean level. Northness also exerted a significant influence, particularly affecting the differentiation of the scree woodlands of *Prunus korshinskyi* from the other montane habitats.

Five habitat types represent novelties, constituting subtypes of broader habitat types described in the national typology (El Zein et al. 2022). They include the description of two types of hedgehog-heaths at the oro-Mediterranean level. The group of *Astragalus echinus* and *Noaea mucronata* exhibits a preference for slopes and thalwegs where exposure to wind and sun is reduced, and the soils is deeper. The group of *Tanacetum densum* and *Astragalus cruentiflorus* thrives on hilltops and south-oriented slopes, showing a preference for xeric and rocky situations. Hedgehog-heaths are unique habitats and constitute relict vegetation poorly studied in the Levant, primarily composed of endemics or rare species belonging to the ancient Mediterranean Tertiary flora (Musarella et al. 2020). Both of these habitats are endemic to Mount Lebanon, Mount Hermon and Anti-Lebanon, indicated by the presence of taxa strictly endemic to these ranges. The first habitat includes *Astragalus coluteoides*, *A. hermoneus*, and *A. nummularius* subsp. *trichopterus*, while the second contains the diagnostic species *A. cruentiflorus*.

Another novelty is the description of a plant group diagnostic of the cliffs at the oro-Mediterranean level in western Mount Hermon. This group comprises twelve taxa, with *Rosularia sempervivum* subsp. *libanotica* having the highest diagnostic value, and the majority of them are endemic to the mountains of South Turkey, Mount Lebanon, Anti-Lebanon and Mount Hermon. We propose categorizing this habitat as a sub-type of "*Mediterranean bare limestone inland cliffs*" (U387) of the national habitat typology, specifically characterizing the oro-Mediterranean limestone cliffs of Mount Hermon in Lebanon. This contributes significantly to our understanding of plant communities on cliffs, as this habitat has remained poorly studied in the Levant, and oro-Mediterranean cliffs of this region were previously undocumented (Davis 1951; Wagensommer 2017).

The scree deciduous montane woodlands of *Prunus korshinskyi* and *Lonicera nummulariifolia* represent a habitat type that has been insufficiently characterised in the past. This unique habitat is distinguished by its specific substrate, notably the screes, and the distinctive aspect of the slope. The formations of *P. korshinskyi* show affinities with the Arabic Peninsula (Zohary 1973), while the presence of *L. nummulariifolia* characterises typical Eastern Mediterranean and Irano-Turanian habitats (Davis et al. 1965). At the Lebanese level, woodlands featuring *P. korshinskyi* are a rarity and are exclusively found on the eastern slopes of Mount Lebanon between Wadi Faara, Ainata and Yammoune in a limited area (Mouterde 1966, 1970). We propose this habitat as a sub-type of "*Lebanese wild fruit trees steppe wood*" of the national typology (T19B9_LB1). The second montane woodland including *P. korshinskyi* in association with *Quercus coccifera* constitutes a second sub-habitat.

Quercus look is a tree endemic to Mount Lebanon, Anti-Lebanon and Mount Hermon (Avishai 2017). The inhabitants of the region of Rachaya historically distinguished this oak species from others, assigning it the name "Look" in Arabic which later became its specific epithet (Avishai 2017). Deciduous montane woodlands of *Q. look* associated with *Acer monspessulanum* subsp. *microphyllum* constitute a unique habitat endemic to the region, specifically occurring in the region of Mount Hermon. Similar *Q. look* woodlands were also identified at the montane-Mediterranean level on the heights of Mount Barouk in Mount Lebanon (Chouchani et al. 1975; Abi-Saleh and Safi 1988). In this area, this tree species was known to form pure stands within the ecological zone of *Cedrus libani*, sometimes co-dominating with the latter. Nevertheless, these woodlands lacked precise documentation in earlier studies, and this research significantly contributes by providing additional insights into their floral composition. These contributions acknowledge the distinctiveness and rarity of the *Q. look* woodlands.

The floristic complexity of the supra-Mediterranean woodlands was highlighted, revealing two main types distinguished by elevation and the prevalence of either *Quercus coccifera* or *Q. infectoria*. However, the floristic composition did not effectively differentiate between degraded forms of these habitats. For instance, the thickets of *Crataegus azarolus*, representing the degraded form of the upper supra-Mediterranean woodlands of *Q. infectoria*, and the gradual transitions were all grouped together. This emphasizes the crucial role that physiognomy of the vegetation plays in interpreting results.

This brings to light an important parameter affecting the habitats of the western slopes of Mount Hermon, namely the impact of the historical anthropic activities that have gradually modified the physiognomy of the vegetation and thus the landscape of the area. The current landscapes of Mount Hermon are made of relict habitats compared to what they used to be (Abel 1933; Vaumas 1954; Mouterde 1966; Mikesell 1969). For example, the deciduous woodlands of *Quercus look* have almost disappeared and only scattered patches remain in Mount Hermon. The current pastoral activities are not allowing a decent regeneration as the seedlings are systematically grazed by goats.

Similar to many areas in the western slopes of Anti-Lebanon range, the woodlands of *Juniperus excelsa* have disappeared due to intense exploitation for firewood (Mouterde 1966). This was the only conifer species observed in our surveys and it was reported to have a wider distribution in the past. Usually, montane-Mediterranean belts are dominated by coniferous formations (Quézel and Barbero 1982) but it is not the case anymore in Mount Hermon. These woodlands have become rare due to past wood exploitation. The presence of *J. excelsa* woodlands on the western slopes of Anti-Lebanon, between 1,700 and 2,800 m a.s.l. (Vaumas 1954; Mouterde 1966), indicates that the relict woodlands present on the Lebanese slopes of Mount Hermon could have once extended over a larger area. Historical documents described Mount Hermon with significant forest cover during the antiquity (Abel 1933; Vaumas 1954; Mikesell 1969). Nevertheless, until now it still constitutes the southernmost edge of the distribution range of this conifer (Douaihy et al. 2011, 2013; Caudullo et al. 2017).

Human activities have significantly influenced the diversity at the landscape level, resulting in a characteristic mosaic of vegetation types. This mosaic consists of an alternating succession of grasslands in linear thalwegs with *Q. infectoria* interspersed among rocky hills dominated by *Q. coccifera*. Below 1,500 meters a.s.l., various habitat types bear traces of ancient agriculture. Old terraces, constructed with rocks, are prevalent remnants of agriculture. Often reclaimed by shrubs or trees, these terraces comprise a mix of rocky micro-habitats and grasslands. Another common trace of past agriculture is the presence of rock heaps, remnants of stones cleared for ploughing, mainly located in thalwegs.

The woodlands on Mount Hermon were previously characterised as similar to those on Mount Lebanon, distinguishing them from those of Anti-Lebanon (Abi-Saleh 1982; Abi-Saleh and Safi 1988). However, some typical Mediterranean taxa were absent in Mount Hermon. For instance, in the supra-Mediterranean belt, *Acer obtusifolium*, *Arbutus andrachne*, *Cercis siliquastrum*, *Laurus nobilis*, *Phillyrea latifolia*, and *Pinus brutia* were absent, and similarly, in the montane-Mediterranean woodlands, *Acer hyrcanum* subsp. *tauricola*, *Fraxinus ornus*, and *Ostrya carpinifolia* were also missing. Intriguingly, additional elements have offered insights into floristic affinities between the eastern slopes of Mount Barouk's and the western slopes Mount Hermon. These indications include the absence of certain Mediterranean tree species that are typical of western Mount Lebanon, and the shared presence of the same narrow endemic taxa, namely *Allium feinbergii*, *Bellevalia hermonis*, *Quercus look*, and *Salvia rubifolia* (Mouterde 1966, 1970, 1984).

Conclusion

This study provides the first comprehensive list of plant taxa of the western slopes of Mount Hermon in Lebanon utilizing a habitat-based approach. The significance of elevation, mean annual temperature, slope and northness in shaping the distribution of taxa and habitat types has been demonstrated. The impact of anthropic activities is also an intriguing aspect that should be more frequently quantified and included in studies. However, understanding historical impacts without proper documentation and verified references can be challenging, and the landscapes stand as the last remaining means to decipher the history of the region.

Floristic affinities with Mount Barouk, located in the south part of Mount Lebanon, were highlighted. The analysis of floristic composition allowed the identification and characterisation of ten habitat types: three at the oro-Mediterranean level, hedgehog-heaths of *Astragalus echinus* and *Noaea mucronata* in thalweg and slopes, hedgehog-heaths of *Tanacetum densum and Astragalus cruentiflorus*, cliffs of *Rosularia sempervivum* subsp. *libanotica*, three at the supra-Mediterranean level, namely grasslands with *Eryngium glomeratum*, woodlands of *Quercus infectoria*, *Q. coccifera* and *Crataegus azarolus*, woodlands of evergreen *Q. coccifera*, and four at the montane level, namely scree deciduous woodlands of *Prunus korshinskyi* and *Lonicera nummulariifolia*, woodlands of deciduous *P. korshinskyi* and evergreen *Q. coccifera*, shrublands of *Astragalus gummifer*, deciduous woodlands of *Quercus look* and *Acer monspessulanum* subsp. *microphyllum*. Five novelties can be added to the national typology of habitat as sub-types.

Our research yielded 383 taxa including twenty-four endemics to Mount Hermon and Mount Lebanon, two taxa endemic to Mount Hermon and Anti-Lebanon, and one exclusively endemic to Mount Hermon. It provides a complementary list of taxa for the region. The oro-Mediterranean hedgehog-heath of *Astragalus echinus* and *Noaea mucronata* hosted the highest number of endemic plant taxa (12), followed by the montane woodlands of *Quercus look* and *Acer monspessulanum* subsp. *microphyllum* (10), the scree deciduous montane woodlands of *Prunus korshinskyi* and *Lonicera nummulariifolia* (6), and by montane thalweg deciduous thickets of *Astragalus gummifer* (5). The vulnerability of specific habitat types, particularly *Q. look* woodlands and *Juniperus excelsa* woodlands, as a result of past exploitations, should be considered. This highlights the need for protective measures aimed at conserving these woodlands and enhancing their restoration. Such initiatives could offer dual benefits by preserving the environment and also supporting pastoralist activities that require shaded areas during hot summer days.

Finally, the habitat mapping serves as a valuable tool for visualizing the distribution of habitats and surrounding human activities. It constitutes a crucial resource for the effective management and conservation of the natural heritage. The comprehensive map reveals that the nature reserve on the western slopes of Mount Hermon encompasses the majority of the identified habitats. The insights gained from this study are instrumental in informing the development of a management plan for the nature reserve, ensuring the preservation of its diversity.

Data availability

The data related to the geographic coordinates and elevation, list of observed plant species, and percentage frequency and diagnostic value for each species within each plant community are provided as Suppl. materials 1–4. The entire data are available upon request to the corresponding author.

Author contributions

HE, LC, SB and CK conceptualized the study, carried out the investigation and designed the visualisation of the results. HE conducted the fieldwork and data collection, curated the data, designed the methodology, carried out the analyses, wrote the original draft and took the photographies. LC, SB, CK, DC and MM supervised the study, reviewed and edited the manuscript, were responsible for acquiring funding and were part of the project administration.

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Supplementary material

Supplementary material 1
Geographic coordinates, elevation and cluster group of the plots (xlsx).
Link: https://doi.org/10.3897/VCS.106377.suppl1

Supplementary material 2
List of the species observed (pdf).
Link: https://doi.org/10.3897/VCS.106377.suppl2

Supplementary material 3
Full synoptic table with percentage frequency and diagnostic value for each species (pdf).
Link: https://doi.org/10.3897/VCS.106377.suppl3

Supplementary material 4
Full synoptic table with percentage frequency and diagnostic value for each species (*.xlsx).
Link: https://doi.org/10.3897/VCS.106377.suppl4

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RESEARCH PAPER

GRASSLANDS OF ASIA

The *Pistacietea verae*: a new class of open, deciduous woodlands in Middle and Southwestern Asia

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Abstract

Aims: To analyse the syntaxonomy of open, deciduous woodlands at the southern margin of the steppe zone in the colline and montane belts of the Pamir-Alai, western Tian Shan and Iranian Mountains (Irano-Turanian region). **Study area:** Tajikistan (Middle Asia) and Iran (Southwestern Asia). **Methods:** We prepared two datasets: the first dataset contained 110 relevés from Tajikistan and Iran representing pistachio groves, the second one was a comparative dataset of 1,276 relevés of pistachio groves and floristically related woody and grassland phytocoenoses from the Irano-Turanian and Mediterranean regions. These two datasets were classified separately with the modified TWINSPAN algorithm with pseudospecies cut levels 0%, 2%, 10% and 25%, and total inertia as a measure of cluster heterogeneity. Diagnostic species were identified using the phi coefficient as a fidelity measure. A NMDS ordination was used to explore the relationships between the distinguished groups. **Results:** We found that *Pistacia* open woodlands are very distinctive in terms of species composition, including numerous endemics. Our observations in Pamir-Alai, Kopet-Dagh, Zagros, Alborz and other Central and southern mountains of Iran proved that pistachio open woodlands form distinct zonal vegetation of the colline-montane belt. We thus propose a new class *Pistacietea verae*, with the order *Pistacietalia verae* and appropriate type alliance *Pistacion verae*, including two associations: *Pistacietum verae* and *Pistacietum khinjuk*. **Conclusions:** Our research has shown that the *Pistacia* open woodlands are a distinct vegetation typical of the Irano-Turanian region and due to its specific ecology, phytogeography and unique species composition, should be regarded as a vegetation class *Pistacietea verae*. It needs further examination and comparison with similar vegetation in the western Irano-Turanian and Hindu Kush regions. Recognizing the unique pistachio open woodlands as a distinct vegetation class in the Irano-Turanian region is crucial for establishing effective conservation strategies in these understudied yet ecologically significant ecosystems, spanning potentially from the Zagros, Alborz and other Central and southern Mountains of Iran to Tajikistan, Afghanistan, Uzbekistan, and Pakistan.

Taxonomic reference: Plants of the World Online (POWO 2023), with World Flora Online (WFO 2023) for some problematic cases and Nobis et al. (2020) for *Stipa* spp.

Syntaxonomic references: Mucina et al. (2016) for SE European syntaxa, Nowak et al. (2022a, 2022b) for all other syntaxa.

Abbreviations: NMDS = Non-metric multidimensional scaling.

Keywords

grove, Iran, Middle Asia, Pamir Alai Mts, phytosociology, *Pistacietea verae*, Southwestern Asia, syntaxonomy, Tajikistan, vegetation classification, wild orchard

Introduction

The concept of the vegetation class as the most comprehensive syntaxonomic unit was introduced by Braun-Blanquet (1928). A class of vegetation refers to a large and usually widely distributed biogeographical unit (Pignatti et al. 1995; Loidi et al. 2020) and is mainly characterised by a specific set of diagnostic taxa, its ecological uniqueness and a distinct pattern of distribution (i.e. chorology; Pignatti et al. 1995). According to Pignatti et al. (1995), a vegetation class is a syntaxon of the highest rank, occupying a common ecological space, having member associations, and being recognisable by the presence of a set of diagnostic taxa that are chorologically homogeneous. According to the fourth criterion proposed by Pignatti et al. (1995), a class is a unique and repeatable structure that exists due to its unique and well-defined ecology. The vegetation class itself is the expression of the ecological and dynamic diversity occurring within it, but it can also express a certain biogeographical-evolutionary legacy (Loidi 2020).

All or only few of the aforementioned criteria have been applied for delimitation of a vegetation class (see example studies: Akhani and Mucina 2015; Noroozi et al. 2017). However, most frequently, the floristic composition and ecological uniqueness have been independently utilised for the delimitation of the vegetation classes. For example, the *Seslerietea variae* Br.-Bl. 1948 was initially characterised by a set of associations colonizing alpine limestone grasslands (Pignatti et al. 1995) whereas the *Querco-Fagetea* Br.-Bl. et Vlieger 1937 was mainly distinguished due to its floristic composition, particularly the occurrence of taxa such as *Lamium galeobdolon* subsp. *galeobdolon*, *Euonymus europaeus*, *Athyrium filix-femina*, *Dryopteris filix-mas*, *Hieracium murorum*, *Lactuca muralis* or *Poa nemoralis* (Mucina et al. 1993). In addition to floristic composition, ecology and phytogeography, vegetation classes might be easily distinguished by their physiognomy and spatial structure. For example, the division of deciduous woody vegetation into forests (*Querco-Fagetea*) and shrubland (*Crataego-Prunetea*) is widely accepted. The latter class is considered as a successional phase towards mature deciduous stands in mesic habitats and is predominantly a result of human activities. However, one should also take into account the floristic composition, ecological characterisation and phytogeographical distinction along with vegetation structure and physiognomy of the vegetation (Pignatti et al. 1995). All these features are often related to the natural history and phylogeny of vegetation in a particular phytogeographical unit. For example, both pistachio open woodlands and juniper stands have common roots in the so-called *proto-šhiblyak* (Kamelin 1967).

The so-called wild orchards, groves and open woodlands were relatively poorly known in Middle Asia. This is mainly due to the fact that they were considered as secondary vegetation replacing forests and thus often ignored in synthetic vegetation studies (see Zapryagaeva 1976). This vegetation constitutes a complex ecosystem of woody and herbaceous plants and is often included into forest-steppe vegetation, which is considered to be shaped by "two worlds" that are very distinct in terms of structure, ecology and function (Erdős et al. 2018). Additionally, there is no unequivocal approach among the Russian and Tajik authors how to treat the so-called *šhiblyak*, i.e. shrubland dominated by such taxa as *Acer* spp., *Crataegus* spp., *Cercis griffithii*, *Celtis* spp., *Ziziphus jujuba*, *Pistacia* spp., *Caragana* spp., *Lonicera* spp., *Zygophyllum* spp., *Prunus* spp. (subg. *Amygdalus*), *Atraphaxis* spp. and *Punica granatum*. Previously, this vegetation was classified into mesophilous forest vegetation (e.g. Ovchinnikov 1957) or into xerophytic open woodlands (redkolesa; e.g. Safarov 2018). It was also considered as part of cold-deciduous open xeromorphic scrub (sensu Frey and Probst 1986; Carle and Frey 1977), which was originally termed "Pistazien-Mandel-Ahorn-Trockenwald" by Bobek (1951). This vegetation type is located in the lower montane and colline belts with a lower precipitation of ca. 200–400 mm/yr compared to the upper montane belt (with ca. 1,500–2,000 mm/yr; Assadi 1986; Safarov 2018; Nowak et al. 2022a). Our recent phytosociological studies have shown that the woody vegetation of Tajikistan should be divided into thermophilous open woodlands (pistachio stands), mesophilous shrubland (*šhiblyak* as a seral vegetation to mesic broad-leaved forests or a thermophilous shrubland on edaphically extreme habitats), juniper stands (with two very different types) and xeric shrubland that develop on initial soils (Nowak et al. 2022b, 2022a; Świerszcz et al. 2022). *Pistacia* woodlands are distributed in the Irano-Turanian and Eastern Mediterranean phytogeographical regions (e.g. Zohary 1973). Middle Asia is considered the centre of pistachio distribution and speciation, including the deciduous species *P. vera*, *P. khinjuk* and *P. eurycarpa*. Based on recent molecular studies, the genus *Pistacia* has evolved in Middle Asia due to the aridification of the climate after the retreat of the Paratethys in the Miocene (Li et al. 2020). They are distributed mainly in colline and montane belts between 500 and 2,000 m a.s.l. Other species of the genus *Pistacia* present in the region are *P. atlantica*, *P. terebinthus*, *P. palaestina*, *P. chinensis*, *P. eurycarpa* and *P. lentiscus* (Bozorgi et al. 2013; Xie et al. 2014; Kozhoridze et al. 2015). However, *P. vera* and *P. khinjuk* are considered as the oldest and most widespread taxa that form zonal open woodlands in the Irano-Turanian region (Zohary 1973). Additionally, in Southeast Caucasus, the similar arid open woodlands of *P. atlantica* were mentioned (Lachashvili et al. 2020).

Given the exceptional composition and distribution in the landscape of pistachio open woodlands in Tajikistan and other areas of the Irano-Turanian region, and obtaining data from the different vegetation units closely related with these woodlands, we decided to check whether pistachio open woodlands are a distinct vegetation type at the class level. We address the following questions: (i) What is the floristic distinction and the biological content of pistachio open woodlands in Irano-Turanian region? (ii) What are the ecological and chorological characteristics of pistachio open woodlands? (iii) How are the distinguished syntaxa related to other similar vegetation types known from Asia and Europe?

Study area

In the current study, the sampling was mainly conducted in the Pamir-Alai in Tajikistan and Zagros Mts in Iran. These are long ranges, mainly stretching from east to west with a number of summits exceeding 4,000 m a.s.l. In the Pamir-Alai the highest summit is Somonii Peak (7,495 m a.s.l.), in Zagros Mts is Zard Kuh (4,548 m a.s.l.).

The eastern outskirts of the study area (in Tajikistan; 36.6743–41.0391°N, 67.3393–75.1250°E) are characterised by spring rather than winter rains and high continentality (Djamali et al. 2012). In southwestern Tajikistan the sub-humid climate predominates. The average temperature in June is around 28 °C in the colline belt, and 13 °C in the alpine belt. The annual precipitation ranges here from about 600 mm in the lowlands to ca. 1,700 mm on the southern slopes of the upper montane belt (Latipova 1968; Narzikulov and Stanyukovich 1968). However, due to differences in altitude, orography and wind conditions, there are significant local deviations from the general bioclimatic patterns. Towards the east, winter temperature minima are more extreme and continentality increases compared to neighbouring Mediterranean and Saharo-Sindian regions (Djamali et al. 2012).

In the western part of the study area, in Iran, Armenia, Azerbaijan and inland Turkey, winter precipitation is lower and summer precipitation slightly higher, reflecting similarity to the Mediterranean climatic pattern. In the area of pistachio grove sampling (Zagros Mts, 29.1062–45.9406°N, 35.1067–52.6405°E), the annual precipitation ranges from 300 mm in the colline belt to 850 mm in the montane belt, with average temperatures ranging from about 30 °C to 15 °C, respectively (Djamali et al. 2012).

In comparison with Euro-Siberian and Mediterranean regions (*sensu* Zohary 1973), both areas of the study area are characterised by distinctive features of the Irano-Turanian climatic region, i.e. relatively low annual precipitation, predominant late winter-spring rainfall, prolonged summer drought, extreme seasonal and diurnal temperature variations, bi-seasonal plant dormancy (in southernmost regions) and extremely low humidity (Djamali et al. 2012).

The uniqueness of the Irano-Turanian region is linked to its extraordinary richness of plants, many of which are endemic. For example, the vascular plant flora consists of more than 8,000 species in Iran (Jalili and Jamzad 1999; Noroozi et al. 2019), 4,300 in Tajikistan (Nowak et al. 2020), 4,300 in Uzbekistan (Sennikov et al. 2016) and 4,000 in Kyrgyzstan (Lazkov and Sultanova 2014). The present characteristics of the woody vegetation have been influenced by the centuries-old use of wood as a building material and energy source, and by pastoralism, especially the grazing of sheep, goats, cows and horses. In addition, in most part of Middle and Southwest Asia there was no glaciation during the Pleistocene, allowing the Tertiary flora to persist (Safarov 2003).

Methods

Data sampling

The first (main) dataset included 110 relevés of pistachio open woodlands and xeric scrubs from Tajikistan and Iran (Figure 1). This dataset was used for floristic and phytogeographical analysis of the pistachio open woodlands. The potential class range was delimited according to the distribution of wild *Pistacia vera* occurrences and the literature with pistachio open woodlands reports, sometimes as *Pistacieta* vegetation (e.g. Kamakhina 1994; Popov 1994; Barazani et al. 2003; Kozhoridze et al. 2015; Tojibaev et al. 2017; Breckle and Rafiqpoor 2020; Lachashvili et al. 2020). Plant material collected during the field studies is preserved at OPUN (Opole University, Poland) and KRA (Jagiellonian University, Poland).

The second dataset consisted of 1,276 relevés including the first dataset, but augmented with a wide range of woody and grassland phytocoenoses growing in the study area and neighbouring regions to determine the relationships of pistachio open woodlands with neighbouring vegetation. For this purpose, we selected vegetation types that show spatial (*Pino-Juniperetea*, *Juniperetea pseudosabinae*, *Carpino-Fagetea*, *Prangetea ulopterae*), ecological (*Quercetea ilicis*, *Quercetea pubescentis*, *Crataego-Prunetea*) or dynamic (*Stipo-Trachynietea distachyae*) relationships with open woodlands of pistachio in the Irano-Turanian or Mediterranean regions. The data set included 110 relevés of pistachio open woodlands and xeric scrubs from Tajikistan (Nowak et al. 2022b) and Iran (A. Naqinezhad unpubl.), 352 of *Carpino-Fagetea* forests from Tajikistan (Nowak et al. 2017a) and Iran, 119 of *Pino-Juniperetea* and *Juniperetea pseudosabinae* stands from Tajikistan (Nowak et al. 2022a), 231 of *Quercetea ilicis* and *Quercetea pubescentis* forests from Italy and Greece (Tsiourlis et al. 2007; Gianguzzi and Bazan 2019), 146 of *Crataego-Prunetea* shrubland from Tajikistan (*šhiblyak*; Nowak et al. 2022b; Świerszcz et al. 2022), 156 of *Prangetea ulopterae* tall-forb communities from Tajikistan (Nowak et al. 2020) and 180 of *Stipo-Trachynietea distachyae* pseudosteppes from Tajikistan (Świerszcz et al. 2020).

Depending on the physiognomy of vegetation, the plot sizes varied from 10 m² in grassland communities to 100 m² in open woodlands and 400 m² in forests in such way to enable providing homogeneity in terms of structure,

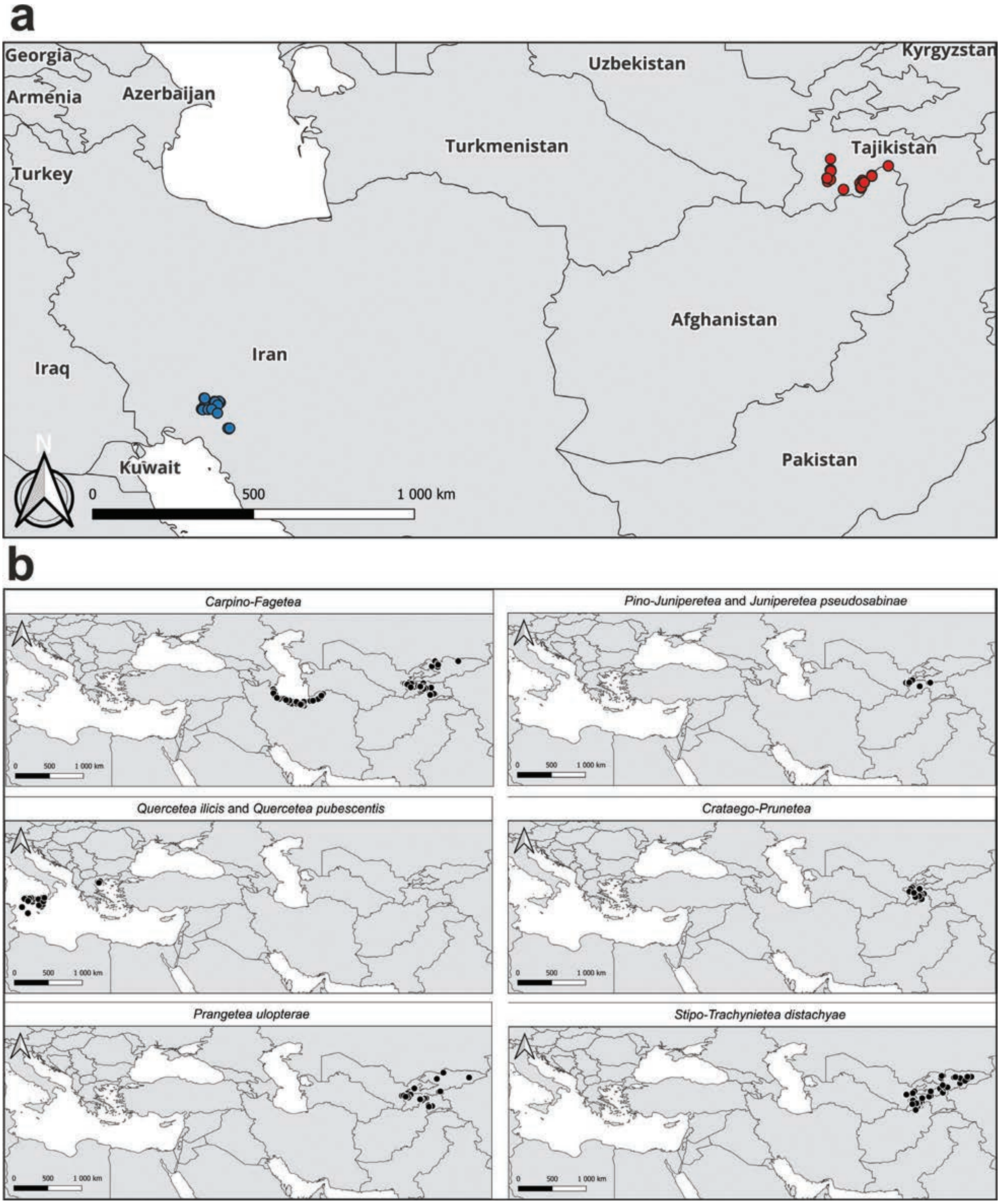

Figure 1. (a) Map showing the distribution of vegetation plots from dataset of pistachio open woodlands (110 relevés) with blue circles represent the *Pistacietum khinjuk*, red circles the *Pistacietum verae*. (b) Map showing distribution of the plots from the second comparative dataset (1,276 relevés) including woody and grassland phytocoenoses with close relationship with analysed vegetation in the Irano-Turanian or Mediterranean regions: *Carpino-Fagetea* forests (352 relevés), *Pino-Juniperetea* and *Juniperetea pseudosabinae* stands (119 relevés), *Quercetea ilicis* and *Quercetea pubescentis* forests from (321 relevés), *Crataego-Prunetea* shrubland (146 relevés), *Prangetea ulopterae* tall-forb communities (156 relevés) and *Stipo-Trachynietea distachyae* pseudosteppes (180 relevés).

species composition and habitat conditions of the phytocoenosis following the Braun-Blanquet approach (Chytrý and Otýpková 2003). For each vegetation plot, all species of vascular plants were recorded with the use of 7-degree cover-abundance scale (r, +, 1, 2, 3, 4, 5; Braun-Blanquet 1928). Species were recorded in five layers of the wood or scrub stands: t1 – higher tree layer (> 7 m), t2 – middle tree layer (3–7 m), t3 – lower tree layer (< 3 m), s1 – shrub layer, hl – herb layer. Geographical coordinates, elevation, aspect and slope inclination were recorded for each relevé. Geographical coordinates of plots were obtained using a GPS device with an accuracy of ± 3 m and the WGS-84 geographic system.

Data analyses

The relevés from Tajikistan were stored in TURBOVEG format (Hennekens and Schaminée 2001) in the Vegetation of Middle Asia Database (GIVD ID AS-00-003; Nowak et al. 2017b). The two datasets were analysed separately in the JUICE software (Tichý 2002). A modified TWINSPAN analysis (Roleček et al. 2009) was performed on the pistachio open woodlands relevé group (90 relevés from Tajikistan and 20 from Iran) in order to classify them with the use of cutoff levels of 0%, 2%, 10% and 25%. Total inertia was used as a measure of cluster heterogeneity (Roleček et al. 2009). Plant species determined only to the genus level were omitted before the analysis. Diagnostic species at the association to order level were identified using the phi coefficient as a fidelity measure (Tichý and Chytrý 2006). The size of all groups was standardised to equal size, and the Fisher's exact test ($p < 0.05$) was applied in order to exclude species with non-significant occurrence optimum in a particular cluster. Species with a phi coefficient ≥ 0.20 and frequency ≥ 20% were considered diagnostic for the *P. vera* stands (excluding species with a wide ecological amplitude or diagnostic for other syntaxonomic units, based on expert judgement), while for a very distinct community of *P. khinjuk* we applied phi ≥ 0.60 and frequency ≥ 45%. Diagnostic species for the class *Pistacietea verae* were identified based on the analysis of the entire dataset used in these studies for all types of naturally occurring woody and grassland phytocoenoses and pistachio open woodlands. For determining a diagnostic value for the class *Pistacietea verae*, we considered species with phi ≥ 0.20, standardised to equal group size. We excluded taxa with wide geographical distribution and ruderal species (e.g. *Anagallis foemina* or *Vicia sativa* subsp. *nigra*) from the diagnostic species group, selected on the base of expert knowledge.

Plot sizes in the available data sources varied greatly from 10 to 400 m^2 between syntaxa and also regions, but this was unavoidable at this current stage as these were the only available data. We acknowledge that plot sizes that vary so greatly will have a significant impact on species constancies and thus phi values when syntaxa sampled with different mean plot sizes are compared (Dengler et al. 2009). Effectively, the frequencies and thus phi values in syntaxa sampled with larger plot sizes are systematically overestimated compared to the frequency and phi-values of syntaxa sample with smaller plot sizes. Since there is no easy way to correct for this bias, we present the raw outcomes, but invite the readers to carefully consult the row with the mean plot sizes to estimate which of the given diagnostic species might be artefacts due to the variation in plot sizes.

A shortened synoptic table of pistachio open woodlands vegetation in Middle and Southwestern Asia with the fidelity and relative percentage frequency of all diagnostic species and other species with frequency > 30% was compiled (Table 1) and the full synoptic table is available in the Suppl. material 1. A synoptic table of the entire dataset used to compare pistachio open woodlands with related vegetation types of forest, shrubland and grassland phytocoenoses is shown in Suppl. material 2. An analytical table of the *Pistacietea verae* is available in Suppl. material 3. New syntaxa are proposed according to the ICPN (Theurillat et al. 2021). In addition, in Table 2, we present species recorded in pistachio open woodlands endemic to Tajikistan, identified based on our field data and the description of the ecology of plants in the Flora of Tajikistan (Ovchinnikov 1957, 1963, 1968, 1975, 1978, 1981; Chukavina 1984; Kochkareva 1986; Kinzikaeva 1988; Rasulova 1991).

To visualize the vegetation grouping and to highlight the relationships between relevés and species, non-metric multidimensional scaling (NMDS) was performed after downweighting of rare species. It was computed using the 'vegan' package version 2.5.4 (Oksanen et al. 2019) in R version 4.2.2 (R Core Team 2022). Species cover data were log-transformed ($\ln(x + 1)$) without down-weighting of rare taxa. Differences in climatic factors (mean annual temperature, temperature annual range, mean temperature of warmest and coldest quarter, sum of annual precipitation, precipitation of warmest and coldest quarter) and richness of phytogeographical elements (Mediterranean, Irano-Turanian, Central Asian and Eurosiberian) between the most similar groups were assessed using the Kruskal–Wallis rank sum test (function kruskal.test) with multiple comparison based on Dunn's test using the *dunnTest* function in the 'FSA' package (Ogle et al. 2018) in R version 4.2.2 (R Core Team 2022). Climatic data were extracted from the CHELSA database, version 2.1 (http://chelsa-climate.org; Karger et al. 2017). The floristic elements were defined on the basis of the species ranges presented in POWO (https://powo.science.kew.org/) and GBIF (https://www.gbif.org/), and according to the phytogeographical divisions of Djamali et al. (2012).

Results

The uniqueness of floristic composition of pistachio open woodlands

The total number of taxa recorded in the dataset from *Pistacia* woodlands in Tajikistan and Iran (110 relevés) was 616. Within this dataset, the most diagnostic taxa

Table 1. Shortened synoptic table of pistachio open woodlands vegetation in Middle and Southwestern Asia belonging to the class *Pistacietea verae* (*Pistacietum verae* and *Pistacietum khinjuk*). The phi values × 100 (in superscript) are only shown when positive. Main values are species frequencies (in percent). Other species with a frequency higher than 30% in the full dataset are also shown. Abbreviations in layer column: t1 – higher tree layer, t2 – middle tree layer, t3 – lower tree layer, sl – shrub layer, hl – herb layer. A full synoptic table is presented in Suppl. material 1.

		Pistacietum verae		***Pistacietum khinjuk***	
Number of relevés		90		20	
Mean plot size (m^2)		100		200	
	Layer	Freq.	phi	Freq.	phi
Ass. *Pistacietum verae*					
Pistacia vera	t2	77	85	0	·
Aegilops triuncialis	hl	70	73	0	·
Bromus popovii	hl	52	67	0	·
Anagallis arvensis subsp. *foemina*	hl	60	62	0	·
Vulpia myuros	hl	42	57	0	·
Prunus verrucosa	sl	40	53	0	·
Brachypodium distachyon	hl	40	53	0	·
Taeniatherum caput-medusae	hl	29	34	0	·
Phlomoides hissarica	hl	26	46	0	·
Eremurus roseolus	hl	23	46	0	·
Ferula tadshikorum	hl	23	43	0	·
Artemisia baldshuanica	hl	22	41	0	·
Asparagus bucharicus	hl	21	39	0	·
Galagania tenuisecta	hl	21	35	0	·
Cousinia grigoriewii	hl	20	33	0	·
Acer pentapomicum	sl	20	26	0	·
Medicago rigidula	hl	31	28	25	20
Avena sterilis subsp. *ludoviciana*	hl	61	58	0	·
Inula orientalis	hl	52	50	0	·
Vicia sativa subsp. *nigra*	hl	44	38	0	·
Amygdalus bucharica	sl	38	43	0	·
Ass. *Pistacietum khinjuk*					
Pistacia eurycarpa	t3	0	·	70	82
Pistacia khinjuk	t3	0	·	60	76
Achillea nobilis subsp. *neilreichii*	hl	0	·	55	72
Arum rupicola	hl	0	·	50	69
Lepidium chalepense	hl	0	·	45	65
Nepeta macrosiphon	hl	0	·	45	65
Centaurea intricata	hl	0	·	45	65
Pyrus glabra	t3	0	·	45	65
Cirsium syriacus	hl	0	·	45	65
Calendula arvensis	hl	0	·	45	65
Other species (sorted alphabetically)					
Anchusa strigosa	hl	0	·	35	57
Arenaria serpyllifolia	hl	49	36	0	·
Asperugo procumbens	hl	1	·	35	49
Asperula glomerata subsp. *eriantha*	hl	0	·	40	61
Astragalus brachycalyx	hl	0	·	40	61
Avena barbata	hl	0	·	40	61
Bellevalia glauca	hl	0	·	35	57
Bromus fasciculatus	hl	0	·	35	57
Bromus oxyodon	hl	46	34	0	·
Bromus tomentellus	hl	0	·	35	56
Bunium paucifolium	hl	0	·	40	61
Centaurea virgata subsp. *squarrosa*	hl	1	·	40	38
Chaerophyllum macropodum	hl	0	·	40	61
Chrozophora tinctoria	hl	0	·	35	57
Cousinia bachtiarica	hl	0	·	40	61
Crepis pulchra	hl	80	54	0	·
Dianthus orientalis	hl	0	·	35	57
Elaeosticta hirtula	hl	50	36	0	·
Eryngium billardieri	hl	0	·	40	61
Euphorbia franchetii	hl	39	35	0	·
Fraxinus ornus	t2	0	·	45	59
Galium aparine	hl	50	24	20	·
Galium spurium	hl	46	27	0	·
Grammosciadium scabridum	hl	0	·	35	57
Helichrysum oligocephalum	hl	0	·	35	57
Hordeum bulbosum	hl	67	46	35	17
Lactuca orientalis	hl	1	·	35	50
Lepyrodiclis stellarioides	hl	31	46	0	·
Linum corymbulosum	hl	32	35	0	·
Lolium temulentum	hl	40	51	0	·
Mentha longifolia var. *asiatica*	hl	0	·	35	39
Nonea persica	hl	0	·	35	57
Notobasis syriaca	hl	0	·	20	43
Parietaria lusitanica subsp. *serbica*	hl	42	48	0	·
Phleum phleoides	hl	39	37	0	·
Phlomis olivieri	hl	0	·	40	61
Phlomis persica	hl	0	·	40	61
Plantago lanceolata	hl	33	14	30	·
Poa bulbosa	hl	43	10	35	·
Rostraria cristata	hl	0	·	35	57
Rumex dentatus subsp. *halacsyi*	hl	0	·	40	60
Salvia persepolitana	hl	0	·	35	57
Salvia syriaca	hl	0	·	40	61
Salvia virgata	hl	0	·	35	55
Sanguisorba minor	hl	0	·	40	59
Scandix pecten-veneris	hl	31	24	35	29
Sonchus asper subsp. *glaucescens*	hl	0	·	35	57
Stachys pilifera	hl	0	·	40	61
Teucrium orientale	hl	0	·	40	61
Torilis leptophylla	hl	7	3	35	51
Veronica arvensis	hl	12	4	40	38

for *Pistacia khinjuk* stands were as follows: *Pistacia eurycarpa*, *Pistacia khinjuk*, *Achillea nobilis* subsp. *neilreichii*, *Arum rupicola*, *Nepeta macrosiphon*, *Notobasis syriaca*, *Centaurea intricata*, *Calendula arvensis*, *Pyrus glabra*, *Lepidium chalepense*. In the group of *Pistacia vera* open woodlands in Tajikistan, the ten species with highest scores of fidelity were: *Pistacia vera*, *Crepis pulchra*, *Anagallis arvensis* subsp. *foemina*, *Brachypodium distachyon*, *Aegilops triuncialis*, *Vulpia myuros*, *Lolium temulentum*, *Vicia sativa* subsp. *nigra*, *Euphorbia franchetii*, *Hordeum bulbosum*. It is worth noting that within the sampled plots some endemic and threatened species occurred, and many of them have the optimum of distribution in pistachio open woodlands (Table 2).

The ecological distinction against other woody or herbaceous vegetation in Middle Asia

Seven main groups determined by using TWINSPAN are shown in the NMDS ordination plot (Figure 2). Although pistachio open woodlands showed much internal heterogeneity in our collection (data from Pamir-Alai and Zagros), they formed a rather distinct group. As expected, the most closely related vegetation type were the pseudosteppes (secondary thermophilous grassland). Open woodlands with *Pistacia vera* had also a close relationship with *šhiblyak* (Figure 2).

The differences in climatic conditions and the habitats of the vegetation types that were most similar to the pis-

Table 2. Endemic species for Tajikistan recorded in pistachio open woodlands. As species endemic to pistachio open woodlands we consider all taxa that were found during our surveys in this certain vegetation type and have endemic status within Tajikistan (not considering their relative frequency against other habitats in which they occur). Endemic species with optimum of distribution in pistachio open woodlands are these that have the highest frequencies in pistachio open woodlands, based on our data set of 5,824 relevés from Middle Asia.

	Endemic species names
Endemic species of pistachio open woodlands	*Allium gypsaceum*, *A. gypsodictyum*, *Amygdalus bucharica*, *Artemisia baldshuanica*, *A. kochiiformis*, *Arum korolkowii*, *Asparagus bucharicus*, *Astragalus ammophilus*, *A. chionanthus*, *A. hissaricus*, *A. nobilis*, *A. retamocarpus*, *A. trachycarpus*, *A. viridiflorus*, *Bunium hissaricum*, *Calophaca grandiflora*, *Cotoneaster hissaricus*, *Cousinia sclerophylla*, *Cuscuta bucharica*, *Dianthus darvazicus*, *Dianthus baldshuanicus*, *Elaeosticta bucharica*, *E. conica*, *E. tschimganica*, *Eremurus bucharicus*, *Eremurus comosus*, *E. olgae*, *E. roseolus*, *E. suworowii*, *Ferula clematidifolia*, *F. decurrens*, *F. tadshikorum*, *Fessia puschkinioides*, *Fritillaria bucharica*, *Gagea paedophila*, *Hypogomphia bucharica*, *Jurinea bucharica*, *Klasea chartacea*, *Korshinskia olgae*, *Ladyginia bucharica*, *Medicago lanigera*, *Nigella bucharica*, *Onosma baldshuanica*, *Paulita ovczinnikovii*, *Phlomoides tadshikistanica*, *Polygonum ovczinnikovii*, *Potentilla kulabensis*, *Primula baldshuanica*, *Ranunculus sewerzowii*, *Rhamnus dolichophylla*, *Rosa huntica*, *R. ovczinnikovii*, *Semenovia bucharica*, *Solenanthus plantaginifolius*, *Taraxacum nuratavicum*, *Tulipa tubergeniana*, *Ungernia tadshicorum*, *Valerianella ovczinnikovii*, *V. vvedenskyi*
Endemic species with optimum of distribution in pistachio open woodlands	*Ajuga turkestanica*, *Allium rosenbachianum*, *Anemone bucharica*, *Artemisia prasina*, *Astragalus babatagi*, *A. brachycalyx*, *A. bucharicus*, *A. corydalinus*, *A. darwasicus*, *A. discessiflorus*, *A. quisqualis*, *A. susianus*, *A. vegetior*, *A. xanthomeloides*, *Asyneuma argutum* subsp. *baldshuanicum*, *Cousinia bachtiarica*, *C. grigoriewii*, *Euphorbia sogdiana*, *Fallopia baldschuanica*, *Galium nupercreatum*, *Iris bucharica*, *I. lineata*, *Onobrychis baldshuanica*, *Oxytropis linczevskii*, *O. tenuirostris*, *Phlomoides baldschuanica*, *Prangos fedtschenkoi*, *Tulipa subquinquefolia*

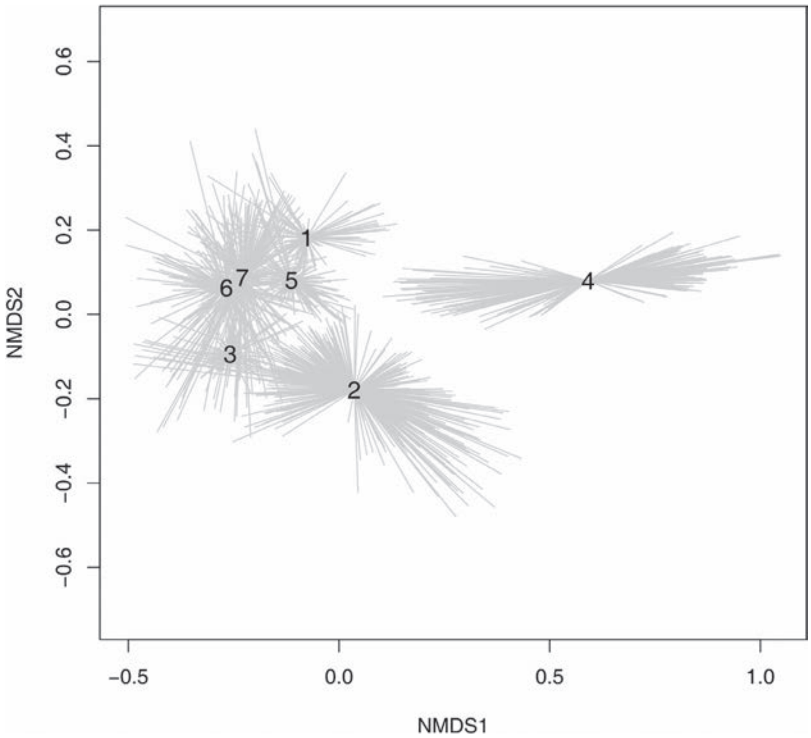

Figure 2. NMDS ordination of 1,276 plots presenting the relationships between pistachio open woodlands all types of naturally occurring woody and related grassland phytocoenoses analysed in this study. Abbreviations: 1 – *Pistacietea verae* (110 relevés, Tajikistan and Iran), 2 – *Carpino-Fagetea* (352 relevés, Tajikistan), 3 – *Pino-Juniperetea* and *Juniperetea pseudosabinae* (119 relevés, Tajikistan), 4 – *Quercetea ilicis* and *Quercetea pubescentis* (213 relevés, Mediterranean Basin), 5 – *Crataego-Prunetea* (146 relevés, Tajikistan), 6 – *Prangetea ulopterae* (156 relevés, Tajikistan) and 7 – *Stipo-Trachynietea distachyae* (180 relevés, Tajikistan).

tachio open woodlands are presented in Figure 3. Interestingly, with exceptions such as the precipitation of the coldest quarter, these conditions were significantly different. The pistachio groves differed mostly in their mean temperature of the coldest quarter and their mean annual temperature (significantly higher than *šhiblyak* and juniper stands). Pistachio groves also had the least precipitation in the warmest quarter.

The vegetation of the pistachio groves showed the highest richness of the Irano-Turanian elements (Figure 4). The richness of Mediterranean species was also quite high (the highest among other Middle Asian vegetation types. Surprisingly, also the proportion of Euro-Siberian elements was indeed the highest amongst the compared vegetation types (although the richness was relatively low: only about 5; Figure 4).

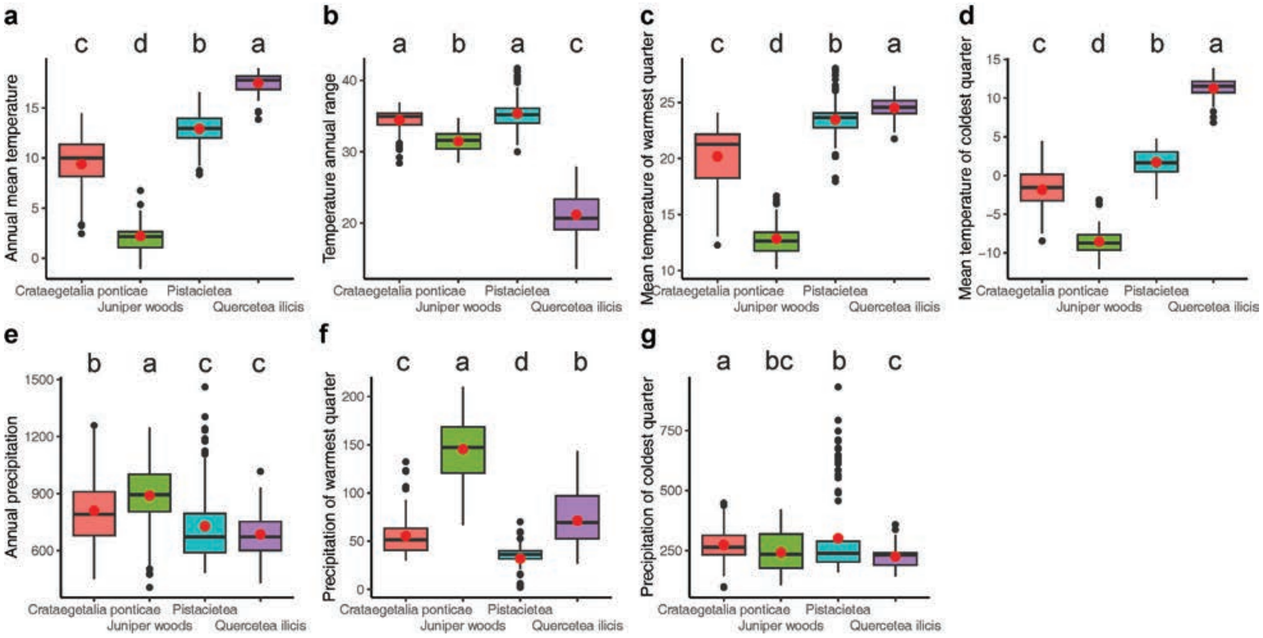

Figure 3. Boxplots showing median (line), mean (red dot), quartiles, outliers and the range of (a) annual mean temperature, (b) temperature annual range, (c) mean temperature of the warmest quarter, (d) mean temperature of the coldest quarter, (e) sum of annual precipitation, (f) precipitation of the warmest quarter and (g) precipitation of the coldest quarter for (from left to right) *šhiblyak* (*Crataego-Prunetea*, Tajikistan), Juniper woods (*Pino-Juniperetea* and *Juniperetea pseudosabinae*, Tajikistan), pistacio open woodlands (*Pistacietea verae*, Tajikistan and Iran) and Mediterranean scrubs (*Quercetea ilicis*, Mediterranean Basin). Different letters indicate significant differences among the groups after the Kruskal–Wallis rank sum test with $p < 0.05$.

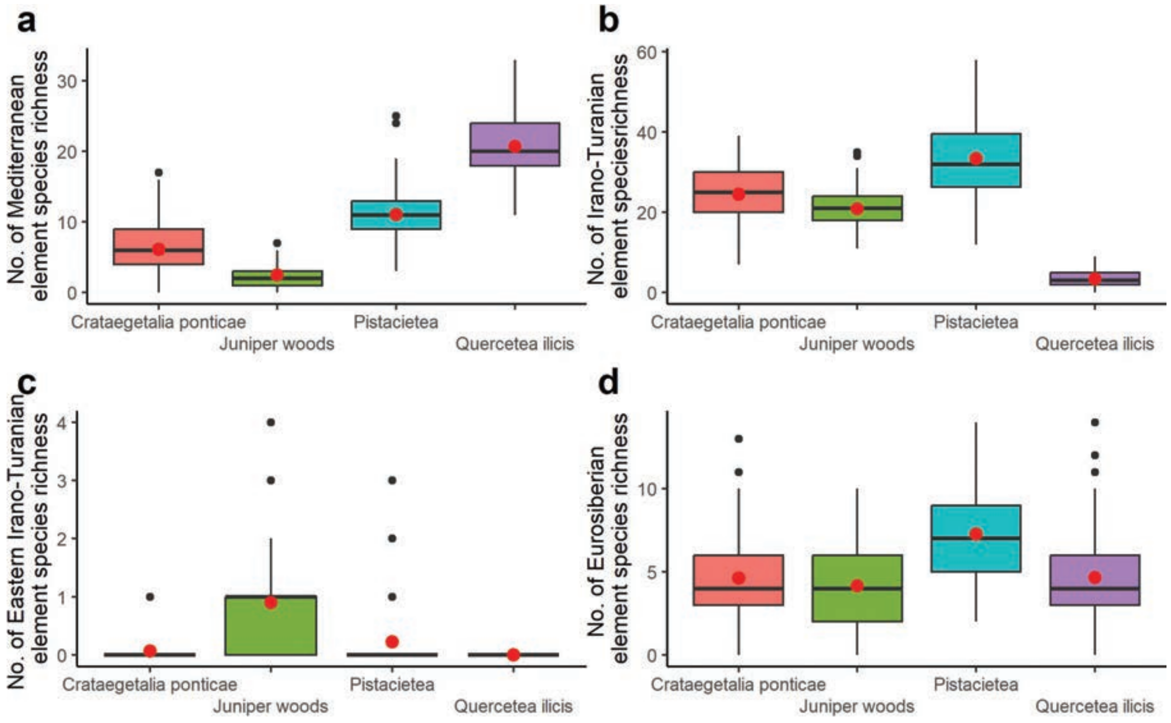

Figure 4. Boxplots showing median (line), mean (red dot), quartiles, outliers and the range of species richness of (a) Mediterranean, (b) Irano-Turanian, (c) Central Asian and (d) Eurosiberian elements for (from left to right) *šhiblyak* (*Crataego-Prunetea*, Tajikistan), Juniper woods (*Pino-Juniperetea* and *Juniperetea pseudosabinae*, Tajikistan), pistacio open woodlands (*Pistacietea verae*, Tajikistan and Iran) and Mediterranean scrubs (*Quercetea ilicis*, Mediterranean Basin). Different letters indicate significant differences among the groups after the Kruskal–Wallis rank sum test with $p < 0.05$.

Proposed syntaxonomic scheme of pistachio open woodlands

Based on the analyses, we propose the following classification for the Irano-Turanian open woodlands in warm, subtropical, semi-arid to sub-humid climate:

- Class: *Pistacietea verae* A. Nowak et al. 2024
  - Order: *Pistacietalia verae* A. Nowak et al. 2024
    - Alliance: *Pistacion verae* A. Nowak et al. 2022
      - A. Eastern group with *Pistacia vera*
        - Association: *Pistacietum verae* A. Nowak et al. 2022
          - Subassociation *Pistacietum verae typicum* A. Nowak et al. 2022
          - Subassociation: *Pistacietum verae cercidetosum griffithii* A. Nowak et al. 2022
      - B. Western group with *Pistacia khinjuk*
        - Association: *Pistacietum khinjuk* A. Nowak et al. 2024

I. *Pistacietea verae* A. Nowak et al. 2024 cl. nov. hoc loco

Holotypus: ***Pistacietalia verae* A. Nowak et al. 2024 (see below)**

General remarks: This vegetation class includes open woodlands with *Pistacia vera* giving them the characteristic appearance of sparse stands with small umbrella-crowned trees or shrubs. This physiognomy resembles savanna-like vegetation, similar to the *Olea europaea* or *Sideroxylon spinosum* open woodlands in the Mediterranean. The canopy density depends on the intensity of grazing and browsing, and the harvesting of the trees by local populations. This vegetation class is well developed in the eastern part of the Irano-Turanian region, where the genus *Pistacia* originated. The shrub layer is poorly developed and the undergrowth is dominated by herbaceous species, often associated with pseudosteppes. Denser forb grasslands develop as a kind of mantle around trees or groups of trees.

Diagnostic species: *Asparagus bucharicus*, *Asperula glomerata* subsp. *eriantha*, *Astragalus brachycalyx*, *A. chionanthus*, *A. kabadianus*, *A. mirabilis*, *A. murinus*, *A. ovinus*, *Avena barbata*, *A. sterilis* subsp. *ludoviciana*, *Bellevalia glauca*, *Brachypodium distachyon*, *Bromus fasciculatus*, *B. oxyodon*, *B. racemosus*, *B. tomentellus*, *Bunium paucifolium*, *Celtis occidentalis*, *Centaurea intricata*, *Cercis griffithii*, *Chaerophyllum macropodum*, *Chrozophora tinctoria*, *Cirsium syriacus*, *Colchicum persicum*, *Consolida stocksiana*, *Convolvulus stachydifolius*, *Cousinia bachtiarica*, *C. grigoriewii*, *C. microcarpa*, *C. multiloba*, *Crambe cordifolia* subsp. *kotschyana*, *Crataegus ambigua*, *C. songarica*, *Dianthus orientalis*, *Ephedra foliata*, *Eremurus roseolus*, *Eryngium billardieri*, *E. caeruleum*, *Euphorbia franchetii*, *Ferula tadshikorum*, *Filago pyramidata*, *Galagania tenuisecta*, *Galium nupercreatum*, *Helichrysum oligocephalum*, *Hordeum bulbosum*, *H. spontaneum*, *Inula orientalis*, *Lallemantia royleana*, *Lathyrus aphaca*, *Lepidium chalepense*, *Linum corymbulosum*, *Malva bucharica*, *Medicago rigidula*, *Nepeta macrosiphon*, *Nigella bucharica*, *Nonea persica*, *Onosma microcarpum*, *Peltaria angustifolia*, *Phleum paniculatum*, *Phlomis olivieri*, *P. persica*, *Phlomoides hissarica*, *Pistacia eurycarpa*, *P. khinjuk*, *P. vera*, *Pseudosedum bucharicum*, *Pyrus glabra*, *Quercus brantii*, *Ranunculus elymaiticus*, *Rostraria cristata*, *Salvia persepolitana*, *S. syriaca*, *S. virgata*, *Scandix iberica*, *S. pecten-veneris*, *Solenanthus plantaginifolius*, *Sonchus asper* subsp. *glaucescens*, *Stachys pilifera*, *Taeniatherum caput-medusae*, *Tanacetum polycephalum*, *Teucrium orientale*, *T. polium*, *Trigonella verae*, *Valerianella coronata*, *Velezia rigida*, *Vulpia myuros*

Geographical range: Eastern Irano-Turanian phytogeographical region (Iran, southern Azerbajan, Afghanistan, Uzbekistan, Turkmenistan, Kyrgyzstan and Tajikistan), particularly the colline and lower montane belts of the Alborz, Zagros, Kopet-Dagh, Pamir-Alai, Tian Shan and Hindu Kush Mts.

Habitat characteristics: It is a typical open woodland vegetation that forms a zonal belt in colline and lower montane elevations of mountain ranges. It develops mainly on fertile to moderately fertile habitats in a semi-arid to subhumid climatic zones. As in the case of other woody vegetation in the region, the abundance and frequency of its undergrowth is strongly influenced by grazing and other types of land use.

Pistacietalia verae A. Nowak et al. 2024 ord. nov. hoc loco

Holotypus: ***Pistacion verae* A. Nowak et al. 2022b (p. 60)**

General remarks: Wild pistachio open woodlands in Tajikistan form a distinct zonal type of vegetation that clearly stands out in the landscape. No occurrence of juniper was recorded in the plots of the community. In many parts of the southwestern part of the country, it has extensive stands, mostly used as fruit plantations or grazing land. *Pistacia vera* woodlands are a distinct vegetation type on the Kopet-Dagh Mts. These are isolated and remnant xerophilous stands of the wild pistachio as subtropical semi-savanna, occurring between altitudes 800 and 1,200 m a.s.l. from the western to eastern Kopet-Dagh Mts (Atashgahi et al. 2022). Due to the low precipitation and high maximum temperature, the understory layer is mainly covered by winter and early-spring ephemeroids, including grasses such as *Poa bulbosa* and the sedge *Carex pachystylis* (Memariani et al. 2016).

Diagnostic species: *Acer pentapomicum*, *Aegilops triuncialis*, *Amygdalus bucharica*, *Artemisia baldshuanica*, *Asparagus bucharicus*, *Avena sterilis* subsp. *ludoviciana*, *Brachypodium distachyon*, *Bromus popovii*, *Cousinia grigoriewii*, *Eremurus roseolus*, *Ferula tadshikorum*, *Galagania tenuisecta*, *Inula orientalis*, *Medicago rigidula*, *Phlomoides hissarica*, *Pistacia vera*, *Prunus verrucosa*, *Taeniatherum caput-medusae*, *Vulpia myuros*.

Geographical range: This order of wild pistachio open woodlands is distributed within the native range of *Pistacia vera*. It mainly includes the colline and montane belt of Eastern Hindu Kush, western Pamir-Alai, western Tian Shan and Kopet-Dagh. The Kopet-Dagh mountain range, northeastern Iran, is the westernmost distribution range of wild pistachio (Atashgahi et al. 2022). It grows between 400 and 2,000 m a.s.l. In Tajikistan, *Pistacia vera* was reported from foothills of Mogol-Tau, Zeravshan, Hissar, Sarsarak, Sangloh, Ak-Tau, Babatag, Darvaz and Hazratishoh Mts (Ovchinnikov 1981).

Habitat characteristics: *Pistacia vera* open woodlands in Pamir Alai are the zonal vegetation inhabiting semi-arid to sub-humid climates with hot summers and mild winters. It shows seasonal changes with intense flowering in early spring and withering of the plants during the hot summer. It thrives on quite fertile loess soils (sometimes also on large rock ledges and slopes on ranker soils), on gentle to moderately steep slopes (Figure 5a). Open groves of *Pistacia vera* are used as pastures for sheep, cows and goats, and are often converted to pistachio plantations. In comparison to other vegetation, pistachio groves are subjected to frequent fires.

A. Eastern group dominated by *Pistacia vera*

See description in Nowak et al. (2022b).

B. Western group dominated by *Pistacia khinjuk*

Pistacietum khinjuk A. Nowak et al. 2024 ass. nov. hoc loco

Holotypus: 2000; 31.04861°N, 50.11139°E; 2216 m a.s.l.; aspect W; slope 9°; plot area 200 m^2; cover tree layer 65%, cover shrub layer 15%, cover herb layer 75%.

Middle tree layer: *Fraxinus ornus* 2, *Morus alba* 1;

Lower tree layer: *Pistacia khinjuk* 3, *Crataegus ambigua* 2, *Crataegus songarica* 2, *Pyrus glabra* 2, *Pistacia eurycarpa* 1, *Cyperus rotundus* +;

Shrub layer: *Vitex pseudonegundo* 2, *Prosopis farcta* +;

Herb layer: *Leiotulus porphyrodiscus* 2, *Parietaria judaica* 2, *Pimpinella affinis* 2, *Achillea nobilis* subsp. *neilreichii* 1, *Allium scabriscapum* 1, *Arum rupicola* 1, *Asperula glomerata* subsp. *eriantha* 1, *Astragalus siliquosus* 1, *Bunium paucifolium* 1, *Carduus pycnocephalus* subsp. *marmoratus* 1, *Chrozophora tinctoria* 1, *Cousinia multiloba* 1, *Crepis sancta* 1, *Echinops cyanocephalus* 1, *Echinops kermanshahanicus* 1, *Erigeron canadensis* 1, *Nonea lutea* 1, *Nonea persica* 1, *Onosma nervosa* 1, *Phlomis olivieri* 1, *Silene conoidea* 1, *Sonchus asper* subsp. *glaucescens* 1, *Tanacetum polycephalum* 1, *Anagallis arvensis* +, *Astragalus susianus* +, *Avena barbata* +, *Avena fatua* +, *Bromus danthoniae* +, *Cirsium syriacus* +, *Convolvulus betonicifolius* +, *Coriandrum sativum* +, *Dionysia bryoides* +, *Echinochloa oryzoides* +, *Grammosciadium scabridum* +, *Haussknechtia elymaitica* +, *Helichrysum oligocephalum* +, *Hordeum spontaneum* +, *Marrubium cuneatum* +, *Mentha longifolia* var. *asiatica* +, *Onosma rostellatum* +, *Plantago lanceolata* +, *Salvia syriaca* +, *Silybum marianum* +, *Smyrnium cordifolium* +, *Trifolium scabrum* +. [relevé number in Suppl. material 3: 105]

Diagnostic species: *Achillea nobilis* subsp. *neilreichii*, *Arum rupicola*, *Centaurea intricata*, *Cirsium syriacus*, *Lepidium chalepense*, *Nepeta macrosiphon*, *Pistacia eurycarpa*, *Pistacia khinjuk*, *Pyrus glabra*.

Geographical range: This association is distributed within the native range of *Pistacia khinjuk* and *P. atlantica*. It mainly includes the colline and montane belt of Zagros, Alborz, central and southern mountains of Iran. Forest-steppes of pistachio-almond occur in lower altitudes of Zagros Mts and other central Iranian ranges down to 750 m a.s.l. However, this vegetation grows between 1,300 and 1,800 m a.s.l. in Alborz and rarely up 3,000 m a.s.l., with a dominance of either *Pistacia atlantica* or *Prunus eburnea* (syn. *Amygdalus scoparius*) (Ravanbakhsh et al. 2013, 2016; Ravanbakhsh and Moshki 2016).

Habitat characteristics: Stands of *Pistacia khinjuk* in Iran form a zonal vegetation inhabiting areas with semi-arid to sub-humid climates (Figure 5b). In general, the *Pistacia-Prunus* (*Amygdalus*) shrubland forms a vegetation belt around the Zagros oak woodland, this belt being broader in the eastern Zagros foothills facing the Central Iranian Plateau (Djamali et al. 2009). Pistachio woodland is better adapted to drier habitats and can withstand the long summer drought. The oak woodland,

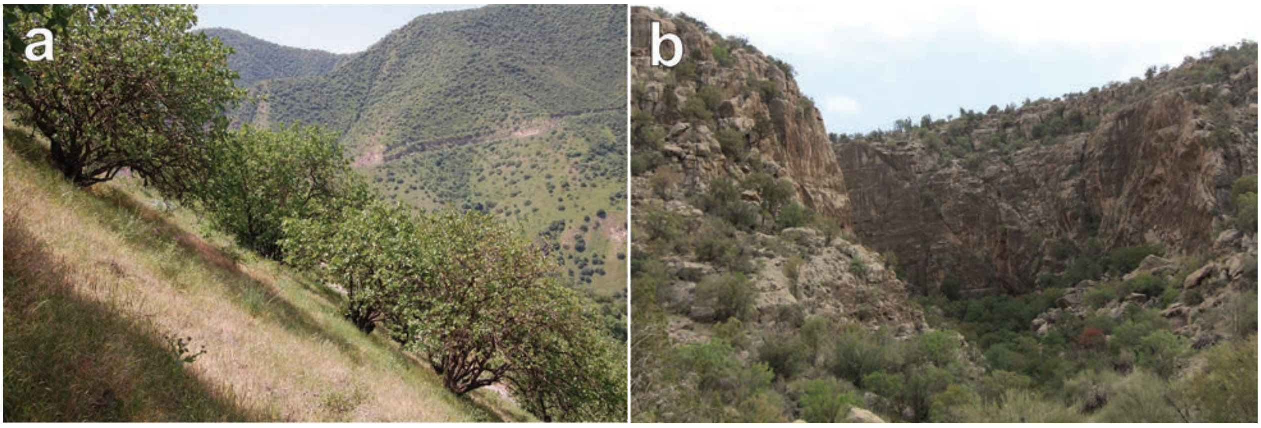

Figure 5. Photographs of pistachio open woodlands: (a) *Pistacietum verae* near Norak, Tajikistan (Photo: S. Świerszcz) and (b) *Pistacietum khinjuk* near Ramhormoz, Iran (Photo: A. Naqinezhad).

however, requires a shorter dry period during the summer and more rain in the spring. The lower limit of the shrubland is determined by the amount of precipitation received (300–350 mm/year).

Remarks: This vegetation type is also called as cold-deciduous open xeromorphic pistachio-almond scrub vegetation (*Pistacia-Amygdalus* steppic woodlands/shrubland) in many mountain ranges of west, south, north and central Iran. They occur between lowland *Artemisia sieberi* semi-desert steppes and thorn-cushion formations of the upper mountains. They once densely covered the many foothills and lower slopes of Iranian steppic mountains and now are remnants that are severely degraded due to anthropogenic effects and fire-cutting management (Djamali et al. 2008, 2009). At the current stage of research, we do not have enough data to accurately build a hierarchical system of this type of vegetation in eastern part of Middle and Southwestern Asia.]

Discussion

How should pistachio open woodlands be treated syntaxonomically?

From the phytosociological point of view, the vegetation type at the highest rank, i.e. class, should be defined by a set of diagnostic taxa (Pignatti et al. 1995). Although at this stage of research, with rather scarce data from the entire potential range of pistachio groves, this set is not complete nor perfect, the high distinctiveness of this class from its neighbouring woody and shrub vegetation types is evident (Figure 2). In particular, the species composition of the pistachio patches differs from the vegetation of the *Quercetea ilicis*, which is typically Mediterranian and occurs far to the west and is characterised by the dominance of oaks (*Quercus rotundifolia*, *Q. pyrenaica*, *Q. ilex*, *Q. pubescens* subsp. *pubescens*, *Q. ithaburensis* subsp. *macrolepis*, *Q. suber*, *Q. coccifera*, *Q. infectoria*), pines (*Pinus halepensis*, *P. pinaster*) or olive (*Olea europaea*). Only in eastern Hindu Kush or western Zagros there are some stands with some oak species such as *Q. brantii*, *Q. libani*, *Q. baloot* or *Q. floribunda* (Erdős et al. 2018; Sagheb-Talebi et al. 2014). Additionally, in *Quercetea ilicis* stands there is a number of herb species that has a typical Mediterranean distribution like, e.g., *Acanthus mollis* subsp. *mollis*, *Asparagus acutifolius*, *Calicotome infesta*, *Cistus salvifolius*, *Cyclamen repandum* subsp. *repandum*, *Daphne gnidium*, *Dioscorea communis*, *Ruta chalepensis*, *Smyrnium olusatrum*. Similarly, the floristic composition of the pistachio groves is totally different than the shrubland vegetation of *Crataegetalia ponticae* in Middle Asia. In these more fertile habitats that are related with broad-leaved forests we can find a number of diagnostic species like *Acer platanoides* subsp. *turkestanica*, *Astragalus darwasicus*, *Brachypodium sylvaticum*, *Caragana turkestanica*, *Corydalis darwasica*, *C. nudicaulis*, *Cotoneaster hissaricus*, *Crataegus pseudoheterophylla*, *Ferula gigantea*, *Malus sieversii*, *Neopaulia ovczinnikovii*, *Potentilla kulabensis*, *Prunus sogdiana*, *Rosa achburensis*, *Vinca erecta* and many others (Świerszcz et al. 2022). Again, the set of diagnostic species as well as the overall composition of thermophilous pistachio open woodlands are largely different. The same is true for the juniper groves that, despite the similar open structure and origin relating to aridification of Central Asia in the Miocene and Pliocene, share almost no common species (no occurence of *Berberis integerrima*, *Juniperus polycarpos* var. *seravschanica*, *Juniperus pseudosabina*, *Juniperus semiglobosa*, *Libanotis schrenkiana*, *Lonicera stenantha*, *Oxytropis capusii*, *O. ovczinnikovii*, *Poa urssulensis*, *Polygonatum roseum* among diagnostic and dominant; Nowak et al. 2022a).

The high floristic distinctiveness of pistachio groves is also due to the high degree of endemism of both vegetation types and their phytogeographical area. The group of endemic taxa which has an ecological optimum in pistachio open woodlands includes, among others: *Ajuga turkestanica*, *Astragalus quisqualis*, *Cousinia grigoriewii*, *Euphorbia sogdiana*, *Fallopia baldschuanica*, *Onobrychis baldshuanica*, *Oxytropis linczevskii*, *Oxytropis tenuirostris*, *Phlomoides baldschuanica* or *Tulipa subquinquefolia* (Table 1). These species are mostly thermophilous and shade-tolerant plants that grow around pistachio trees or groups of pistachio trees forming a specific mantle. It is worth noting that if we had been able to collect more data from the entire *Pistacia vera* and *P. khinjuk* range, there would probably be many more such national or regional endemics. The vast majority of species that build pistachio open woodlands have an Irano-Turanian distribution. Certainly, further research in Turkmenistan, Afghanistan and eastern Iran should confirm this pattern, as this phytogeographical region has its own distinct natural history and bioclimate (Djamali et al. 2009, 2012).

It is also worth noting that the overall richness of this vegetation is impressive, in 110 relevés we found 616 species of vascular plants. This number is high compared to mesic shrubs (120 plots of 100 m^2 mean size, 566 species), pseudosteppes (200 plots of 10 m^2 mean size, 770 species), steppes (eastern Middle Asia: 274 plots, 503 species and western: 148 plots of 20 m^2 mean size, 384 species), deciduous forests 201 plots of of 200 m^2 mean size, 545 species) and even tall-forb communities (244 plots of 10 m^2 mean size, 810 species) studied so far in Middle Asia (Nowak et al. 2017a, 2018, 2020, 2022b). Of course, an important group characterising pistachio open woodlands are the species of the herbaceous undergrowth that is often dominated by plants typical of pseudosteppes. Their considerable proportion and high frequency in our plots is due to the dynamic relationship between pistachio stands and surrounding grasslands and the effect of the ecotonal nature (transitional character), the removal of open woodlands and intensive grazing. A similar relationship and overlap of diagnostic species groups is found in seral or marginal vegetation like *Crataego-Prunetea* and *Carpino-Fagetea*, *Trifolio-Geranietea* and *Crataego-Prunetea* or *Paliuretalia* and *Quercetea pubescentis* (see Mucina et al. 2016; Chytrý 2013).

Taking the above arguments into account, in our opinion pistachio groves have a distinct species composition in comparison to neighbouring vegetation types, including a set of diagnostic, dominant and frequent taxa of typical Irano-Turanian distribution. This also indicates the potential extent of this vegetation and shows that its rank should be related to wide phytogeographical unit, that means the floristic region as suggested by Pignatti et al. (1995). In our opinion, the extent of the proposed class is sufficient and, in addition, quite uniform with respect to the phytogeographical division. This is because it covers almost all mountain ranges of the Irano-Turanian region. A wide range of this vegetation type, as well as the high rate of endemism of the floras of the mountains of the Irano-Turanian region, will result in a high variety of associations.

Relationship with other vegetation types in the Irano-Turanian and Mediterranean area

At the initial stages of phytosociological research of the Irano-Turanian region, pistachio open woodlands were included in the class *Junipero-Pistacietea* (Zohary 1973). Apart from the fact that this class was described invalidly (Art. 2b, see Mucina et al. 2016), it seems that current knowledge does not justify including both types – juniper and pistachio groves – into one class of vegetation. In the mountains of Pamir-Alai and Tian Shan (in Uzbekistan, Tajikistan and Kyrgyzstan), they are clearly climatically separated in the landscape and form two distinct elevational belts of vegetation (see Figure 3). The juniper stands grow in upper montane to lower subalpine belts and only occasionally overlap with the pistachio woodlands (some plots of *J. seravshanica* in the Khodzhamumin and Babatag Mts). In our data from Tajikistan, juniper was not found in pistachio woodlands and we noticed only two occurrences of juniper in *šhiblyak* shrubland (*Calophaca grandiflora* stands). Even in the original species lists and descriptions provided by Zohary (1973), there were no plots that contained both junipers and pistachios with significant cover. Juniper stands and pistachio woodlands were also distinct and separated in the description of vegetation in north-eastern Iran (Memariani et al. 2016), probably also due to different climatic conditions (particularly precipitation and mean temperature in the warmest qurter) as it was found in the area of Tajikistan (Figure 3; Nowak et al. 2022a). In Turkmenistan, in the Badghyz region, two large open pistachio woodlands of Kushka and Pulikhatum have been described as distinct zonal vegetation dominated solely by *P. vera* with some admixture of *Ficus carica* and *F. afghanica* (Popov 1994). The same zonation with separate pistachio and juniper vegegation is reported from Iori plateau in eastern Georgia (Lachashvili et al. 2020) and Hindu Kush Mts (Freitag 1971). Only towards the southern, more arid and warm territories of Hindu Kush, Zagros and Kopet-dagh, pistachia form mixed stands with *Cercis griffithii*. It can be one of the main canopy species or form a pure stands of a more shrubby physiognomy.

We have checked also the similar vegetation in Eastern Mediterranean and Southwestern Asia – the Kurdo-Zagrosian forest-steppe. All of the known vegetation types, including sclerophilous oak stands of the thermo- to supramediterranean belts of Southwestern Asia (*Quercetea brantii* Zohary 1973) and several vegetation types from the *Quercetea ilicis* (sclerophilous oak and conifer forests and associated macchia in the thermo- to supramediterranean belts of the Eastern Mediterranean – *Quercetalia calliprini*, thermo-mesomediterranean pine forests of the Central and Eastern Mediterranean – *Pinetalia halepensis*, mesomediterranean evergreen endemic golden oak forests of Cyprus – *Quercion alnifoliae*, thermo-mesomediterranean low-grown matorral, macchia and garrigue of the Mediterranean Basin - *Pistacio lentisci-Rhamnetalia alaterni*, thermomediterranean calcicolous macchia of the Liguro-Tyrrhenian Seaboards with evergreen *Olea europaea*, *Ceratonia siliqua* and *Pistacia lentiscus* stands with a closed tree canopy in the drought-prone lowlands and foothills of the Mediterranean and Macaronesia – *Oleo-Ceratonion siliquae*, Mesomediterranean sclerophyllous garrigue of the Eastern Mediterranean – *Pistacio terebinthi-Rhamnion alaterni*, evergreen calcicolous mesic kermes oak forests of the Eastern Mediterranean - *Arbuto andrachnes-Quercion cocciferae*, thermo-mesomediterranean evergreen oak forests on deep soils of the Iberian Peninsula and North Africa - *Oleo sylvestris-Quercion rotundifoliae*) vary considerably in terms of the ecology, seasonality, physiognomy, floristic composition, range, evolution of the main species that make up the communities.

Structure, ecology and origin of pistachio open wooldlands

For anyone visiting countries such as Iran, Turkmenistan, Uzbekistan, Tajikistan, Kyrgyzstan or Afghanistan, the vegetation of open woodlands with pistachio trees proves to be one of the most distinctive vegetation types and landscape features. It forms a distinct zone in the colline and montane belts of most ranges throughout the warm and sub-humid areas in Middle Asia and the entire Irano-Turanian region. For years, it has been the subject of research by botanists who coined the term *redkolese* (from Russian for sparse forest), or just grove, open arid forest, open woodland, wild orchard, or open scrubs (e.g. Frey and Probst 1986; Zohary 1973; Popov 1974, 1994; Kamelin and Rodin 1989; Memariani et al. 2016; Nowak et al. 2022a) or Pistacieta arid open woodlands (see Lachashvili et al. 2020). Other scientists have created some confusion by considering these ecosystems to be a type of thermophilous mesic continental shrubland called *šhiblyak* (e.g. Ovchinnikov 1948; Popov 1994; Safarov 2018). We have discussed in detail this misleading classification in our recent work (Nowak et al. 2022b), and considered pistachio open woodlands, a savanna-like vegetation in Middle Asia, as well settled. In addition to its spatial distinction in the landscape and specific “floristic content”, the vegetation with *Pistacia vera* dominance is characterised by a number of other features that allow it to be considered a distinct type at the highest rank according to the widely accepted criteria (Pignatti et al. 1995; Loidi 2020).

One of these features is the open structure of the stands due to grazing and browsing, and also the climatic and edaphic conditions. Recent intensification of grazing and logging have led to a loss of the canopy compactness, rising light intensity and the encroachment of heliophilous plants from the surrounding pseudosteppes as well as many ruderal plants. The southern parts of Middle Asia have been used as grazing lands for centuries by the ancient Indus Valley civilisation (Shortugai) or the local Bactrian Kingdom people (Lawler 2007; Chew and Sarabia 2016; Sinha et al. 2019). This situation is very analogous to vegetation in Mediterranean countries such as olive or argan groves in Morocco, Italy or Greece. It is not easy to determine what the natural density of the pistachio canopy was in pre-historic times, when goats and sheep were not grazing. The wild herbivores that naturally occur in the pistachio open woodlands were mainly *Saiga tatarica* (saiga), *Gazella subgutturosa* (dzheyran), *G. bennettii* (chinkara), *Ovis vignei* (urial) and *Equus hemionus* (kulan). During the long history of megafauna extirpation by humans across Southwestern and Middle Asia the populations of these animals have drastically decreased and most of them are currently considered as critically endangered or extinct in some countries (e.g. Abdusalyamov 1988). After the first global human-driven megafauna extinctions in the Quaternary period (approx. 50,000 to 10,000 years ago; Barnosky 2008; Smith et al. 2018), the large herbivores of Middle Asia were gradually replaced by herds of domesticated goats, sheep, donkeys and cows. To what extent the current state reflects the situation before the introduction of intensive livestock grazing in Asia is difficult to say. What is undeniable, however, is that at the southern limit of the range of woody vegetation, in areas where herds of herbivorous megafauna and accompanying predators such as *Panthera leo* subsp. *leo* (Persian lions), *Panthera tigris* subsp. *tigris* (Caspian tigers) and *Hyaena hyaena* (stripped hyenas) lived in the wild, there was a belt of open vegetation dominated by pistachio. The herbivore pressure is still preserved today and is evident in the high proportion of herbs in the undergrowth and the characteristic ‚savanna' physiognomy of the umbrella-like canopy of pistachio crowns. It is worth mentioning that such a loose structure of this vegetation is also evident on the larger rock ledges (e.g. in southern Hazratishoh range), which are not accessible to grazing animals, but only to wild urials.

An important distinguishing feature of the vegetation at class level is its well-defined ecology (Pignatti et al. 1995; Loidi 2020). In entire Middle Asia, the pistachio open woodlands reveal strong seasonal variation of plant cover. In early spring the colourful geophyte aspect is apparent while during the hot summer the herbaceous layer easily wither to the bareland. The closely related thermophilopus *Juniperus seravschanica* open woods, which evolved also from *proto-šhiblyak* (Kamelin 1967), have apparently different seasonality, precipitation and temperature requirements related to elevation and subalpine vegetation. Additionally, *Pistacia* groves during hot summers are exposed to frequent fires. Young seedlings are resistant to it and due to the high nutrient content in large seeds, can rapidly develop deep roots which secure the young trees' survival in the first, most critical year of their life (Popov 1994). Wild fires are observed frequently in Khatlon province, both in plantations and wild pistachio woodlands, resulting in a very scarce shrub layer and a preference for fire-avoiding or resistant species - such as geophytes - in the undergrowth.

Today, the wide native distribution of *P. vera* and *P. khinjuk* is well characterised, and Middle Asia is believed to be a primary center of origin and diversity of these species. This opinion is supported by many botanists, among others Popov (1929), Morozov (1929), Vavilov (1931), Whitehouse (1957), Zohary (1996). *Pistacia vera* is also considered the most economically important species of the genus (FAOSTAT 2023), whereas *P. atlantica* and *P. khinjuk* that grow in Southwestern Asia (Rechinger 1969; Khatamsaz 1988; Behboodi 2003) did not receive commercial acceptance and have not been extensively cultivated. However, their nuts are used mainly as traditional food or for their medicinal properties (Bozorgi et al. 2013).

The phylogenetic data show that *P. vera* and *P. khinjuk* are the oldest (Kozhoridze et al. 2015) and genetically closely related representatives of the genus (Zarei and Erfani-Moghadam 2021). Palaeobotanical data indicate that before the Pleistocene, *P. vera* was one out of four species of this genus that inhabited Middle Asia (Popov 1994; Zlotin 1994). Loidi (2020), in his discussion of vegetation class delimitation, emphasises the importance of the common evolution of species and vegetation that creates a given type of high rank vegetation. The ancestral vegetation that gave rise to the pistachio groves was most likely the Mesozoic flora of warm and subtropical climates called Tethys Flora. In the early Palaeogene (from the Palaeocene to Eocene; 66 to 33.9 M years ago) this flora was probably close to the known Eocene flora of Badghyz (Kurbanov 1994; Hurka et al. 2019). This palaeoflora was dominated by e.g. *Rhus turkomanica*, species of *Prunus*, *Pistacia*, evergreen species of *Quercus* and some *Lauraceae* taxa (Korovin 1934; Kurbanov 1994). It is possible that this vegetation gave rise to the xerophylic tree and shrub communities of *proto-šhiblyak* during the Tertiary period (66 to 2.6 M years ago; Kamelin 1970, 1973), which was composed of sclerophyllous and thermophilous shrubs and small trees (Kurbanov 1994). Contemporary *šhiblyak* vegetation still includes Tertiary taxa like *Ziziphus jujuba*, *Rhus coriaria*, *Celtis caucasica*, *Cercis griffithii*, *Punica granatum* and *Ficus carica*. However, it lacks oak species that were common in Palaeogen (*Quercus ilex*, *Q. balloot* and *Q. castaneifolia*). Aridisation of climate and steppe formations in Miocene and Pliocene caused the xerophytisation of *proto-šhiblyak*. This ancient zonal vegetation type could be regarded as a shrinking relict refuge of a number of paleoendemic taxa. Examples are, e.g., *Prunus bucharica*, *Calophaca grandiflora*, *Cephalorhizum micranthum*, *Eversmannia sogdiana*, *Lipskya insignis*, *Mediasia macrophylla* or *Oedibasis tamerlanii*. As a consequence of aridisation, the withdrawal of the para-Tethys sea and climate oscillation during the Pleistocene, *proto-šhiblyak* has formed a variety of vegetation formations from pistachio open woodlands in the lowest and warmest areas, through the deciduous forests of *Juglans regia* occupying the valleys in the mid-latitudes, to the juniper woods inhabiting subalpine belt. It is worth noting that important compositional elements of woodlands like *Prunus*, *Pyrus* and *Malus* evolved during this aridification. In mid-Miocene (ca. 14 M years ago), *Rosaceae* also diversified, most likely in response to increasingly less humid climate (Töpel et al. 2012). Also in the Late Miocene the divergence time of *Calophaca* took place in Middle Asia (Zhang et al. 2015). The community of the latter species occupies large areas in central Tajikistan and occupies an intermediate position between pistachio open woodlands and typical *šhiblyak* (Nowak et al. 2022b).

Ethnobotanical evidence showing the extent of pistachio open woodlands in Middle Asia

The name for pistachio originated from Middle Asian languages. In Uzbek and Tajik, it is *pista*, in Kazakh *psta*, in Turkmen *pisse*, and in Kyrgyz *miste* (Khalmatov et al. 1984). Evidence of these formerly extensive open woodlands can be found in the many pistachio related names of villages, small streams, waterfalls, and gorges (Khanazarov et al. 2009). Pistachio groves are culturally significant to Tajik (and neighbouring) people not only for their fruit production or livestock grazing, but also for their fruit trees cultivation tradition and scenic value of their homeland. It is very common for pistachio trees to be planted in home gardens. Also, many places derive their names from the local name for pistachios. Often these names occur in areas that are now 100% occupied by pseudosteppe vegetation, with only single trees growing next to buildings, e.g. Pistimazor near Vahdad, ca. 700 m a.s.l., Pistimazor near Kulob, ca. 600 m a.s.l. These two names also show the connection between pistachios and religion: “Mazor” or “Mazar” means mausoleum of holy people and is surrounded by religious worship. The name *Pistimazor* can therefore be translated as “sacred place under the pistachio”. Other names related to pistachio come from the Ferghana Basin and western Pamir Alai: Gulpista (means flower of pistachio, Tajikistan), Pista Mazor, Pistamazar (Pstamazar), Pista Quduq, Pystalik (Pistalik; Uzbekistan), Jeke-Miste (Kyrgyzstan). There are even pistachio mountains Pistalitau in Uzbekistan (Alibekov and Alibekov 2007). Probably also Psa Mandeh and Pstigrom in Afghanistan are based on the pistachio name.

Conclusions and outlook

In this paper we propose to recognise the *Pistacietea verae* as a distinct and new vegetation class. It was compared with similar vegetation of the eastern Mediterranean and Irano-Turanian vegetation of shrublands, mesic and Mediterranean woodlands, juniper open woods, tall-forb communities and pseudosteppes. Taking into account species composition, rate of endemism, phytogeography, ecology and seasonal dynamics, range and use before the development of pastoral civilisation and today, this research suggests that the new vegetation class is a distinct vegetation type stretching across the entire region. Further research in the Hindu Kush, Kopet-Dagh, Zagroz Mts and south-eastern Caucasus (Iori plateau in Georgia and Turian-Chay State Reserve in Azerbajan) will certainly yield interesting data on the internal diversity of this vegetation. Based on our data, we could only describe one association from the western part of the range - *Pistacietum khinjuk*. This open woodland with *Pistacia* spp. dominance is a heterogeneous vegetation with its distribution center in the Irano-Turanian phytogeographical region. Previously it had been described as an arid open woodland, thicket, thin forest, grove, savanna or savanna-like steppe woodland, open arid forest or wild orchard (Zohary 1973; Kayimov et al. 2001; Kaya et al. 2010; Fayvush and Aleksanyan 2016; Gianguzzi and Bazan 2019; Ambarlı et al. 2020; Lachashvili et al. 2020). Unfortunately, strong negative impacts by humans through intensive grazing, logging and burning, on pistachio woodlands together with the lack of effective conservation measures and forest management are causing a gradual decline in the range of this species-rich vegetation, which harbours many rare, endemic and relict taxa.

Data availability

The datasets of the current study are available from the corresponding author on reasonable request.

Author contributions

ANo conceived the idea of the vegetation class, ANo, SŚ, ANa and MN planned the research, conducted the field sampling and identified the plant species. ANo and SŚ performed statistical analyses, while all the authors participated in the writing of the manuscript and verification of plants in herbarium.

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Supplementary material

Supplementary material 1
Synoptic table of pistachio open woodlands vegetation in Middle and Southwestern Asia belonging to the class *Pistacietea verae* (*.xlsx)
Link: https://doi.org/10.3897/VCS.104841.suppl1

Supplementary material 2
Synoptic table of the full dataset used for comparing the pistachio open woodlands with related vegetation types of naturally occurring woody and grassland phytocoenoses in Middle and Southwestern Asia (*.xlsx)
Link: https://doi.org/10.3897/VCS.104841.suppl2

Supplementary material 3
Analytical table of class *Pistacietea verae* (*.xlsx)
Link: https://doi.org/10.3897/VCS.104841.suppl3

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RESEARCH PAPER AFRICAN VEGETATION STUDIES

Potential distribution of major plant units under climate change scenarios along an aridity gradient in Namibia

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Abstract

Objectives: Climate change is expected to have major impacts on plant species distribution worldwide. These changes can affect plant species in three ways: the timing of seasonal activities (phenology), physiology and distribution. This study aims to predict the effect of shifting climatic conditions on the major vegetation units along an aridity gradient through Namibia. **Study area:** Namibia's vegetation is characterised by open woodland in the northeast to low open shrubland in the southern part of the country. These differences are a result of increasing aridity from north to south with a rainfall gradient from 100 mm to 600 mm. Namibia is projected to have an increase in annual mean temperature of 2°C by the end of the 21st century. **Methods:** A vegetation classification was done for 1,986 relevés using cluster analysis, a Multi-Response Permutation Procedure and indicator species analysis. The current distribution of the vegetation classes was modelled with Random Forest. Future projections for the most important climate variables were used to model the potential distribution of the vegetation units in 2080. This modelling approach used two scenarios of Representative Concentration Pathways (4.5 and 8.5) from two Global Climate Models – the IPSL–CM5A–LR and HAdGEM2–ES. **Results:** The predicted distribution shows a high expansion potential of *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas, *Combretum africanum-Terminalia sericea* broad-leafed savannas and *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas towards the south under both scenarios. **Conclusions:** The model indicated the ability to classify and predict vegetation units to future climatic conditions. Half of the vegetation units are expected to undergo significant contraction. Overall, RCP8.5 conditions favour the proliferation of certain vegetation types, particularly *Combretum collinum-Terminalia sericea* broad-leafed savannas and *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, potentially displacing other vegetation types.

Taxonomic reference: Klaassen and Kwembeya (2013) for vascular plants, except Kyalangalilwa et al. (2013) for the genera *Senegalia* and *Vachellia* s.l. (*Fabaceae*).

Abbreviations: CDM = Community Distribution Model; CMIP5 = Coupled Model Inter-comparison Project Phase 5; EVI = Enhanced Vegetation Index; GCM = General Circulation Model; IV = Indicator Value; ISA = Indicator Species Analysis; MAP = mean annual precipitation; MAT = mean annual temperature; MRPP = Multi-Response Permutation Procedure; NMS = Non-Metric Multidimensional Scaling; RF = Random Forest; RCPs = Representative Concentration Pathways; SDM = species distribution model.

Keywords

climate change scenarios, distribution, indicator species, Namibia, potential distribution, rainfall gradient, vegetation units, vegetation classification

Introduction

Namibia is the driest country in southern Africa. Despite its arid conditions, Namibia is home to more than 4,500 plant species covering four major biomes: Namib Desert, Succulent Karoo, Nama-Karoo, and tree and shrub savanna (Midgley et al. 2005). The vegetation supports communal and commercial livestock and wildlife farming, the sectors on which Namibia is highly dependent (Reid et al. 2008). Therefore, the tree and shrub savanna that covers up to 84% of the land is economically vital to Namibia. It also provides ecosystem services such as capturing carbon dioxide from the atmosphere and regulating the climate (Snyder et al. 2004). Economically important species in the savanna provide food, traditional medicine, building materials and timber products to local people (Barnes et al. 2012).

However, these savannas are at risk of global climate change that affects many species worldwide (Pounds et al. 2005; Parmesan 2006; Feehan et al. 2009; Lenoir et al. 2010; Chen et al. 2011). It has resulted in species range shifts to cooler areas such as towards the poles and high elevations (Pounds et al. 2005; Feehan et al. 2009; Sintayehu 2018). However, warming challenges species already inhabiting the highest elevations because they do not have new habitats to colonise, leading to possible local extinction (Thuiller et al. 2005; Manish et al. 2016). Species with a low dispersal capability, such as herbs (Ash et al. 2017) are noted to also be at risk as they cannot disperse over a long distance, thus accelerating warming may surpass the rate of migration of these species.

In southern Africa, a change in weather patterns has been noted over the last decennia. For example, the second half of the 20th century observed a reduction in rainfall in mainly Angola, Democratic Republic of Congo and Namibia (Niang et al. 2014). The mean temperature in southern Africa has increased from 1.04°C to 1.44°C between 1961 and 2015 (Trisos et al. 2022).

Midgley et al. (2005) found that 53% of the long–term weather stations in Namibia and the Northern Cape experienced an increased temperature of 0.2°C and a 33% decreased rainfall over a 25 to 60–year period. Future climate projections indicate significant impacts from climate change, including changes in temperature such as a projected mean annual warming between 2°C and 6°C (Reid et al. 2008; Barnes et al. 2012) by the end of the 21st century (Turpie et al. 2010). The projected high temperature will cause an increase in evaporation, resulting in severe water shortages, thereby exacerbating the country's aridity (Reid et al. 2008). The latter is likely to have significant effects on Namibia's vegetation, including changes in species composition and distribution, as well as the overall health and productivity of ecosystems.

By 2050 and 2080, it is expected that the endemic plants in Namibia, such as perennial herbs, geophytes, and trees, will experience adverse effects (Thuiller et al. 2006). Midgley et al. (2005) found that by 2080, a range expansion with 43% of desert–adapted vegetation types, should be expected. A range contraction of desert–adapted species such as *Aloe dichotoma* to higher elevations is also likely. The temperature and rainfall change will result in some plants shifting their ranges towards the north–eastern part of Namibia (Midgley et al. 2005; Thuiller et al. 2006), such as the timber tree *Pterocarpus angolensis* (De Cauwer et al. 2016).

Namibia's vegetation has been studied by several researchers as indicated by Burke and Strohbach (2000) with the most widely accepted classification being the preliminary vegetation map of Namibia by Giess (1998). This map categorizes Namibia's vegetation into 14 different vegetation types. The vegetation varies from desert scrub to woodland. The preliminary vegetation map that is widely used in Namibia is based on ground observations that were then extrapolated to the national level using expert knowledge (Giess 1998; Westinga et al. 2020). A comprehensive vegetation map based on vegetation surveys does not exist yet for Namibia. In addition to the preliminary vegetation map of Namibia, other studies have focused on specific regions or types of vegetation, such as the classification of savanna vegetation in the central parts of Namibia (Strohbach 2002, 2019).

Many studies have used species distribution models (SDMs) to investigate the effects of climate change on species' potential distribution. SDMs are computer algorithms that are widely used to predict species distribution by relating species occurrences to environmental variables at known locations and using this relationship to predict species distribution across space and time (Elith and Graham 2009; Manish et al. 2016). In Namibia, there have been studies on the effect of climate change on species distribution, indicating that the country's vegetation is likely to experience significant shifts in vegetation types and distribution, while others found that the country's savanna ecosystem will change in composition and some species becoming dominant over the others (Midgley et al. 2005).

Unlike SDMs, the examination of large–scale vegetation patterns can be conducted through the application of a community distribution model (CDM) by employing the species compositional approach (Ferrier and Guisan 2006; Potts et al. 2013). Community–level modelling integrates information from various species which are grouped through numerical classification, to provide insights into the spatial distribution at a collective community level which provides an opportunity to integrate a complex dataset (Ferrier and Guisan 2006). Just like SDMs, CDMs are subject to multiple uncertainties such as geographical sampling bias which can limit model generalisation, the assumption of unchanging species interactions, and groups or species that have not been homogeneously described across their distribution range (Thuiller et al. 2004a; Midgley and Thuiller 2011). CDMs share similarities with SDMs in terms of methods and data type (Keane et al. 2020). The CDM's response variable is the vegetation type or community instead of individual species as in SDMs (Franklin 2013). The machine learning models used to predict species distribution also predict community distribution (Jiménez-Alfaro et al. 2018; Keane et al.

2020). An example of an algorithm that has popularly been used in individual species and community modelling is the Random Forest algorithm (Keane et al. 2020).

Namibia exhibits a south–north rainfall gradient. Consequently, the country's vegetation transitions from sparse shrubs with scattered trees in the south to open woodland in the northeast. This rainfall and vegetation gradient offers an ideal national–scale transect for studying vegetation change.

This study aims to use Random Forest models to predict the response of vegetation units along a south–north rainfall gradient to projected global climate change scenarios in Namibia. The above was achieved through the following objectives: classify the vegetation along the gradient, identify the environmental factors responsible for the distribution of vegetation units, model the vegetation for the current climate, and predict the distribution of vegetation units for the future using climate scenarios. The present study used vegetation data collected over many years by various researchers and has therefore the potential to provide a good synthesis of the vegetation distribution in Namibia.

Methods

Study area

The study was conducted along a south-north transect of 1,383 km long and 30 km wide following a rainfall gradient. Rainfall typically begins in the first three months of summer (October to December), but peaks in February (Dreber and Esler 2011). The northern part of the study area receives 600 mm of annual rainfall, while the southern parts of the study area receive 100 to 160 mm, indicating a gradient of decreasing annual rainfall from the north to the south of the transect, as shown in Figure 1a (Mendelsohn et al. 2002). The yearly maximum mean temperature of the hottest month along the study site is 34°C (Turpie et al. 2010). The transect crosses four landscapes: the Kalahari Basin in the north, the Central Plateau, the Khomas Hochland Plateau in the central, and the Nama-Karoo in the south (Figure 1b).

In the far north–east, the topography of the Kalahari basin is flat to nearly flat, with elevations ranging between 900 m and 1,200 m a.s.l. (Mendelsohn et al. 2002) with Ferralic Arenosols as dominant soils. The Central Plateau stretches from the central northeast (near Grootfontein) to the Khomas Hochland (near Okahandja) in central Namibia. For most parts, it is a flat to undulating plain, interrupted by occasional inselbergs and the foot slopes in the north of the Otavi Mountain Land. Altitudes range between 1,100 and 1,600 m a.s.l. In the far north–east, shallow Mollic Leptosols, often with calcrete, prevail, whilst in the central and southern parts deeper Cambisols occur (ICC et al. 2000). The Khomas Hochland forms part of the escarpment and ranges between 1,600 to well over 1,800 m a.s.l. It is a rolling to steep mountainous highland overlaid by lithic Leptosols that are generally shallow and often covered by quarz pebbles (Joubert et al. 2008; Strohbach 2017). The Nama-Karoo forms part of the Central Plateau, however with a distinctly arid climate. It consists of various landforms ranging from dissected plains to mountains and generally lies at approximately 800 to 1,200 m a.s.l. (Mendelsohn et al. 2002).

Data sampling and analysis

This research study used relevé data collected from 1990 to 2016 for the vegetation survey of the Namibia project (Strohbach and Kangombe 2012). The data collection followed the Braun-Blanquet sampling procedure (Strohbach 2014) within a plot size of 20 m × 50 m. This plot size is considered adequate and commonly used for vegetation surveys in Namibia (Burke and Strohbach 2000; Strohbach 2001, 2014). The abundance for each species in a plot was assessed by visually estimating the cover and recorded as a percentage.

The vegetation surveys do not cover the whole country; therefore, a countrywide analysis was not possible. Sufficient data were available for the transect of our study, which represents most of the rainfall gradient in Namibia and hence a wide variety of vegetation units present in the country. The data were grouped into vegetation classes using cluster analysis in PC-ORD version 7 (McCune et al. 2002). Given the length of the gradient, and thus the size and heterogeneity of the data set, it was assumed that less than six groups would not adequately reflect the turnover in habitat and plant diversity. Therefore, the clustering was started with a minimum of six and a maximum of twelve groups. The classification was based on the Sørensen distance measure and Flexible Beta (Beta = -0.25) as a group linkage method (Perrin et al. 2006). There are multiple distance measures available, but all are dependent on the nature of the ecological question to be answered and the type of data collected. For example, the Sørensen distance measure used in this analysis is good for ecological community data analysis because it is less prone to extreme values (outliers) and can retain sensitivity to heterogenous data sets (McCune et al. 2002; Perrin et al. 2006; Peck 2010).

To find the ideal number of groups for the classification, the statistical outcomes from the Multi-Response Permutation Procedure (MRPP) and Indicator Species Analysis (ISA) in PC-ORD are compared for each number of groups. MRPP was used to test the similarity within groups using the Sørensen distance measure. The difference among the groups was interpreted from a test statistic (T) and the chance–corrected within–group Agreement (A). A high negative T–value indicates a greater separation between the groups, while a low negative T–value indicates less separation (Everhart et al. 2008). The classification with the optimal number of groups would have the lowest negative T–value. The A–value shows how homogenous or heterogenous the groups are (Brinkmann et al. 2009). An optimal number of groups gives a high A–value. The A–value ranges between 0–1, with values between

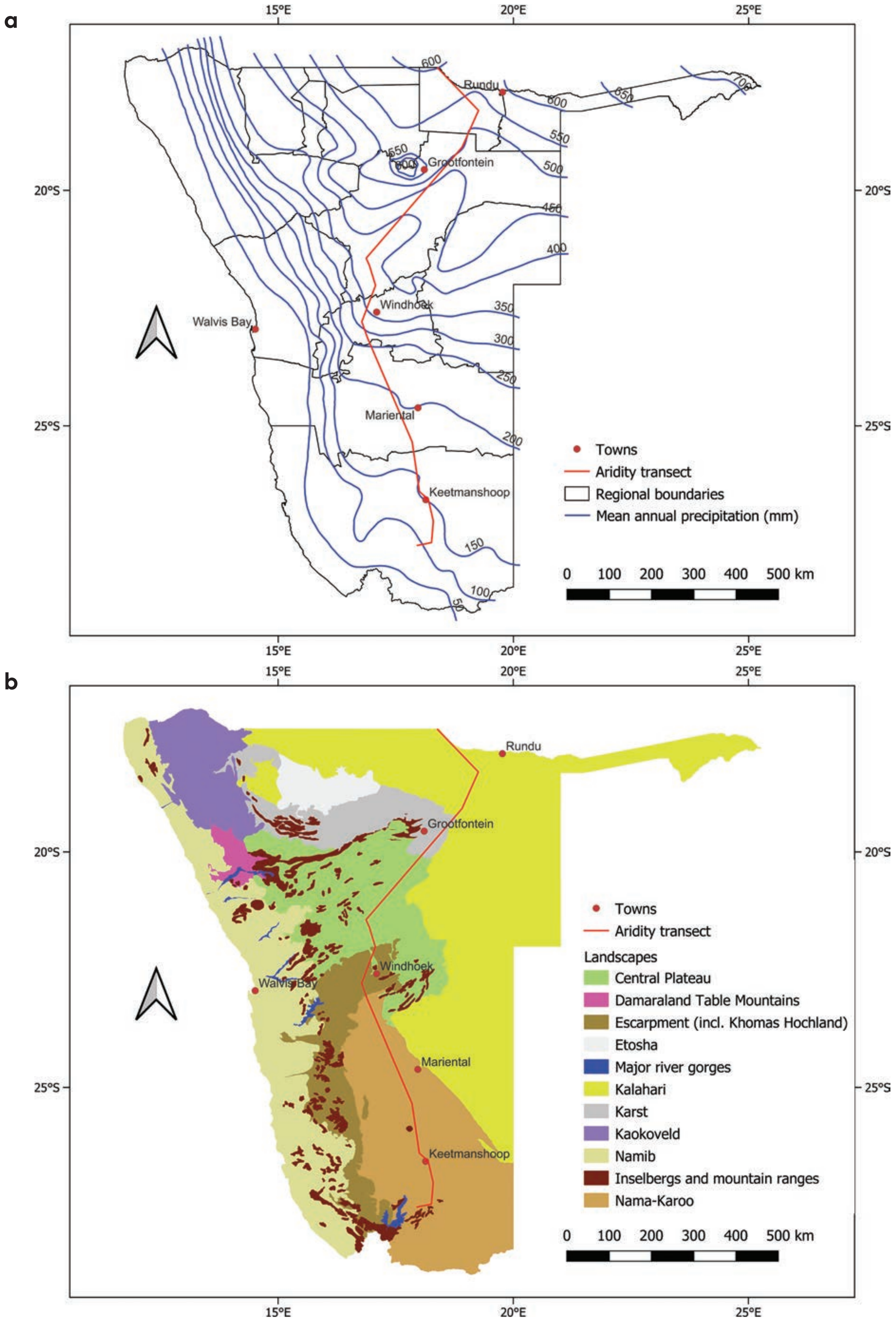

Figure 1. (a) Map of the study area indicating a north–south transect across an aridity gradient. (b) Major landscapes. Maps adapted from De Pauw et al. (1998).

0.3–1 showing that the homogeneity in the groups did not occur by chance (Everhart et al. 2008).

The ISA analysis determined indicator values (IV) for each species, as well as their statistical significance with a Monte Carlo test, to determine species with robust association to specific vegetation groups. A threshold level for IV of 20% with p–value ≤ 0.05 was chosen as the cut–off for identifying indicator species (Dufrêne and Legendre 1997; Khan et al. 2011). ISA contributed to determining the ideal number of vegetation groups in the classification (Brinkmann et al. 2009) by comparing the mean probability (p) value and mean IV for each group. The identified constant and dominant species in each group were used to name the vegetation types. Constant species are species with frequent occurrence, while dominant species frequently occur with a high percentage of cover in a particular vegetation unit (Kusbach et al. 2012). The naming of vegetation units in this study does not follow the International Code of Phytosociological Nomenclature (Theurillat et al. 2021) and are thus named as vegetation units that are not attached to any hierarchical order.

The ISA results were imported into the JUICE program (Tichý 2002) to generate a list of diagnostic species for each vegetation unit through the synoptic table routine. The numbers of relevés were standardised following Tichý and Chytrý (2006). Species with phi ≥ 40 were considered diagnostic. Species above 60% frequency were regarded as constant species and above 10% frequency as dominant species (Marcenò et al. 2018). Diagnostic species have a distinct concentration of occurrence or abundance in a particular vegetation unit and help identify the vegetation units (Chytrý and Tichý 2003). The threshold fidelity value for diagnostic species was 30%, while the cut–off frequency value for constant species was 40%, and 10% for dominant species (Marcenò et al. 2018). This follows standard procedures used for the Vegetation Survey of the Namibia project (Strohbach 2021).

An initial non–parametric ordination technique, non–metric multidimensional scaling (NMS) was performed in PC-ORD using the Sørensen distance measure (McCune et al. 2002). The NMS iterations recommended a two–dimensional ordination space. NMS scores were saved at plot level and correlated to a range of environmental variables

Environmental variables determining the current distribution of the vegetation units

Environmental factors significantly impact vegetation growth and distribution (Anderson and Herlocker 1973; Ahmad et al. 2020). The selection of environmental factors used to define the ecological niche of vegetation units is a critical step in the classification and modelling process because these variables determine the quality of the model output (Guisan and Zimmermann 2000; Araújo and Guisan 2006). A large set of environmental variables (Table 1) was tested for their relevance to the vegetation model. Firstly, highly correlated environmental variables were removed. Spearman's rank correlations were determined in R statistical software version 4.1.0 (R Core Team 2021). For each pair of highly correlated variables (> 0.80) (Pecchi et al. 2019), the variable with the lowest NMS score, explaining the least of the ordination, was removed.

Table 1. Environmental variables used for the current distribution of the vegetation units.

Variable description	Source
Monthly Soil water content (SWC), Priestley–Taylor alpha coefficient (Pt–alpha) – a measure of evapotranspiration rate of water bodies such as lakes and oceans.	CGIAR–CSI (Consortium for Spatial Information, Zomer et al. 2006) Global aridity and PET database
Global aridity index, Monthly potential evapotranspiration (PET).	(Trabucco and Zomer 2018)
19 bioclimatic variables for 1970–2000, with a spatial resolution of 30 arcsec, approximately 1 km at the equator available as GeoTiff files. Data were derived from the average monthly climatic data min, mean, max temperature and precipitation.	WorldClim: version 2 http://www.worldclim.org (Fick and Hijmans 2017; Vega et al. 2017)
Digital soil layer downloaded as GeoTiff at five–arcsecond spatial resolution. Soil digital layers with a spatial resolution of 250 m for 1970–2000 are available in GeoTiff files. The following layer was downloaded:	ISRIC World soil information **http://www.data.isric.org/**
Sand content (60–100 cm) at 5 standard depths in g/100 g was predicted using two sets of African soil profile data.	(Hengl et al. 2015)
Enhanced Vegetation Index (EVI) provides a measure of the greenness of the vegetation and ranges between -1 and 1, where an EVI value close to zero represents less vegetation while a value close to one represents abundant vegetation (Gurung et al. 2009).	Moderate–resolution Imaging Spectroradiometer (MODIS) sensor. African Soil Information Services (AfSIS): Remote Sensing Land Collection
EVI data were obtained as monthly and yearly means between 2000–2018, at a spatial resolution of 250 m.	http://africasoils.net/services/data/remotesensing/land/ Average time–series of Africa
Soil types, and dominant soils (DOM) soil of Namibia	Soil map of Namibia (Coetzee 2020, unpubl.). Accurate soil data for each relevés is not available, and thus the use of a more generalised soil map.
Namibia 2011 census population data. Data extracted from a shapefile.	Namibia Statistic Agency
Cattle density	FAO http://www.fao.org/livestock-systems/global-distributions/en/
Climatic Water Deficit (CWD) downloaded as GeoTiff at 2.5 arcs minute spatial resolution (Chave et al. 2014)	http://chave.ups-tlse.fr/pantropical_allometry.htm
Global Land Cover (GLC) 2006	http://www.landcover.org

Random Forest model

The current and future distribution of vegetation units were modelled with Random Forest. Random Forest uses a collection of computer–grown decision trees (an ensemble of trees) to solve regression and classification problems (Breiman 2001). For this study, environmental variables as predictors and vegetation unit as response were added as input variables into the model. The algorithm selects a group of decision learners in a process known as bagging. Approximately 63% of the data is used for bagging, with the remainder used as an out–of–bag estimate to the test prediction accuracy of the classification (Liaw and Wiener 2002; Cushman and Huettmann 2009). Two parameters (mtry and ntree) are defined as the number of random variables and the number of trees used at each node, respectively (Naidoo et al. 2012). The model of this study used 500 trees (Nguyen et al. 2020) and three randomly chosen variables at each node.

Two models for the current vegetation distribution were fitted with the non–correlated environmental variables as predictors, however, one model used 10 variables, including two satellite–derived Enhanced Vegetation Indices (EVI). Another model was fitted with eight variables, excluding the two EVI variables. Vegetation indices such as the EVI are important predictors for the classification of vegetation and the creation of two models aimed to assess to what extent climate and static data such as topography and soil can predict the current vegetation distribution. Stanton et al. (2012) and Zangiabadi et al. (2021) indicated that using only dynamic climate variables reduces model performance compared to when static variables are included. The model without EVI was the basis for the models that projected the distribution of the vegetation units based on future climate data.

Further selection of the final variables was done through Variable Importance selection under the Random Forest package (Liaw and Wiener 2014) using the Mean Decrease Gini coefficient (MDG) (Naidoo et al. 2012; Han et al. 2016). The MDG measures the decrease in node impurity and how well the data is split among the trees. All variables with an MDG value above 70 were selected to be used in fitting the model. After the selection, the model is rerun with only the selected variables. Partial dependence plots were used to visualise the effect of the most important variables.

Model accuracy assessment

Model calibration was performed using the out–of–bag error. The ratio of 70:30 was used to divide the data into training and testing data, respectively (Duque-Lazo et al. 2016; Sahragard et al. 2018). The confusion matrix was produced to show the correctness of the predicted classes against the actual class values and calculate the misclassification error per class. Additionally, an accuracy score and Kappa statistic (Cohen's Kappa) (Congalton 1991) were used to validate the model from test data. The scale of the statistic ranges as follows; 0.81–1 = almost perfect, 0.61–0.80 = substantial, 0.41–0.60 = moderate, 0.21–0.40 = fair, and 0–0.20 = fail (Heikkinen et al. 2006).

Future climate change scenarios

This study used future climate scenarios for one time period, 2070 (average for 2061–2080) based on emission scenarios from the General Circulation Model of CMIP5, downscaled and calibrated using WorlClim 1.4 as baseline climate. CMIP5 data were used because the CMIP6 downscaled and calibrated data were not available at the time of analysis for this study. The future projection was based on the Representative Concentration Pathways (RCPs 4.5 and 8.5) of IPSL CM5A LR and HadGEM2–ES general circulation models. Future bioclimatic raster layers were reprojected to WGS 84, cropped to the study area, and resampled to ensure that they all have the same extent and resolution. All datasets were resampled to 0.083 degrees resolution, approximately 1 km at the equator.

Results

Vegetation classification along the transect

The grouping statistics of the seven classifications done with PC-Ord Cluster analysis are provided in Table 2. Based on the MRPP and ISA criteria described earlier, a classification of twelve groups was chosen as the best result.

Table 2. The summary of Multi–Response Permutation Procedure (MRPP) and Indicator Species Analysis (ISA) illustrating the statistical values for each classification level or number of classified groups (Gr). The bolded value represents the best result of each statistical test. The values in italic fonts show the second–best value in each category. *T* = Test statistic *T*, *A* = chance–corrected within–group agreement, *p* = mean probability and IV = Indicator Value.

Number of Groups		**6 Gr**	**7 Gr**	**8 Gr**	**9 Gr**	**10 Gr**	**11 Gr**	**12 Gr**
MRPP	***T***	**-753**	-741	*-744*	-743	-737	-732	-720
	A	0.11	**0.12**	0.13	0.14	0.15	*0.16*	**0.17**
ISA	No. of Indicator species	562	612	*668*	666	**669**	630	642
	Mean *p*	0.25	0.21	*0.20*	***0.20***	0.20	0.21	**0.20**
	Indicator value (IV)	4.9	4.8	5.2	5.2	5.4	*5.5*	**5.5**

Environmental variables and their influence on the distribution of vegetation units along the transect

A description of the twelve vegetation units is described below. A bridged synoptic table of vegetation units, their species composition and species frequency is presented in Table 3.

Unit 1. Senegalia mellifera-Monechma genistifolium *thornbush savanna*

This vegetation unit consists of 138 relevés and 53 species. It occurs sparsely in the south of the Otjozondjupa region as well as towards the north of the Karas region. The vegetation is highly dominated by *Senegalia mellifera* and diagnostic species such as *Monechma genistifolium*, *Leucosphaera bainesii* and *Senegalia tortilis* (Table 3). The probability of occurrence drops as the mean temperature increases above 20°C (Figure 3a). Figure 2a shows a typical example of this unit.

Unit 2. Monelytrum luederitzianum-Senegalia hereroensis *mountain savanna*

The vegetation unit consists of 175 species in 217 plots. The vegetation occurs in the rocky outcrops from the Otavi mountain range to the Omatako mountains of the

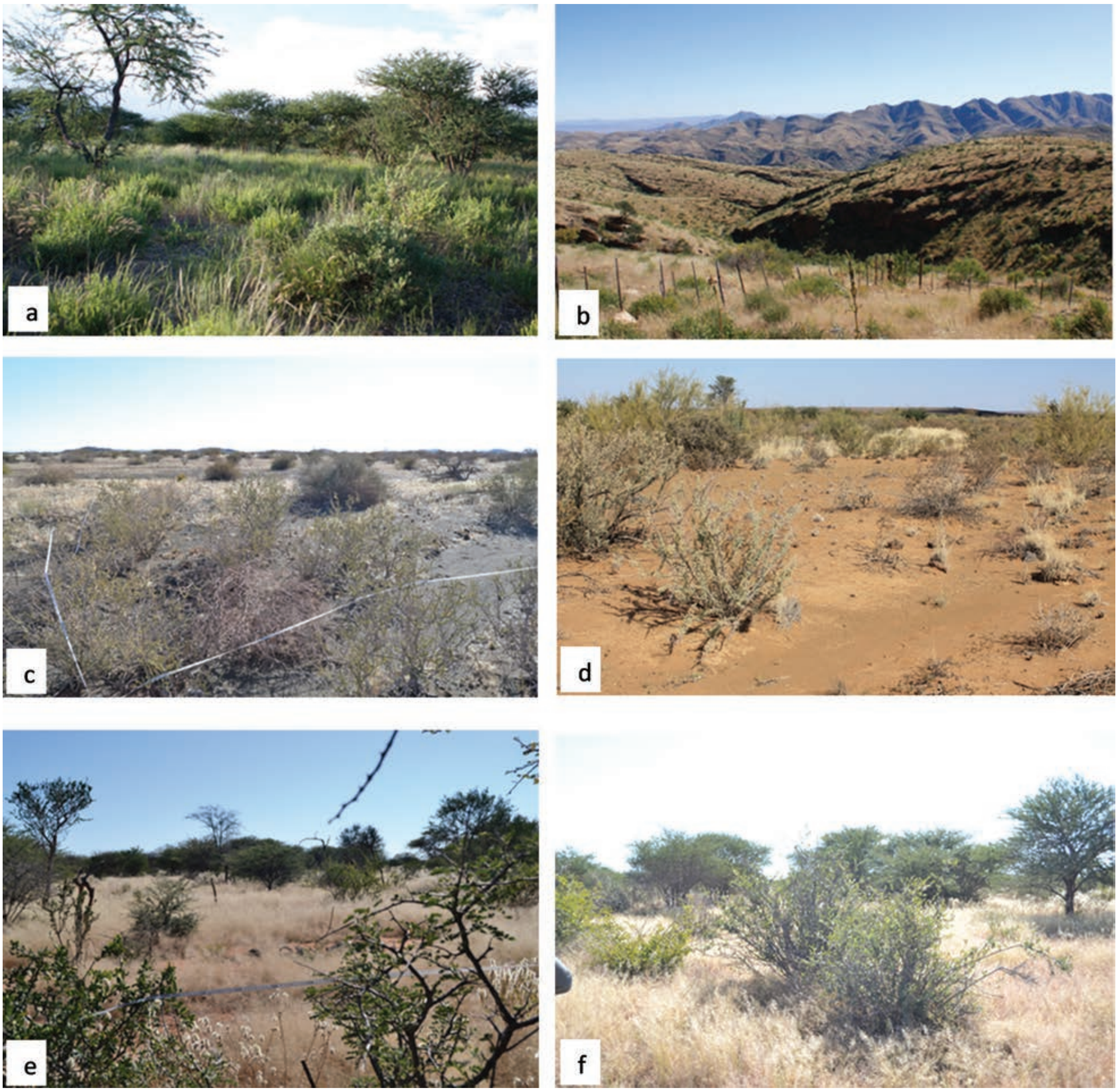

Figure 2. Typical representations of the vegetation units. (a) unit 1, the *Senegalia mellifera-Monechma genistifolium* thornbush savanna; (b) unit 2, the *Monelytrum luederitzianum-Senegalia hereroensis* mountain savanna; (c) unit 3, the *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savanna; (d) unit 4, the *Salsola-Tetragonia schenckii* dwarf shrub savanna; (e) unit 5, the *Dichrostachys cinerea-Senegalia mellifera* thornbush savanna; (f) unit 6, the *Stipagrostis uniplumis-Senegalia mellifera* thornbush savanna. Photo credit: (a) and (d) Ben Strohbach; (b), (c), (e) and (f) Leena Naftal.

Table 3. Abridged synoptic table of all the vegetation units along the transect. Vegetation units are labelled as follows: **1**. *Senegalia mellifera-Monechma genistifolium* thornbush savanna, **2**. *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas, **3**. *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas, **4**. *Salsola-Tetragonia schenckii* dwarf shrub savannas, **5**. *Dichrostachys cinerea-Senegalia mellifera* thornbush savannas, **6**. *Stipagrostis uniplumis-Senegalia mellifera* thornbush savannas, **7**. Thornbush savanna – Nama-Karoo transition, **8**. *Aristida congesta-Senegalia mellifera* thornbush savannas, **9**. *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, **10**. *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas, **11**. *Combretum collinum-Terminalia sericea* broad-leafed savannas, **12**. *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas. **F** = percentage frequency; **P** = the phi coefficient of fidelity × 100. The highlighted values are for species with Phi > 0.30, and Freq > 40%, meeting the predetermined criteria for the respective vegetation units.

Vegetation units	**1**		**2**		**3**		**4**		**5**		**6**		**7**		**8**		**9**		**10**		**11**		**12**	
Number of plots	**138**		**217**		**101**		**173**		**175**		**157**		**115**		**168**		**305**		**84**		**301**		**52**	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Monechma genistifolium	73	41	10	---	12	---	21	---	18	---	22	---	23	---	31	9	6	---	12	---	.	---	2	---
Cenchrus ciliaris	74	36	37	10	7	---	10	---	37	10	26	---	16	---	30	---	28	---	10	---	.	---	4	---
Leucosphaera bainesii	88	36	50	11	19	---	17	---	32	---	38	---	37	---	69	24	20	---	14	---	.	---	6	---
Hermannia damarana	19	36	4	---	.	---	.	---	1	---	.	---	.	---	1	---	1	---	.	---	.	---	.	---
Vachellia tortilis	60	35	6	---	.	---	1	---	27	8	24	---	1	---	49	26	19	---	.	---	.	---	13	---
Monelytrum luederitzianum	10	---	39	40	.	---	.	---	9	---	4	---	1	---	5	---	8	---	.	---	.	---	.	---
Hirpicium gazanioides	4	---	40	40	3	---	6	---	7	---	5	---	.	---	2	---	10	---	1	---	.	---	.	---
Eriocephalus luederitzianus	20	16	39	40	1	---	5	---	4	---	4	---	3	---	2	---	1	---	.	---	.	---	.	---
Senegalia hereroensis	.	---	30	40	..	---	.	---	4	---	4	---	.	---	1	---	8	---	.	---	.	---	2	---
Eragrostis nindensis	14	---	71	40	14	---	10	---	11	---	33	11	24	---	10	---	18	---	8	---	2	---	15	---
Microchloa caffra	4	---	39	36	2	---	2	---	8	---	9	---	.	---	11	---	7	---	1	---	3	---	2	---
Hibiscus discophorus	1	---	21	36	.	---	.	---	2	---	3	---	.	---	2	---	1	---	.	---	.	---	.	---
Fingerhuthia africana	13	---	39	35	2	---	5	---	10	---	6	---	2	---	.	---	11	---	5	---	.	---	.	---
Panicum lanipes	.	---	19	34	.	---	1	---	4	---	3	---	.	---	.	---	2	---	.	---	.	---	.	---
Ursinia nana	.	---	18	32	.	---	1	---	2	---	3	---	.	---	.	---	2	---	1	---	.	---	.	---
Hermannia affinis	1	---	24	30	5	---	5	---	1	---	2	---	.	---	.	---	2	---	8	---	.	---	.	---
Plinthus sericeus	.	---	17	30	.	---	2	---	3	---	2	---	.	---	.	---	2	---	.	---	.	---	.	---
Stipagrostis anomala	.	---	.	---	45	56	2	---	.	---	.	---	1	---	.	---	.	---	11	8	.	---	.	---
Zygophyllum simplex	.	---	1	---	30	44	6	---	.	---	.	---	2	---	.	---	1	---	2	---	.	---	.	---
Xerocladia viridiramis	1	---	.	---	19	40	1	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---
Calicorema capitata	.	---	.	---	39	40	4	---	.	---	3	---	2	---	.	---	.	---	30	29	.	---	.	---
Tribulus cristatus	1	---	1	---	37	39	11	6	.	---	3	---	18	15	.	---	.	---	2	---	.	---	.	---
Zygophyllum rigida	1	---	1	---	19	35	6	8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---
Petalidium parvifolium	.	---	.	---	10	30	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---
Stipagrostis ciliata	7	---	11	---	26	13	68	52	.	---	1	---	21	8	1	---	2	---	10	---	.	---	.	---
Cadaba aphylla	1	---	1	---	6	---	31	33	.	---	9	---	14	10	1	---	1	---	7	---	.	---	.	---
Salsola species	3	---	1	---	17	18	25	31	.	---	.	---	5	---	.	---	1	---	2	---	.	---	.	---
Boscia foetida	27	5	6	---	30	7	27	5	1	---	38	14	74	41	5	---	4	---	29	---	.	---	.	---
Lycium cinereum	.	---	11	---	16	---	9	---	1	---	25	13	48	35	1	---	1	---	25	13	.	---	.	---
Triraphis ramosissima	2	---	6	---	1	---	.	---	1	---	17	16	29	32	.	---	5	---	1	---	.	---	.	---
Vachellia nebrownii	.	---	1	---	10	---	17	10	.	---	16	9	36	30	1	---	.	---	17	9	.	---	.	---
Ondetia linearis	6	---	6	---	.	---	.	---	12	---	3	---	.	---	40	43	2	---	.	---	.	---	4	---
Indigofera rautanenii	5	---	5	---	.	---	.	---	18	9	14	---	2	---	45	38	5	---	.	---	.	---	13	---
Geigeria acaulis	14	---	8	---	1	---	.	---	15	---	16	---	1	---	43	36	5	---	1	---	.	---	2	---
Lycium eeni	57	21	31	---	.	---	1	---	38	9	38	8	7	---	76	35	18	---	12	---	.	---	31	---
Achyranthes aspera	54	21	22	---	.	---	1	---	57	23	25	---	5	---	71	33	26	---	7	---	4	---	21	---
Phaeoptilum spinosum	36	11	32	8	16	---	3	---	24	---	25	---	14	---	65	33	7	---	18	---	.	---	10	---
Eragrostis porosa	51	14	38	---	3	---	5	---	35	---	50	13	42	---	79	32	25	---	20	---	1	---	13	---
Boscia albitrunca	59	15	25	---	3	---	2	---	59	15	46	7	17	---	84	31	39	---	17	---	10	---	62	17
Aristida rhiniochloa	30	12	11	---	.	---	.	---	42	22	9	---	3	---	52	31	23	6	.	---	.	---	17	---
Combretum apiculatum	1	---	6	---	.	---	.	---	3	---	1	---	1	---	2	---	20	30	.	---	.	---	.	---
Schmidtia kalahariensis	7	---	11	---	19	---	17	---	.	---	33	7	62	28	1	---	7	---	93	50	.	---	25	---
Stipagrostis hirtigluma	12	---	22	4	37	16	20	---	6	---	5	---	8	---	5	---	5	---	68	42	.	---	12	---
Eragrostis cylindriflora	.	---	6	---	3	---	1	---	.	---	.	---	.	---	3	---	4	---	27	38	.	---	.	---
Aizoanthemum galenioides	.	---	1	---	.	---	3	---	.	---	.	---	.	---	.	---	.	---	19	38	.	---	.	---
Combretum collinum	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	.	---	83	85	6	---
Ochna pulchra	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	.	---	72	79	6	---
Terminalia sericea	.	---	.	---	.	---	.	---	5	---	1	---	.	---	1	---	10	---	.	---	89	79	17	---
Burkea africana	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	62	77	.	---
Baphia massaiensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	70	76	10	---
Bauhinia petersiana	.	---	1	---	.	---	.	---	3	---	.	---	.	---	.	---	9	---	.	---	82	73	23	---
Eragrostis pallens	.	---	.	---	.	---	1	---	.	---	1	---	.	---	.	---	1	---	.	---	55	72	.	---
Aristida stipitata	.	---	.	---	.	---	.	---	2	---	.	---	2	---	2	---	3	---	.	---	62	72	2	---
Combretum psidioides	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	52	68	2	---
Xenostegia tridentata subsp. *angustifolia*	.	---	1	---	.	---	.	---	5	---	1	---	.	---	.	---	5	---	.	---	57	64	6	---

Vegetation units	1		2		3		4		5		6		7		8		9		10		11		12	
Number of plots	138		217		101		173		175		157		115		168		305		84		301		52	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Baissea wulfhorstii	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	40	60	2	---
Panicum kalaharense	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	37	59	.	---
Pterocarpus angolensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	37	59	.	---
Senegalia ataxacantha	.	---	.	---	.	---	.	---	1	---	1	---	.	---	.	---	4	---	.	---	44	58	4	---
Jacquemontia tamnifolia	.	---	.	---	.	---	.	---	1	---	1	---	.	---	1	---	3	---	.	---	43	56	6	---
Ozoroa schinzii	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	39	56	6	---
Combretum engleri	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	37	55	4	---
Lophiocarpus tenuissimus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	31	54	.	---
Acrotome angustifolia	.	---	.	---	.	---	.	---	4	---	.	---	.	---	1	---	3	---	.	---	38	54	.	---
Cyperus margaritaceus	.	---	.	---	.	---	.	---	2	---	2	---	.	---	.	---	4	---	.	---	50	53	19	---
Megaloprotachne albescens	.	---	.	---	.	---	.	---	2	---	.	---	.	---	.	---	1	---	.	---	31	50	2	---
Commiphora angolensis	.	---	2	---	.	---	.	---	14	---	1	---	.	---	4	---	9	---	.	---	59	49	33	23
Perotis patens	.	---	.	---	.	---	.	---	1	---	.	---	.	---	.	---	1	---	.	---	26	49	.	---
Diplorhynchus condylocarpon	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	25	48	.	---
Croton gratissimus	.	---	1	---	.	---	.	---	19	---	.	---	.	---	.	---	18	12	.	---	50	48	6	---
Ipomoea chloroneura	.	---	.	---	.	---	.	---	3	---	.	---	.	---	.	---	3	---	.	---	33	46	6	---
Tristachya superba	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	22	46	.	---
Indigofera filipes	.	---	.	---	.	---	.	---	.	---	1	---	.	---	1	---	1	---	.	---	28	45	4	---
Syncolostemon bracteosus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	24	44	2	---
Guibourtia coleosperma	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	20	44	.	---
Tephrosia lupinifolia	.	---	.	---	.	---	.	---	2	---	.	---	.	---	1	---	1	---	.	---	25	43	2	---
Strychnos pungens	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	19	42	.	---
Oxygonum alatum	2	---	6	---	.	---	.	---	13	---	26	---	1	---	13	---	18	---	4	---	67	42	40	20
Polydora steetziana	.	---	.	---	.	---	.	---	5	---	4	---	.	---	.	---	5	---	.	---	31	42	2	---
Baikiaea plurijuga	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	19	42	.	---
Limeum fenestratum	.	---	1	---	.	---	1	---	3	---	6	---	3	---	6	---	8	---	.	---	44	42	19	---
Rhynchosia venulose	.	---	2	---	.	---	.	---	1	---	.	---	.	---	.	---	7	---	.	---	27	41	.	---
Phyllanthus omahakensis	.	---	.	---	.	---	.	---	1	---	.	---	.	---	.	---	2	---	.	---	25	41	4	---
Gardenia brachythamnus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	18	41	.	---
Chamaecrista absus	.	---	.	---	.	---	.	---	2	---	.	---	.	---	1	---	1	---	.	---	23	41	2	---
Sesamum alatum	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	16	39	.	---
Philenoptera nelsii	.	---	.	---	.	---	.	---	5	---	1	---	.	---	.	---	6	---	.	---	31	39	12	---
Dichapetalum cymosum	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	16	38	.	---
Diospyros chamaethamnus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	15	38	.	---
Pavonia clathrate	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	1	---	.	---	19	37	2	---
Indigofera baumiana	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	15	37	.	---
Clerodendrum ternatum	.	---	1	---	.	---	.	---	14	---	5	---	.	---	2	---	16	---	.	---	47	36	38	28
Combretum zeyheri	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	14	36	.	---
Acanthosicyos naudinuanus	.	---	1	---	.	---	.	---	6	---	13	---	.	---	4	---	8	---	4	---	41	36	23	---
Bulbostylis hispidula	2	---	6	---	.	---	.	---	8	---	9	---	5	---	8	---	15	---	14	---	53	35	44	27
Tephrosia purpurea	1	---	.	---	.	---	.	---	5	---	3	---	.	---	1	---	3	---	.	---	29	35	13	---
Raphionacme velutina	1	---	23	22	.	---	.	---	4	---	3	---	.	---	1	---	5	---	.	---	32	34	.	---
Chamaecrista biensis	.	---	.	---	.	---	.	---	3	---	1	---	.	---	1	---	5	---	2	---	26	34	10	---
Phyllanthus pentandrus	6	---	3	---	1	---	1	---	6	---	10	---	2	---	14	---	15	---	2	---	44	32	31	19
Strychnos cocculoides	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	11	31	.	---
Pogonarthria squarrosa	.	---	2	---	.	---	.	---	7	---	1	---	.	---	.	---	8	---	5	---	31	31	19	---
Grewia flavescens	5	---	4	---	.	---	1	---	22	---	5	---	1	---	15	---	17	---	.	---	46	31	31	---
Triraphis schinzii	.	---	1	---	.	---	.	---	2	---	1	---	.	---	.	---	4	---	.	---	21	31	10	---
Eragrostis dinteri	1	---	1	---	.	---	.	---	6	---	3	---	.	---	4	---	10	---	1	---	27	31	6	---
Tricholaena monachne	.	---	.	---	.	---	.	---	3	---	1	---	.	---	.	---	2	---	1	---	16	31	.	---
Commiphora africana	.	---	1	---	.	---	1	---	12	---	.	---	.	---	1	---	3	---	.	---	32	30	31	29
Psydrax livida	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	10	30	.	---
Entada arenaria	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	10	30	.	---
Chamaecrista mimosoides	.	---	.	---	.	---	.	---	.	---	2	---	.	---	.	---	1	---	.	---	13	30	.	---
Gloriosa superba	.	---	.	---	.	---	.	---	1	---	.	---	.	---	1	---	1	---	1	---	15	30	2	---
Eragrostis rigidior	.	---	2	---	1	---	1	---	27	8	23	5	1	---	17	---	19	---	.	---	15	---	98	65
Rhigozum brevispinosum	1	---	.	---	.	---	.	---	12	7	4	---	.	---	4	---	10	5	.	---	1	---	42	45
Urochloa panicoides	.	---	.	---	.	---	.	---	.	---	1	---	.	---	1	---	2	---	.	---	.	---	25	45
Ozoroa paniculosa	.	---	2	---	.	---	.	---	11	---	4	---	.	---	1	---	16	10	.	---	7	---	44	43
Solanum elaeagnifolium	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	4	3	1	---	.	---	23	40
Geigeria schinzii	.	---	1	---	.	---	.	---	.	---	1	---	.	---	1	---	3	---	.	---	.	---	21	40
Pavonia senegalensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2	---	4	3	.	---	1	---	21	39
Rhynchosia totta	1	---	1	---	.	---	.	---	7	---	1	---	.	---	1	---	8	---	.	---	15	12	35	38
Peltophorum africanum	.	---	2	---	.	---	.	---	15	8	2	---	.	---	.	---	18	12	.	---	15	8	40	37
Indigofera holubii	1	---	1	---	.	---	.	---	1	---	1	---	.	---	5	---	3	---	.	---	.	---	23	36
Evolvulus alsinioides	9	---	10	---	.	---	.	---	35	11	31	8	1	---	28	---	29	7	1	---	27	5	67	36
Camptorrhiza strumosa	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	12	33
Grewia flava	59	13	27	---	.	---	2	---	74	22	51	8	26	---	61	14	46	5	7	---	15	---	90	32
Commiphora glandulosa	1	---	6	---	.	---	.	---	18	10	6	---	7	---	.	---	18	10	.	---	8	---	38	32

Vegetation units	**1**		**2**		**3**		**4**		**5**		**6**		**7**		**8**		**9**		**10**		**11**		**12**	
Number of plots	**138**		**217**		**101**		**173**		**175**		**157**		**115**		**168**		**305**		**84**		**301**		**52**	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Brachiaria brizantha	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2	---	.	---	1	---	13	32
Rhus tenuinervis	.	---	1	---	.	---	.	---	6	---	.	---	.	---	.	---	6	5	.	---	3	---	21	31
Combretum hereroense	.	---	6	---	.	---	.	---	26	20	3	---	.	---	.	---	20	13	.	---	7	---	37	31
Lapeirousia otaviensis	.	---	.	---	.	---	.	---	1	---	.	---	.	---	.	---	.	---	.	---	.	---	12	31
Ipomoea hochstetteri	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2	---	2	---	.	---	.	---	13	31
Hibiscus mastersianus	.	---	.	---	.	---	.	---	1	---	.	---	1	---	1	---	2	---	.	---	19	24	23	30
Digitaria seriata	.	---	1	---	.	---	.	---	7	---	3	---	.	---	.	---	11	---	.	---	83	64	48	32
Commelina africana	.	---	12	---	.	---	.	---	10	---	3	---	.	---	2	---	10	---	.	---	53	41	42	30
Senegalia cinerea	1	---	1	---	.	---	.	---	16	---	5	---	.	---	4	---	21	8	2	---	48	32	52	36
Talinum arnotii	30	---	19	---	1	---	1	---	29	---	40	13	1	---	52	22	20	---	12	---	1	---	60	27
Lantana angolensis	14	---	12	---	.	---	.	---	30	16	6	---	.	---	13	---	23	9	2	---	12	---	42	27
Pogonarthria fleckii	8	---	41	10	.	---	2	---	45	13	39	9	3	---	52	18	37	7	8	---	18	---	65	26
Schmidtia pappophoroides	4	---	38	11	1	---	2	---	25	---	32	---	3	---	17	---	32	---	10	---	58	25	58	25
Ehretia rigida	38	11	16	---	.	---	1	---	47	18	18	---	6	---	48	18	25	---	12	---	6	---	54	23
Ziziphus mucronata	23	---	31	---	1	---	2	---	50	20	15	---	17	---	24	---	43	15	1	---	8	---	54	23
Dichrostachys cinerea	17	---	13	---	.	---	.	---	61	21	33	---	2	---	61	21	52	15	13	---	42	8	62	21
Urochloa brachyura	26	---	19	---	.	---	.	---	55	15	42	---	3	---	55	15	49	11	7	---	63	20	63	20
Senegalia mellifera subsp. *dentinens*	91	20	61	---	15	---	17	---	100	26	74	10	35	---	96	23	72	9	42	---	8	---	88	19
Eragrostis trichophora	20	---	23	---	.	---	1	---	54	25	13	---	3	---	39	14	28	---	4	---	16	---	44	18
Phyllanthus maderaspatensis	34	10	24	---	.	---	.	---	39	14	18	---	2	---	42	16	21	---	4	---	20	---	44	18
Aristida congesta	18	---	35	6	11	---	6	---	41	11	37	8	6	---	67	29	24	---	13	---	4	---	48	15
Tragus berteronianus	39	12	28	---	5	---	3	---	30	---	24	---	11	---	42	14	25	---	18	---	3	---	42	14
Stipagrostis uniplumis	72	---	58	---	48	---	18	---	62	---	100	22	97	20	74	---	55	---	39	---	72	---	87	14
Barleria lanceolata	48	23	16	---	3	---	.	---	35	13	17	---	1	---	54	28	12	---	2	---	2	---	31	---
Enneapogon cenchroides	78	24	51	7	10	---	24	---	43	---	75	22	61	13	68	17	32	---	20	---	3	---	12	---
Rhigozum trichotomum	9	---	13	---	63	27	65	28	1	---	29	---	63	26	1	---	5	---	54	20	.	---	.	---
Kyphocarpa angustifolia	25	---	52	18	.	---	8	---	43	13	28	---	4	---	57	22	32	---	12	---	5	---	38	---
Cyperus palmatus	20	---	15	---	.	---	.	---	19	---	21	9	.	---	41	28	9	---	1	---	1	---	15	---
Chloris virgata	28	---	24	---	9	---	7	---	28	7	15	---	8	---	46	21	21	---	15	---	1	---	23	---
Hermannia modesta	18	---	41	22	3	---	3	---	18	---	19	---	10	---	48	27	11	---	4	---	.	---	12	---
Otoptera burchellii	46	20	27	---	1	---	1	---	28	---	43	17	23	---	28	---	17	---	6	---	1	---	17	---
Ptycholobium biflorum	34	7	27	---	7	---	5	---	22	---	48	17	28	---	60	25	12	---	13	---	.	---	40	---
Aristida adscensionis	55	10	68	18	13	---	5	---	59	12	45	---	42	---	79	25	37	---	33	---	8	---	31	---
Melinis repens	33	---	62	12	4	---	10	---	47	---	59	---	30	---	61	11	53	---	20	---	70	17	65	---
Gisekia africana	4	---	12	---	7	---	8	---	17	---	48	15	41	10	29	---	17	---	38	---	55	20	38	---
Vachellia luederitzii	56	19	28	---	1	---	1	---	60	21	26	---	3	---	51	15	42	9	11	---	11	---	48	---
Enneapogon desvauxii	54	22	32	7	50	19	21	---	8	---	20	---	38	11	10	---	10	---	30	---	.	---	.	---
Dicoma capensis	6	---	23	9	33	18	12	---	5	---	13	---	35	20	5	---	3	---	20	---	.	---	.	---
Catophractes alexandrii	52	11	50	10	22	---	24	---	21	---	59	16	70	23	39	---	22	---	39	---	1	---	12	---
Vachellia hebeclada subsp. *hebeclada*	24	---	28	7	.	---	1	---	23	---	31	9	10	---	40	17	26	6	12	---	1	---	27	---

Central Plateau and Khomas highlands, at a mean altitude of 2,000–2,500 m (Strohbach 2017, 2019). Figure 2b shows a typical example of this unit which consists of diagnostic species of grasses such as *Monelytrum luederitzianum*, *Eragrostis nindensis*, *Pogonarthria fleckii*, and bushes such as *Monechma genistifolium*, *Catophractes alexandrii* and *Searsia marlothii* (Table 3), forming semi–open shrublands on shallow soils. The probability of occurrence of this vegetation type increases with the Mean Annual Precipitation (MAP) between 200 mm and 350 mm (Figure 3b).

Unit 3. Calicorema capitata-Rhigozum trichotomum *dwarf shrub savanna*

These are dwarf shrub savannas occurring in the Nama–Karoo (Figure 2c) in areas with mean annual rainfall below 250 mm (Figure 3c). Diagnostic species include *Stipagrostis anomala*, *Tetraena simplex*, *Xerocladia viridiramis*, *Calicorema capitata*, *Tribulus cristatus*, *Zygophyllum rigidum* and *Petalidium parvifolium*. Constant species include *Rhigozum trichotomum* and *Enneapogon desvauxii* (Table 3).

Unit 4. Salsola-Tetragonia schenckii *dwarf shrub savanna*

This vegetation is mainly associated with washes, floodplains, pans and other ephemeral wetland systems of the Nama-Karoo (Strohbach and Jankowitz 2012). The vegetation unit occurs around the mean rainfall of 250 mm per year (Figure 3d). The dwarf Karoo shrubs, mainly *Rhigozum trichotomum* and *Tetragonia schenckii*, but also *Zygophyllum microcarpum*, *Vachellia nebrownii* and *Salsola* species dominate the unit. Grass species such as *Stipagrostis ciliata* and *Stipagrostis obtusa* form part of the dominant species of the unit (Table 3) Figure 2d shows a representation of this vegetation unit.

Unit 5. Dichrostachys cinerea-Senegalia mellifera *thornbush savanna*

These savanna types comprise 175 plots and 90 species, characterised by a woody layer with constant species *Grewia flava*, *Ziziphus mucronata*, *Senegalia mellifera* subsp. *dentinens* and *Dichrostachys cinerea* (Table 3) usually forming open to closed bushland (Figure 2e). The lower strata consist of herb species

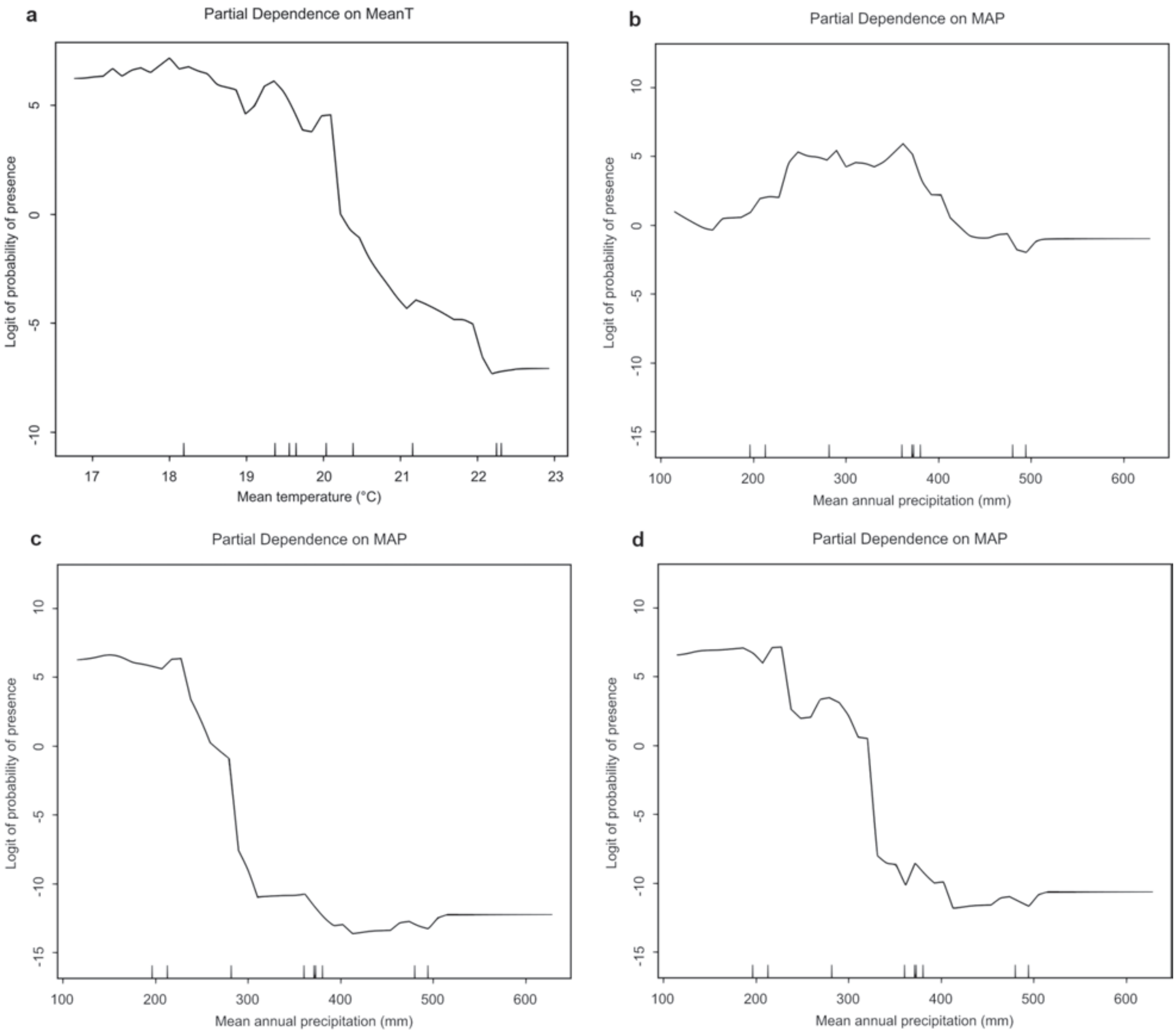

Figure 3. Partial dependence plots showing the effect of various environmental factors on the distribution of vegetation units. (a) Mean annual temperature (MAT) influencing the distribution of unit 1, the *Senegalia mellifera-Monechma* thornbush savanna; (b) Mean annual precipitation (MAP) influencing the distribution of unit 3, the *Monelytrum luederitzianum-Senegalia hereroensis* mountain savanna; (c) MAP influencing the distribution of unit 3, the *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savanna; (d) MAP influencing the distribution of unit 4, the *Salsola-Tetragonia schenckii* dwarf shrub savanna.

such as *Achyranthes aspera*, which according to field observation, are mostly shade–loving, taking up cover under trees with big canopies. Other herb species include *Pavonia burchellii* and *Pollichia campestris*. Dominant grass species include *Urochloa brachyura*, *Pogonarthria fleckii* and *Melinis repens* subsp. *grandiflora*. The vegetation occurs in an area with MAP between 250 mm and 500 mm (Figure 4a).

Unit 6. Stipagrostis uniplumis-Senegalia mellifera *thornbush savanna*

This vegetation unit consists of 157 plots and 30 species. The unit is distributed within the mean annual rainfall range of 230 mm and 400 mm (Figure 4b), but also an altitudinal range of between 1100 and 1300 m asl (Figure 4c). The species composition of this vegetation includes the following dominant species: *Catophractes alexandrii*, *Grewia flava*, *Eragrostis porosa*, *Senegalia mellifera* subsp. *dentinens*, *Vachellia reficiens* and *Schmidtia pappophoroides* (Table 3). An overview of the vegetation unit is shown in Figure 2e.

Unit 7. Thornbush savanna – Nama-Karoo transition

This vegetation unit is distributed in areas with MAP below 300 mm (Figure 6a). The vegetation unit comprises 115 plots and 52 species. Diagnostic species of the group include species such as *Boscia foetida*, *Lycium cinereum*, *Triraphis ramosissima* and *Vachellia nebrownii*. Species such as *Stipagrostis uniplumis*, *Catophractes alexandrii*, *Rhigozum trichotomum* and *Schmidtia kalahariensis* dominate the unit (Table 3). An example of the vegetation is shown in Figure 5a.

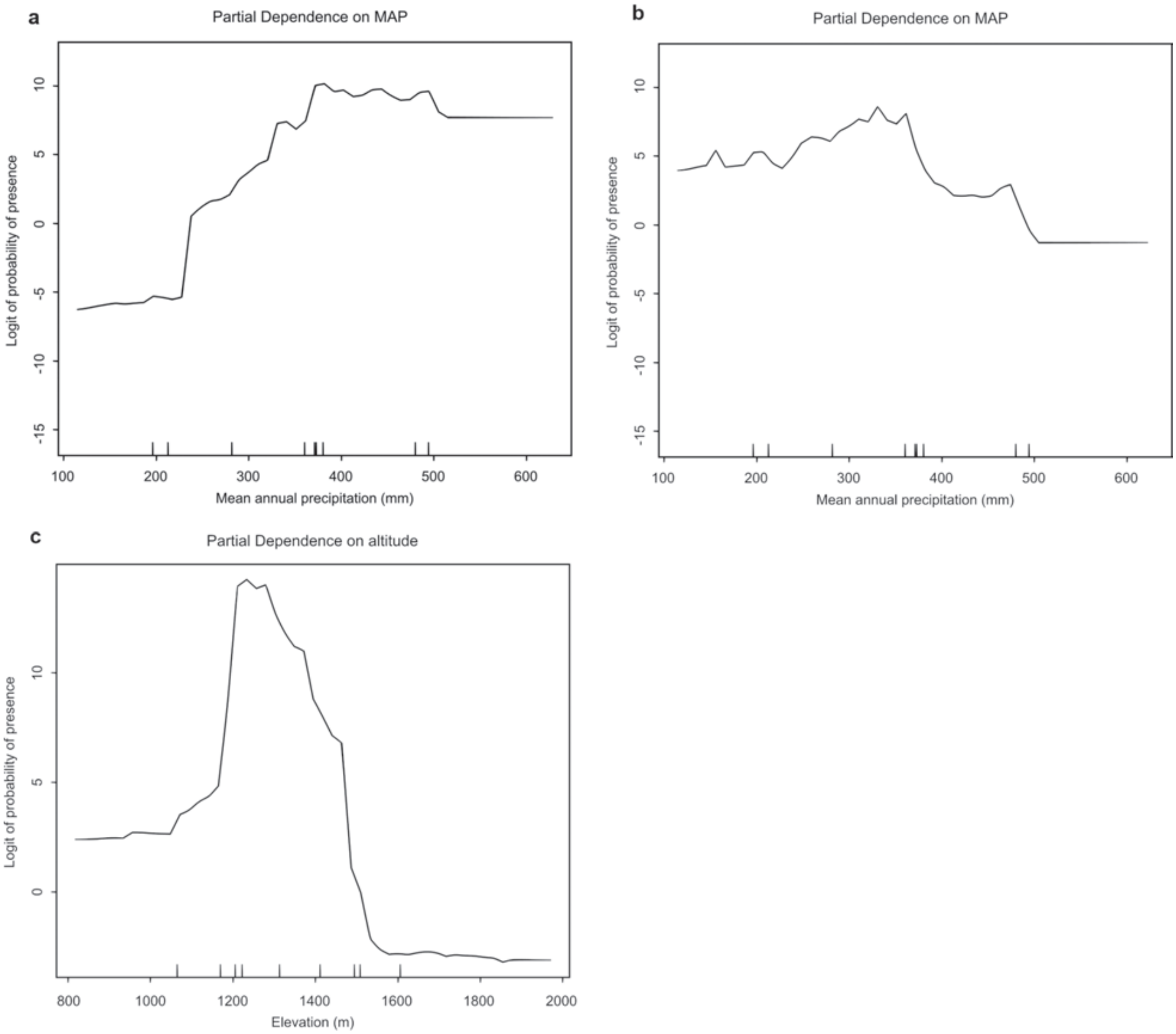

Figure 4. Partial dependence plots showing the effect of various environmental factors on the distribution of vegetation units. (a) MAP influencing the distribution of unit 5, the *Dichrostachys cinerea-Senegalia mellifera* thornbush savanna; (b) MAP influencing the distribution of unit 6, the *Stipagrostis uniplumis-Senegalia mellifera* thornbush savanna; and (c) altitude also influencing the distribution of unit 6, the *Stipagrostis uniplumis-Senegalia mellifera* thornbush savanna.

Unit 8. **Aristida congesta-Senegalia mellifera** *thornbush savanna*

The distribution of this vegetation unit occurs between the mean rainfall range of 200 mm to 400 mm (Figure 6b). Species diagnostic of the group include *Lycium eenii*, *Achyranthes aspera*, *Phaeoptilum spinosum*, *Eragrostis porosa*, *Boscia albitrunca*, *Aristida rhiniochloa*, with dominating species *Senegalia mellifera* subsp. *dentinens*, *Aristida adscensionis*, *Stipagrostis uniplumis* and *Leucosphaera bainesii* (Table 3). A typical example of the vegetation of this unit can be seen in Figure 5b.

Unit 9. **Senegalia mellifera-Dichrostachys cinerea** *degraded thornbush savanna*

This unit is the most widely distributed, occurring in areas that receive a mean rainfall of 200 mm to 500 mm (Figure 6c). It occurs in mosaic with many other thornbush savanna units, often associated with a dense shrublayer dominated by the woody species *Senegalia mellifera* subsp. *dentinens*, *Grewia flava*, *Dichrostachys cinerea* and *Vachellia reficiens*, whilst the herb layer is generally sparser with the grasses *Urochloa brachyura*, *Stipagrostis uniplumis*, *Melinis repens* subsp. *grandiflora* and *Eragrostis trichophora.* Bush encroachment is regarded as a serious form of degradation in the savannas of Namibia and southern Africa (De Klerk 2004; Laufs et al. 2024). An example of vegetation occurring in this unit can be seen in Figure 5c. A more detailed species composition can be found in Table 3.

Unit 10. **Schmidtia kalahariensis-Rhigozum trichotomum** *arid thornbush savanna*

This savanna type is distributed within the mean rainfall range of 100–300 mm (Figure 6d). Constant species of this unit are as follows: *Schmidtia kalahariensis*, *Stipagrostis hirtigluma* and *Eragrostis cylindriflora.* Species such as *Chloris virgata*, *Senegalia mellifera* subsp. *dentinens*,

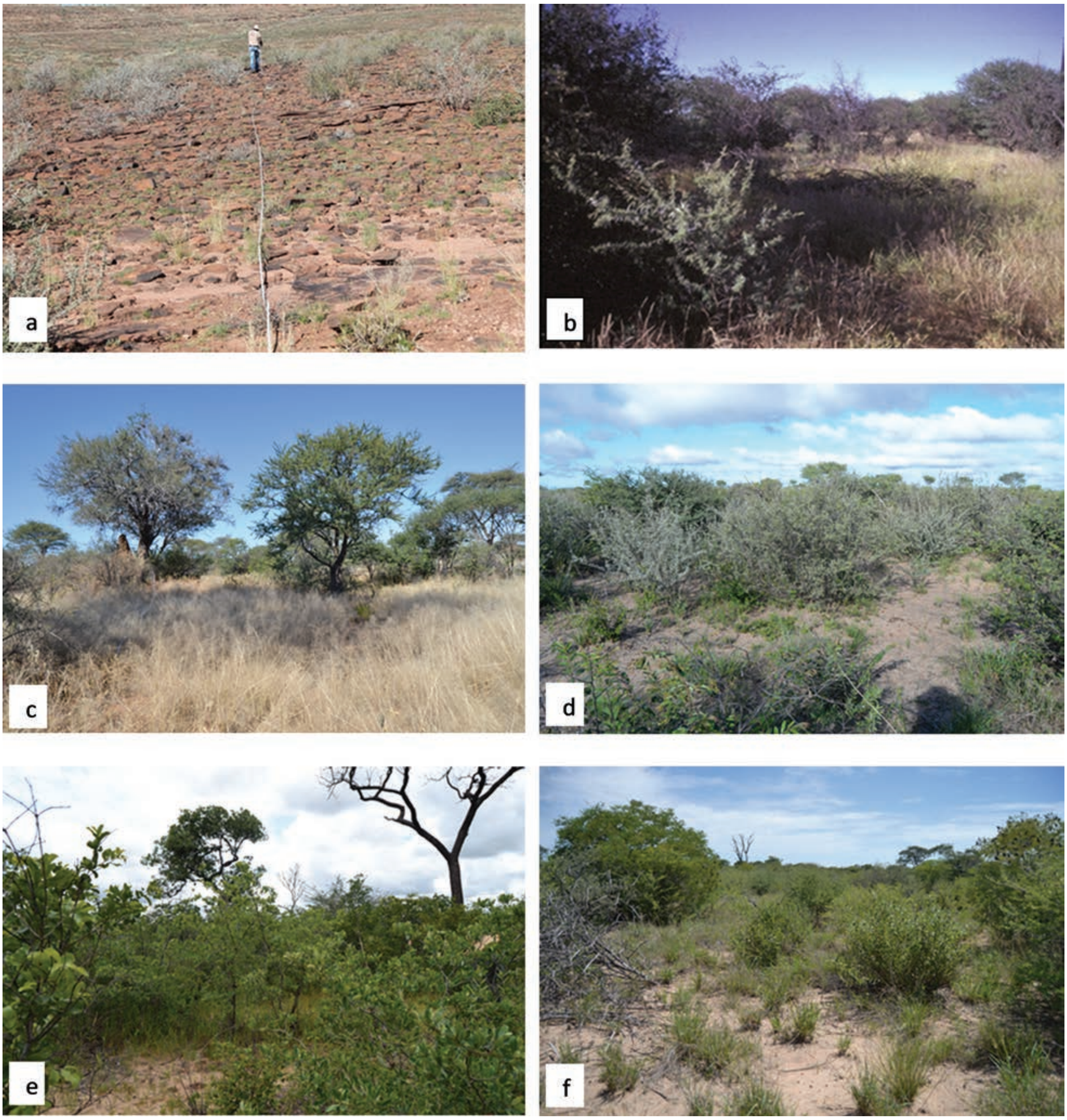

Figure 5. Typical representations of the vegetation units. (a) unit 7, the Thornbush savanna – Nama-Karoo transition, (b) unit 8, the *Aristida congesta-Senegalia mellifera* thornbush savanna, (c) unit 9, the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savanna, (d) unit 10, the *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savanna; (e) unit 11, the *Combretum collinum-Terminalia sericea* broad-leafed savanna; and (f) unit 12, the *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savanna. Photo credit: (a) Johanna Nghishiko, (b) Ben Strohbach, (c–f) Leena Naftal.

Catophractes alexandrii and *Vachellia reficiens* dominate the unit (Table 3). An example of this vegetation unit is shown in Figure 5d.

Unit 11. Combretum collinum-Terminalia sericea *broad-leafed savanna*

This vegetation unit has a high species diversity compared to other vegetation units. The diagnostic species forming up the woody layer include *Combretum collinum*, *Ochna pulchra*, *Terminalia sericea*, *Burkea africana*, *Baphia massaiensis*, *Bauhinia petersiana* and *Pterocarpus angolensis*, amongst others (Figure 5e). Herbs and grasses such as *Xenostegia tridentata* subsp. *angustifolia*, *Digitaria seriata* and *Panicum kalaharense* are also found. Species within these savannas occasionally form open to close woodlands and shrublands (Strohbach and Petersen 2007). The unit occurs on deep Kalahari sand, mostly on Ferralic Arenosols (Strohbach and Petersen 2007). The probability

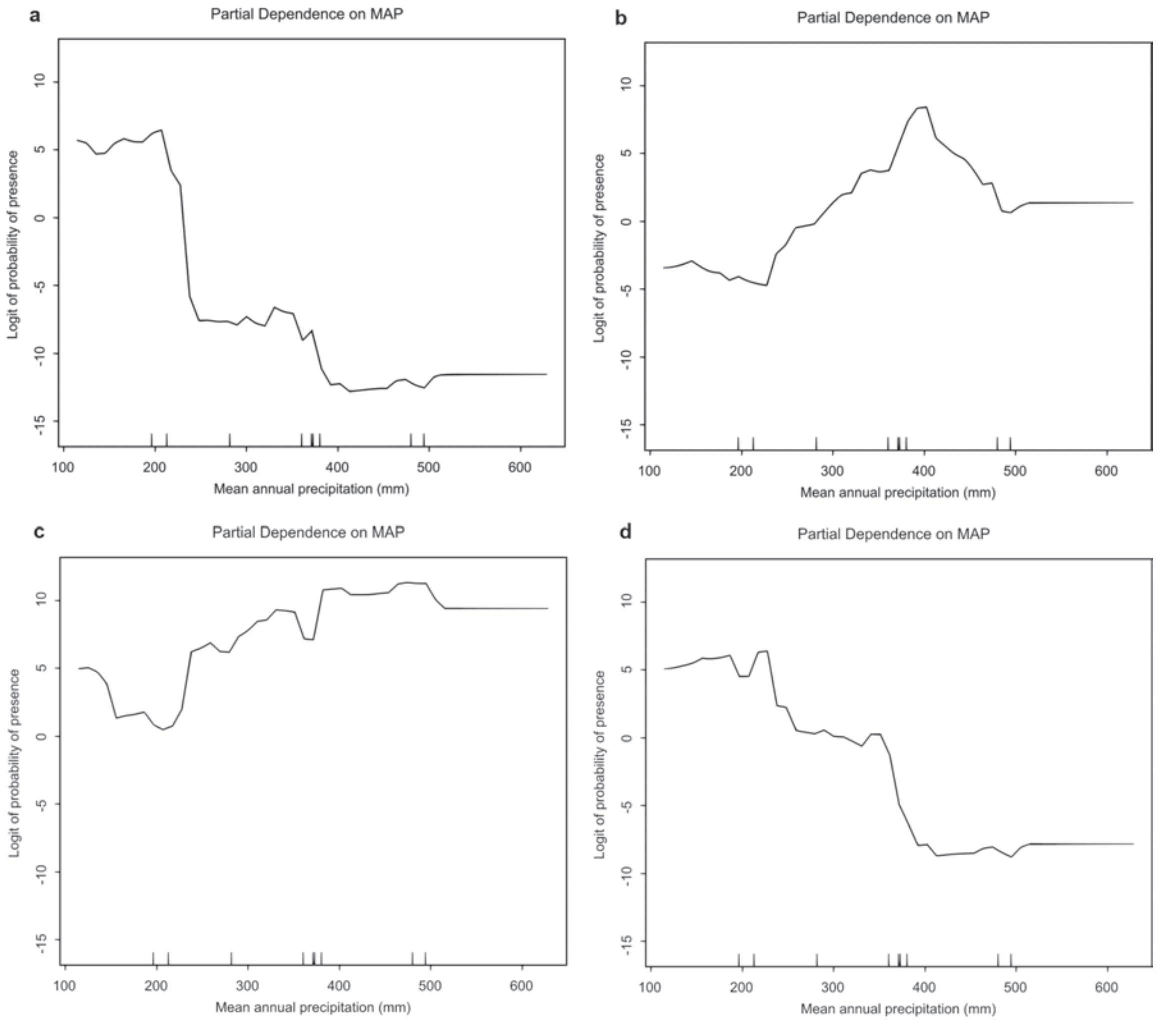

Figure 6. Partial dependence plots showing the effect of various environmental factors on the distribution of vegetation units. (a) MAP influencing the distribution of unit 7, the Thornbush savanna – Nama-Karoo transition; (b) MAP influencing the distribution of unit 8, the *Aristida congesta-Senegalia mellifera* thornbush savanna; (c) MAP influencing the distribution of unit 9, the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savanna; (d) MAP influencing the distribution of unit 10, the *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savanna.

of occurrence increases when the mean annual rainfall is above 400 mm (Figure 7a).

Unit 12. **Eragrostis rigidior-Peltophorum africanum** *mesic thornbush savanna*

This vegetation unit is distributed in areas with MAP of 350 mm to 500 mm and a Mean Annual Temperature (MAT) of over 25°C (Figure 7b, c). The composition of this vegetation unit includes woody species such as *Rhigozum brevispinosum*, *Senegalia cinerea*, *Vachellia erioloba* and *Peltophorum africanum*. Grass species such as *Urochloa panicoides*, *Eragrostis rigidior* and *Schmidtia pappophoroides* (Figure 5f). A detailed list of species occurring in this unit is presented in Table 3.

Modelling vegetation classes with Random Forest

Model performance evaluation

The model prediction with EVI indices had an overall classification accuracy of 94%, a Kappa value of 94% (Suppl. material 1), and an out-of-bag error of 17.1%. The accuracy of the model without EVI indices was 82% and Kappa 80%, as well as an out-of-bag error rate of 17.4% (Suppl. material 2). The environmental variables driving the current distribution and therefore used to predict the future distribution of the vegetation units are shown in Table 4.

The potential distribution of the vegetation units for the current and future under climate change scenarios

The current vegetation distribution results show that some vegetation units have a broad distribution, such as unit 9, *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, unit 11, *Combretum collinum-Terminalia sericea* broad-leafed savannas, unit 2, *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas and unit 4, *Salsola-Tetragonia schenckii* dwarf shrub savannas. While others such as unit 12, *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas and unit 1, the *Senegalia mellifera-Monechma genistifolium* thornbush savanna, have a restricted distribution (Figure 8). The total area covered by the current distribution for each

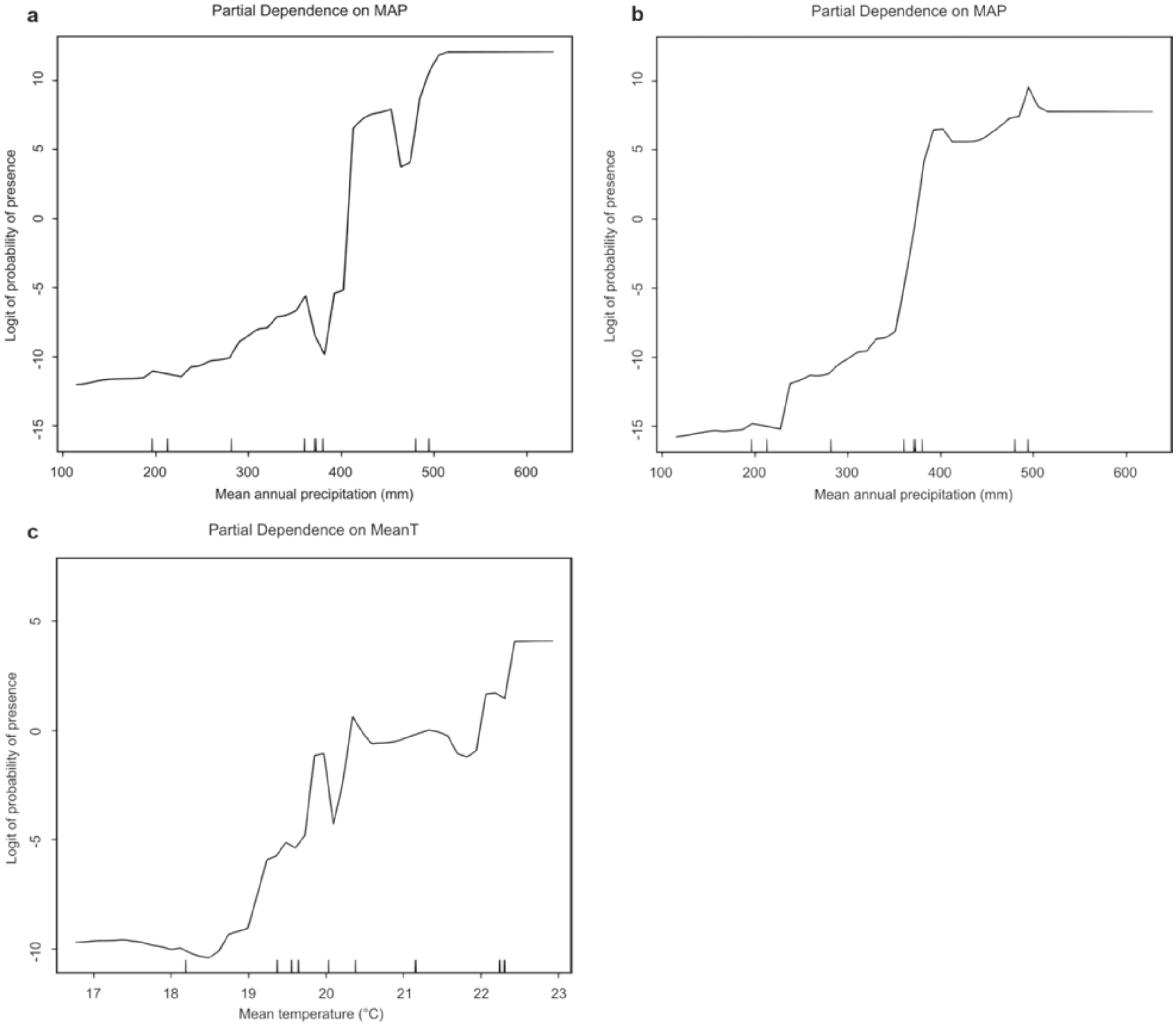

Figure 7. Partial dependence plots showing the effect of various environmental factors on the distribution of vegetation units. (a) MAP influencing the distribution of unit 11, the *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savanna; (b) MAP influencing the distribution of unit 12, the *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savanna; (c) MAT influencing the distribution of unit 12, the *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savanna.

Table 4. The Mean Decrease Gini (MDG) index and the importance per unit for the predictor variables used to fit the final model. Vegetation units are labelled as follows; unit **1**. *Senegalia mellifera-Monechma genistifolium* thornbush savanna, unit **2**. *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas, unit **3**. *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas, unit **4.** *Salsola-Tetragonia schenckii* dwarf shrub savannas, unit **5**. *Dichrostachys cinerea-Senegalia mellifera* thornbush savannas, unit **6**. *Stipagrostis uniplumis-Senegalia mellifera* thornbush savannas, unit **7**. Thornbush savanna – Nama-Karoo transition, unit **8**. *Aristida congesta-Senegalia mellifera* thornbush savannas, unit **9**. *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, unit **10**. *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas, unit **11**. *Combretum collinum-Terminalia sericea* broad-leafed savannas, and unit **12**. *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas.

Variable	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5	Unit 6	Unit 7	Unit 8	Unit 9	Unit 10	Unit 11	Unit 12	Mean decrease gini
Precipitation of the wettest month	15.7	19.2	29.6	33.5	18.3	15.8	21.7	16.3	15.9	25.4	24.2	17.8	191.71
Mean annual precipitation	18.9	15.2	18.8	26	18	15.6	24.1	16.1	14.5	24.1	18.7	17	195.21
Mean temperature of driest quarter	17.7	24.7	9.2	11.9	18.6	9.5	10.5	10.9	11.5	19.7	15.4	20.6	189.68
Mean temperature	19.6	28.9	12.6	15.3	15	13.5	16.4	14.8	10.7	22.7	11.5	19.9	205.95
Sand_sl4	16.6	6	9.4	8.7	7.5	5.9	7.2	7.5	4.4	7.7	13.3	16.3	168.08
Precipitation of February	17.5	16.9	26.7	29.1	18.1	16.7	24.2	18.5	13.8	28.1	20.7	18.3	182.97
Dominant soil	12.2	18.1	21.2	18.4	25.6	27.8	37	11.7	24.9	20.6	5	11.9	238.19
Altitude	26.1	25.8	25.8	20.6	37.1	32.1	29	24.4	29.2	29.4	12	26.3	366.27

Table 5. A comparison of the percentage change in the future distribution of the vegetation units relative to the current distribution using projected (2061–2080) climatic conditions for moderate (RCP4.5) and high (RCP8.5) scenarios under the IPSL–CM5A–LR and HadGEM2–ES General Circulation Models relative to the current potential distribution.

vegetation type name	Number of relevés	Area covered Current		RCP4.5		RCP8.5	
		km²	%	IPSL–CM5A–LR % Change	HadGEM2–ES % Change	IPSL–CM5A–LR % Change	HadGEM2–ES % Change
Unit 1. *Senegalia mellifera-Monechma genistifolium* thornbush savannas	138	469.15	0.36	-99.46	-70.71	-100	-99.82
Unit 2. *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas	217	16,228.09	12.56	-70.56	-85.91	164.10	-98.77
Unit 3. *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas	101	6,985.11	5.41	-98.26	-91.09	-99.29	-10.95
Unit 4. *Salsola-Tetragonia schenckii* dwarf shrub savannas	173	18,648.03	14.44	-76.79	-34.85	-86.32	6.60
Unit 5. *Dichrostachys cinerea- Senegalia mellifera* thornbush savannas	175	5,514.37	4.27	-95.06	-98.35	-100	-100
Unit 6. *Stipagrostis uniplumis-Senegalia mellifera* thornbush savannas	157	2,829.78	2.19	-85.67	22.94	-100	-95.75
Unit 7. Thornbush savanna – Nama-Karoo transition	115	12,003.75	9.29	-98.29	-90.96	-100	-100
Unit 8. *Aristida congesta-Senegalia mellifera* thornbush savannas	168	8,632.81	6.68	-13.99	63.30	-83.24	2.14
Unit 9. *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas	305	34,049.07	26.36	-10.50	68.44	-18.19	65.77
Unit 10. *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas	84	1,624.7	1.25	-77.79	49.20	-100	-95.91
Unit 11. *Combretum collinum-Terminalia sericea* broad-leaved savannas	301	21,987.78	17.02	267.30	60.06	336.04	70
Unit 12. *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas	52	162.13	0.13	-97.40	32.94	-66.76	-96.88

vegetation unit is presented in Table 5, and the potential current distribution map is presented in Figure 8.

The HadGEM2–ES under the RCP4.5 predicted a potential expansion in unit 11, *Combretum collinum-Terminalia sericea* broad-leafed savannas, unit 9, *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, unit 1, *Senegalia mellifera-Monechma genistifolium* thornbush savannas, unit 10, *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas, unit 12, *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas and unit 6, *Stipagrostis uniplumis-Senegalia mellifera* thornbush savannas, towards the south of the transect (Figure 9a). Half of the vegetation types in the HadGEM2–ES are predicted to highly contract relative to the current distribution (Table 5).

The IPSL–CM5A–LR (RCP4.5) (Figure 9b) predicts a high potential expansion of mostly unit 11, *Combretum collinum-Terminalia sericea* broad-leafed savannas, are projected to cover most of the transect from the north to the central parts of the Khomas Highland in the Khomas region as well as sparsely down south. Most of the vegetation types are predicted to lose over 70% of their habitats and will be forced to live in restricted areas under this scenario.

The IPSL–CM5A–LR under the RCP8.5 (Figure 10b) predicts harsher conditions with five vegetation units predicted to go extinct while most of the vegetation types are predicted to lose up to 70% of their habitats. On the other hand, under the HadGEM2–ES (RCP8.5), only two vegetation types are predicted to go extinct while others will be on the verge of losing all their areas of occupancy (Table 5).

The HadGEM2–ES under the business–as–usual scenarios (RCP8.5) (Figure 10a) indicates an expansion shifting a bit towards the south of the transect with a few patches of unit 11, the *Combretum collinum-Terminalia sericea* broad-leafed savannas, down south. of Vegetation units such as unit 8, *Aristida congesta-Senegalia mellifera* thornbush savannas, unit 4, *Salsola-Tetragonia schenckii* dwarf shrub savannas, and unit 9, *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas are predicted to expand.

The RCP8.5 conditions will favour the vegetation types such as the widely spread unit 11, *Combretum collinum-Terminalia sericea* broad-leafed savannas, and unit 9, *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, will expand at the expense of the other vegetation types.

Discussion

Comparison of the vegetation units to existing classification

The vegetation units derived from this analysis can be compared with existing classifications. Giess (1998) broadly described the vegetation of the whole Nama-Karoo as dwarf shrub savanna. Two vegetation units (*Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas and *Salsola-Tetragonia schenckii* dwarf shrub savannas) can be associated with Giess' (1998) classification of the dwarf shrub savanna. The same unit is similar to *Salsolo-Tetragonietum schenckii* as Strohbach and Jankowitz (2012) described for the phytosociology classification of farm Haribes in the Nama-Karoo biome.

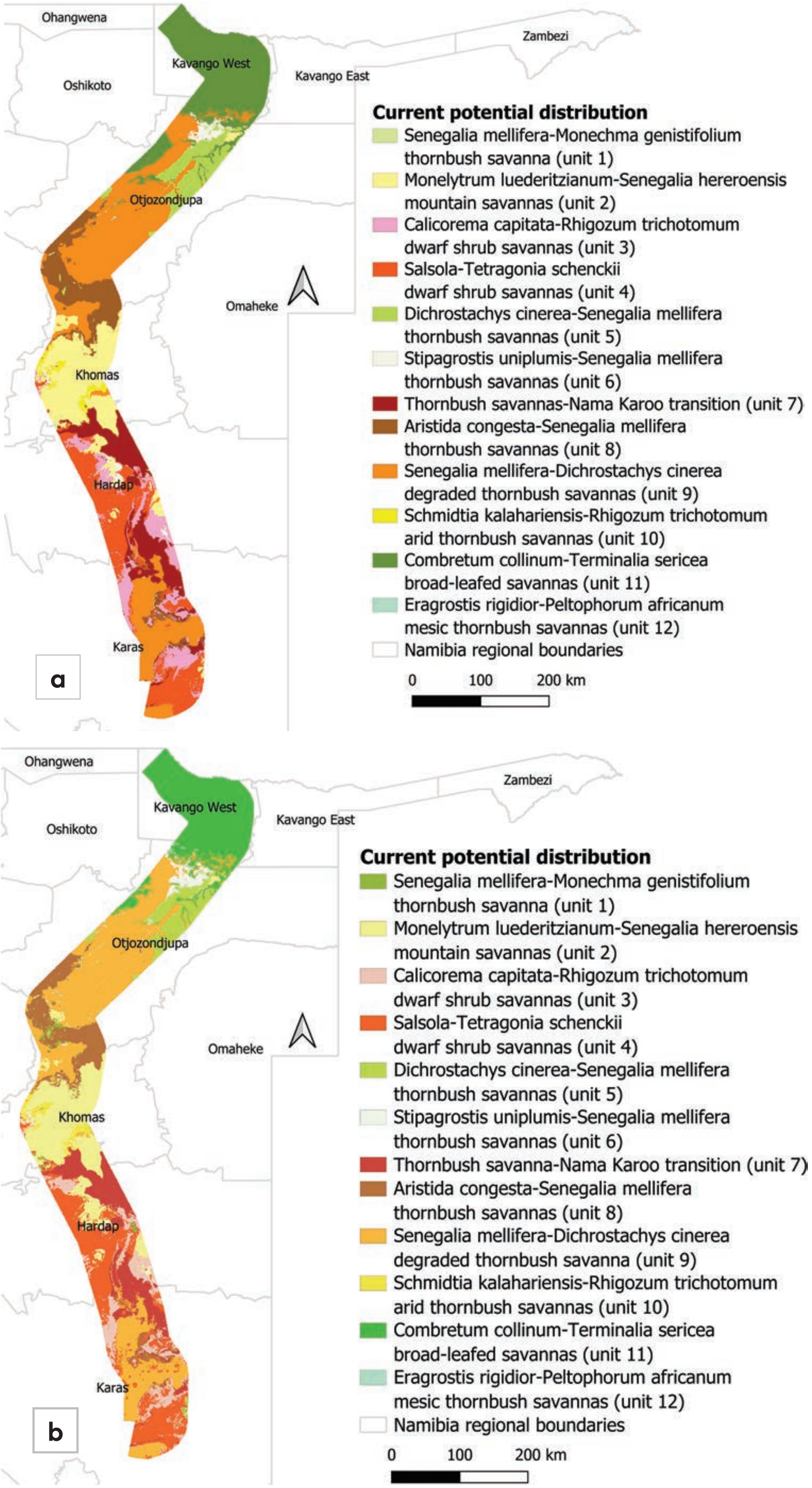
Ohangwena
Oshikoto
Kavango West
Kavango East
Zambezi
Otjozondjupa
Omaheke
Khomas
Hardap
Karas
a
Current potential distribution
Senegalia mellifera-Monechma genistifolium thornbush savanna (unit 1)
Monelytrum luederitzianum-Senegalia hereroensis mountain savannas (unit 2)
Calicorema capitata-Rhigozum trichotomum dwarf shrub savannas (unit 3)
Salsola-Tetragonia schenckii dwarf shrub savannas (unit 4)
Dichrostachys cinerea-Senegalia mellifera thornbush savannas (unit 5)
Stipagrostis uniplumis-Senegalia mellifera thornbush savannas (unit 6)
Thornbush savannas-Nama Karoo transition (unit 7)
Aristida congesta-Senegalia mellifera thornbush savannas (unit 8)
Senegalia mellifera-Dichrostachys cinerea degraded thornbush savannas (unit 9)
Schmidtia kalahariensis-Rhigozum trichotomum arid thornbush savannas (unit 10)
Combretum collinum-Terminalia sericea broad-leafed savannas (unit 11)
Eragrostis rigidior-Peltophorum africanum mesic thornbush savannas (unit 12)
Namibia regional boundaries
0 100 200 km
Ohangwena
Oshikoto
Kavango West
Kavango East
Zambezi
Otjozondjupa
Omaheke
Khomas
Hardap
Karas
b
Current potential distribution
Senegalia mellifera-Monechma genistifolium thornbush savanna (unit 1)
Monelytrum luederitzianum-Senegalia hereroensis mountain savannas (unit 2)
Calicorema capitata-Rhigozum trichotomum dwarf shrub savannas (unit 3)
Salsola-Tetragonia schenckii dwarf shrub savannas (unit 4)
Dichrostachys cinerea-Senegalia mellifera thornbush savannas (unit 5)
Stipagrostis uniplumis-Senegalia mellifera thornbush savannas (unit 6)
Thornbush savanna-Nama Karoo transition (unit 7)
Aristida congesta-Senegalia mellifera thornbush savannas (unit 8)
Senegalia mellifera-Dichrostachys cinerea degraded thornbush savanna (unit 9)
Schmidtia kalahariensis-Rhigozum trichotomum arid thornbush savannas (unit 10)
Combretum collinum-Terminalia sericea broad-leafed savannas (unit 11)
Eragrostis rigidior-Peltophorum africanum mesic thornbush savannas (unit 12)
Namibia regional boundaries
0 100 200 km

Figure 8. The current potential distribution of the vegetation units modelled under existing environmental conditions. The climate variables are averaged over 1970–2000. Two models were performed for the baseline classification: (a) a classification excluding EVI variables, (b) a classification including EVI of August and EVI of March as variables.

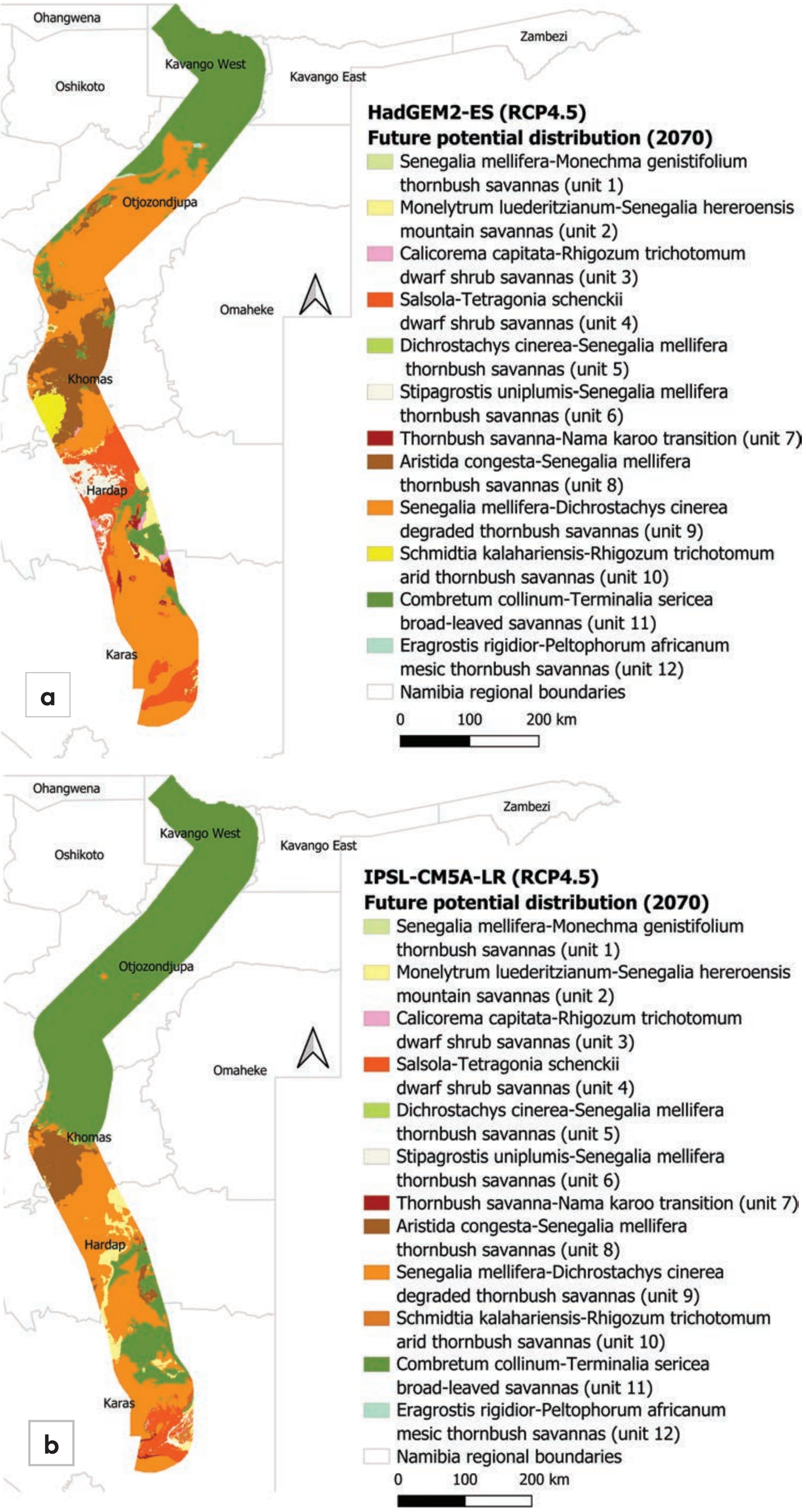
Ohangwena
Zambezi
Kavango West
Oshikoto
Kavango East
HadGEM2-ES (RCP4.5)
Future potential distribution (2070)
Senegalia mellifera-Monechma genistifolium thornbush savannas (unit 1)
Monelytrum luederitzianum-Senegalia hereroensis mountain savannas (unit 2)
Calicorema capitata-Rhigozum trichotomum dwarf shrub savannas (unit 3)
Salsola-Tetragonia schenckii dwarf shrub savannas (unit 4)
Dichrostachys cinerea-Senegalia mellifera thornbush savannas (unit 5)
Stipagrostis uniplumis-Senegalia mellifera thornbush savannas (unit 6)
Thornbush savanna-Nama karoo transition (unit 7)
Aristida congesta-Senegalia mellifera thornbush savannas (unit 8)
Senegalia mellifera-Dichrostachys cinerea degraded thornbush savannas (unit 9)
Schmidtia kalahariensis-Rhigozum trichotomum arid thornbush savannas (unit 10)
Combretum collinum-Terminalia sericea broad-leaved savannas (unit 11)
Eragrostis rigidior-Peltophorum africanum mesic thornbush savannas (unit 12)
Namibia regional boundaries
Otjozondjupa
Omaheke
Khomas
Hardap
Karas
a
0 100 200 km
Ohangwena
Zambezi
Kavango West
Oshikoto
Kavango East
IPSL-CM5A-LR (RCP4.5)
Future potential distribution (2070)
Senegalia mellifera-Monechma genistifolium thornbush savannas (unit 1)
Monelytrum luederitzianum-Senegalia hereroensis mountain savannas (unit 2)
Calicorema capitata-Rhigozum trichotomum dwarf shrub savannas (unit 3)
Salsola-Tetragonia schenckii dwarf shrub savannas (unit 4)
Dichrostachys cinerea-Senegalia mellifera thornbush savannas (unit 5)
Stipagrostis uniplumis-Senegalia mellifera thornbush savannas (unit 6)
Thornbush savanna-Nama karoo transition (unit 7)
Aristida congesta-Senegalia mellifera thornbush savannas (unit 8)
Senegalia mellifera-Dichrostachys cinerea degraded thornbush savannas (unit 9)
Schmidtia kalahariensis-Rhigozum trichotomum arid thornbush savannas (unit 10)
Combretum collinum-Terminalia sericea broad-leaved savannas (unit 11)
Eragrostis rigidior-Peltophorum africanum mesic thornbush savannas (unit 12)
Namibia regional boundaries
Otjozondjupa
Omaheke
Khomas
Hardap
Karas
b
0 100 200 km

Figure 9. Potential future distribution of the vegetation units using projected (2061–2080) climatic conditions for moderate scenarios (RCP4.5) under the (a) HadGEM2–ES and (b) IPSL–CM5A–LR General Circulation Models.

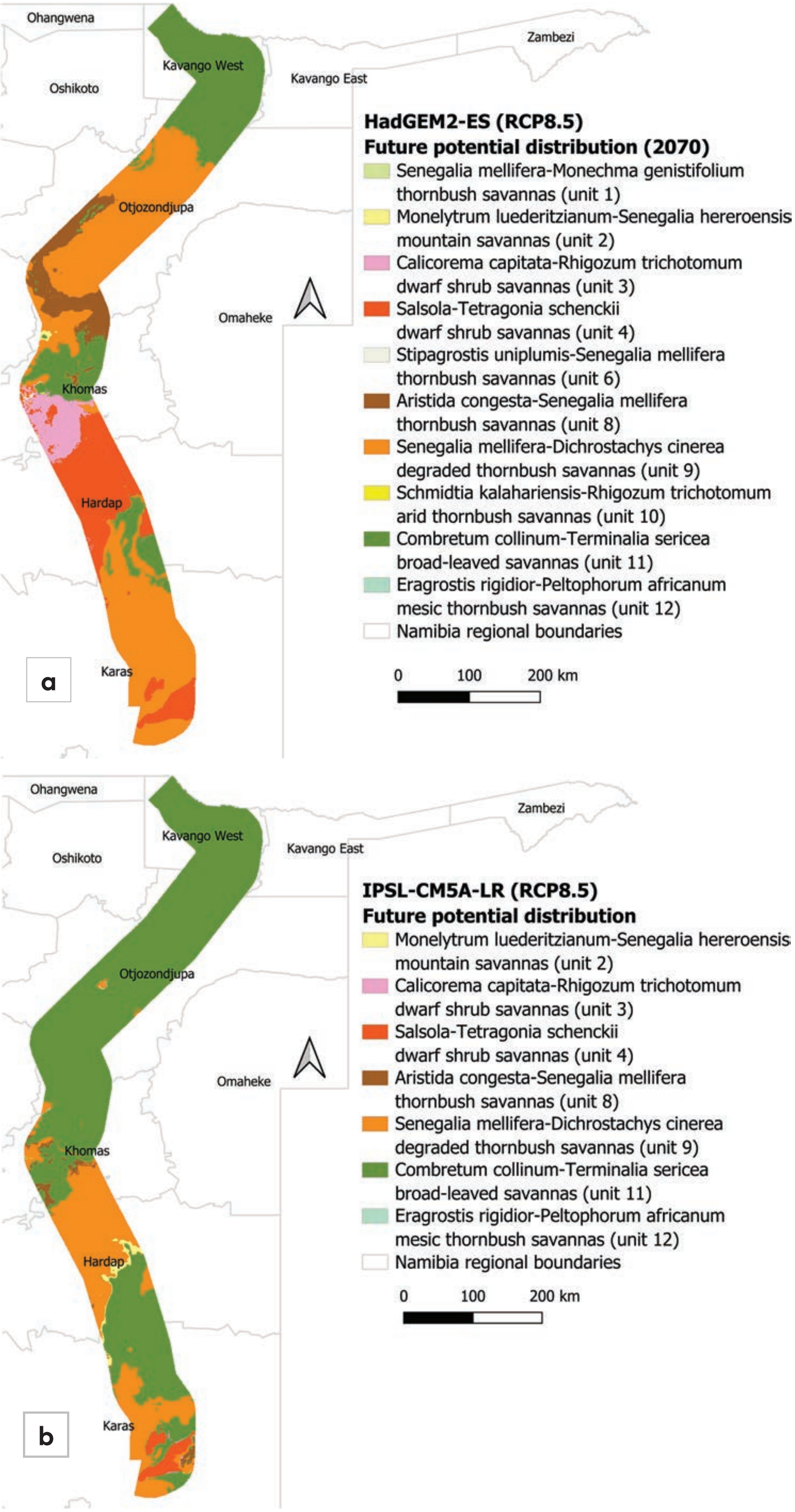
Ohangwena
Zambezi
Kavango West
Oshikoto
Kavango East
HadGEM2-ES (RCP8.5)
Future potential distribution (2070)
Senegalia mellifera-Monechma genistifolium thornbush savannas (unit 1)
Monelytrum luederitzianum-Senegalia hereroensis mountain savannas (unit 2)
Calicorema capitata-Rhigozum trichotomum dwarf shrub savannas (unit 3)
Salsola-Tetragonia schenckii dwarf shrub savannas (unit 4)
Stipagrostis uniplumis-Senegalia mellifera thornbush savannas (unit 6)
Aristida congesta-Senegalia mellifera thornbush savannas (unit 8)
Senegalia mellifera-Dichrostachys cinerea degraded thornbush savannas (unit 9)
Schmidtia kalahariensis-Rhigozum trichotomum arid thornbush savannas (unit 10)
Combretum collinum-Terminalia sericea broad-leaved savannas (unit 11)
Eragrostis rigidior-Peltophorum africanum mesic thornbush savannas (unit 12)
Namibia regional boundaries
Otjozondjupa
Omaheke
Khomas
Hardap
Karas
a
0 100 200 km
Ohangwena
Zambezi
Kavango West
Oshikoto
Kavango East
IPSL-CM5A-LR (RCP8.5)
Future potential distribution
Monelytrum luederitzianum-Senegalia hereroensis mountain savannas (unit 2)
Calicorema capitata-Rhigozum trichotomum dwarf shrub savannas (unit 3)
Salsola-Tetragonia schenckii dwarf shrub savannas (unit 4)
Aristida congesta-Senegalia mellifera thornbush savannas (unit 8)
Senegalia mellifera-Dichrostachys cinerea degraded thornbush savannas (unit 9)
Combretum collinum-Terminalia sericea broad-leaved savannas (unit 11)
Eragrostis rigidior-Peltophorum africanum mesic thornbush savannas (unit 12)
Namibia regional boundaries
Otjozondjupa
Omaheke
Khomas
Hardap
Karas
b
0 100 200 km

Figure 10. Potential future distribution of the vegetation types using projected (2061–2080) climatic conditions for high scenarios (RCP85) under the (a) HadGEM2–ES and (b) IPSL–CM5A–LR General Circulation Models.

Unit 2, the *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas, include the vegetation orders *Brachiario nigropedatae-Senegalietalia hereroensis* and *Senegalio hereroensis-Tarchonanthoetalia camphorati* as described by Strohbach (2021). This unit is also referred to as the Highland Savanna *sensu* Giess (1998).

Unit 1, the *Senegalia mellifera-Monechma genistifolium* thornbush savanna, occurs in what Giess (1998) referred to as the Thornbush savanna. It includes the *Senegalia mellifera-Monechma genistifolium* association and *Boscia foetida-Leucosphaera bainesii* association, but also elements of the *Monechma genistifolium-Vachellia tortilis* association described by Strohbach (2002, 2019).

Unit 7, Thornbush savanna – Nama-Karoo transition, is similar to *Acacio senegal-Catophractetum alexandri* described by Strohbach and Jankowitz (2012). This unit forms a transition between the Nama-Karoo (Dwarf Shrub Savanna *sensu* Giess 1998) and thornbush savanna, with elements of both biomes present.

Unit 9, the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas are closely related to various other thornbush savanna units, especially units 5, 6 and 8. The composition of the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas is a highly variable, but generally depauperated form of the related thornbush savannas and may have been impacted by overgrazing, severe bush encroachment and/or injudicious bush control interventions.

Unit 11, the *Combretum collinum-Terminalia sericea* broad-leafed savannas, are similar to the Northern Kalahari dry forests and woodlands described by Giess (1998). The vegetation unit consists of elements of small–scale studies such as the classes *Burkeo-Pterocarpetea* described by Strohbach and Petersen (2007) and the *Combreto-Terminalietea sericeae* as proposed by Strohbach (2014). De Cauwer et al. (2016) described this vegetation unit as part of southern Africa's tropical dry forest transition zone, which forms part of the WWF ecoregions Zambesian-*Baikiaea* Woodlands (Vetter 2001) and Kalahari *Acacia-Baikiaea* woodlands (Spriggs 2001).

Unit 12, the *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas, is a *Senegalia*–dominated savanna with several mesic species, including broad-leafed species such as *Philenoptera nelsii* and *Terminalia sericea* on sandy soils (Giess 1998). It includes elements of the *Acacia erioloba-Stipagrostis uniplumis* bushlands and the *Lonchocarpus nelsii-Eragrostis rigidior* bushlands described by Strohbach (2002), as well as the *Stipagrostio uniplumis-Acacietum melliferae* described by Strohbach (2014).

Modelling the vegetation units with the current climate

Model accuracy assessment

The model obtained a prediction accuracy of 82%. According to the accuracy scale statistic range (Heikkinen et al. 2006), this accuracy is very good for such a large area and in comparison to other studies such as the classification of eight peatland communities by Thomas et al. (2003) that obtained a classification accuracy of 62%. Other classification studies obtained prediction accuracies of 69% (Dirnböck et al. 2003) and 75% (Dobrowski et al. 2008). However, the prediction accuracy for this study would have been much higher (94%) with the inclusion of EVI indices.

Environmental variables responsible for the distribution of the vegetation units along the transect

Overall, the distribution of the vegetation units is controlled by altitude and soil as indicated by the Mean Decrease Gini. However, each vegetation unit has different variables that control its distribution. In other studies, MAP and MAT were the main factors in plant species distribution, such as in Ghana (Amissah et al. 2014). Another study has found mean temperature to be the leading factor in the distribution of plant species along an elevational gradient in the Himalayas (Maharjan et al. 2022).

Namibia has a high climatic variability, especially in mean annual rainfall. When creating a classification along an extended transect, it is important to choose a classification with many groups to accurately account for climatic variability. This approach prevents grouping species in a manner that does not truly reflect their specific current climatic requirements. The partial plots indicate that three vegetation units occur at the much drier end of the transect, namely unit 4. *Salsola-Tetragonia schenckii* Dwarf shrub savannas, unit 3, *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas, and unit 7, Thornbush savanna – Nama-Karoo transition. The occurrence of vegetation units in these dry areas is facilitated by the heterogeneity of the local topography and landform patterns. The degree of slope and rivers create microhabitats with distinct microclimatic conditions (Abd El-Ghani 1996), allowing for different plant species communities to coexist. The species within these units possess sclerophyllous leaves, an adaptive characteristic enabling them to withstand high evapotranspiration rates induced by high evaporation in the area. Additionally, species in more arid areas tend to have smaller leaves as an adaptive mechanism to limit water loss by reducing the exchange area with air, as stated by Thuiller et al. (2004b).

Other vegetation types presented occur at the wetter end of the gradient, where the MAT and rainfall are high. On the northern end of the transect, the vegetation unit comprises mesophyll-leaved tall trees and high shrubs, which are believed to be influenced by the deep, coarse sands of the Kalahari basin (Strohbach 2014). The broad leaves of the species in this unit allow for maximum light absorption.

Prediction of the future distribution of the vegetation types

The projected expansion for the *Combretum collinum-Terminalia sericea* broad-leafed savannas around the high altitude areas such as the Karstveld towards the Khomas highland under the IPSL–CM5A LR (RCP4.5) may be due to the overestimation of precipitation south of the equator in the IPSL–CM5A LR model (Boucher et al. 2020). Boucher et al. (2020) explain that the overall global rainfall rate in the IPSL–CM5A LR model was generally overestimated, which explains the shift of all the other vegetation units towards the south of the transect following the high predicted rainfall in the RCP8.5 (Suppl. material 3: A).

A southward expansion of several vegetation units for both models under the RCP4.5 and RCP8.5 scenarios towards the central areas with high mean annual rainfall (Suppl. material 3: B–D) and projected low mean temperature (Suppl. material 3: E–F) is surprising, as it does not agree with models used in other studies which predict species to be shifting their distributional range towards the north because of the predicted lower rainfall (Midgley et al. 2005; De Cauwer 2016; Zhang et al. 2019). However, several authors have discovered that not all species are shifting their distribution because of projected changes in rainfall, but some are moving to higher elevations where the temperature is less high (Parmesan 2006; Feehan et al. 2009; Lenoir et al. 2010; Harsch and HilleRisLambers 2016; Sintayehu 2018). The extinction of vegetation units such as *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas in both GCMs supports the idea that warming challenges species at high elevation as they may not have a place left to migrate to when the high elevation areas become warmer (Manish et al. 2016).

Because of the potential human impact on the composition of the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, it is possible that the predicted expansion includes that of unit 5 with which many species are shared.

The projected distributions of vegetation units such as the *Combretum collinum-Terminalia sericea* broad-leafed savannas in the RCP4.5 and RCP8.5 of both GCMs may not be possible because of distributional barriers such as the rate of dispersal, soil type and terrain. Species within the *Combretum collinum-Terminalia sericea* prefer deep sand, high rainfall and high temperature, contradicting the predicted future distribution.

SDMs assume that a model trained in one location can make reliable predictions in another. These models work on the assumption that species are in sync with their surroundings, thriving where conditions are optimal and dying off where conditions are less favourable. However, transferability tests indicate that most statistical models may fail to accurately extrapolate beyond the climate data range used during model training (Higgins et al. 2021; Meyer and Pebesma 2021). The future projections must therefore be interpreted with caution because some of the variables, notably the expected rainfall patterns derived from HadGEM2–ES, exceed the range of the data the models were trained on. For instance, the forecast from the HadGEM2—ES indicates a potential increase of up to 550 mm in northeastern Namibia (Figure 3d), resulting in a MAP exceeding 1000 mm well beyond the 0 to 600 mm rainfall range historically observed in Namibia.

While SDMs predict individualistic responses exhibited by individual species (Baselga and Araújo 2009), this study focuses on CDMs whereby changes in vegetation units, characterised by a group of dominant and indicator species, in response to climate change are predicted. The underlying assumption is based on the idea that species sharing similar ecological niches are likely to have analogous distributions and, consequently, co-occur. This approach considers not only the individual responses of species but also acknowledges the potential influence of ecological interactions such as facilitation and symbiosis within vegetation units (Brooker et al. 2008). As a result, some scientists began modelling higher levels of ecological organization, such as communities (Maguire et al. 2015). Analysing vegetation units or communities offers several advantages, including more efficient processing of species distribution data, increased ability to detect shared patterns of environmental response across species, and improved capacity to synthesize complex data into formats readily interpretable by scientists and decision-makers (Ferrier and Guisan 2006). A limitation is that the interactions between species in a vegetation unit may change under different climate scenarios.

There is a need for the development of projected vegetation indices data, for example, EVI, because they proved to be important in this model. This can be done by averaging the EVI data over many years and interpolating the data similarly to the projection for climate variables.

Despite the limitations, our vegetation predictions provide useful insights into potential future scenarios and can feed into initial risk assessment, future research, and the design of monitoring programs (Midgley and Thuiller 2011).

Conclusion

Vegetation along the aridity gradient was successfully classified into twelve vegetation units. These units were mapped under current climate conditions with very high accuracy (94%) and modelled to assess the influence of future climatic conditions using a Random Forest machine learning algorithm. The projected shift in vegetation units suggests a movement towards the southern end of the transect. Specifically, it is expected that unit 11, the *Combretum collinum-Terminalia sericea* broad-leafed savannas, and unit 9, the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, will exert a notably higher dominance compared to other units currently confined to specific habitats, especially the mountainous areas. This includes units like unit 2, the *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas, unit 3, the *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas and unit 10, the *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas. Consequently, these latter units are projected to experience a reduction in their area of occupancy, potentially bordering on imminent loss.

Data availability

The data used for this publication forms part of the Namibian Phytosociological Database (GVID ID AF–NA–001) and can be provided on request by Ben Strohbach. All data of GVID ID AF–NA–001 has been shared with the sPlot database as well as the GBIF database.

Author contributions

All authors planned the research, worked on the vegetation classification and revised the manuscript, LN and BS conducted the field sampling, LN performed the modelling assisted by VDC, LN led the writing.

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Supplementary material

Supplementary material 1
Confusion matrix for Random Forest classification with EVI indices (pdf)
Link: https://doi.org/10.3897/VCS.99050.suppl1

Supplementary material 2
Confusion matrix for Random Forest classification without EVI indices (pdf)
Link: https://doi.org/10.3897/VCS.99050.suppl2

Supplementary material 3
Projected change in MAP and MAT in Namibia for the IPSL–LR and HadGeM2–ES general circulation models (pdf)
Link: https://doi.org/10.3897/VCS.99050.suppl3

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RESEARCH PAPER

NEOTROPICAL VEGETATION

A coupled cartographic approach between bioclimatology and vegetation formations of Mexico

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Abstract

Aims: The task of classifying and naming Mexican vegetation types has been undertaken by previous botanists, ecologists, and mapping agencies. However, discrepancies remain due to the lack of criteria and joint efforts from a geographical and botanical perspective. We aim to unravel the complex interactions between climate and vegetation in Mexico using climatic data and advanced mapping techniques, display in maps the transition from land cover to vegetation maps and couple geobotanical and bioclimatological approaches to provide a sound, unified system for identifying Mexican bioclimatic physiognomic patterns. **Methods:** Bioclimatic mapping was developed from the Digital Climatic Atlas of Mexico data source. In addition, land cover and vegetation data were obtained from the National Institute of Statistics and Geography of Mexico regrouped as described by the Standardized Hierarchical Vegetation Classification. These data were analysed via standard map crossing technics using geographic information systems. **Results and conclusions:** The results revealed five ombrotypes and five thermotypes, leading to the identification of 13 different bioclimatic classes, which, when combined with physiognomic types, led us to recognize 11 forests, 3 shrublands and 3 herbaceous formations (at a scale of 1:4,000,000). The core outcome is a detailed bioclimatic/physiognomic vegetation map including forests, shrublands and areas dominated by Herbaceous/Non-Vascular formations. The map highlights the critical importance of harmonising methodologies to ensure comprehensive and accurate insights into Mexico's bioclimatic diversity.

Taxonomic reference: Villaseñor et al. (2005).

Syntaxonomic reference: Velázquez et al. (2021).

Abbreviations: INEGI = Instituto Nacional de Estadística y Geografía; SECLAVEMEX = Standardized Hierarchical Vegetation Classification; WBCS = Worldwide Bioclimatic Classification System.

Keywords

bioclimatology, geobotanical approach, land use, mapping techniques, Mexico, sustainable management, vegetation classification

Introduction

The study of vegetation, ranging from its traditional use in medicinal practices (Yuan et al. 2016; Khatoon Shaikh and Kanase 2022) to its contemporary applications such as carbon capture, disaster mitigation, and climate regulation, is gaining prominence (Fawzy et al. 2020). Traditional vegetation science, deeply rooted in ancient wisdom and practices, focuses on the responsible use of pristine ecosystems and the protection of biodiversity (Molnár and Babai 2021). On the other hand, modern vegetation science has transformed into a discipline focused on processes (Grime 2006), elucidating the mechanisms that govern species coexistence within plant communities (Saiz et al. 2016).

Over the past decade, we have witnessed the accumulation of vast amounts of information on vegetation. Nonetheless, data coverage and quality can vary significantly between regions, affecting the ability to fully classify vegetation types. Some countries, benefiting from initiatives such as the European Vegetation Archive database with its comprehensive data coverage, have been able to achieve more detailed classifications of vegetation types (Chytrý et al. 2016). However, not all countries have information that allows them to effectively apprehly this kind of information to classification systems to address the specific conditions unique to each country (De Cáceres et al. 2015). This challenge underscores the need for innovative proposals based on robust classification and syntaxonomical frameworks linked to new scientific advances such as bioclimatic approaches (Cano-Ortiz et al. 2022; del Río et al. 2024). As the study of vegetation evolves to encompass diverse aspects, it is imperative to advance our understanding and effectively combine the potential trends of vegetation in relation to climatic conditions (Afuye et al. 2021).

Bioclimatology: origin and outreach

Naturalists and scientists have long acknowledged the profound influence of climate on the distribution, behaviour, and adaptation of diverse species (Smit et al. 1996; Huey et al. 2012; Keenan 2015). Bioclimatology delves into the study of long-term weather patterns and its relation to biotic responses (Thompson and Perry 2013; Bonan 2015). Its origins trace back to early observations highlighting the intricate relationships between climate and living organisms. The establishment of bioclimatology as an independent discipline gained momentum in the 20th century, driven by technological advancements, refined data collection methods, and an escalating awareness of the effects of climate change (Rehfeldt et al. 2014a, 2014b; Heymann 2019).

Pioneers in this field, including notable scientists such as Alexander von Humboldt and Carl Troll, explored the intricate links between climate and vegetation (Holtmeier 2015; Hoorn et al. 2022). The development of climate classification systems, exemplified by the Köppen Climate Classification, further enriched our understanding of how various climates shape ecosystems and influence the organisms found in specific regions (Lohmann et al. 1993; Beck et al. 2005). Bioclimatology, as an ecological discipline, meticulously explores the links between climatic conditions and the distribution of living organisms and vegetation patterns on a global scale. Salvador Rivas-Martínez contributed significantly to unravelling the relationship between climate and vegetation, developing the Worldwide Bioclimatic Classification System (WBCS) by connecting bioclimatic units to vegetation models and climate values (Rivas-Martínez et al. 2011). This enhanced understanding of vegetation distribution, coupled with changes in the structure and composition of potential vegetation, and allows scientists to identify critical bioclimatic thresholds for vegetation types. This is particularly crucial in addressing climate change concerns, where vegetation stands as both a prime indicator and a landscape component profoundly affected by environmental shifts.

Relevance of understanding vegetation patterns of megadiverse countries

The study of vegetation patterns is critical as nations grapple with imminent threats such as habitat loss, climate change, and resource overexploitation (Kumar and Verma 2017; Sáenz-Romero et al. 2020). Latin American countries such as Colombia, Bolivia, Peru, Brazil and Mexico exemplify high complexity due to their rich biodiversity and varied geophysical conditions (Rangel Churio et al. 1997; Navarro and Maldonado 2002; Ulloa Ulloa et al. 2017; Velázquez et al. 2021). Noteworthy classification initiatives in these nations employ both phytosociological and bioclimatic approaches. However, despite their significance, these initiatives fall short in providing comprehensive cartography that clarifies the intricate relationships between climate and vegetation. The study of plant formations in megadiverse countries stands at the forefront of scientific research, offering valuable insights into plant interactions, evolutionary processes, and ecological dynamics (Villaseñor et al. 2005; Carpio 2018; Hoveka et al. 2020). The approach of those studies not only enhance our scientific knowledge but also underscores the interconnectedness of ecological research and conservation efforts, emphasizing the importance of global collaboration in safeguarding the world's biodiversity.

Mexico is acknowledged as a megadiverse nation (Velazquez et al. 2021; Canet 2023), based on the criteria established by Mendoza-Ponce et al. (2020). In this regard, understanding the intricate vegetation patterns and biodiversity assumes paramount importance in addressing global challenges for biodiversity conservation. Moreover, vegetation patterns facilitate the identification of key habitats, biodiversity hotspots, and ecologically significant areas, forming the basis for targeted conservation strategies (Sloan et al. 2014; Topp and Loos 2019; Mendoza-Ponce et al. 2020). In addition to biodiversity conservation, a profound understanding of vegetation patterns plays a crucial role in climate resilience and adaptation efforts. These patterns serve as indicators of climate change impacts, offering insights into plant species responses to environmental changes and guiding predictions and strategies for mitigation and adaptation (de Boer 1983; Wu et al. 2015; Afuye et al. 2021). The diverse vegetation in megadiverse regions also contributes significantly to ecosystem services, influencing water purification, pollination, climate regulation, and resource provision, thereby directly affecting human well-being on a global scale (Power 2010; Haines-Young and Potschin 2012).

Mexico holds extensive phytotaxonomic knowledge; however, it lacks a standardized phytosociological classification system that, on one hand, merges vegetation knowledge and, on the other, facilitates an understanding of its spatial distribution based on geobotanical standards (Pedrotti 2004; Mas et al. 2009; Velázquez et al. 2021). Over time, there have been attempts to fill this gap dating to the late 19th century with the works of Ramírez (1899), Harshberger (1911) and Ochoterena (1918; quoted by Velázquez et al. 2016) amongst others, each one contributing with formal maps delineating geobotanical regions in Mexico. In the latter stage of this progression, the vegetation classification system assumes a central role and starts to be integrated into cartographic legends. An example of this integration is found in the “Map of vegetation types of the Mexican Republic” by Flores Mata et al. (1971), with a scale of 1:2000,000. In this comprehensive work, the authors differentiate 25 types of vegetation, contributing to a more nuanced understanding of Mexico’s diverse botanical knowledge. These sequential efforts underscore the evolving nature of vegetation classification in Mexico, emphasizing the continuous refinement and integration of botanical knowledge into mapping frameworks.

Objectives

We pursue a dual objective, to both apply, for the first time (as far we know), a novel bioclimatic mapping methodology in Mexico, and to analyse its relationship with hierarchical land cover-vegetation physiognomic data. The newly mapped Mexican vegetation patterns are further discussed in terms of their relevance for predicting place-based climatic impacts on natural vegetation. This innovative approach allows for the prediction of site-specific bioclimatic patterns and vegetation physiognomy. This research represents a pioneering effort to integrate bioclimatic mapping with hierarchical land cover-vegetation physiognomy data in Mexico, highlighting its originality and contribution to the field of bioclimatic analysis and conservation planning.

Methods

Study area

Mexico, located in the southern region of North America, covers an area of approximately 1.96 million km^2, making it the third largest country in Latin America and the fourteenth largest in the world (World Bank Group 2023). Bordered by the United States to the north, the country is flanked by the Pacific Ocean to the south and west, Guatemala, Belize and the Gulf of Mexico to the southeast, and the Caribbean Sea to the east. Mexico’s diverse geography encompasses a wide range of climates and geographical regions, from arid deserts to lush tropical rainforests. Moreover, the country is rich in biodiversity and has a varied topography, including mountains, plains, coastlines, and plateaus (Koleff et al. 2018; Alcocer and Aguilar-Sierra 2019). Mountain ranges such as the Sierra Madre Occidental and Oriental cross the country, influencing climate patterns, vegetation and contributing to the formation of distinct geographical regions. The convergence of the Nearctic and Neotropical biogeographic regions in Mexico creates a unique intersection of flora resulting in exceptional biodiversity (Silva-Flores et al. 2014; Sosa and Loera 2017).

Bioclimatic map of Mexico

In terms of bioclimatic cartography, our primary data source was the Digital Climatic Atlas of Mexico (DCAM). The atlas is mainly constructed from climatic data that include monthly and annual averages for precipitation and temperature from 1902 to 2011, obtained from the National Meteorological System (SMN) (Fernández Eguiarte et al. 2014). We followed the Gopar-Merino et al. (2015) methodology to analyse data from the DCAM. With the obtained precipitation and temperature data, several bioclimatic parameters and indices were calculated following the bioclimatic classification system proposed by Rivas-Martínez et al. (2011) (Table 1). The Rivas Martinez et al. (2011) classification system is based on:

- The close interrelationship between climate, vegetation, and geography, where there must be a relationship between bioclimate, vegetation series and biogeography. The bioclimate forms the basis of the system, the vegetation series comprises plant associations related to the same climax stage, and the “Tesela” serves as the basic unit of biogeography.
- Of particular importance in this system is the seasonality of precipitation, which refers to how it is distributed throughout the year. This, together with temperature and continentality, determines the existence of bioclimates (such as tropical pluvial, tropical pluvial-seasonal, etc.) within macrobioclimates.
- Continentality refers to the thermal amplitude and the difference between the months with the highest and lowest temperatures. Consideration of continentality is critical to the development of certain plant communities. This system nuances the existing vegetation responses within the same macrobioclimate, establishing a predictive and hierarchical bioclimatic typology.

Table 1. Bioclimatic parameters and indices as defined by Rivas-Martínez et al. (2011) and applied to the climatic data of the National Meteorological System for Mexico.

Abbreviation	Name	Definition
T	Annual Mean Temperature	Annual mean temperature in degrees Celsius (°C).
P	Annual Precipitation	Annual precipitation in millimetres (mm).
Pp	Positive Precipitation	Sum of the mean precipitation in millimetres for months with a mean temperature above 0°C.
Tp	Positive Temperature	Sum of temperatures for months with a mean temperature above 0°C, expressed in tenths of a degree.
Ic	Continentality Index	Expresses the difference or oscillation between the mean temperature of the warmest month (Tmax) and the coldest month of the year (Tmin). Ic = Tmax – Tmin.
It	Thermicity Index	The sum in tenths of a degree of the annual mean temperature (T), the mean temperature of the coldest month (m), and the mean temperature of the warmest month (M). It can also be calculated as the annual mean temperature plus twice the temperature of the coldest month, all multiplied by ten. It is an index that weighs the intensity of cold, a limiting factor for many plants and vegetal communities. (T + M + m) * 10 <=> (Tmed + 2 * Tmin) * 10.
Itc	Compensated Thermicity Index	An index that attempts to weigh the value of the thermicity index (It) due to the "excess" of cold or temperance that occurs during the cold season in continental or hyperoceanic territories on Earth. Itc = It if Ic (8–18). They will be different if Ic <8 or Ic >18; then, a correction factor (Ci) must be calculated. If Ic >18, then Itc = It + Ci. If Ic < 8, then Itc = It - Ci. Ci is a compensation factor calculated according to the proposal of Rivas-Martínez et al. (2011). This index allows the determination of the thermotype each of which can be differentiated into an upper and lower horizon.
Io	Annual Ombrothermic Index	This index is the ratio of Positive Precipitation (Pp) to Positive Temperature (Tp), multiplied by ten. Io = (Pp / Tp) * 10. This index allows the determination of the ombrotype. It can be differentiated into upper and lower horizons.
Iod_2	Ombrothermic Index of the Dryest Bimonth	$Iod_2 = (Ppd_2 / Tpd_2)$. This index is derived from the total precipitation of the two driest months within the driest fourth-monthly period of the year (Ppd_2), divided by the total temperature of the two driest months within the driest fourth-monthly period of the year (Tpd_2).

The climatic units recognised in this system includes:

- Macrobioclimates, as the highest typological units, include Tropical (0–35° N-S), Mediterranean (23–52° N-S), Temperate (23–66° N-S), Boreal (42–72° N, 49–56° S) and Polar (53–90° N-S) regions. The basic unit is the bioclimate, of which there are 28 types. Bioclimatic variants allow for nuances within bioclimates. Within a bioclimate, we can specify the bioclimatic belt, which is determined by the combination of thermal (thermotype) and shading (ombrotype) components. Finally, by combining these bioclimatic factors as indices operating within an area, we have the isobioclimate. It is worth noting that mountainous areas are altitudinal variants of thermotypes and ombrotypes within a macrobioclimate.

The preliminary bioclimatic outcome depicted gradients of precipitation (ombro) and temperature (thermic) conditions clustered into bioclimatic patterns depicting all possible combinations of ombro and thermic indices. Due to scale issues, some of these bioclimatic classes were re-grouped on basis of their resemblance and correlation to the closely related adjacent index. This enabled us to construct a novel bioclimatic map of Mexico (sensu Gopar-Merino et al. 2015).

Vegetation physiognomic land cover map of Mexico

Cartographically, inputs were obtained from the National Institute of Statistics and Geography of México (scale 1:250,000; INEGI 2016, series VI). The vector input data were regrouped into two major cartographic classes, cultural and natural, as described by the Standardized Hierarchical Vegetation Classification (SECLAVEMEX) (Velázquez et al. 2016). To accomplish the objectives of this research, the vector layer map was reclassified into three classes of vegetation physiognomic categories using ArcMap GIS 10.5. The three classes were: forest (tree-dominated), shrubland (shrub-dominated), Herbaceous and Non-Vascular (herb-dominated) as described in Table 2. Water bodies and cultural land cover types were also depicted using data from Velazquez et al. (2021). We focused on a scale of 1:4,000,000 so that polygons smaller than 256 km^2 (< 4 mm^2 on the map) were merged with the adjacent larger polygon, taking the assigned category of that polygon.

Map crossing and correlation analyses

Mexican vegetation patterns were obtained by crossing the bioclimatic as well as the vegetation physiognomic land cover maps using ArcMap GIS 10.5. Correlations among cartographic classes were used to either maintain or cluster classes accordingly to their climatic and physiognomic affinity. The complete methodological steps and the sources of information used to elaborate the core product of the present research are presented in Figure 1. Actual surface in km^2 and in percentage values were computed to describe the final Mexican vegetation formation bioclimatic map.

Table 2. Description of vegetation physiognomic categories used for this survey. Tree (forests), shrub (shrublands), herbaceous and non-vascular plants (grasslands and Non-Vascular plants) categories are based on dominant attributes and specific growth forms and height characteristics. Dominant refers to life forms covering ≥ 60% of the surface of the polygons (Velázquez et al. 2016, 2021).

Criteria	Dominant attributes	Qualifiers, definition and description of the dominant elements or attributes
Physiognomy (form of growth)	Tree	Forests. Dominated by woody-stemmed plants over 5 m tall.
	Shrub	Shrublands. Dominated by plants with one or more woody or succulent stems. Mostly less than 5 m tall or plants with arborescent or arborescent or arbofrutescent habit greater than 5 m tall.
	Herbaceous and Non-Vascular plants	Grassland. Dominated by plants without a woody base and Non-Vascular plants with no or primitive vascular system.

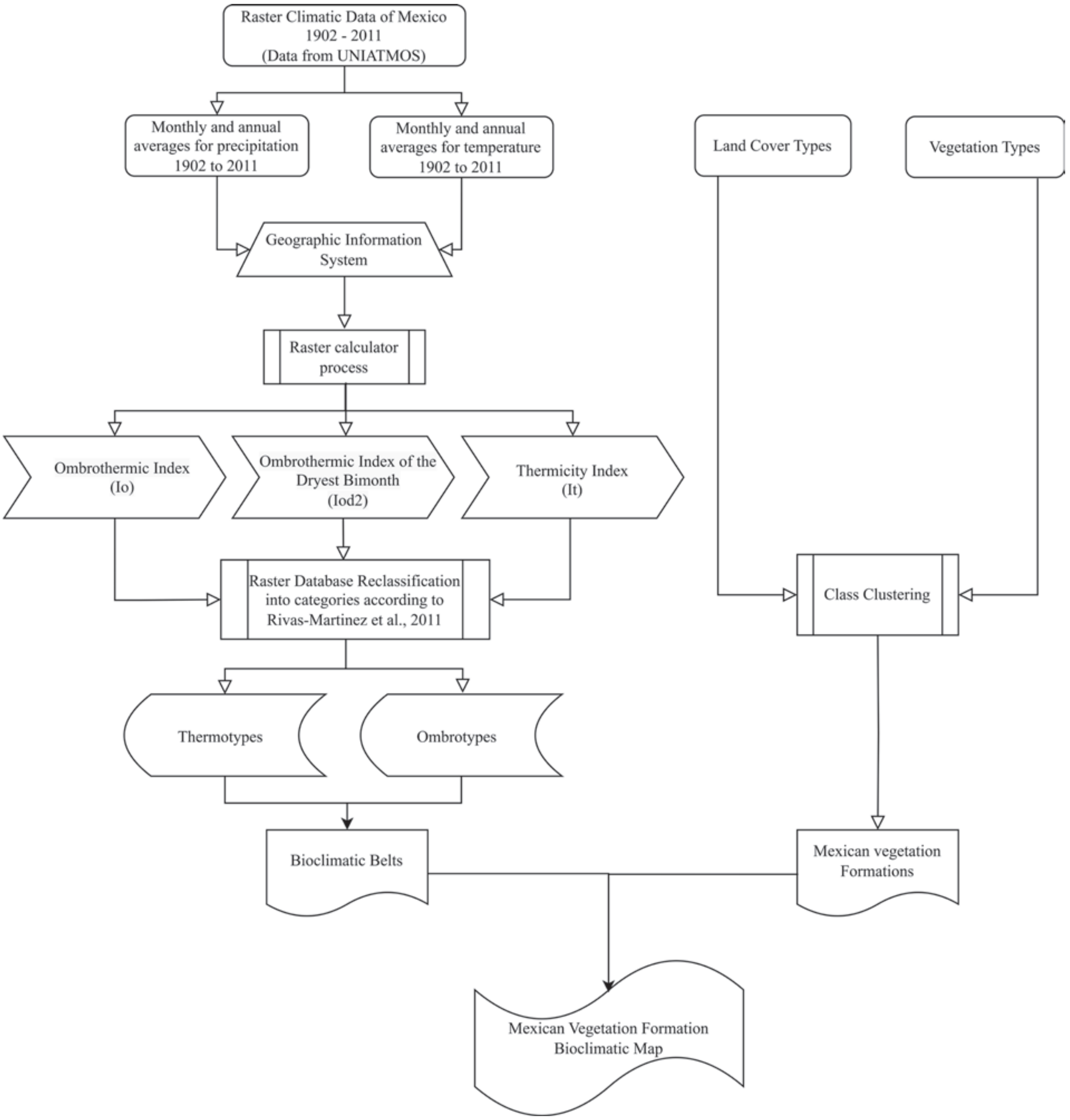

Raster Climatic Data of Mexico
1902 - 2011
(Data from UNIATMOS)
Monthly and annual averages for precipitation 1902 to 2011
Monthly and annual averages for temperature 1902 to 2011
Land Cover Types
Vegetation Types
Geographic Information System
Raster calculator process
Ombrothermic Index (Io)
Ombrothermic Index of the Dryest Bimonth (Iod2)
Thermicity Index (It)
Raster Database Reclassification into categories according to Rivas-Martinez et al., 2011
Class Clustering
Thermotypes
Ombrotypes
Bioclimatic Belts
Mexican vegetation Formations
Mexican Vegetation Formation Bioclimatic Map

Figure 1. Flow chart illustrating step by step methods and the sources of information applied to compute the Mexican vegetation formation bioclimatic map (sources: INEGI 2016; Velázquez et al. 2016).

Results

Bioclimatic map of Mexico

Using climatic data as input, we showed five ombrotypes and five thermotypes as major bioclimatic classes of Mexico. The former includes (Hyper)Arid, (Semi)Arid, Subhumid, Humid, and Hyper-Ultra Humid precipitation classes, whereas the latter comprises Infra, Thermo, Meso, Supra and Oro tropical temperature classes. Arid ombrotypes cover 55.6%, whereas, Subhumid (29.8%) and Humid (13.8%) together cover 43% of the total surface of Mexico. However, the combination of these classes only permitted the cartographic expression of 13 bioclimatic classes. The dominant bioclimate in Mexico obtained was the (Semi)Arid Mesotropical (33.5% of the total Mexican surface). (Semi)Arid and Subhumid both Thermotropical bioclimate belts were the next best represented, 14.8% and 13.2% of the total Mexican surface, respectively (Table 3).

Distributions of the vegetation formations of Mexico

Within the Forest, the Infra-Thermo-Meso-Supratropical region covers 22,132 km^2 in (Hyper/Semi) Arid conditions and 134,085 km^2 in Dry environments. This is mainly containing spiny deciduous trees locally named Mezquital and partially, Deciduous Dry Forests. Infratropical areas show a shift from Subhumid to Humid climate areas (94,977 km^2) with forests. This also comprises Deciduous broadleaved forest types intermingle with columnari- thorn forest life forms. The Thermotropical and the Mesotropical thermotypes show a spectrum from Subhumid to Humid ombrotypes, covering 328,002 km^2; the former comprise Subdeciduous broad-leaved forests, and the latter are dominated by needle-leaved conifer forests. Supratropical Subhumid and humid forests cover 82,918 km^2, represent transitions that are mainly restricted to mountainous landscapes. The first contains an ecotone from Subdeciduous (Mainly broad-leaved) to Perennial (mainly scale and needle leaved) forests locally representing the Mexican timber line. The Orotropical Hyper-Ultra humid often represents evergreen perennial broad-leaved forests.

Shrublands, which predominate in the Dry Thermo-Meso-Supratropical zone, cover 532,521 km^2 and represent a significant proportion of climates under water stress for long periods of the year. These shrublands include the Xerophitic shrubland that comprises a large number of vegetation communities such as Cardonal (dominated by *Pachycereus pringlei*), Tetetzal (*Neobuxbaumia tetetzo*), Izotal (*Yucca periculosa*), Nopaleras (*Opuntia* spp.), Magueyal (*Agave cupreata*, *A. durangensis*; *A. cerulata*), and arid sandy desert vegetation. One portion of these shrublands correspond mainly to the Mediterranean Macrobioclimate (158,117 km^2); and this vegetation type is locally known as Chaparral shrublands (dominated by *Adenostoma*, *Arctostaphylos*, *Ceanothus*, *Quercus*, *Hechita*, and other genera) and is found in Baja California and expands largely into Chihuahua and isolated remnants in the central Plateau of Mexico. North American Chaparral is best represented in California and New Mexico states (Rivas-Martínez et al. 2011; González-Pérez et al. 2023).

The Herbaceous and Non-Vascular physiognomy is distributed in different bioclimatic belts spread over 84,862 km^2 in (Hyper/Semi) Arid and 80,616 km^2 are in the (Semi)Dry Infra-Thermo-Meso-Supratropical belts.

Water bodies, widespread across several bioclimatic levels, are critical for the maintenance of aquatic biodiversity and cover 12,958 km^2, while extensive human activities, land-use changes and urbanisation are reflected in the 529,794 km^2 of cultural areas (27.3%), which predominate in the (Semi)Dry Meso-Supratropical regions. This reveals the intricate ecological mosaic that characterises each physiognomic level across different climatic and geographical parameters. Cultural areas, prevalent in the (Semi)Dry Meso-Supratropical, indicate extensive human activities, land use change and urbanisation. Overall, the complex relationship of thermotypes, ombrotypes and vegetation physiognomic land cover types highlights the diverse ecological and bioclimatic belts of Mexico and emphasises the need for sustainable management and conservation efforts. Understanding these patterns is crucial for informed land management and conservation strategies.

The core output of the present research focuses on depicting specific regions where bioclimatic conditions may face changes. Figure 2 displays (at scale 1:4,000,000) 17 vegetation types, including the 11 forests, 3 shrubland and 3 herb-dominated ecosystems of the present Mexican vegetation physiognomy as depicted from climatic patterns. The 17 types are summarized as the legend of Figure 3.

Table 3. Data (percentage) depicting the 13 different bioclimatic belts of Mexico mappable at scale 1:4,000,000.

			Ombrotypes			TOTAL
	(Hiper)Arid	**(Semi)Arid**	**Subhumid**	**Humid**	**Hiper-Ultra Humid**	
Infratropical			23.1	2.4		9.1
Thermotropical	7.3	14.9	13.2	5.8	1.40	42.6
Mesotropical		33.5	6.6	3.4		43.5
Supratropical			2.6	2.2		4.8
Orotropical				0.0		0.0
TOTAL	7.3	48.3	29.2	13.8	1.4	100.00

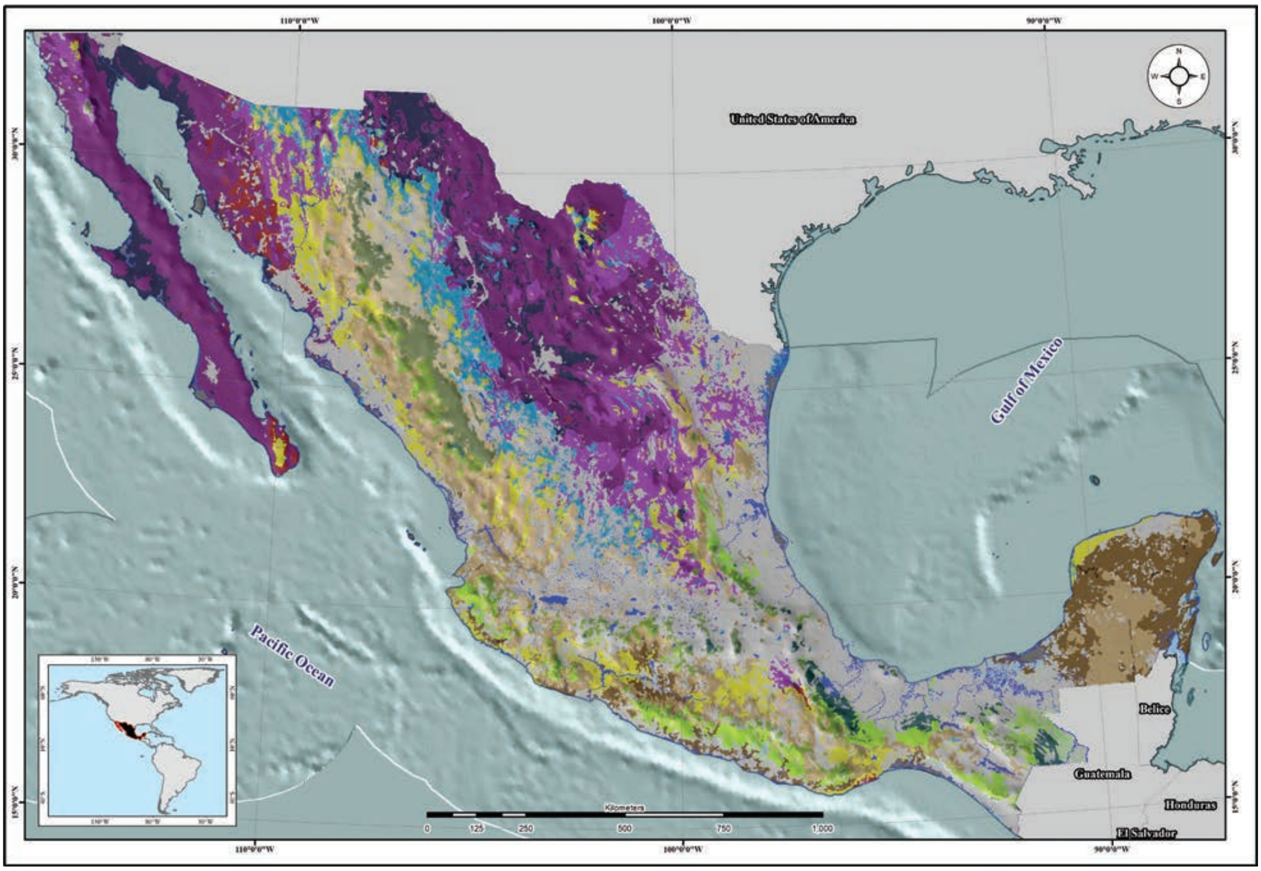
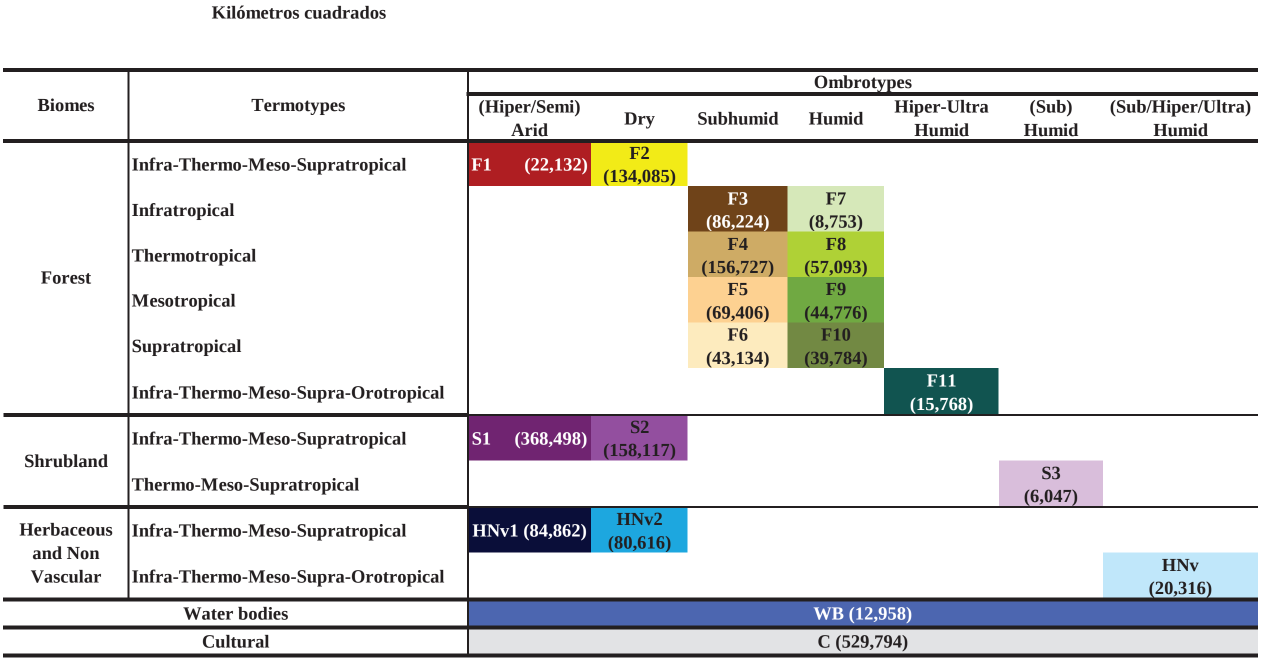


Figure 2. Vegetation pattern map of Mexico. On the whole, 17 native vegetation types, as a result of bioclimate and physiognomic land cover date map crossing, were depicted.



Kilómetros cuadrados

Biomes	Termotypes	Ombrotypes (Hiper/Semi) Arid	Dry	Subhumid	Humid	Hiper-Ultra Humid	(Sub) Humid	(Sub/Hiper/Ultra) Humid
Forest	Infra-Thermo-Meso-Supratropical	F1 (22,132)	F2 (134,085)					
	Infratropical			F3 (86,224)	F7 (8,753)			
	Thermotropical			F4 (156,727)	F8 (57,093)			
	Mesotropical			F5 (69,406)	F9 (44,776)			
	Supratropical			F6 (43,134)	F10 (39,784)			
	Infra-Thermo-Meso-Supra-Orotropical					F11 (15,768)		
Shrubland	Infra-Thermo-Meso-Supratropical	S1 (368,498)	S2 (158,117)					
	Thermo-Meso-Supratropical						S3 (6,047)	
Herbaceous and Non Vascular	Infra-Thermo-Meso-Supratropical	HNv1 (84,862)	HNv2 (80,616)					
	Infra-Thermo-Meso-Supra-Orotropical							HNv (20,316)
Water bodies		WB (12,958)						
Cultural		C (529,794)						

Figure 3. Legend of the vegetation pattern map of Mexico. Colours relate to map cartographic classes. Numbers in brackets correspond to km^2 covered by each class.

The forests corresponding to the hyper-arid and Semi-arid ombrotypes, with thermotypes ranging from infra to Supratropical in red, and the forests that thrive in the Dry ombrotype and in thermotypes ranging from infra to Supra-tropical are in yellow. In the Sub-Humid ombrotype, forests range from Infra-tropical (brown) to Supra-tropical (cream) depending on the thermotype in which they develop. In the Humid ombrotype, forests develop from Infratropical (light green) to Supratropical (army green). Forests developing in the Hyperhumid and Ultra-Humid ombrotypes are shown as dark green for all thermotypes. In the case of shrub formations, we have a range of purple colours. In Hyperarid and Semi-arid (including infra- to Supratropical thermotypes) the colour is purple. The shrubs found in the areas with dry ombrotypes in the infra- to Supratropical thermotypes are represented by a strong violet colour, and the formations that develop in the bioclimatic belt with sub-humid and humid ombrotypes in the Thermo-, Meso- and Supratropical thermotypes are defined by a soft violet colour. Finally, the category of Herbaceous and Non-vascular plants is represented by shades of blue; when they develop on bioclimatic belt with hyper-arid and semi-arid ombrotypes, with thermotypes ranging from infra- to Supratropical, we have defined them as dark blue. If they are found in the arid and thermotypes ranging from infra- to Supratropical, the colour assigned is intense blue, and finally, if we find elements of this category in the Sub-humid to Utra-Humid ombrotypes in all thermotypes (Infra-Orotropical), the colour assigned is light blue. Water bodies are shown in dark blue. Cultural areas are shown in grey. In the case of the forests, we find three different shades of colour. Vegetation communities nested within the native ecosystems described here are yet to be correlated at finer scales (e.g., 1:250,000) since spatially explicit floristic vegetation types are not yet available for the whole country (e.g., Velazquez et al. 2021).

Discussion

Bioclimatic map of Mexico

By using advanced bioclimatic and land cover mapping techniques, we are able to delineate the spatial distribution of different plant formation classes, providing insights into the extent and status of diverse ecosystems (Wolff et al. 2015; Velázquez et al. 2021; Sharma et al. 2022). This exploration of land cover patterns goes beyond mere cartography; it serves as a lens through which the transformation of ecosystems unfolds. This method has allowed us to illustrate vegetation physiognomy patterns in Mexico and explore their significance and relationships with bioclimate belts and vice versa.

Mapping the vegetation formations of Mexico is not novel. Ochoterena's contribution (1937) offered a detailed description of the geographical distribution of plants in Mexico. This contribution includes rigorous floristic lists organized in a hierarchical classification system that spans from formations to "sinucias", yet cartographic rigor was absent. Subsequently, the cartographic representation of Mexican vegetation gained prominence so that authors such as Dice (1943), Smith and Johnston (1945), Goldman and Moore (1946), and Leopold (1950), among others, made significant attempts. Climatic mapping efforts have been perhaps the most demanding and lagged behind other efforts. The outstanding work of Enriqueta García to adapt the Köppen climatic system to the Mexican conditions became a landmark (García 2004). García also produced a climatic zone map of Mexico at the scale of 1:500,000 containing three tropical, four dry, eight temperate, and one polar group classes. These were further split into types, subtypes, and variables. The dominance of temperate group classes (inherited from the Köppen classification system) has always remained a major constraint in the Mexican transitional Nearctic-Neotropical context.

Our work highlights a number of key bioclimatic characteristics of Mexico. The dominance of Arid-(Humid)-(Thermo) Mesotropical types in the present bioclimatic map, covering 64.7% of Mexico's surface area, reflects the ecological significance of these bioclimatic conditions, especially in Arid ombrotypes. Given global climatic trends, regions experiencing arid conditions may encounter challenges related to water scarcity and desertification. Conversely, shifts from Humid into Subhumid ombrotypes may be expected (Pontifes et al. 2018; Lee et al. 2021).

Vegetation formations of Mexico

The tabulated data provide a complex overview of the different physiognomic level and their respective thermotypes and ombrotypes, each making a distinctive contribution to the ecological mosaic (Figure 2). Currently, Mexico's land has undergone anthropogenic change, with unprecedent agricultural and urban encroachment. Our present study reveals that 27.3% surface of the whole country is irreversibly changed into cultural land cover. Land cover types (cultural and water bodies) are misrepresented due to minimum cartographic area, so that small patches of crops were immersed into neighbouring vegetation formations (Table 4). The probable scenario of

Table 4. Dominant land cover and vegetation types clustered into the land cover physiognomic formations used in the present research. Vegetation types derived from polygons where taxonomic families, genus or species prevail combined with a specific phenology of the foliage (Velázquez et al. 2016). Physiognomic formations are distinguished by dominant life forms (INEGI 2016). A detailed and extended explanation and all vegetation types of Mexico and how they have been clustered into physiognomic formations may be found in Velázquez et al. (2016, Appendix A.8.).

Land cover classes and vegetation types	Land cover and Physiognomic formations
Towns	Cultural
Cities	
Cropland (irrigation & humid)	
Cropland (annual basis)	
Conifers	Forest
Conifers & broad-leaved	
Broad-leaved	
Mountain cloud forest	
Perennial & sub-perennial	
Deciduous & sub-deciduous	
"Mezquital"	Shrubland
Xerophytic scrubland	
Grassland	Grassland
Hygrophilous vegetation	
	Water bodies

small polygons merging into larger polygons jeopardizes 51% of the whole country to be converted into cultural within the years. Large polygons of native arid ecosystems are also threatened by global trends of climatic changes. The importance of comprehending present vegetation and land cover patterns stems from its far-reaching implications. Negative impacts on biodiversity, and alterations in hydrology and biogeochemical cycles are some of the already noticeable consequences (Rogé et al. 2014; Koleff et al. 2018;). Mapping these changes is essential for assessing and formulating land-use policies that compromise land use and conservation of native ecosystems. In the context of Mexico's megadiversity, vegetation mapping provides a platform for identifying and foreseen challenges and opportunities. Mapping provides a place/based platform for identifying and foreseen challenges and opportunities.

This study sheds light on the complex interplay between climate and vegetation in Mexico and highlights the central role of bioclimatology. The detailed bioclimatic and vegetation maps presented provide a comprehensive overview of the ecological mosaic, revealing the diverse bioclimatic conditions that characterise this megadiverse nation. However, it's important to recognise the limitations and perspectives of this comparison, especially when considering the broader context of biogeographic classifications. In addition, further research should consider other environmental factors such as soils.

The combination of bioclimatic data and vegetation maps reveals Mexico's ecological diversity, ranging from semi-arid to humid bioclimates, and from forest formations to shrublands. These findings underscore the complexity of Mexico's ecosystems and highlight the importance of sustainable management and informed conservation efforts.

Conclusion

The present survey provides a novel attempt to correlate bioclimatic classification data with physiognomic vegetation types of Mexico, as a long-term objective to delineate plant formations representing spatially explicit ecosystem types. Detailed data on types within formation (e.g. order and alliances) and vegetation communities (associations) are yet to compiled and analysed so that proper classification and cartographic analyses are simultaneously performed. Joint vegetation classification and climatic cartographic semi-detailed analyses are an important tool for biodiversity assessments but are rather limited, to our knowledge, in scientific literature. This is a core need in some megadiverse countries where biodiversity is rapidly vanishing, and environmental policies would benefit from geobotanical spatially explicit data.

Data availability

Bioclimatic data are available under request to the authors.

Author contributions

FG-M and AV leaded the contributions of all authors; FG-M performed bioclimatic, land cover and statistical and geographical analyses; AV conceived the research framework, collected data, performed statistical analyses, and wrote the paper; AGP performed statistical and bioclimatic geographical analyses; SRG conceived the research framework, and collected data; JFMC performed statistical and geographical analyses; AP collected data, performed botanical and statistical analyses.

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NOMENCLATURAL PROPOSAL
PHYTOSOCIOLOGICAL NOMENCLATURE

Proposal (39) to conserve the name *Koelerietalia splendentis* Horvatić 1973 as a *nomen conservandum*

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Abstract

After a nomenclatural revision of the available names for the order of rocky grasslands of the Balkan Peninsula within the class *Festuco-Brometea*, based on Article 52 ICPN we propose the conservation of the name *Koelerietalia splendentis* against the name *Halacsyetalia sendtneri*. In syntaxonomic concepts not combining the limestone and serpentine rocky grasslands of the Balkans in a single order, the latter name would still be available as it is based on a different nomenclatural type.

(39) *Koelerietalia splendentis* Horvatić 1973 nom. cons. propos.
Typus: *Chrysopogono grylli-Koelerion splendentis* Horvatić 1973 (holotypus)

(=) *Halacsyetalia sendtneri* Ritter-Studnička 1970
Typus: *Potentillion visianii* Ritter-Studnička 1970 (lectotypus: Kuzmanović et al. 2016)

Taxonomic reference: Mucina et al. (2016).

Abbreviations: ICPN = International Code of Phytosociological Nomenclature, 4th edition (Theurillat et al. 2021).

Keywords

Balkan, dry grassland, Europe, *Festuco-Brometea*, *Halacsyetalia sendtneri*, *Koelerietalia splendentis*, *nomen conservandum*, phytosociological nomenclature, rocky grassland, *Scorzoneretalia villosae*, syntaxonomy

Introduction

Recent broad-scale syntheses involving the Balkan dry grassland syntaxa suggest re-arrangement of some alliances and orders within the class *Festuco-Brometea* compared to the view reflected in the EuroVegChecklist (Mucina et al. 2016; see updates at https://floraveg.eu/vegetation/). On the one hand, various authors suggest that the meso-xeric grasslands of the alliance *Scorzonerion villosae* Horvatić ex Kovačević 1959 should be transferred from the Balkan order *Scorzoneretalia villosae* Kovačević 1959 to the almost pan-European order of meso-xeric grasslands *Brachypodietalia pinnati* Korneck 1974 nom. conserv. propos. (Willner et al. 2019; Dengler and Willner 2023; Vassilev et al. 2024). On the other hand, Vassilev et al. (2024) recently suggested merging the limestone and serpentine rocky grassland of the Balkans into one order because of many joint species as well as similar structure and ecology. When following these two suggestions, the application of the ICPN (Theurillat et al. 2021) demands using the priority name *Halacsyetalia sendtneri* Ritter-Studnička 1970 in a sense (1) alien to common use, (2) not intended by the authors of the order nor, (3) according to our present knowledge, ever applied so before. We consider this a source of potential misinterpretation and thus propose here a solution that establishes a non-ambiguous name for the combined order.

Review of the situation and proposal

The dry rocky grasslands of the Balkan Peninsula usually have been referred to as order *Koelerietalia splendentis* Horvatić 1973 or *Scorzoneretalia villosae* Kovačević 1959 (both names appear in literature also with other, incorrect, author citations) (see Terzi 2015; Mucina et al. 2016). The latter was established as the oldest valid name (Terzi 2015; Mucina et al. 2016). According to Mucina et al. (2016) and Preislerová et al. (2022), the alliances of the *Scorzoneretalia villosae* are widely distributed in regions of the Balkan and Italian Peninsulas. However, if the nomenclatural type alliance *Scorzonerion villosae* Horvatić ex Kovačević 1959 is excluded from that order as suggested by recent studies (Willner et al. 2019; Dengler and Willner 2023; Vassilev et al. 2024), the name *Scorzoneretalia villosae* is no longer applicable for the rocky xerophytic grasslands of the Balkan and Italian Peninsulas. A possible solution would be to take up the name *Koelerietalia splendentis* which has already repeatedly been used, if in synonymy, to comprise amphi-adriatic calcareous xerophytic grasslands (Terzi 2015; Mucina et al. 2016). The oldest valid description of this order is by Horvatić (1973). Prior to this date another order of rocky dry grasslands in the Balkan Peninsula had been validly described, the *Halacsyetalia sendtneri* (Ritter-Studnička 1970). The latter name, however, has never been used for Balkanic rocky dry grasslands in general, but exclusively for serpentine rocky grasslands in the Central and Western Balkans (see Kuzmanović et al. 2016; Mucina et al. 2016). The concept of the *Halacsyetalia sendtneri* is much narrower, both geographically and ecologically, than that of the *Koelerietalia splendentis*. According to Preislerová et al. (2022), the type alliance of the *Halacsyetalia sendtneri* (*Potentillion visianii* Ritter-Studnička 1970, according to Mucina et al. 2016 a syntaxonomic synonym of the *Polygonion albanicae* Ritter-Studnička 1970) occurs in two geographic entities for sure and three more with question mark, while the type alliance of the *Koelerietalia splendentis* (*Chrysopogono grylli-Koelerion splendentis*) occurs in four geographic entities for sure and six more with question mark. Also, within the same geographic units, the serpentine rocky grasslands are usually much rarer than the non-serpentine rocky grasslands (see maps in Vassilev et al. 2024). Taking up the name *Halacsyetalia sendtneri* for an order that comprises both the limestone and serpentine rocky grasslands (as the results by Vassilev et al. 2024 suggest; see also their Appendix S25), would give rise to confusion and, as the name-giving plant *Halacsya sendtneri* (Boiss.) Dörfler is a regional Southwest Balkan endemic and serpentine specialist, cause misunderstandings.

We thus propose to conserve the name *Koelerietalia splendentis* Horvatić 1973 against the name *Halacsyetalia sendtneri* Ritter-Studnička 1970 according to ICPN Art. 52. Since the two names have different types (see Terzi 2015; Kuzmanović et al. 2016), the name *Halacsyetalia sendtneri* Ritter-Studnička 1970 could still be used as usual after acceptance of this proposal, if limestone and serpentine rocky grasslands of the Balkans are separated at order level. Only if the *Halacsyetalia sendtneri* (or at least their type alliance) are included in a wider order of Balkanic (and Apennine) rocky dry grasslands, the name *Koelerietalia splendentis* Horvatić 1973 would have precedence. Adoption of this proposal would thus support nomenclatural clarity without excluding different syntaxonomic viewpoints.

Author contributions

JD conceived the idea of this paper and prepared a first draft, while all authors revised and approved it.

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FORUM PAPER

Determinants of citation impact

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Abstract

This article aims to quantitatively assess how different formal aspects – beyond the relevance and quality of a study – influence how often a scientific paper is cited. As a case study, I retrieved all publications co-authored by myself from the Scopus database, of which 174 could be used for regression modelling. The citation impact was quantified as Field-Weighted Citation Impact (FWCI), which is the citation number normalised by year, subject area and article type. I examined 13 easily accessible numeric and binary predictor variables, including the Source Normalized Impact per Paper (SNIP), open access, special feature, number of authors, length of article and title, as well as formal aspects of the title. In the minimal adequate model, these formal aspects explained 50.2% of the variance in FWCI, with the SNIP alone explaining only 26.8%. Other strong positive predictors were title brevity, article length, special feature and the use of a colon in the title. By contrast, open access and the formulation of titles as factual statements did not have a significant effect. For authors who wish to make their articles more impactful, the main recommendation is to shorten the title and to disregard using factual statements that make the title longer.

Abbreviations: FWCI = Field-weighted Citation Impact; JIF = Journal Impact Factor; OA = open access; SNIP = Source Normalized Impact per Paper: VCS = Vegetation Classification and Survey.

Keywords

article impact, article title, bibliometrics, citation rate, Field-Weighted Citation Impact (FWCI), normalised citation rate, open access, research assessment, Scopus database, special feature, vegetation ecology, Web of Science

Introduction

Authors of scientific papers normally want to achieve impact with their publications, and likewise editors of scientific journals want the published articles to be as impactful as possible. Therefore, the big question is "what makes a paper successful?" Admittedly, the scientific impact of a paper depends on the content, such as the relevance of the topic, state-of-the art techniques in the analyses and well-founded conclusions. Secondly, one would think that the writing style and the appeal of the figures play a role. Both are doubtlessly true, and it is hard to give generic advice on the first point while the second is nicely addressed in various textbooks on scientific writing (Gustavii 2008; Cargill and O'Connor 2009). Moreover, both groups of factors are so diverse that they could hardly be analysed quantitatively.

However, there is a third group of factors that should not be underestimated. These are formal aspects, such as the choice of the journal and of the language, the style of the title and the length of the article. Authors and editors alike invest considerable efforts here. However, there is a lack of empirical studies that test which measures might be effective and to which degree they contribute to the success of a paper. My long-standing impression as co-author and editor is that this field is dominated by either ignorance or strong beliefs, but hardly by empirical facts. To fill this gap, I conducted a quantitative study on how different "formal aspects" influence the citation impact of articles.

Methods

For this study I used all papers (co-)authored by me and available in the Scopus database (https://www.scopus.com) on 1 May 2024. This process allowed me to discuss individual papers without exposing other researchers in an undue manner. Moreover, using the papers of a single author reduces variation resulting from different skills of different authors and from different subject fields in which they work. Of course, the list of co-authors and thus their skills as well as the detailed subject fields still vary, but the latter appear to represent a typical set for vegetation ecologists who publish in the journals of the International Association for Vegetation Science (IAVS).

Data extraction yielded 189 entries, of which four were duplicates, six were from 2024 (i.e. with very limited chance to garner citations, and indeed four were without citations so far) and two were from pre-2003 resulting from unsystematic databasing at that time (one conference abstract, one book review). These 12 entries were excluded, leaving 177 observations to be used in the modelling (Suppl. material 1). These observations stem from 54 journals and two book series, with Journal of Vegetation Science ($n = 25$), Tuexenia (21), Vegetation Classification and Survey (13), Phytocoenologia (12) and Applied Vegetation Science (11) being the most frequent (for more details, see Suppl. material 2).

I used the Field-Weighted Citation Impact (FWCI) as of 1 May 2024, provided by the Scopus database as the measure of scientific impact (dependent variable). FWCI normalises the citations of each paper in the year of the publication and the three following years compared to all papers of a certain year, subject area and article type (e.g. "Article", "Review"). Thus, a FWCI of 1 means that an article was cited as often as the average of all articles in the group; a FWCI of 2 means that it received twice as many citations etc. Unlike the raw citation rates, which are strongly dependent on the time elapsed since the publication, FWCI values are directly comparable between articles published in different years, between reviews and research articles or between different disciplines. Another advantage of the FWCI is that Scopus also provides an analogous measure at the journal level, called Source Normalized Impact per Paper (SNIP), where SNIP is essentially the average of the FWCI values of all articles in the respective period. For one article from 2022 and two articles from 2023 which therefore possessed a FWCI of 0, I inserted half of the minimum of all other FWCI values of that year instead (0.05 and 0.30, respectively) to allow modelling (see below). For readers who are more familiar with Journal Impact Factors (JIFs) from the Web of Science, I calculated the relationship of the two metrics for the year 2022 for those 46 journals that were also included in the Web of Science with linear regression after log-transformation of both variables to meet the assumptions of linear models: $\log_{10}(\text{JIF.2022}) = 0.42 + 1.32 \log_{10}(\text{SNIP.2022})$. This means that a SNIP of 1 corresponds to a JIF of 2.6 and a SNIP of 2 to a JIF of 6.6.

As predictor variables, I used formal and quantitative features of the journal, of the article, its titles and authors, where there is some plausible relationship to citation impact and that could be derived from the data provided by Scopus, or I could easily extract this from pdf's (Table 1). The relevant variables, such as the number of authors, were extracted from the downloaded file from Scopus via text functions in MS Excel, followed by careful manual checking. For the question whether a title contains a dash, all different types of dashes used in Scopus were considered. In cases where Scopus included two language versions in the title field, only that in the language of the article was retained. I considered those articles as "open access" that were categorized as Gold OA, Hybrid Gold OA or Bronze OA in Scopus, while those labelled as Green OA were checked on the journal webpage for free accessibility of the definitive article version. Articles of five journals that are indeed gold or diamond open access, but not or only partly categorized as such in Scopus (Tuexenia, Lazaroa, Preslia, Ecography, Diversity and Distributions) were also assigned to the OA category in the analyses. The FWCI of each article as well as the SNIP.2022 of the journals were taken directly from the Scopus website. One article from a journal whose coverage was discontinued in Scopus and thus did not have a recent SNIP value, received an arbitrary value of half of the minimum of all other SNIPs assigned (0.034). Whether an article was part of a special feature was derived from the pdf's.

Table 1. Variables used in the regression modelling of the 177 articles and some further citation metrics, their value distribution and their handling in the modelling.

Variable	Mean	Min	Max	Modelling
Dependent variable				
FWCI 2024.5	2.94	0.05	32.05	$\log_{10}$
Independent variables (numeric)				
SNIP 2022	1.15	0.03	11.59	$\log_{10}$
Year	2017	2003	2023	
Pages	16.50	1	262	$\log_{10}$
Authors	25.72	1	601	$\log_{10}$
Title characters	94.49	14	209	excluded because of high correlation with Title words
Title words	12.62	1	31	
Independent variables (binary)				
Book chapter	Yes =	3		modelled separately
Open access	Yes =	101		
Special feature	Yes =	63		
English	Yes =	170		
Title with statement*	Yes =	14		
Title with word play**	Yes =	6		
Title with "?"	Yes =	4		
Title with ":"	Yes =	47		
Title with dash	Yes =	27		
Further citation metrics (not used in the modelling)				
Citations	49.02	0	1025	
delta (FWCI vs. SNIP)	1.68	-7.89	30.66	
log-ratio (FWCI vs. SNIP)	0.18	-1.26	1.46	

* "title with statement" means factual statements with a verb, e.g. "Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs"

** "title with word play" means any title where words are used in unusual or metaphoric manner, e.g. "Step(pe) up!" or "Midas touches"

All statistical modelling was done in R version 4.2.2 (R Core Team 2022), assuming a significance threshold of 0.05. The highly skewed variables FWCI, SNIP, Pages and Authors were $\log_{10}$-transformed to achieve approximate normal distribution. The regressions were run with the command 'lm', and the compliance of the final models with the assumptions of linear models was verified via visual inspection of the residual plots (Quinn and Keough 2002). Since books do not have FWCI values in Scopus, the differences in citation rates between book chapters and journal articles were initially tested, while all further modelling was done only for the 174 remaining journal articles. For this purpose, all potential numeric and binary predictor variables of Table 1 were first subjected to a correlation analysis to detect pairs of highly correlated variables. Accordingly, Title. characters was excluded from further modelling as it was highly positively correlated with Title.words ($r = 0.94$). The remaining 12 predictor variables defined the global model, which then was refined stepwise until only significant terms remained (minimal adequate model; see Crawley 2014). With each of the predictor variables of the minimal adequate model, I also conducted simple linear regressions with the log-transformed FWCI as response variable. Since FWCI was modelled on a $\log_{10}$-scale, the raw estimates (given in Table 2) in the following text were back-transformed to linear scale to allow easier interpretation.

Results

The log-transformed FWCI was significantly higher in book chapters than in journal articles ($p = 0.017$; $R^2_{\text{adj.}} = 0.026$). The estimate (0.748) suggests that on average my book chapters are cited 5.6 times more often than my journal articles. In the multiple regression for journal articles only, among the 12 predictor variables in the global model, seven remained as significant terms in the minimal adequate model (Table 2).

Table 2. Minimal adequate model to explain the $\log_{10}$-transformed Field-Weighted Citation Impact (FWCI). The estimates for the predictors in the multiple and simple linear regressions as well as the associated $R^2_{\text{adj.}}$ values are given. n.s. = non-significant.

	Multiple regression				Simple regressions	
Variable	**Estimate**	***t* value**	***p*-value**	**$R^2_{\text{adj.}}$**	**Estimate**	**$R^2_{\text{adj.}}$**
(Intercept)	0.329	2.009	0.046	0.502		
$\log_{10}$(SNIP 2022)	0.780	7.001	<0.001		0.800	0.268
Special feature	0.158	2.444	0.016			n.s.
Year - 2003	-0.030	-4.620	<0.001			n.s.
$\log_{10}$(Pages)	0.324	2.819	0.005		0.307	0.020
$\log_{10}$(Authors)	0.282	4.067	<0.001		0.416	0.172
Title words	-0.038	-5.692	<0.001		-0.038	0.105
Title with ":"	0.169	2.566	0.011			n.s.

The most influential variable (i.e. the one with the highest absolute *t*-value) in the multiple regression was the log-transformed **SNIP**. The estimate suggests that with each doubling of the SNIP, the FWCI increases on average by 43%. However, in a simple regression SNIP explained only 26.8% of the overall variance in FWCI. Conversely, the minimal adequate model leaving out SNIP explained 31.5% of the variance (not shown).

The **number of title words** had the second-strongest influence in the minimal adequate model. The estimate suggests that each additional word decreases the FWCI by 8.4%, and likewise each word less increases it by 9.1%. Also, the log-transformed **number of authors** was highly significant in the minimal adequate model and was the second-most influential variable among the bivariate models (17.2% explained variance in FWCI). According to the estimate in the minimal adequate model, each doubling of the author numbers would lead to a 13.9% higher FWCI. The **year of publication** had a highly significant negative impact on the FWCI, with an estimated decrease of FWCI per year by 6.7%. By contrast, in the simple regression model year of publication was not significant. The log-transformed **number of pages** was significant, with an estimated increase of the FWCI for each doubling of the page number by 16.1%. The presence of a **colon** (":") in the title had a significant positive impact on the FWCI (+48%) as had the question whether an article was published in a **special feature/special collection** (+44%).

By contrast, the variables **open access** (yes vs. no), **language of the article** (English vs. German) as well as the use of **factual statements**, **questions**, **word plays** or **dashes** in the title had no significant influence on the FWCI in the multiple regression model and thus were not included in the minimal adequate model.

Discussion

Potential mechanisms behind the patterns

Among the tested variables, SNIP was the strongest predictor both in the multiple regression and among the bivariate regressions. It is self-evident that there must be a positive relationship between the FWCI of the articles and the SNIP values of the journals as the latter essentially are the averaged FWCI values of the included articles. That articles in journals with higher SNIP are more cited can be explained by three mechanisms that act together: (1) authors tend to submit their better manuscripts to the better journals; (2) higher-ranked journals likely have the more experienced editors and reviewers who can help more to improve the manuscript than in lower-ranked journals; and (3) publications in higher-ranked journals likely attract more readers as a high SNIP/JIF to many readers suggests high quality. Given all these obvious links, it is somehow astonishing that SNIP explained only a little more than one quarter of the variance in FWCI and thus less than the other formal aspects combined. This is mainly driven by the fact that the citations rates among different articles in the same journal vary dramatically (Figure 1, see Suppl. material 1 and Table 3). For example, the FWCI values of my articles in Vegetation Classification and Survey ranged from 0.10 to 18.45 (185-fold difference) and those in Journal of Vegetation Science from 0.30 to 22.82 (76-fold difference, noting that the lowest values in both cases were 0, but these were replaced according to the Methods). A subordinate reason for the relatively low explained variance could be that for simplicity I used the SNIP values of the year 2022 and not of the publication year, thus not accounting for potential systematic changes in the relative positions of journals over the years, which, however, are usually small and gradual. An interesting finding is that the estimate for SNIP was 0.78 in the analysed dataset, whereas across all articles of any authors it should be 1 given that SNIPs essentially are averaged FWCIs. This deviation suggests that for lower-ranked journals my papers are much more cited than the journal average, but this relative difference decreases with increasing journal impact (SNIP). This can be seen also in Table 3 and in Suppl. material 2, if sorted by the difference of FWCI vs. SNIP: The differences are on average highest for relatively low-rank journals and become smaller or even negative for many higher-ranked journals.

Interestingly, the second-most influential predictor was the title length, with articles being on average much more cited when the title is shorter. It is not directly intuitive why title brevity is so influential. Likely, the main reason is that a short title is normally achieved by getting rid of as many non-necessary words as possible. As people find articles mainly via search engines, the title essentially should be a sequence of probable keywords for which people might search (“search engine optimisation”). The top-ranked journal Nature apparently is fully aware of the importance of short titles as their author guidelines strictly forbid any title longer than 75 characters, including spaces (which typically corresponds to 7 to 11 words).

By contrast, the two other numeric indicators, number of authors and number of pages, had a positive effect on citation rates. The particularly strong effect of the number of authors (third-strongest predictor) can be explained by a set of non-exclusive mechanisms. First, a higher number of authors is typically related to larger datasets that allow more comprehensive analyses. Second, if more authors with their experiences are involved in paper preparation, this will likely lead to a higher manuscript quality. Last, a higher number of authors also means that more people (the authors and their networks) are aware of the paper and thus likely to cite it. It is not so obvious why also a greater length of the paper is beneficial. Most likely it is because a greater length allows incorporation of more different subtopics, meaning that the paper contains relevant information for a wider range of other studies.

Among the different binary article typologies, only book chapters vs. journal articles and special features vs.

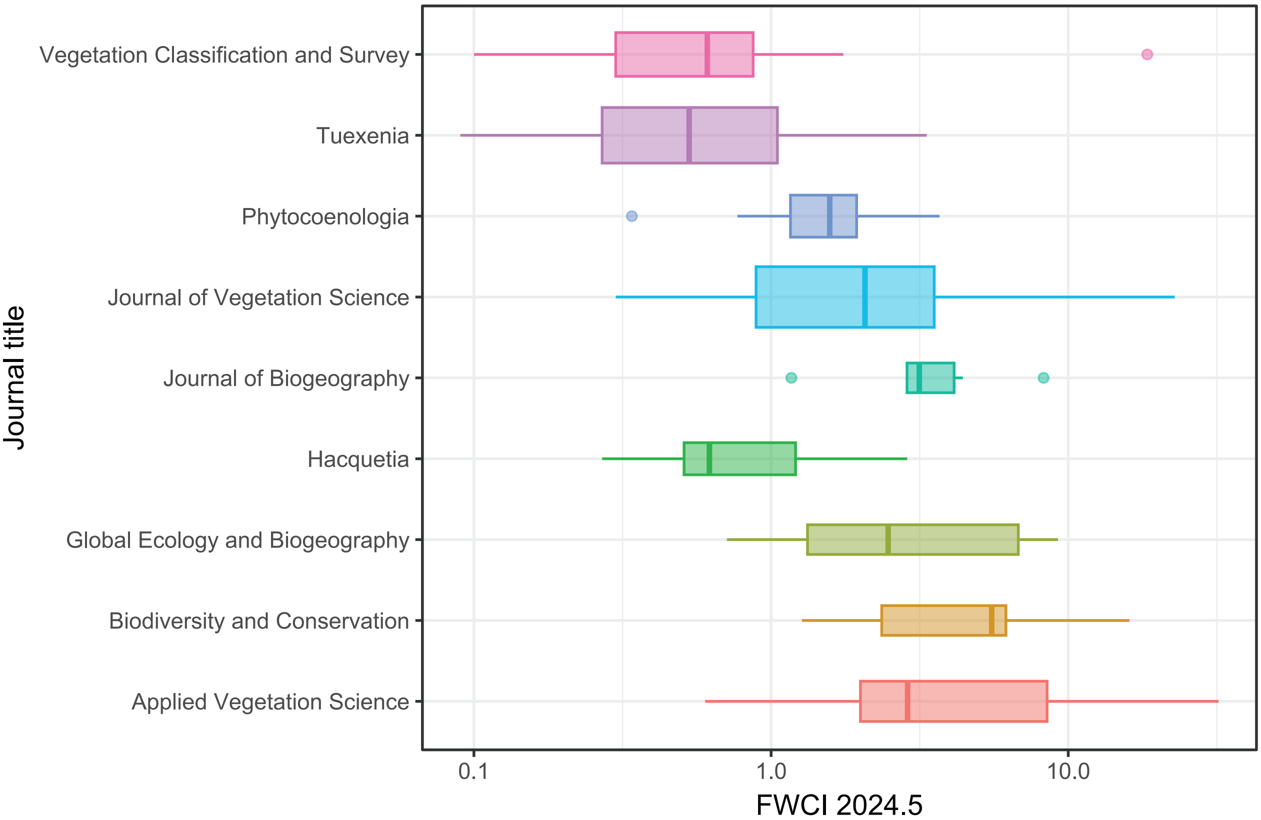

Figure 1. Variation of FWCI values of articles in journals represented by at least five articles in the sample. The height of boxplots is proportional to the number of articles included in the sample. Note that the *x*-axis has a log-scaling. The length of the box-whisker plots indicates that except for Journal of Biogeography, the most-cited article in the sample performs at least 10 times better than the least cited one, while the difference was as big as 185 times in the case of Vegetation Classification and Survey.

regular articles had a positive effect, but not so open access or English language. The unexpectedly much higher citation rate of book chapters compared to journal articles can probably be attributed to the narrow selection of books that are currently covered by Scopus. In my case, these are two "encyclopedias" that provide authoritative mini reviews on the current state of knowledge across a wide range of topics and thus are relevant for many studies as background information. If the coverage of books in Scopus was as wide as for journals, this citation advantage probably would disappear. The citation advantage of articles in special features is not a big surprise. Being part of a special feature automatically increases the visibility as there is usually an editorial that highlights the relevance of each included paper, plus often some additional "advertising" activities. Moreover, editors of special features are specialised in its narrow topic and thus might be able to contribute more to the improvement of the submitted manuscripts than normal editors can in journals where they must handle manuscripts of a much wider range of topics. Surprisingly, publishing OA did not bring any benefit in terms of citation rates. Naively, one would imagine that OA increases the visibility of articles and thus the chance of being cited – and previously there have been some studies that showed such a positive effect (Hajjem et al. 2005), but it is always hard to control for confounding factors. English language probably did not play a significant role in the multiple regression model because most journals publish in one language only and therefore the almost surely existing lower citation rates of German vs. English articles was already accounted for by the journal SNIP. In this dataset, only one journal contained articles in different languages (Tuexenia), and the sample size thus was too small to detect a pattern even if was there.

Among the other characteristics of the article titles beyond the length, only the presence of a colon (":") had a significant positive effect, while using a dash or a word play or phrasing the title as a question or factual statement had no significant effect – despite many authors seem to believe that it is beneficial to do so. In fact, using questions or statements even has an implicit negative effect on citation rates as reformulating a "conventional" title as question or statement requires additional words, while the number of words has a strong negative effect on citation rates. By contrast, the use of colons and dashes allows conveying the same information in a title but with less words, e.g. "Dry grasslands of Southern Europe: Syntaxonomy, management and conservation" instead of "Dry grasslands of Southern Europe with a focus on syntaxonomy, management and conservation". Therefore, it is logical that the use of a colon or dash to separate a subtitle from a title are beneficial for citation rates via the strong effect on title brevity. However, it remains unclear why the colon has an additional strong positive effect while the dash – despite almost identical usage – has not.

Last but not least, there was the surprising result that my citation impact per article highly significantly decreased over the years in the multiple regression model, while the simple regression suggested no change over time. This is unexpected, as one should assume that in this 20-year period, I should have gained experience and now be able to write articles with higher impact than before. Perhaps I did, but it may be that other scientists improved even faster, and this then is reflected in a decrease in mean FWCI per paper – since FWCI values are normalised to the average in the respective research field and year. However, the absence of a change in the bivariate regression points in another direction: I may have improved various things over time, such as targeting higher-impact journals, shorter titles or more co-authors, but these improvements were accounted for already by the other predictors in the model.

Regression model exemplified for this paper

The regression model developed in Table 2 allows one to forecast the FWCI of this paper itself. It has the following parameters: SNIP.2022 = 0.65, SF = 0, Year = 2024, Pages = 9, Authors = 1, Title.words = 4, Title.colon = 0. Inserted into the equation, this would yield a predicted FWCI of 0.504, i.e. below the current average of the journal (SNIP.2022 = 0.65). It should be noted that (a) about half of the variation in the citation rate is not explained by the seven formal variables used in the model and (b) the model is for May 2024 and the then current SNIP and FWCI values. Therefore, if readers should find the content of the paper interesting and useful, it could still become as much cited as average VCS papers or even more.

This estimate helps to explain how different simple choices under my influence as author would have altered the outcome. Originally, I thought of the title "What makes a paper successful?" but abandoned it, when I realised that questions do not improve citation rates but lead to longer titles (in this case: + 1 word). The prediction for this title would be a FWCI of 0.462, i.e. a 8% lower citation rate. If I had chosen to follow the trend to state the main findings in the title, e.g. "Title brevity and article length increase the citation rates of articles", the predicted FWCI would be 0.275, i.e. 45% lower than for the chosen solution. On the other hand, if I had found three more co-authors or expanded the paper with more content to 18 pages, it would likely get more cited (+48% and +25%, respectively).

Limitations

Evidently, the strongest limitation of this study is the small sample size of < 200 articles. Thus, this study cannot (and is not intended to) replace a comprehensive analysis with a much broader dataset. However, since the sample covers a relatively wide range of > 50 journals relevant to vegetation ecologists, the findings still can claim some generality. This is particularly true when focussing on the two strongest predictors (those with the lowest p- and highest R^2-values) after the journal impact (SNIP), i.e. number of authors and number of title words. Actually, the same two variables had turned out to be highly influential in the same direction in an unpublished study conducted by Meelis Pärtel sometime ago, for all the articles published in Journal of Vegetation Science and Applied Vegetation Science over several years.

Also, the metric of citation impact used here, FWCI, while it was chosen for its obvious advantages over metrics such as the mere citation count, still has limitations. On the Scopus website it is pointed out that the FWCI of an article is less meaningful when its calculation was based on averaging a small group of articles where a single high-impact article could have undue effects. However, this is not the case in the subject areas studied here, each of which is populated by numerous journals, together publishing >> 1000 articles per year. Moreover, the subject area classification by Scopus (ASJC = All Science Journal Classification) as any typology has arbitrary elements. However, these are to some extent levelled out by the fact that most journals are assigned to multiple subject areas; Vegetation Classification and Survey for example to 1110 ("Plant Science"), 1101 ("Agricultural and Biological Sciences (miscellaneous)") and 1105 ("Ecology, Evolution, Behavior and Systematics"). Evidently, assignment to other subject areas would have led to slightly different FWCI values. However, in the current study this potential bias was counteracted by the fact that the journal SNIP is based on exactly the same subject areas as the FWCI of an article.

Recommendations for different stakeholders

Authors

This study underlines that trying to get a certain paper accepted in the journal with the highest possible SNIP or JIF will, if successful, on average lead to higher citation rates, as is in agreement with common sense. However, the study also makes clear that the average impact of the journal only determines slightly more than one quarter of the impact of an article, while the latter should be the focus of authors. This means that it could be more efficient for authors to work on the other formal aspects addressed here, which together have more influence on the article impact than the level of the journal has. For example, instead of trying to publish in a journal with a twice as high journal impact (measured as SNIP), they could shorten their title in a meaningful way by 62%, which probably would cost only a small fraction of the time. Likewise, authors should question the current fashion to formulate the main results in the title as a factual statement, as I could show that by itself it is not beneficial for the impact but leads to a much longer title, resulting in a lower impact (e.g. in the example of the previous section: –45%).

Table 3. The top-5 over- and underperforming papers in the analysed portfolio of 174 journal articles compared to the average citation rates of the respective journals. The ranking was done by absolute differences (delta), while additionally the relative differences are given as ratios and log-ratios. Note that some articles are underperforming relative to the average of the journal in which they were published, but still are overperforming relative to all articles in the subject area and year (i.e. have a FWCI > 1).

Authors	Year	Title	Publication venue	Citations	FWCI 2024.5	SNIP 2022	delta (FWCI vs. SNIP)	ratio (FWCI vs. SNIP)	log-ratio (FWCI vs. SNIP)
Mucina et al.	2016	Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities	Applied Vegetation Science	1025	32.05	1.389	30.66	23.07	1.363
Tichý et al.	2023	Ellenberg-type indicator values for European vascular plant species	Journal of Vegetation Science	35	22.82	0.901	21.92	25.33	1.404
Dengler et al.	2023	Ecological Indicator Values for Europe (EIVE) 1.0	Vegetation Classification and Survey	22	18.45	0.647	17.80	28.52	1.455
Bruelheide et al.	2018	Global trait–environment relationships of plant communities	Nature Ecology and Evolution	394	20.30	3.989	16.31	5.09	0.707
Wilson et al.	2012	Plant species richness: The world records	Journal of Vegetation Science	609	17.19	0.901	16.29	19.08	1.281
[...]									
Klotz et al.	2022	Plasticity of plant silicon and nitrogen concentrations in response to water regimes varies across temperate grassland species	Functional Ecology	1	0.26	1.645	-1.39	0.16	-0.801
Laughlin et al.	2023	Rooting depth and xylem vulnerability are independent woody plant traits jointly selected by aridity, seasonality, and water table depth	New Phytologist	1	0.62	2.490	-1.87	0.25	-0.604
Vetter et al.	2020	Invader presence disrupts the stabilizing effect of species richness in plant community recovery after drought	Global Change Biology	18	1.04	3.007	-1.97	0.35	-0.461
Jandt et al.	2022a	ReSurveyGermany: Vegetation-plot time-series over the past hundred years in Germany	Scientific Data	5	0.58	2.887	-2.31	0.20	-0.697
Jandt et al.	2022b	More losses than gains during one century of plant biodiversity change in Germany	Nature	27	3.70	11.591	-7.89	0.32	-0.496

Editors, reviewers and publishers

Most editors probably would agree that their job is to select those articles that are not only topic-wise but also impact-wise matching the journal, i.e. avoid articles that will become much less cited than the journal average. This study suggests that editors are not very good in this selection as the variation of article impact within the individual journals is extreme (see Suppl. material 2). Taking only the small subset of articles co-authored by me, the variation of FWCI in those five journals where I had at least 10 papers ranged from 11- to 185-fold (and similarly for all journals with at least five papers, see Figure 1), meaning that the range of all articles in these journals must be even wider. While editors can be happy if authors submit articles that then perform much better than the average of the other articles in the journal, one could argue that they make a misjudgement if they accept articles that are far less cited than expected for an average article in that journal. The most extreme examples of negative and positive mismatches among my portfolio are shown in Table 3.

I hope that this Forum contribution can raise the awareness among editors that currently they are often not doing a particularly good service to their journals in deciding which manuscripts to accept or reject, at least not from the perspective of scientific impact. I believe that editors could and should be trained much better to forecast the potential scientific impact of submitted manuscripts – which evidently concerns not only the 31.5% of variance explained just by formal issues discussed here, but also the 49.8% of (probably mostly content-wise issues) not addressed here. This refers both to avoid rejections of potential high-impact papers, and acceptances of papers that likely will be much less attractive than average articles in that journal. For example, the article by Bruelheide et al. (2018) from Table 3 was originally submitted to Nature but rejected – and now has citation rates almost twice as high as average Nature papers (FWCI = 20.30 vs. SNIP.2022(Nature) = 11.59). From Nature perspective, this editor decision was thus not beneficial.

Another simple issue that journals could ask themselves is whether the strict upper thresholds for article length defined in many author guidelines are still appropriate, given that longer papers receive significantly more citations after taking all other aspects into consideration. Page limits made sense in the old times when articles were still printed on paper and journal issues sent by mail, i.e. each additional page came with substantial additional costs, but in times of electronic publishing when a few pages more cost hardly anything, this does not appear wise. But of course, editors should only accept longer articles when the additional pages are justified by the content.

Science funders and universities

This study calls into question several widespread practices of science funders and universities.

In many countries, researchers are strongly pushed to publish their results in "high-rank" journals, often defined as the first and second quarter of JIFs in the Web of Science database. I consider this practice clearly unethical. First, it removes the decision on what is valuable science from scientists and puts it into the hands of a commercial enterprise (Clarivate) and their arbitrary and intransparent decisions as to which journals to include in their database at all.

Second and perhaps more importantly, the variation of citation rates within most (if not all) of the journals is so extreme that it is arbitrary and unfair to assess the impact of an article by the average impact of all articles in that journal. Why should the Nature article by Jandt et al. (2022) (Q1 in Web of Science) be more valuable than the Ecological Indicator Values for Europe (Dengler et al. 2023) (not included in the Journal Citation Report of Web of Science so far and, if included, probably Q3) despite the latter having a five times higher citation impact (both are far above the average citation rates in their disciplines; Suppl. material 1)? This misuse of journal-based metrics for the assessment of scientists has been repeatedly criticised (CoARA 2022), still it seems to be the prevailing practice in many countries as I hear from my colleagues abroad. In the past, there might have been some sense in using a ranking based on JIF, CiteScore or SNIP of the journals, when there were no meaningful article-based metrics. However, now we have the FWCI, which directly measures the normalised impact of each article, and is readily available not only for the journals in the Web of Science but for the much wider selection of journals in the Scopus database, and becomes available latest one year after publication (see also Dengler et al. 2024).

Thirdly, this study calls into question one of the major motivations for the OA movement: to make scientific results better accessible (BOAI 2002; Tennant et al. 2016). In the earlier days of OA, studies claimed to have found significant citation advantages (Hajjem et al. 2005). However, in the dataset analysed here, being published behind a paywall apparently did not create any relevant impediment for other scientists to access the articles. Actually, universities have still subscribed to thousands of non-OA journals, which makes the access easy. But even if not, it is not a real challenge to get an article – just write an e-mail to the authors and nearly always they will be happy to send you a copy. This has become even easier today when you can use Research Gate (https://www.researchgate.net) to find an article and, when it is not open access, just press a button and an automated email to the authors is generated. I can say that in my life as a scientist I have received all articles I requested, but I (or my university) have never paid any article fee for that – despite being at small- to medium-size universities that had subscription access only to a limited number of journals. Therefore, one might ask whether it is a wise allocation of public money to spend millions of Euros or dollars on OA if this does not lead to substantially better access, in particular if most of the money just ends up as profit in the pockets of a few mega-publishing houses, whether predatory or not (Dengler 2023).

Among the national science funders who did and still do push OA publishing massively is the Swiss National Science Foundation (SNSF), which recently started to admit that there are some negative side effects. In consequence of that, they stopped paying OA fees for articles in special features (SNSF 2023) instead of stopping payments to predatory publishers and journals. While it is true that many predatory journals have a particularly high fraction of articles in special features (Hanson et al. 2023), it appears unethical to ban the financial support of all special features, even those in serious journals where they typically contain the most prestigious content (Ibrahim et al. 2024). The latter assumption has been ascertained by this study that found 44% higher citation impact for special feature contributions, all other things being equal (and there is no predatory journal in my publication portfolio).

Bibliometric databases

It should be highlighted that this whole study became only possible by the Scopus database providing the matching pair of normalised citation indices, both for the journals (SNIP) and the individual articles (FWCI). The normalisation makes studies across subject areas with different citation practices and across years (with different numbers of articles, e.g. the publication peak in the COVID-19 years: Dengler 2023) possible and is similarly available in the Web of Science under the name Journal Citation Indicator (JCI). In this respect, both SNIP and JCI are much more informative indicators than the more widely used CiteScore (Scopus) and JIF (Web of Science) (see also Dengler et al. 2024). However, only Scopus currently provides a matching meaningful indicator at the article level, which is the one thing that is really needed in fair impact assessment of scientists. Unfortunately, Scopus still does not advertise the FWCI as prominently as they could, and it is still not particularly user-friendly to get the data. Unlike the absolute numbers of citations, which can be automatically downloaded for a larger list of articles, the FWCI currently must be retrieved manually for each article separately. Smaller issues with the use of the SNIP and FWCI concern the fact that book chapters currently do not have a SNIP and that the article categorizations used for the normalisation are not always consistently applied (e.g. some editorials currently are coded as editorial, others as reviews), which has an influence on the SNIP and FWCI calculation in a smaller fraction of cases. However, already now, according to my experience, the combination of SNIP and FWCI offers more informative analyses than any of the indices available in the Web of Science do.

Conclusions

I would like to emphasize that authors, reviewers, editors and science funders should primarily aim for high-quality science. However, I have shown here that the impact of one specific paper is not only defined by its scientific qualities, but to a non-negligible part also by simple formal aspects. As author, it is worth being aware of these mechanisms and take advantage of them to make your own high-quality papers as impactful as they can be. Likewise, reviewers and editors could use this empirical knowledge to give better advice to their authors. I thus hope that this contribution opens a wider discussion on the relevance of formal aspects for the scientific impact of articles. Evidently, this was just an example study based on a small sample from a single vegetation ecologist. However, the results largely coincide with an unpublished study by Meelis Pärtel who several years ago analysed the publication output of Journal of Vegetation Science and Applied Vegetation Science over several years. Hopefully this Forum Paper will spur much more comprehensive follow-up studies across multiple authors and disciplines to test how general the reported patterns are.

Data availability

All data used are provided in the Supplementary materials.

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I would like to thank Meelis Pärtel who, several years ago when he was the Chair of the Chief Editors of *Applied Vegetation Science* and *Journal of Vegetation Science*, conducted a similar study on articles published in these two journals. His study came to similar conclusions as this one, but unfortunately was never published. This motivated me to finally get something citable on the topic. Many thanks to François Gillet and Idoia Biurrun who made very useful suggestions to a former versions of the manuscript. Further, I am grateful to Stephen Bell for linguistic revision of this article.

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Supplementary material

Supplementary material 1

Overview of the 177 articles analysed, broken down to publication venue with journal- and article-based citation metrics and the analysed predictor variables (*.xlsx).

Link: https://doi.org/10.3897/VCS.126956.suppl1

Supplementary material 2

Overview of the 54 journals and two book series included in the analysis, with journal-based and article-based metrics and their relationships (*.xlsx).

Link: https://doi.org/10.3897/VCS.126956.suppl2

VEGETATION CLASSIFICATION AND SURVEY
International Association for Vegetation Science (IAVS)

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SHORT COMMUNICATION
PHYTOSOCIOLOGICAL NOMENCLATURE

Comments on nomenclature of the order *Rhododendro tomentosi-Laricetalia gmelinii* and validation of the alliance *Pino sibiricae-Laricion sibiricae*

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Abstract

Zonal light-coniferous forests are widespread on long-frozen soils in Southern Siberia. Their individuality was first recognised in 1982 by Guinochet, who proposed a new suballiance for them, *Pino-Laricenion sibiricae*, within the alliance *Vaccinio-Piceion*. Later, attempts were made to raise the suballiance to the rank of an alliance. However, they failed to publish the name *Pino sibiricae-Laricion sibiricae* validly according to the International Code of Phytosociological Nomenclature (ICPN). Therefore, the name is validated here after discussing the reasons for rejecting all previous proposals. The validity of the corrected and mutated syntaxon names *Rhododendro tomentosi-Laricetalia gmelinii* and *Rhododendro tomentosi-Laricion gmelinii*, which are related to the alliance *Pino sibiricae-Laricion sibiricae*, is confirmed. Corrections and mutations of two association names are also performed.

Taxonomic reference: World Flora Online Plant List (WFO) (https://wfoplantlist.org/) [accessed 28 July 2024].

Abbreviations: ICPN = International Code of Phytosociological Nomenclature (Theurillat et al. 2021); WFO = World Flora Online Plant List.

Keywords

boreal, forest, *Ledo-Laricetalia*, nomenclature, phytosociology, Siberia, *Vaccinio-Piceetea*

Introduction

The alliance name *'Pino sibiricae-Laricion sibiricae'* is related to a peculiar regional category of light-coniferous forests occurring on long-frozen soils in the southern part of Siberia and adjacent areas of Northern Mongolia (Ermakov et al. 2002; Ermakov 2019, 2023). The syntaxon was proposed by Guinochet (1982) as a suballiance under the invalid name *'Pino-Laricenion sibiricae'* after analyzing two new associations made by him in the Eastern Sayan mountains. The detailed history describing the raise of the suballiance to the rank of an alliance under the name *'Pino sibiricae-Laricion sibiricae'* has been discussed by Anenkhonov (2023) in this journal. According

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to Anenkhonov, the name '*Pino sibiricae-Laricion sibiricae* Guinochet ex Dostálek et al. 1988' is the correct name of the alliance. The aims of our work are (1) to present arguments on the invalidity of all previous attempts to describe the alliance name *Pino sibiricae-Laricion sibiricae*, and (2) to validate the name *Pino sibiricae-Laricion sibiricae* in accordance with the ICPN.

On the nomenclature of the name *Pino sibiricae-Laricion sibiricae* and names of related syntaxa

Guinochet (1982) extended the range of the alliance *Vaccinio-Piceion* Braun-Blanquet in Braun-Blanquet, Sissingh et Vlieger 1939 in Siberia eastwards with two new associations, the '*Rhododendro-Pinetum sibiricae* Guinochet' and the '*Piceo obovatae-Abietetum sibiricae* Guinochet', within the new suballiance '*Pino-Laricenion* Guinochet'. However, the name '*Rhododendro-Pinetum sibiricae*' (p. 296 and relevés 1 and 2 in table 1) is invalidly published because no type relevé was designated (Art. 5a) and also because it is not clear which species of *Rhododendron* is the name-giving taxon since *R. dauricum* occurs in both relevés and *R. aureum* occurs in relevé 2 (Art. 3g). In the same way, the name '*Piceo obovatae-Abietetum sibiricae*' (p. 296 and relevés 3 and 4 in table 1) was invalidly published because no type relevé was designated (Art. 5a). Consequently, the name '*Pino-Laricenion*' (p. 296 and table 1) was also invalidly published because the diagnosis contained only two invalidly published associations ('*Rhododendro-Pinetum sibiricae* Guinochet 1982' nom. inval. and '*Piceo obovatae-Abietetum sibiricae* Guinochet 1982' nom. inval.).

In their study of some North Korean *Rhododendron* species, Dostálek et al. (1988) described on p. 33 the new association '*Rhododendro aurei-Laricetum olgensis*', which they attributed to the '*Pino-Laricenion*' of Guinochet (1982). However, they considered that the communities of East Siberian larch woodlands did not correspond to a suballiance but to a vicariant alliance of the '*Piceion excelsae* Pawłowski in Pawłowski, Sokołowski et Wallisch 1928'. Consequently, they raised Guinochet's suballiance to alliance level, using the name '*Pino sibiricae-Laricion sibiricae* (Guinochet 1982) Dostálek, J. Dostálek, Mucina et Ho-Dzun 1988' [recte: *Pino sibiricae-Laricion sibiricae* Dostálek, J. Dostálek, Mucina et Ho-Dzun 1988]. They also attempted to validate the invalid '*Rhododendro-Pinetum sibiricae*' published by Guinochet by selecting a type from Guinochet's two relevés. However, despite the designation of a type (as "lectotypus") and an unambiguous reference (Art. 2b, Note 4) to Guinochet (1982), the name '*Rhododendro-Pinetum sibiricae* Guinochet ex Dostálek in Dostálek, J. Dostálek, Mucina et Ho-Dzun 1988' was still not validly published in Dostálek et al. (1988) because it is still not clear which species, *Rhododendron dauricum* or *R. aureum*, is the name-giving taxon (Art. 3g). Consequently, the name '*Pino sibiricae-Laricion sibiricae* Dostálek, J. Dostálek, Mucina et Ho-Dzun 1988' is invalidly published in Dostálek et al. (1988) because the name '*Rhododendro-Pinetum sibiricae*', which they designated as its type association, is not validly published.

In their paper on modelling the distribution of the forests in the southern part of the mountains of the Western Sayan (Southern Siberia), Ermakov and Alsynbayev (2004) provided a syntaxonomic scheme for this region and described a new order, two new alliances and one new association. The association was named '*Carici iljinii-Laricetum sibiricae*', and it was validly published on pp. 701–702, although the Latin word "typus" was not used to designate the type relevé, which was designated with the Russian word "Номенклатурный тип" ("nomenclatural type", in the sense of the holotype). However, for a name published on or after 1 January 2002 and before 1 January 2021, the single relevé published on p. 701 for the association, being the only suitable element for the typification, automatically became the holotype (Art. 5a, Ex. 5). Among the two new alliances, the '*Ledo palustris-Laricion cajanderi* Ermakov' was validly published on p. 701 because (1) the diagnosis of the alliance contains only a single association, the '*Ledo palustris-Laricetum cajanderi* Ermakov, Cherosov et Gogoleva 2002' that is designated as the nomenclatural type (in Russian: "Номенклатурный тип") (Art. 5a), (2) there is an unambiguous reference (Art. 2b Note 4) to Ermakov et al. (2002) where the name is validly published on p. 82 with a single relevé designated as the "nomenclatural type" (Art. 5a), which contains the two name-giving taxa *Ledum palustre* L. and *Larix cajanderi* Mayr (Art. 3g); and (3) this relevé also contains three of the seven diagnostic species indicated for the alliance. Ermakov (2023) erroneously considered the name '*Ledo palustris-Laricion cajanderi*' to have been invalidly published in Ermakov and Alsynbayev (2004) (see below).

In contrast, the name of the new alliance '*Pino sibiricae-Laricion sibiricae* Ermakov' was not validly published on p. 701 although in the original diagnosis there was only one suitable element designated as the nomenclatural type ("Номенклатурный тип", in Russian) (Art. 5a), namely the validly published association '*Carici iljinii-Laricetum sibiricae* Ermakov in Ermakov et Alsynbayev 2004'. The invalidity is due to the fact that the same association is also the type of another new alliance name on p. 701, the '*Ledo-Laricion sibiricae*'. Actually, the name '*Ledo-Laricion sibiricae*' is a typing error for '*Pino-Laricion sibiricae*' since the '*Carici iljinii-Laricetum sibiricae*' is indeed the type designated for the '*Pino-Laricion sibiricae*'. Nevertheless, although no type was designated for the name '*Ledo-Laricion sibiricae*', its diagnosis contains only one suitable element to be designated as the type of the name, the '*Carici iljinii-Laricetum sibiricae*'. Indeed, the names of the two other associations mentioned ('*Ledo-Laricetum sibiricae* Zhitlukhina et Alimbekova 1987' and '*Bergenio-Pinetum sibiricae* Zhitlukhina et Alimbekova 1987') are not effectively published names (nomina inedita) since in the bibliography of Ermakov and Alsynbayev (2004) all the references to Zhitlukhina and/ or Alimbekova published in 1987, namely references 6, 7 and 8, correspond to VINITI papers, which are not qualified as effective publications (Art. 1). Therefore, although the name *'Ledo-Laricion sibiricae'* appeared as technical error, it is validly published (Art. 5a). As a result, the two names *'Pino sibiricae-Laricion sibiricae'* and *'Ledo-Laricion sibiricae'*, having the same type, are homotypic synonyms published at the same time and implicitly correspond to alternative names (Def. VI), which are invalidly published on or after 1 January 2002 (Art. 3j).

Regarding the new order proposed to represent the light-coniferous larch (*Larix cajanderi*) forests occurring on frozen soils in Central Yakutia, the name *'Ledo palustris-Laricetalia cajanderi'* was validly published in Ermakov and Alsynbayev (2004) because its original diagnosis contains only one suitable alliance, the new, validly published '*Ledo palustris-Laricion cajanderi* Ermakov', which was designated as the type, even if the Latin word "typus" was not used (Art. 5a). Indeed, the two other alliances *'Pino sibiricae-Laricion sibiricae'* and *'Ledo-Laricion sibiricae'* included in the order being invalid, the '*Ledo palustris-Laricion cajanderi* Ermakov in Ermakov et Alsynbayev 2004' remains the only suitable element in the diagnosis of the order name, and two species (*Ledum palustre* L. and *Vaccinium uliginosum*) among the eleven diagnostic species indicated for the order (Art. 8) occur in the single relevé of the unique association validly published for the order, the *'Ledo palustris-Laricetum cajanderi'*. However, Ermakov (2023) erroneously considered the name *'Ledo palustris-Laricetalia cajanderi'* to have been invalidly published in Ermakov and Alsynbayev 2004 (see below).

Later, Ermakov (2019, 2023) suggested that the two names '*Pino sibiricae-Laricion sibiricae* Guinochet ex Dostalek et al. 1988' and '*Rhododendro-Pinetum sibiricae* Guinochet 1982' are both invalid and nomina dubia. As seen above, these names are indeed invalid, but not for the reasons given by Ermakov, who rejected the latter association name as nomen dubium (Art. 37) on the grounds that it was described on two floristically incomplete relevés. In fact, the values given for the cover of the moss layer of these relevés are 90% and 100%, respectively, but no bryophyte species are mentioned, which makes it impossible to correctly identify the association. However, the syntaxonomic content has no influence on the validity of a name, which depends only on objective formal requisites (articles 2 through 9, see Def. IV). In addition, a nomen dubium can only be designated by a decision of the GPN Assembly (Art. 37).

In his overview of the order *'Ledo palustris-Laricetalia cajanderi'*, Ermakov (2023) superfluously re-published the alliance and the order names *'Ledo palustris-Laricion cajanderi'* and *'Ledo palustris-Laricetalia cajanderi'*, respectively, because he considered them invalidly published in Ermakov and Alsynbayev (2004). Therefore, the validly published name '*Ledo palustris-Laricion cajanderi* Ermakov 2023' with the association '*Ledo palustris-Laricetum cajanderi* Ermakov, Cherosov et Gogolova 2002' as its holotype is a later superfluous name (Art. 29c). For the order *'Ledo palustris-Laricetalia cajanderi'*, the erroneous reason given in Ermakov (2023) for its invalidity in Ermakov and Alsynbayev (2004) was that its type, the alliance *'Ledo palustris-Laricion cajanderi'*, was invalidly published, which was not the case as shown above. Therefore, the validly published name '*Ledo palustris-Laricetalia cajanderi* Ermakov 2023' is also a later superfluous name (Art. 29c).

Anenkhonov (2023) considered on p. 319 the name *'Rhododendro-Pinetum sibiricae'* as validly published in Dostálek et al. (1988). Contrary to the author's assertion this is not the case under Art. 3g (see above). In addition, the correct citation of the name in accordance with Rec. 10C and 46D is not '*Rhododendro dahurici-Pinetum sibiricae* Guinochet ex Dostálek in Dostálek, J. Dostálek, Mucina et Ho-Dzun 1988', as indicated on p. 320, "because *Rhododendron dahuricum* is the only *Rhododendron* species present in the type relevé designated by Dostálek et al. (1988)" (namely relevé 1, table 1 in Guinochet 1982). In fact, as seen above, in their attempt to validate the *'Rhododendro-Pinetum sibiricae'* of Guinochet (1982), Dostálek et al. (1988) implicitly accepted the whole diagnosis of Guinochet for the name, i.e. relevés 1 and 2 in table 1, with *R. dauricum* occurring in both relevés and *R. aureum* in relevé 2 (Art. 3g). Consequently, the name *'Pino sibiricae-Laricion sibiricae'* was invalidly published in Dostálek et al. (1988) because of the invalidity of the type association, the *'Rhododendro-Pinetum sibiricae'* (Arts. 5a, 17). Contrary to Ermakov (2019, 2023), Anenkhonov (2023) did not consider the *'Rhododendro-Pinetum sibiricae'* to be a nomen dubium because relevé 1 in table 1 in Guinochet (1982), selected as the type of the association name, can be easily classified at the class, order and even alliance level just by the vascular plant species. Although bryophytes are physiognomically important in boreal coniferous forests, they are not good diagnostic species at the association level due to their ubiquity. Therefore, their absence is not a reason to consider Guinochet's relevé incomplete for an association-level classification.

Validation of the name *Pino sibiricae-Laricion sibiricae* and other nomenclatural novelties

Following the nomenclatural analysis performed above, we validate here the name *Pino sibiricae-Laricion sibiricae* Ermakov et Theurillat all. nov. The holotypus of the alliance is the association *Carici iljinii-Laricetum sibiricae* Ermakov in Ermakov et Alsynbayev 2004 (Ermakov and Alsynbayev 2004, pages 701–702). The diagnostic species of the alliance are *Pinus sibirica*, *Calamagrostis obtusata*, *Carex iljinii*, *Luzula parviflora* and *Poa sibirica*.

The alliance includes the larch and pine-larch (*Pinus sibirica*, *Larix sibirica*) forests widespread in the upper part of the forest belt in the continental and ultra-continental climatic sectors of Southern Siberia and adjacent areas of Northern Mongolia, where they occupy north-facing mountain slopes at altitudes of 1400–2000 m a.s.l. At present, the alliance *Pino sibiricae-Laricion sibiricae* includes nine associations described in Anenkhonov and Chytrý (1997), Ermakov and Alsynbayev (2004), Ermakov and Makhatkov (2011), Makunina (2011, 2020), Ermakov (2014), and Ermakov and Polyakova (2022).

The names '*Rhododendro-Pinetum sibiricae* Guinochet 1982' and '*Piceo-Abietetum sibiricae* Guinochet 1982' are not validated here. The reason is that the former name is floristically very close to the validly published association *Bergenio crassifoliae-Laricetum sibiricae* Makunina 2011, of which it can be considered a synonym. It is also close to the associations *Vaccinio uliginosi-Laricetum sibiricae* Makunina 2020 and *Linnaeo borealis-Pinetum sibiricae* Ermakov et Polyakova 2022. As far as the '*Piceo-Abietetum sibiricae*' is concerned, we do not validate the name here because the association cannot be placed in the order *Rhododendro-Laricetalia* (= *Ledo-Laricetalia*, see below).

Ledum palustre L. 1753, the name-giving taxon of the order *Ledo palustris-Laricetalia cajanderi* Ermakov et Alsynbayev 2004 (Ermakov and Alsynbayev 2004, p. 700, 701), is now considered to belong to the genus *Rhododendron* as *R. tomentosum* Harmaja 1990 in several floras (e.g., Euro+Med Plant Base, https://europlusmed.org; WFO; Flora of North America, http://beta.floranorthamerica.org; Flora Germanica, Hassler and Muer 2022). In addition, *Larix gmelinii* (Ruprecht) Kuzeneva 1920 and *Larix cajanderi* Mayr 1906 are considered the same taxon (e.g., in WFO; GBIF, https://www.gbif.org; The Gymnosperm Database, https://www.conifers.org), and the former is the correct name at the species rank (basionym: *Abies gmelinii* Ruprecht 1845). Therefore, in accordance with Art. 45, we mutate the order name with *Rhododendron tomentosum* instead of *Ledum palustre* and, in accordance with Art. 44, we correct it with *Larix gmelinii* instead of *L. cajanderi*, namely *Rhododendro tomentosi-Laricetalia gmelinii* Ermakov et Alsynbayev 2004 nom. corr. et mut. nov. In the same way, we mutate and correct the alliance name *Ledo palustris-Laricion cajanderi* Ermakov in Ermakov et Alsynbayev 2004 (Ermakov and Alsynbayev 2004, p. 701) to *Rhododendro tomentosi-Laricion gmelinii* Ermakov in Ermakov et Alsynbayev 2004 nom. corr. et mut. nov., and we also mutate and correct two association names, *Ledo palustris-Pinetum sibiricae* Ermakov et Makhatkov 2011 (Ermakov and Makhatov 2011, p. 202) to *Rhododendro tomentosi-Pinetum sibiricae* Ermakov et Makhatkov 2011 nom. mut. nov., and *Ledo palustris-Laricetum cajanderi* Ermakov, Cherosov et Gogoleva 2002 (Ermakov et al. 2002, p. 440) to *Rhododendro tomentosi-Laricetum gmelinii* Ermakov, Cherosov et Gogoleva 2002 nom. corr. et mut. nov.

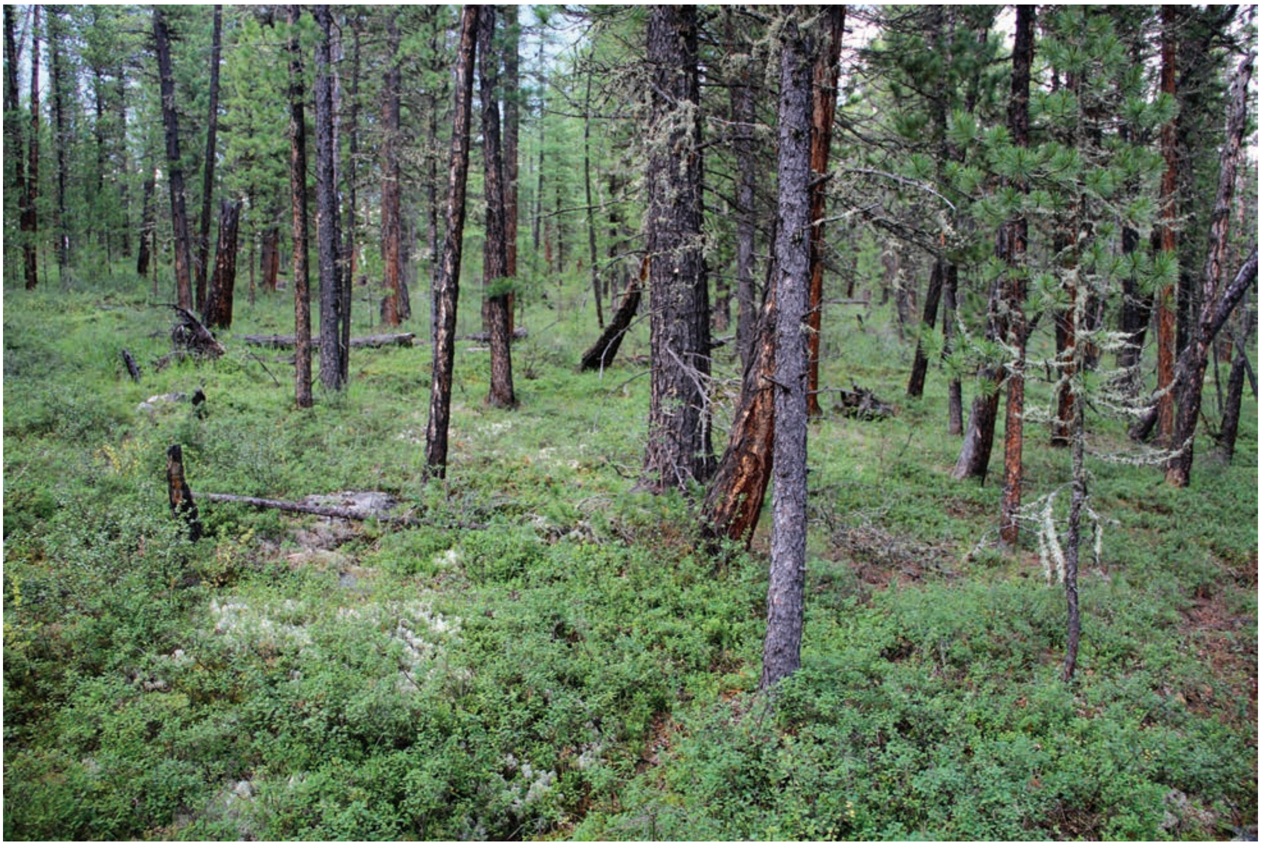

Figure 1. Boreal forests of larch (*Larix sibirica*) and pine (*Pinus sibirica*) of the association *Carici iljinii-Laricetum sibiricae* Ermakov in Ermakov et Alsynbayev 2004 (alliance *Pino sibiricae-Laricion sibiricae* Ermakov et Theurillat all. nov.) from the Eastern Altai (Southern Siberia).

Syntaxonomic synopsis

Cl. *Vaccinio-Piceetea* Braun-Blanquet in Braun-Blanquet, Sissingh et Vlieger 1939

Ord. *Rhododendro tomentosi-Laricetalia gmelinii* Ermakov in Ermakov et Alsynbayev 2004 nom. corr. et mut. nov. (Art. 44 and alternative form of the name, Art. 45)

Synonyms: *Ledo palustris-Laricetalia gmelinii* Ermakov et Alsynbayev 2004 nom. corr.; *Ledo palustris-Laricetalia cajanderi* Ermakov et Alsynbayev 2004 nom. inept. (Art. 44); *Ledo palustris-Laricetalia cajanderi* Ermakov 2023 (Art. 29c)

All. *Pino sibiricae-Laricion sibiricae* Ermakov et Theurillat all. nov.

Synonyms: *Pino-Laricenion* Guinochet 1982 nom. inval. (Art. 5; corresponding name); *Pino sibiricae-Laricion sibiricae* Dostálek, J. Dostálek, Mucina et Ho-Dzun 1988 nom. inval. (Art. 5); *Pino sibiricae-Laricion sibiricae* Ermakov in Ermakov et Alsynbayev 2004 nom. inval. (Art. 3j)

Ass. *Carici iljinii-Laricetum sibiricae* Ermakov in Ermakov et Alsynbayev 2004

Ass. *Carici iljinii-Pinetum sibiricae* Ermakov 2014

Ass. *Calamagrostio obtusatae-Laricetum sibiricae* Chytrý, Anenkhonov et Valachovic in Anenkhonov et Chytrý 1998

Ass. *Melampyro pratensis-Laricetum sibiricae* Ermakov et Makhatkov 2011

Ass. *Rhododendro tomentosi-Pinetum sibiricae* Ermakov et Makhatkov 2011 nom. mut. nov. (alternative form of the name, Art. 45)

Synonym: *Ledo palustris-Pinetum sibiricae* Ermakov et Makhatkov 2011

Ass. *Bergenio crassifoliae-Laricetum sibiricae* Makunina 2011

Synonyms: *Rhododendro-Laricetum sibiricae* Guinochet 1982 nom. inval. (Art. 3g, 5a); *Bergenio-Pinetum sibiricae* Zhitlukhina et Alimbekova 1987 nom. inval. (Art. 1)

Ass. *Vaccinio uliginosi-Laricetum sibiricae* Makunina 2020

Ass. *Carici globularis-Pinetum sibiricae* Ermakov et Polyakova 2022

Ass. *Linnaeo borealis-Pinetum sibiricae* Ermakov et Polyakova 2022

All. *Rhododendro tomentosi-Laricion gmelinii* Ermakov in Ermakov et Alsynbayev 2004 nom. corr. et mut. nov. (Art. 44 and alternative form of the name, Art. 45)

Synonyms: *Ledo palustris-Laricion gmelinii* Ermakov in Ermakov et Alsynbayev 2004 nom. corr; *Ledo palustris-Laricion cajanderi* Ermakov in Ermakov et Alsynbayev 2004 nom. inept. (Art. 44); *Ledo palustris-Laricion cajanderi* Ermakov 2023 (Art. 29c)

Rhododendro tomentosi-Laricetum gmelinii Ermakov, Cherosov et Gogoleva 2002 nom. corr. et. mut. nov. (Art. 44 and alternative form of the name, Art. 45

Synonyms: *Ledo palustris-Laricetum gmelinii* Ermakov, Cherosov et Gogoleva 2002 nom. corr.; *Ledo palustris-Laricetum cajanderi* Ermakov, Cherosov et Gogoleva 2002 nom. inept. (Art. 44)

Conclusion

The name *Pino sibiricae-Laricion sibiricae* was not validly published either in Dostálek et al. (1988) (Art. 5) or in Ermakov and Alsynbayev (2004) (Art. 3j). It is validated in the present paper as *Pino sibiricae-Laricion sibiricae* Ermakov et Theurillat all. nov., together with the correction and/or mutation of other syntaxon names of Siberian forests.

Author contributions

NE planned the research and performed the syntaxonomic analysis; JPT did the nomenclature analysis. Both authors contributed critically to the writing of the paper.

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RESEARCH PAPER
GRASSLANDS OF ASIA

Plant biogeography, endemism and vegetation types of Dena Mts, Zagros, West Iran

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Abstract

Questions: The highest mountain peak of Zagros is located in the Dena mountain system (4409 m a.s.l.), which is identified as the second richest center of plant endemism of Zagros. In this study we (1) investigate floristic affinities of Dena Mts to adjacent mountain ranges based on the endemic species of the Iranian Plateau, (2) identify the species reaching the subnival zone, and (3) characterize the plant communities of the subnival zone of Dena Mts. **Study area:** Dena Mts is a calcareous mountain system in southern Zagros, Iran. **Methods:** The list of taxa endemic to the Iranian Plateau present also in Dena Mts was taken from our previously published data. Novel vegetation data were collected using the methodology of Braun-Blanquet. Classification was carried out in JUICE using the Modified TWINSPAN method. **Results:** Of the 242 taxa endemic to the Iranian Plateau present in Dena Mts, 22 taxa are endemic to the latter. Dena Mts have the strongest floristic affinity with the Yazd-Kerman massif, with which they share 84 taxa compared to 51 taxa shared with Alborz, 37 taxa shared with the Azerbaijan Plateau, and 15 taxa shared with Kopet Dagh-Khorassan. In Dena Mts, 38 taxa reach the subnival zone, most of them being endemic to the Iranian Plateau (68%). From scree habitats in the subnival zone, two new plant associations are described, *Aethionemetum umbellati* and *Zerdanetum anchonioidei*. These constitute a newly described alliance *Galion pseudokurdici*, classified within the class *Didymophyso aucheri-Dracocephaletea aucheri*. **Conclusions:** Although Dena Mts lie within a protected area, this will not prevent shrinking of alpine and subnival habitats due to global warming. Consequently, strong attention to the conservation of all range-restricted species of this mountain system, especially of alpine and subnival species, is highly recommended.

Taxonomic reference: Flora of Iran (Assadi et al. 1989–2021) and, for families not yet covered in the previous source, Flora Iranica (Rechinger 1963–2015).

Keywords

biogeography, conservation, Dena Mts, endemism, subnival zone, vegetation, Zagros

Introduction

Global biodiversity hotspots, many of which are located in mountainous areas, are known as regions with high conservation priorities due to their rich endemic diversity and, at the same time, high pressure from human activities (Myers et al. 2000; Mittermeier et al. 2005, 2011). One such hotspot is the Irano-Anatolian biodiversity hotspot, which is a mountainous region in South-West Asia with very heterogenous climate and topography (Zohary 1973; Djamali et al. 2012) and, consequently, harboring a rich endemic diversity, especially at high elevations (Mittermeier et al. 2011; Noroozi et al. 2021). The Irano-Anatolian biodiversity hotspot includes several areas of endemism that are strongly associated with the major mountain ranges (Noroozi et al. 2019a, 2019b).

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Zagros mountain range, the most extensive mountain range of Iran (Figure 1), is one of the richest areas of endemism of the region with numerous centers of endemism, mostly located in areas with very high elevations (Noroozi et al. 2019a). Among those areas, Dena Mts are the highest mountain system, reaching 4409 m a.s.l. at its highest peak (Figure 1). Dena Mts are the second-richest center of plant endemism in Zagros and the fourth-richest in Iran (Noroozi et al. 2019a). The Austrian botanist Theodor Kotschy (1813–1866), the most important collector of natural history objects active in the nineteenth century in South-West Asia (Edmondson and Lack 2006), was the first botanist to collect plants from the alpine and subnival zones of Dena Mts (in 1842), and many of the numerous collected plants were described as new species by Edmond Boissier in his Flora Orientalis (Boissier 1867–1884). Although Dena Mts have been frequently visited by national botanists, only few botanists have ascended to the high alpine and subnival zones after Kotschy, so that data pertaining to these elevation zones remained scarce and became potentially outdated. This is also the case for the “Flora of Dena Mts.” (Jafari Kokhedan 2003). Despite the prominent role as a center of biodiversity in Zagros, endemic diversity, biogeography, vegetation as well as conservation aspects of Dena Mts have only been poorly studied.

The subnival flora is an important component in SW Asia contributing a high proportion of endemics that are highly threatened (Noroozi et al. 2011). Although exploration of the alpine and subnival flora of Dena Mts dates back to Kotschy, a thorough survey of it has been lacking. Connected to the poor exploration of the alpine zone, little is known about the vegetation types in this area, especially in a phytosociological context.

As a basis for putative conservation strategies, we here provide a biogeographic characterization of Dena Mts with a focus on the particularly poorly studied high elevation zones. To this end, we use the following approaches: (1) The floristic affinities and thus biogeographic connections of Dena Mts to other mountain ranges of the region are analyzed; (2) a full account of the subnival plant diversity of Dena Mts is given; (3) plant communities from the subnival zone are described and classified.

Study area

Dena Mts is a calcareous mountain system in southern Zagros, ca. 60 km long and ca. 10 km wide. Nearly 100 peaks exceed 4000 m a.s.l., with the highest one reaching 4409 m a.s.l., being the highest summit of the entire Zagros mountain range (Figure 1). Dena Mts have a Mediterranean precipitation regime with cold-wet winters and warm-dry summers (Figure 2). Western slopes receive more precipitation than eastern slopes, and in the alpine zone the annual precipitation exceeds 1000 mm (Jafari Kokhedan 2003).

The main vegetation types of the study area can be summarized as follows (see Noroozi et al. 2020 and references therein):

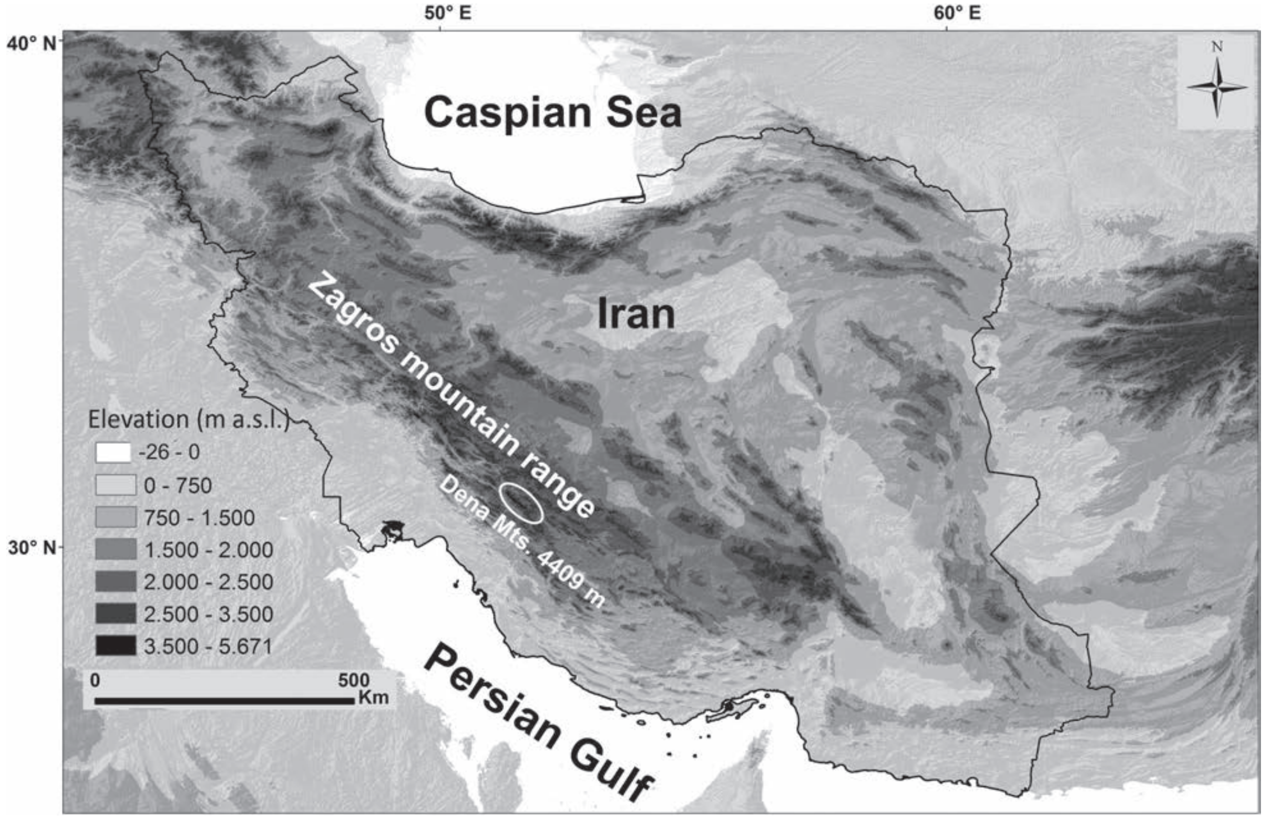

Figure 1. Location of Dena Mts in the Zagros mountain range in Iran.

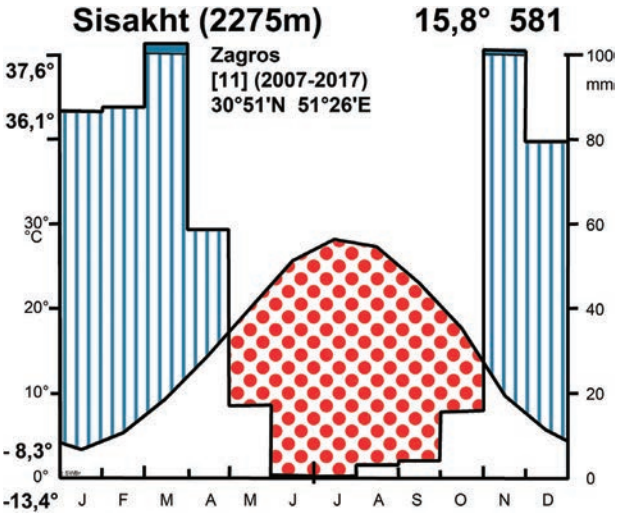

Figure 2. Climate diagram of the study region.

***Quercus* woodlands** (Figure 3A) occupy the montane zone of Dena Mts, especially on the western slopes up to 2700 m a.s.l. These woodlands are dominated by *Quercus* species, especially *Q. brantii* (Jafari Kokhedan 2003). Other frequent shrubs and trees are *Cotoneaster luristanica*, *Daphne mucronata*, *Lonicera nummularifolia*, *Pistacia khinjuk* and *Rhamnus kurdica*.

Subalpine tall-umbelliferous vegetation types (Figure 3B) mostly cover steep slopes with scree in elevations ranging from ca. 2500 to 3500 m a.s.l. In term of physiognomy, environmental features and species composition, they can be classified in the provisional class *Prangetea ulopterae*, described from Alborz mountain range (Klein 1988, 2001). The most dominant species of this vegetation type in Dena Mts is *Ferulago angulata* (Figure 3B).

Chasmophyte vegetation types (Figure 3C, D) have a high elevational amplitude from the montane to the subnival zone. Characteristic species in these habitats include *Arenaria minutissima*, *Dielsiocharis kotschyi*, *Dionysia bryoides* (Figure 3C), *D. termeana* (Figure 3D), *Graellsia saxifragifolia*, *Pentanema multicaule*, *Rhamnus cornifolia*, and *Tanacetum kotschyi*.

Subalpine and alpine thorn-cushion grasslands (Figure 4A, B) are the main formation of the subalpine and alpine zone, having more developed soils compared to other communities of these zones. In the subalpine zone, up to 3500 m a.s.l., the main dominant thorn-cushion species is *Astragalus brachycalyx*, mostly accompanied by *Bromus tomentellus*, *Daphne mucronata*, *Euphorbia polycaulis*, *Fritillaria imperialis*, and *Tulipa systola*. In the alpine zone, from ca. 3500 m a.s.l. up to ca. 4100 m a.s.l., this formation is dominated by *Astragalus murinus* (Figure 4A, B) and *A. myriacanthus*. Other accompanying species are *Acantholimon melananthum*, *Arenaria persica*, *Arnebia euchroma*, *Cousinia bakhtiarica*, *Euphorbia microsciadia*, *Marrubium astracanicum*, *Micrantha multicaulis*, *Phlomis anisodonta* subsp. *occidentalis*, *Scorzonera subaphylla*, and *Tanacetum dumosum*.

Alpine snowbeds (Figure 4C, D) are mostly found at elevations between ca. 3500 m a.s.l. and 4100 m a.s.l., where snow cover can persist till July and August. The growing season of these vegetation types is short, and most of the species are small hemicryptophytes. Structure and composition (mostly at the generic level) of these communities are the same as those from Alborz, which belong to the order *Taraxaco brevirostris-Polygonetalia serpyllacei*. The most important character species of the order present in Dena Mts is *Polygonum serpyllaceum*. Other characterstic species in the region are *Arenaria balansae*, *Plantago atrata*, *Primula capitellata*, and *Ranunculus elymaiticus* (Figure 4C, D).

Alpine and subnival scree vegetation types (Figure 5) occur, where the ground is mostly covered by scree and big stones. They harbor only scattered vegetation and have a low species richness. Phytosociologically, these vegetation types belong to the class *Didymophyso aucheri-Dracocephaletea aucheri* described from Alborz and mountains of NW Iran (Noroozi et al. 2014). Character species of this class occurring in Dena Mts are *Didymophysa aucheri* (rare), *Elymus longearistatus*, *Astragalus melanodon* (Figure 5A), *Bromus frigidus* (Figure 5B), *Euphorbia aucheri* (Figure 5C), *Galium pseudokurdicum* (Figure 5D), *Physoptychis gnaphalodes* (Figure 5E), and *Stachys obtusicrena* (Figure 5F). The highest elevations of this mountain system, above ca. 4100 m a.s.l., are mostly covered with subnival scree vegetation types.

Methods

The list of taxa (species, subspecies and varieties) endemic to the Iranian Plateau and also present in Dena Mts was prepared using the list of all endemic vascular plant species of Iran published by Noroozi et al. (2019b) and our updated data (Table 1). Presence of these taxa in the adjacent mountain ranges, i.e., the Azerbaijan Plateau, Alborz, Kopet Dagh, and Yazd-Kerman, was used to quantify the floristic connections between Dena Mts and these mountain ranges. To explore the flora and vegetation of the subnival zone, an expedition dedicated to the high elevations of this mountain was undertaken in summer 2019. The plots were taken at subnival scree sites at elevations above 4100 m a.s.l. The alpine grasslands and subnival scree vegetation types are easily distinguishable in this area. Vegetation data from 19 plots, each 10 m × 10 m, were collected following the methodology of Braun-Blanquet (Braun-Blanquet 1964; Dengler et al. 2008). The proportional covers of the vegetation, scree, soil, and rock were estimated in each plot. The plot data were stored in Turboveg (Hennekens and Schaminée 2001). Classification was carried out in JUICE version 7.1 (Tichý 2002) using the Modified TWINSPAN and four cutlevel values (0%, 5%, 25%, 50%). A synoptic table was constructed based on the percentage frequency and fidelity of the species in each described association. We followed the phytosociological nomenclature code (Theurillat et al. 2020) to describe and propose new syntaxa. Associations were delimited according to Willner (2006). We used the phi value as fidelity measure and a threshold of 0.3. A synoptic table showing the character species of both the three alliances previously described for high alpine and subnival scree vegetation types of the Iranian Plateau and the alliance newly described in this paper is presented.

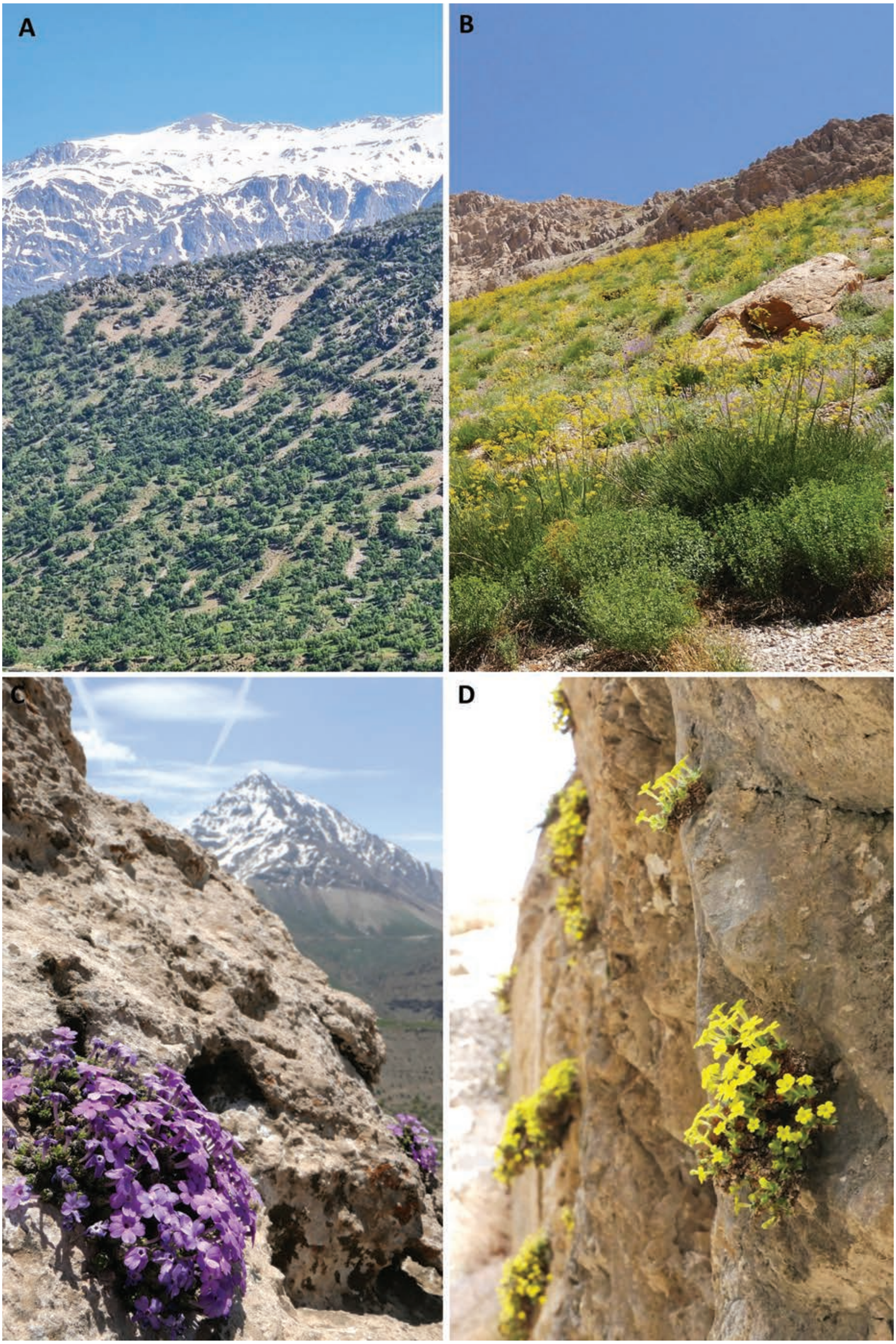

Figure 3. A) *Quercus brantii* woodlands (2000–2600 m a.s.l.). **B)** Umbelliferous vegetation types and *Ferulago angulata* as dominant species (2500–3500 m a.s.l.). **C)** Chasmophyte habitats, *Dionysia bryoides* (2800 m a.s.l.). **D)** Chasmophyte habitats, *Dionysia termeana* (2500 m a.s.l.).

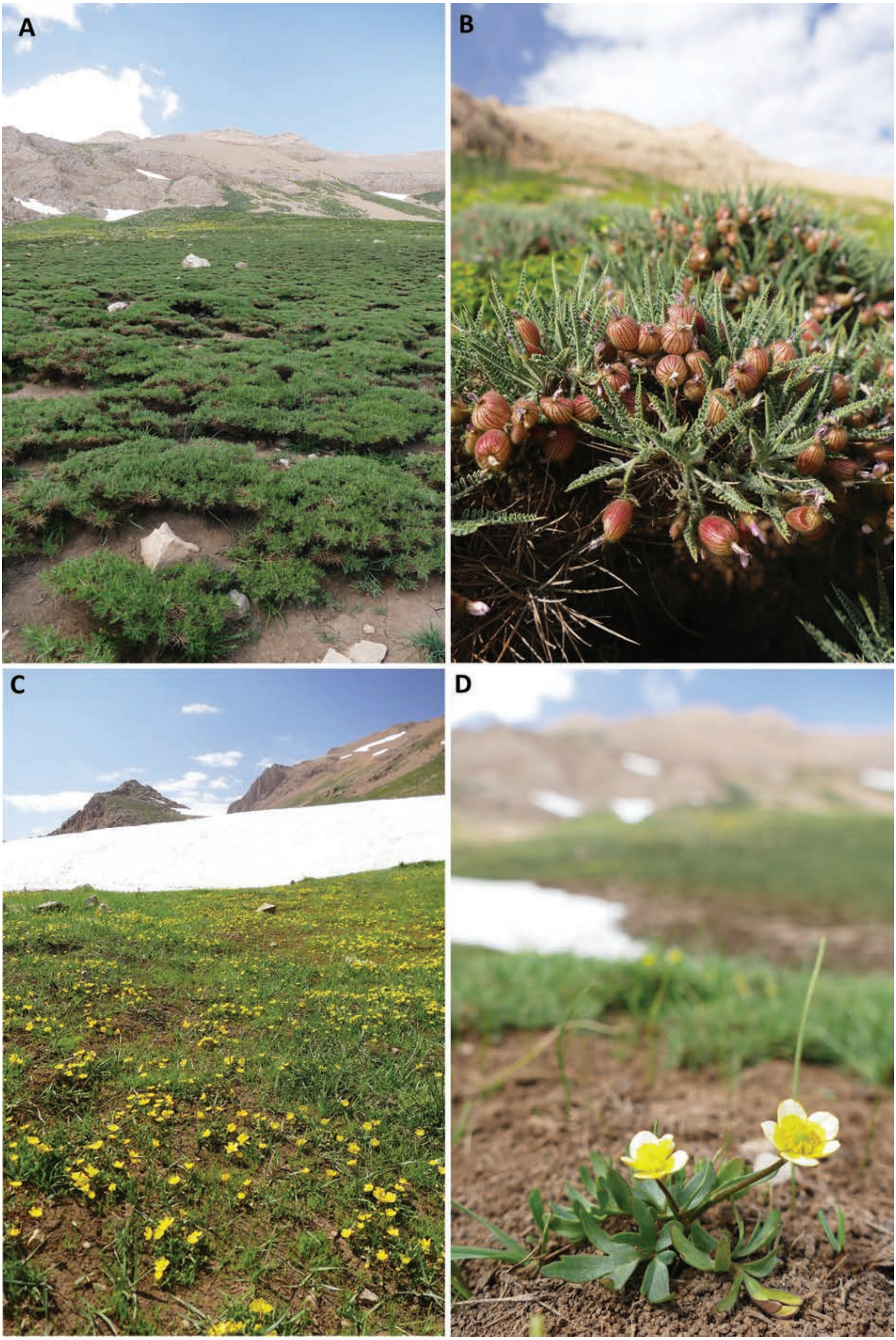

Figure 4. A, B) Thorn-cushion grasslands and *Astragalus murinus* as dominant species (3800 m a.s.l.). **C, D)** Snowbed vegetation types and *Ranunculus elymaiticus* as dominant species (3800 m a.s.l.).

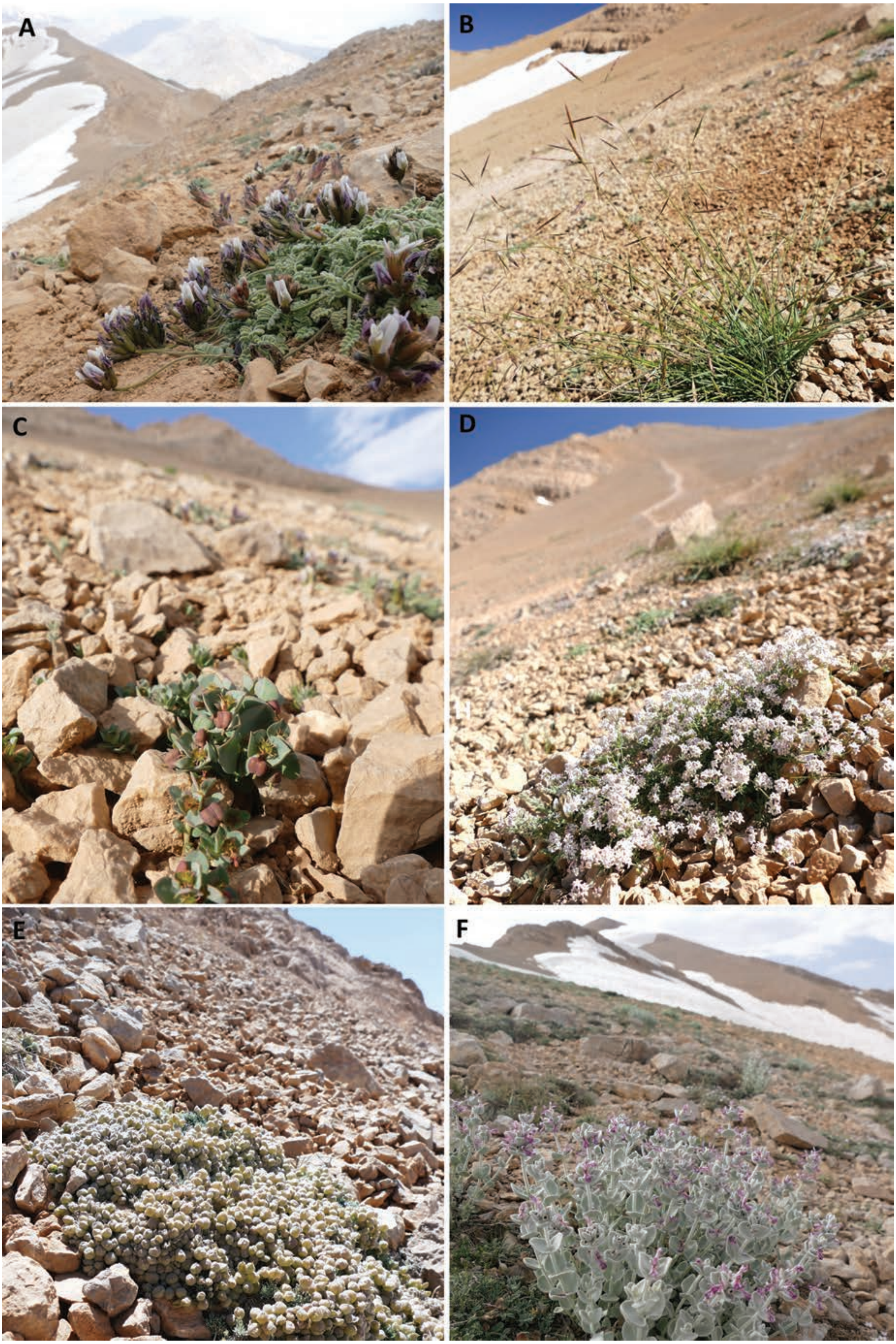

Figure 5. Subnival scree vegetation types (4100–4409 m a.s.l.). **A)** *Astragalus melanodon* (4150 m a.s.l.). **B)** *Bromus frigidus* (4200 m a.s.l.). **C)** *Euphorbia aucheri* (4200 m a.s.l.). **D)** *Galium pseudokurdicum* (4150 m a.s.l.). **E)** *Physoptychis gnaphalodes* (4250 m a.s.l.). **F)** *Stachys obtusicrena* (4200 m a.s.l.).

Table 1. Endemic taxa of the Iranian Plateau recorded in Dena Mts. For each species, the following information is provided: family, distribution in different areas of endemism (Al: Alborz; Az: Azerbaijan Plateau; Ke: Yazd-Kerman; Ko: Kopet Dagh-Khorassan; Za: Zagros, endemics of Dena Mts given in bold) based on Noroozi et al. (2019b), elevational range in the entire geographical range of the species, and main habitat types (Alp. Scree: Alpine Scree; Chasm.: Chasmophytic vegetation; M Grass.: Montane Grasslands; Oak W.: Oak Woodland; Subn. Scree: Subnival Scree; Th.-Cu.: Thorn-Cushion vegetation; Umb.: Umbelliferous vegetation).

Species	Family	Distribution	Elevation range (m)	Main Habitat
Allium austroiranicum R.M. Fritsch	Alliaceae	Za, Ke	1700–3300	Umb., Th.-Cu.
Allium brachyodon Boiss.	Alliaceae	Za, Ko	3000–3200	Th.-Cu.
Allium kazerouni Parsa	Alliaceae	Za	1660–2900	Th.-Cu.
Allium kotschyi Boiss.	Alliaceae	Za, Ke	2500–3600	Th.-Cu.
Kochia prostrata (L.) Schrad. var. *alpina* Bornm.	Amaranthaceae	Za	2500–3000	Th.-Cu.
Astrodaucus persicus (Boiss.) Drude in Engler & Prantl	Apiaceae	Za, Al, Az, Ko	1000–2750	Oak W., Th.-Cu.
Dorema aucheri Boiss.	Apiaceae	Za, Ke	1700–3250	Umb., Th.-Cu.
Echinophora cinerea (Boiss.) Hedge & Lamond	Apiaceae	Za	2000–3300	Umb., Th.-Cu.
Ferula microcolea (Boiss.) Boiss.	Apiaceae	Za, Al, Az	1600–3050	Umb.
Ferulago angulata (schlecht.) Boiss.	Apiaceae	Za, Al, Az, Ke, Ko	2000–3700	Umb.
Ferulago carduchorum Boiss. & Haisskn.	Apiaceae	Za, Az, Ke	1700–3990	Umb.
Ferulago contracta Boiss. & Hausskn.	Apiaceae	Za, Ke	1700–2500	Umb.
Johreniopsis scoparia (Boiss.) Pimenov	Apiaceae	Za	2370–3000	Umb.
Leutea cupularis (Boiss.) M. Pimen.	Apiaceae	Za, Al	1800–3700	Umb.
Pimpinella deverroides (Boiss.) Boiss.	Apiaceae	Za	1500–3500	Umb., Th.-Cu.
Pimpinella dichotoma (Boiss. et Hausskn.) Wolff	Apiaceae	Za, Ke	1500–2750	Umb., Th.-Cu.
Pseudotrachydium kotschyi (Boiss.) Pimenov & Kljuykov	Apiaceae	Za	1950–3900	Th.-Cu., Alp. Scree
Rhabdosciadium aucheri Boiss.	Apiaceae	Za	1830–3960	Th.-Cu., Alp. Scree
Semenovia dichotoma (Boiss.) Manden.	Apiaceae	Za	2800–4200	Th.-Cu.
Semenovia frigida (Boiss.) Hausskn.	Apiaceae	Za, Ke	2400–3500	Th.-Cu.
Semenovia tragioides (Boiss.) Manden.	Apiaceae	Za, Al, Az, Ko	1500–3550	Th.-Cu.
Tetrataenium lasiopetalum (Boiss.) Manden.	Apiaceae	Za	2000–4000	Umb., Alp. Scree
Thecocarpus meifolius Boiss.	Apiaceae	Za, Ke	1500–3200	Th.-Cu.
Trachydium depressum Boiss.	Apiaceae	Za, Al, Ke	2100–3800	Th.-Cu.
Trachydium kotschyi (Boiss.) Boiss.	Apiaceae	Za	2000–3900	Th.-Cu.
Zeravschania aucheri (Boiss.) Pimenov	Apiaceae	Za, Al, Az	1300–3300	Th.-Cu.
Bellevalia heweri Wendelbo	Asparagaceae	**Za**	2200–2300	Wetland
Ornithogalum pycnanthum Wendelbo	Asparagaceae	Za	2400–3200	Th.-Cu.
Centaurea persica Boiss.	Asteraceae	Za	1550–3000	Oak W.
Cephalorrhynchus microcephalus (D.C.) Schchian	Asteraceae	Za, Al, Az	700–2800	Oak W.
Cicerbita polyclada (Boiss.) Beauverd	Asteraceae	**Za**	3300–3500	Oak W.
Cirsium bracteosum DC.	Asteraceae	Za, Ke, Al, Az	1800–3200	Oak W., Th.-Cu.
Cirsium spectabile DC.	Asteraceae	Za, Ke	1750–3000	Th.-Cu.
Cousinia albida DC.	Asteraceae	**Za**	2300–2600	Th.-Cu.
Cousinia amplissima (Boiss.) Boiss.	Asteraceae	Za, Al, Az	1000–2300	Oak W., Th.-Cu.
Cousinia araneosa DC.	Asteraceae	Za, Ke	1653–3600	Th.-Cu.
Cousinia assadii Attar	Asteraceae	**Za**	3000–3400	Th.-Cu.
Cousinia bachtiarica Boiss. & Hausskn.	Asteraceae	Za	2400–3000	Umb., Th.-Cu.
Cousinia barbeyi C.Winkl.	Asteraceae	Za	1570–2400	Th.-Cu.
Cousinia calcitrapa Boiss.	Asteraceae	Za, Ke	2100–3000	Th.-Cu.
Cousinia canescens DC.	Asteraceae	Za, Az	1850–2500	Th.-Cu.
Cousinia denaensis Attar & Djavadi	Asteraceae	Za	1800–2900	Oak W., Th.-Cu.
Cousinia gracilis Boiss.	Asteraceae	Za	2700–2800	Th.-Cu.
Cousinia iranshahriana Attar & Maroofi	Asteraceae	Za	2000–2800	Th.-Cu.
Cousinia kotschyi Boiss.	Asteraceae	Za, Ke	1200–3000	M Grass., Umb., Th.-Cu.
Cousinia longifolia C. Winkl. & Bornm.	Asteraceae	Za, Ke	3000–3400	Th.-Cu.
Cousinia oligocephala Boiss.	Asteraceae	**Za**	3200–3700	Th.-Cu.
Crepis heterotricha DC.	Asteraceae	Az, Al, Za, Ke	3000–4300	Th.-Cu., Alp.-Subn. Scree
Echinops ceratophorus Boiss.	Asteraceae	Za, Ke	1500–2800	Th.-Cu.
Echinops iranshahrii Rech.f.	Asteraceae	**Za**	1600–1800	Oak W.
Echinops kotschyi Boiss.	Asteraceae	**Za**	3000–3200	Th.-Cu.
Echinops macrophyllus Boiss. & Hausskn. var. *laciniatus* Mozaff.	Asteraceae	Za	1000–2500	Oak W.
Echinops macrophyllus Boiss. & Hausskn. var. *papillosus* Mozaff.	Asteraceae	Za, Al	1600–2500	Oak W.
Echinops mosulensis Rech.f. var. *papillosus* Mozaff.	Asteraceae	Za	500–2500	Oak W.
Echinops viscidulus Mozaff.	Asteraceae	Za	1500–3200	Umb., Th.-Cu.
Erigeron daenensis Vierh.	Asteraceae	Za	3700–4300	Chasm., Subn. Scree
Helichrysum artemisioides Boiss & Hausskn	Asteraceae	Za	1400–2100	Th.-Cu.
Helichrysum oligocephalum DC.	Asteraceae	Za, Al, Az	1600–3600	Umb., Th.-Cu.
Iranecio paucilobus (DC.) B. Nord.	Asteraceae	Za, Al, Ke	1800–3600	Th.-Cu., Alp. Scree
Lactuca denaensis N. Kilian & Djavadi	Asteraceae	**Za**	3600–4000	Chasm.

Species	Family	Distribution	Elevation range (m)	Main Habitat
Lactuca polyclada Boiss.	Asteraceae	Za	3200–3400	Th.-Cu.
Myopordon persicum Boiss.	Asteraceae	Za	3800–4400	Subn. Scree
Pentanema multicaule Boiss.	Asteraceae	Za	2100–3750	Chasm.
Phagnalon persicum Boiss.	Asteraceae	Za, Ke	1700–3400	Chasm.
Picris strigosa M.Bieb. subsp. *gonicaula* (Boiss.) Lack	Asteraceae	Za, Al, Ke	1250–2800	Th.-Cu.
Psychrogeton chionophilus (Boiss.) Krasch.	Asteraceae	**Za**	3500–3700	Th.-Cu., Snowbed
Scorzonera calyculata Boiss.	Asteraceae	Za, Al, Az, Ke	1000–3000	Oak W., Th.-Cu.
Scorzonera stenocephala Boiss.	Asteraceae	Za, Al, Az, Ko	2400–3600	Th.-Cu.
Scorzonera subaphylla Boiss.	Asteraceae	Za	2700–3400	Th.-Cu.
Senecio kotschyanus Boiss.	Asteraceae	Za, Ke	3800–4200	Subn. Scree
Tanacetum dumosum Boiss.	Asteraceae	Za	2100–3300	Th.-Cu.
Tanacetum persicum (Boiss.) Mozaff.	Asteraceae	Za, Al, Az, Ke, Ko	1700–3800	Chasm.
Tanacetum polycephalum Sch.Bip. subsp. *farsicum* Podl.	Asteraceae	Za, Ke	1500–3990	Th.-Cu.
Taraxacum kotschyi Soest	Asteraceae	Za	1640–2800	Chasm.
Tragopogon caricifolius Boiss.	Asteraceae	Za, Al, Az, Ke	1000–4000	Th.-Cu.
Alkanna frigida Boiss.	Boraginaceae	Za, Al	1500–3400	Oak W., Th.-Cu.
Caccinia kotschyi Boiss.	Boraginaceae	Za	1500–2500	Oak W., Chasm.
Onosma kilouyense Boiss. & Hausskn	Boraginaceae	Za, Al	1500–3500	Th.-Cu.
Onosma kotschyi Boiss.	Boraginaceae	Za, Al, Ke	1220–3150	Th.-Cu.
Onosma platyphylla H.Riedl	Boraginaceae	Za	1400–3000	Th.-Cu.
Onosma stenosiphon Boiss.	Boraginaceae	Za, Al, Ke, Ko	3000–4000	Th.-Cu.
Trichodesma aucheri DC.	Boraginaceae	Za, Ke	1500–3050	Th.-Cu.
Aethionema alpinum Moazzeni & Noroozi	Brassicaceae	Za, Ke	3000–4000	Alp. Scree
Aethionema umbellatum (Boiss.) Bornm.	Brassicaceae	**Za**	3900–4300	Subn. Scree
Didymophysa aucheri Boiss.	Brassicaceae	Za, Al, Az, Ko	3000–4800	Subn. Scree
Dielsiocharis kotschyi (Boiss) O.E. Schulz	Brassicaceae	Za, Ke, Al, Az, Ko	1300–4000	Chasm.
Fibigia umbellata (Boiss.) Boiss.	Brassicaceae	Za, Al, Ke	1900–3900	Th.-Cu.
Micrantha multicaulis (Boiss.) Dvorak	Brassicaceae	Za	1200–3600	Th.-Cu.
Physoptychis gnaphalodes Boiss.	Brassicaceae	Za, Al, Az, Ke	3000–4700	Alp.-Subn. Scree
Pseudocamelina aphragmodes (Boiss.) N. Busch	Brassicaceae	Za	3000–4200	Alp.-Subn. Scree
Pseudocamelina glaucophylla (DC.) N. Busch	Brassicaceae	Za, Al, Az, Ke	2500–3800	Alp.-Subn. Scree
Zerdana anchonioides Boiss.	Brassicaceae	Za,Ke	3500–4400	Subn. Scree
Campanula luristanica Freyn	Campanulaceae	Za	2000–2800	Chasm.
Acanthophyllum crassifolium Boiss.	Caryophyllaceae	Za, Al, Az	1100–3000	Th.-Cu.
Arenaria minutissima Rech.f. & Esfand.	Caryophyllaceae	Za, Ke	3700–4200	Alp.-Subn. Scree
Arenaria persica Boiss.	Caryophyllaceae	Za, Ke	3000–4200	Th.-Cu.
Bufonia kotschyana Boiss.	Caryophyllaceae	Za, Al, Az	1600–3100	Th.-Cu.
Bufonia macrocarpa Ser.	Caryophyllaceae	Za, Al	1300–3000	Th.-Cu.
Dianthus austroiranicus Lemperg	Caryophyllaceae	Za, Ke	1600–2300	Th.-Cu.
Dianthus denaicus Assadi	Caryophyllaceae	**Za**	2600–3700	Th.-Cu.
Dianthus orientalis Adams subsp. *aphanoneurus* Rech.f.	Caryophyllaceae	Za	2000–4140	Th.-Cu., Chasm.
Dianthus orientalis Adams subsp. *scoparius* (Fenzl ex Boiss.) Bornm.	Caryophyllaceae	Za	2300–2500	Th.-Cu., Chasm.
Dianthus stenocephalus Boiss.	Caryophyllaceae	Za	2100–2500	Th.-Cu.
Minuartia sublineata Rech.f.	Caryophyllaceae	Za, Az	1650–4200	Chasm.
Silene albescens Boiss.	Caryophyllaceae	Za	1315–3000	Th.-Cu.
Silene daenensis Melzh.	Caryophyllaceae	Za	3000–4400	Alp.-Subn. Scree
Silene elymaitica Bornm.	Caryophyllaceae	Za	1700–3350	Chasm.
Silene farsistanica Melzh.	Caryophyllaceae	Za	1800–3000	Th.-Cu.
Silene gynodioica Ghaz. subsp. *glandulosa* Melzh.	Caryophyllaceae	Za, Ko	1900–3500	Th.-Cu.
Silene gynodioica Ghaz. subsp. *peduncularis* (Fenzl ex Boiss.) Melzh.	Caryophyllaceae	Za, Az, Ke	1150–3500	Th.-Cu.
Silene nurensis Boiss. & Hausskn.	Caryophyllaceae	Za, Ke	3600–4400	Subn. Scree
Silene persica Boiss.	Caryophyllaceae	Za	2400–3500	Chasm.
Silene rhynchocarpa Boiss.	Caryophyllaceae	Za	2000–3000	Chasm.
Silene tragacantha Fenzl ex Boiss.	Caryophyllaceae	**Za**	3800–4000	Th.-Cu.
Colchicum wendelboi K. Persson	Colchicaceae	Za	850–3000	Wetland
Convolvulus urosepalus Pau	Convolvulaceae	Za	2500–3450	Umb.
Sedum callichroum Boiss.	Crassulaceae	Za	1300–3000	Oak W.
Sedum kotschyanum Boiss.	Crassulaceae	Za, Ke	2100–4000	Alp.-Sub. Scree
Cephalaria juncea Boiss.	Dipsacaceae	Za, Az	1500–3100	Oak W.
Pterocephalus persicus Boiss.	Dipsacaceae	Za, Ke	1600–3100	Oak W.
Euphorbia hebecarpa Boiss.	Euphorbiaceae	Za, Ke, Az	3000–3800	Th.-Cu.
Euphorbia plebeia Boiss.	Euphorbiaceae	Za	2000–2500	Oak W., Th.-Cu.
Astragalus argyrostachys Boiss.	Fabaceae	Za	1650–2400	Oak W.
Astragalus brachycalyx Fisch. subsp. *eriostylus* (Boiss. & Hausskn.) Zarre	Fabaceae	Za	2000–3200	Th.-Cu.

Species	Family	Distribution	Elevation range (m)	Main Habitat
Astragalus campylanthus Boiss.	Fabaceae	Za, Ke	1550–3100	Th.-Cu.
Astragalus cephalanthus DC.	Fabaceae	Za, Ke	1150–3000	Th.-Cu.
Astragalus chalaranthus Boiss. & Hausskn.	Fabaceae	**Za**	2200–3050	Th.-Cu.
Astragalus chartostegius Boiss. & Hausskn.	Fabaceae	Za	2500–4000	Th.-Cu.
Astragalus cyclophyllon Beck	Fabaceae	Za, Az	1000–2800	Oak W.
Astragalus daenensis Boiss.	Fabaceae	Za, Ke	3300–4200	Alp.-Subn. Scree
Astragalus fragiferus Bunge	Fabaceae	Za	1700–3600	Th.-Cu.
Astragalus horridus Boiss.	Fabaceae	Za	2400–3700	Th.-Cu.
Astragalus ibicinus Boiss. & Haussk.	Fabaceae	Za	1600–3250	Th.-Cu.
Astragalus inexspectatus Maassoumi & Podlech	Fabaceae	Za	2400–3000	Umb., Th.-Cu.
Astragalus ischredensis Bunge	Fabaceae	Za, Ke	1000–3100	M Grass.
Astragalus johannis Boiss.	Fabaceae	Za, Ke	1300–3780	Oak W., Th.-Cu.
Astragalus lateritiiformis Zarre	Fabaceae	Za	2102–3100	Th.-Cu.
Astragalus maassoumii Podl.	Fabaceae	Za	2000–2400	Th.-Cu.
Astragalus managettae Sirj. & Rech.f.	Fabaceae	Za	1800–2200	Oak W.
Astragalus melanodon Boiss.	Fabaceae	Za	3500–4400	Alp.-Subn. Scree
Astragalus microphysa Boiss.	Fabaceae	Za, Ke	1900–3800	Th.-Cu.
Astragalus murinus Boiss.	Fabaceae	Za	2500–3900	Th.-Cu.
Astragalus myriacanthus Boiss.	Fabaceae	Za, Ke	2000–3800	Th.-Cu.
Astragalus plagiophacos Maassoumi & Podlech	Fabaceae	Al	2200–3900	Th.-Cu.
Astragalus plebejus Boiss.	Fabaceae	Za	1800–3650	Th.-Cu.
Astragalus ptychophyllus Boiss.	Fabaceae	Za	1600–3000	Oak W., Th.-Cu.
Astragalus quinquefoliolatus Bunge	Fabaceae	Za	1600–2400	Th.-Cu.
Astragalus rhodosemius Boiss. & Hausskn.	Fabaceae	Za, Az, Ke	1300–3500	Th.-Cu.
Astragalus sisakhtianus Podlech & Maassoumi	Fabaceae	**Za**	2400–2500	Oak W.
Astragalus spachianus Boiss. & Buhse	Fabaceae	Za, Ke	1200–3300	Th.-Cu., Oak W.
Astragalus sphaeranthus Boiss.	Fabaceae	Za	2200–3800	Th.-Cu.
Astragalus susianus Boiss. subsp. *sericeus* Tietz	Fabaceae	Za	1210–3355	Th.-Cu.
Astragalus susianus Boiss. subsp. *susianus*	Fabaceae	Za	1400–3040	Th.-Cu.
Astragalus tenuiscapus Freyn & Bornm.	Fabaceae	Za, Ke	2450–3950	Umb.
Astragalus turgidus Podlech	Fabaceae	Za	2700–3900	Alp. Scree
Astragalus zerdanus Boiss.	Fabaceae	Za	3500–4400	Subn. Scree
Cicer spiroceras subsp. *spiroceras* Jaub. & Spach	Fabaceae	Za, Ke	1500–3700	Umb.
Cicer tragacanthoides Jaub. & Spach	Fabaceae	Za, Al, Ke, Ko	2600–4000	Alp.-Subn. Scree
Hedysarum criniferum Boiss.	Fabaceae	Za	1600–3000	Th.-Cu.
Onobrychis melanotricha Boiss.	Fabaceae	Za, Al	900–3200	Th.-Cu., Oak W.
Oxytropis chrysocarpa Boiss.	Fabaceae	Za, Al, Ko	1900–3000	Oak W.
Vicia ciceroidea Boiss.	Fabaceae	Za, Al, Az	2600–4200	Alp.-Subn. Scree
Vicia kotschyana Boiss.	Fabaceae	Za	2400–4100	Alp.-Subn. Scree
Ajuga austro-iranica Rech. f.,F	Fabaceae	Za	400–3600	Chasm.
Ajuga chamaecistus Ging. ex Benth.	Lamiaceae	Za, Al, Az, Ko	1200–2800	M Grass.
Dracocephalum kotschyi Boiss.	Lamiaceae	Za, Al, Az	1500–3500	M Grass., Umb.
Dracocephalum surmandinum Rech.f.	Lamiaceae	Za	3000–3900	Th.-Cu.
Mentha longifolia (L.) Hudson var. *kermanensis* Rech.f.	Lamiaceae	Za, Al, Ke	1300–3800	Wetland
Nepeta glomerulosa Boiss.	Lamiaceae	Za, Al, Ke, Ko	200–3800	Umb.
Nepeta kotschyi Boiss.	Lamiaceae	Za	1100–2930	Umb.
Nepeta lasiocephala Benth.	Lamiaceae	Za, Ke	3500–4400	Subn. Scree
Nepeta macrosiphon Boiss.	Lamiaceae	Za, Az	1800–3800	Umb.
Nepeta oxyodonta Boiss.	Lamiaceae	Za, Ke	1000–3300	Chasm.
Nepeta schiraziana Boiss.	Lamiaceae	Za, Al, Ko	1500–3000	Oak W.
Phlomis anisodonta Boiss. subsp. *occidentalis* Jamzad	Lamiaceae	Za	950–3300	Th.-Cu.
Phlomis persica Boiss.	Lamiaceae	Za, Al	0–2800	Oak W., Th.-Cu.
Phlomoides adenantha Jaub. & Spach	Lamiaceae	Za, Ke	150–2900	Oak W.
Satureja bachtiarica Bunge	Lamiaceae	Za, Ke	1550–3000	Chasm.
Scutellaria multicaulis Boiss.	Lamiaceae	Za, Al, Ke	3000–4200	Alp.-Subn. Scree
Stachys acerosa Boiss.	Lamiaceae	Za, Ke	1700–3500	Th.-Cu.
Stachys ixodes Boiss. & Hausskn. ex Boiss.	Lamiaceae	Za	1700–2860	Chasm.
Stachys obtusicrena Boiss.	Lamiaceae	Za, Ke	3500–4200	Subn. Scree
Stachys persepolitana Boiss.	Lamiaceae	Za, Ke	800–2600	Chasm.
Stachys pilifera Benth.	Lamiaceae	Za	1700–3350	Th.-Cu.
Thymus daenensis Celak.	Lamiaceae	Za, Al, Az, Ke	1100–3100	Th.-Cu.
Linum persicum Ky. ex Boiss.	Linaceae	Za	1900–3200	Th.-Cu.
Alcea iranshahrii Pakravan	Malvaceae	**Za**	2400–2600	Umb.
Fraxinus angustifolia Vahl. subsp. *persica* (Boiss.) Azadi	Oleaceae	Za	850–2500	Oak W.
Acantholimon flexuosum Boiss. & Hausskn. ex Bunge	Plumbaginaceae	Za, Al, Ke	1600–3000	Th.-Cu.
Acantholimon melananthum Boiss.	Plumbaginaceae	Za	2500–3500	Th.-Cu.
Acantholimon oliganthum Boiss.	Plumbaginaceae	Za, Ke	1600–3500	Th.-Cu.

Species	Family	Distribution	Elevation range (m)	Main Habitat
Acantholimon tomentellum Boiss.	Plumbaginaceae	Za	3100–4200	Alp.-Subn. Scree
Bromus frigidus Boiss. & Hausskn.	Poaceae	Za	3500–4200	Alp.-Subn. Scree
Colpodium violaceum (Boiss.) Griseb.	Poaceae	Za	3000–3400	Snowbed
Elymus gentryi (Melderis) Melderis var. *ciliatiglumis* Assadi	Poaceae	**Za**	2500–3000	Th.-Cu.
Elymus zagricus Assadi	Poaceae	**Za**	2800–2900	Th.-Cu.
Piptatherum denaense Hamzehee & Assadi	Poaceae	**Za**	3200–3300	Th.-Cu.
Polygonum aridum Boiss. & Hausskn.	Polygonaceae	Za	1700–2800	Th.-Cu.
Rheum persicum Los.	Polygonaceae	Za	1650–2200	Umb.
Primula gaubaeana Bornm.	Primulaceae	Za, Ke	700–2800	Chasm.
Dionysia bryoides Boiss.	Primulaceae	Za	1850–3200	Chasm.
Dionysia diapensiifolia Boiss.	Primulaceae	Za	1000–2500	Chasm.
Dionysia revoluta Boiss. subsp. *canescens* (Boiss.) Wendelbo	Primulaceae	Za, Ke	1600–3300	Chasm.
Dionysia revoluta Boiss. subsp. *revoluta*	Primulaceae	Za, Ke	1700–3700	Chasm.
Dionysia termeana Wendelbo	Primulaceae	**Za**	2680–3500	Chasm.
Dionysia zagrica Grey-Wilson	Primulaceae	**Za**	2050–2850	Chasm.
Delphinium saniculifolium Boiss.	Ranunculaceae	Za, Ke	1700–2700	Umb.
Ranunculus elymaiticus Boiss. & Hausskn.	Ranunculaceae	Za	2200–4200	Snowbed
Rhamnus cornifolia Boiss. & Hohen. var. *cornifolia*	Rhamnaceae	Za, Az	1700–3700	Chasm.
Rhamnus cornifolia Boiss. & Hohen. var. *denudata* Bornm.	Rhamnaceae	Za	2400–3000	Chasm.
Amygdalus elaeagnifolia Spach subsp. *elaeagnifolia*	Rosaceae	Za, Ke	1300–3467	Th.-Cu.
Amygdalus elaeagnifolia Spach subsp. *leiocarpa* (Boiss.) Browicz	Rosaceae	Za, Ke	1600–3400	Th.-Cu.
Amygdalus haussknechtii (C.K.Schneider.) Bornm.	Rosaceae	Za	1400–2900	Oak W.
Cerasus brachypetala Boiss. var. *bornmuelleri* (C. K. Schneid.) Browicz	Rosaceae	Za	2100–3000	Chasm.
Cerasus brachypetala Boiss. var. *brachypetala* Boiss.	Rosaceae	Za	2100–3600	Chasm.
Cerasus microcarpa (C.A.Mey.) Boiss. subsp. *diffusa* (Boiss. & Hausskn.) Browicz	Rosaceae	Za, Al	800–2400	Oak W.
Cotoneaster persicus Pojark.	Rosaceae	Za, Ke	1000–3300	Oak W.
Potentilla elvendensis Boiss. et Hohen.	Rosaceae	Za	2200–2800	Th.-Cu.
Potentilla flaccida Th. Wolf	Rosaceae	Za, Al	2600–3750	Snowbed
Potentilla lignosa Willd. ex D. F. K. Schltdl	Rosaceae	Za, Al	2000–3200	Chasm.
Potentilla nuda Boiss.	Rosaceae	Za, Al, Az, Ke	2000–3900	Snowbed
Potentilla nurensis Boiss. & Hausskn.	Rosaceae	Za, Az	1650–3350	Wetland
Pyrus glabra Boiss.	Rosaceae	Za	1578–2600	Oak W.
Asperula fragillima Boiss. & Hausskn. ex Boiss.	Rubiaceae	Za	1800–3300	Chasm.
Asperula glomerata (M.Bieb.) Griseb. subsp. *condensata* (Ehrend.) Ehrend.	Rubiaceae	Za	3200–3500	Umb.
Asperula glomerata (M.Bieb.) Griseb. subsp. *dasycarpa* Ehrend. & Schönb.-Tem.	Rubiaceae	Za	1500–3500	Umb.
Asperula glomerata (M.Bieb.) Griseb. subsp. *filiformis* (Bornm.) Ehrend. & Schönb.-Tem	Rubiaceae	Za, Ke	3000–4200	Alp.-Subn. Scree
Asperula rechingeri Ehrend. & Schönb.- Tem	Rubiaceae	Za	2000–3900	Umb., Th.-Cu.
Crucianella gilanica Trin. subsp. *glauca* (A. Rich ex D.C.) Ehrend.	Rubiaceae	Za	1530–3204	Chasm.
Galium anguineum Ehrend & Schönb.-Tem.	Rubiaceae	Za	2150–4000	Wetland
Galium pseudokurdicum (Ehrend.) Schönb.-Tem.	Rubiaceae	Za	3500–4200	Alp.-Subn. Scree
Galium schoenbeck-temesyae Ehrend.	Rubiaceae	**Za**	2400–2900	Chasm.
Rubia albicaulis Boiss.	Rubiaceae	Za, Ke	1300–2800	Umb.
Rubia pauciflora Boiss.	Rubiaceae	Za	3000–4200	Alp.-Subn. Scree
Salix issatissensis Maassoumi, Moeeni & Rahimin.	Salicaceae	Za, Ke	1800–2500	Wetland
Scrophularia crassiuscula Grau	Schrophulariaceae	Za	1300–3300	Chasm.
Scrophularia subaphylla Boiss.	Schrophulariaceae	Za, Al, Az, Ke	3000–4150	Alp.-Subn. Scree
Verbascum austroiranicum Hub.-Mor.	Schrophulariaceae	**Za**	1900–2400	Oak W.
Verbascum hasarense Freyn & Bornm.	Schrophulariaceae	Za, Ke	2400–3600	Th.-Cu.
Veronica kurdica Benth. subsp. *filicaulis* (Freyn) M. A. Fischer	Schrophulariaceae	Za, Ke	3000–4300	Th.-Cu., Subn. Scree
Veronica rubrifolia Boiss. subsp. *rubrifolia*	Schrophulariaceae	Za, Al, Ke	1800–3000	Snowbed, Th.-Cu.
Ulmus boissieri Graudz	Ulmaceae	Za, Ke	1300–2600	Oak W.

Results and discussion

Endemicity and biogeography

Of the 242 Iranian endemic taxa recorded from the study area, a total of 22 taxa (21 species, 1 variety; Table 1) are restricted to Dena Mts, 122 taxa (105 species, 10 subspecies, 7 varieties; Table 1) are endemic to Zagros as a whole, and 120 taxa (104 species, 13 subspecies, 3 varieties) are shared with outher mountain ranges of the Iranian Plateau (Figure 6, Table 1). From these 120 taxa, 84 taxa are also present in Yazd-Kerman, 51 taxa in Alborz, 37 taxa in the Azerbaijan Plateau, and 15 taxa in Kopet Dagh-Khorassan (Figure 6). Thus, Dena Mts have the strongest floristic affinity to the closest mountain range, the Yazd-Kerman massif. The elevational belt of 2200–2600 m a.s.l. has the richest endemic diversity. Number of endemic species decrease gradually at both lower and higher elevations (Figure 7). From the 22

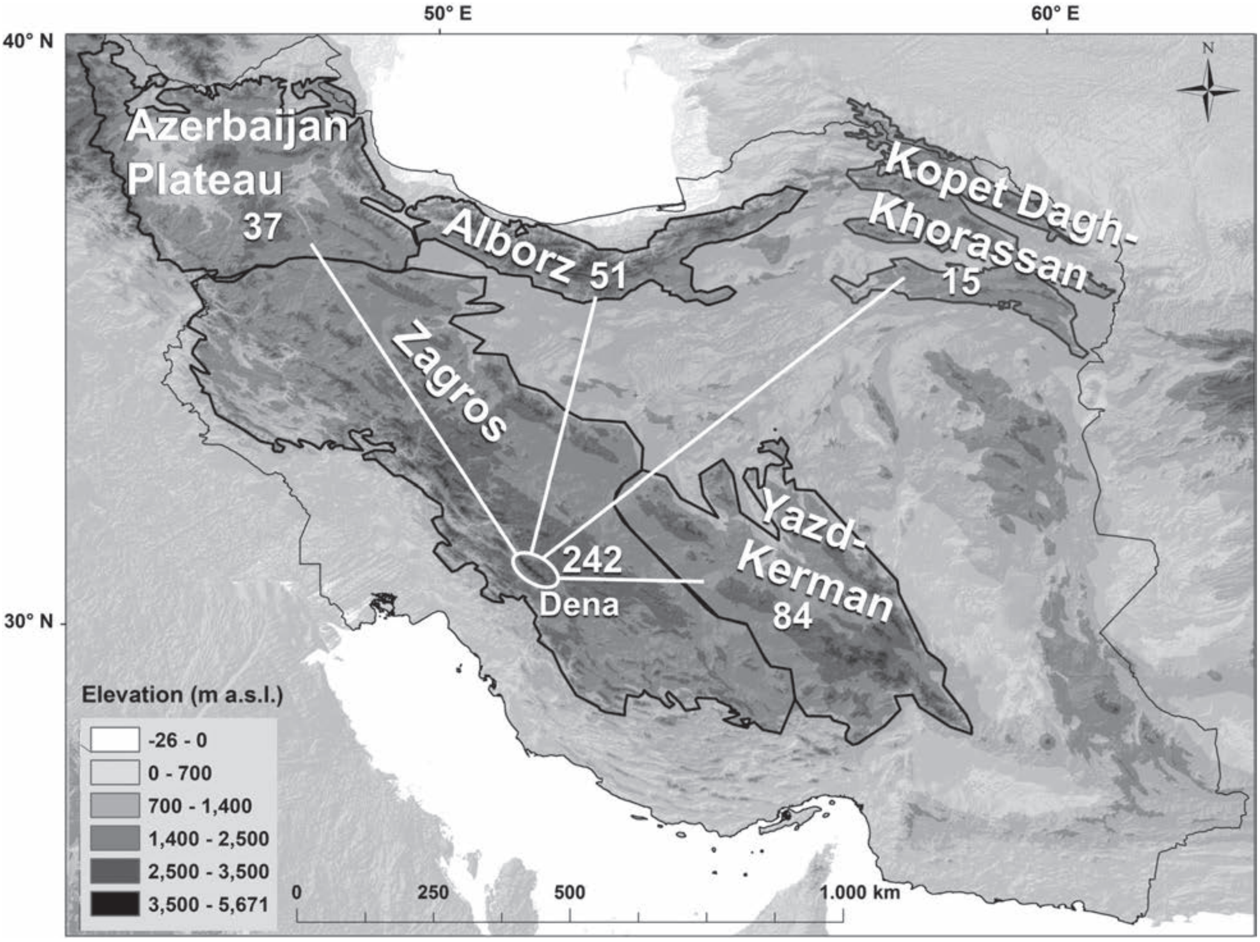

Figure 6. Floristic relationships between Dena Mts and other mountain ranges of Iran (areas of endemism), based on the endemic flora of Iran (the numbers written in each area are taxa shared with Dena Mts).

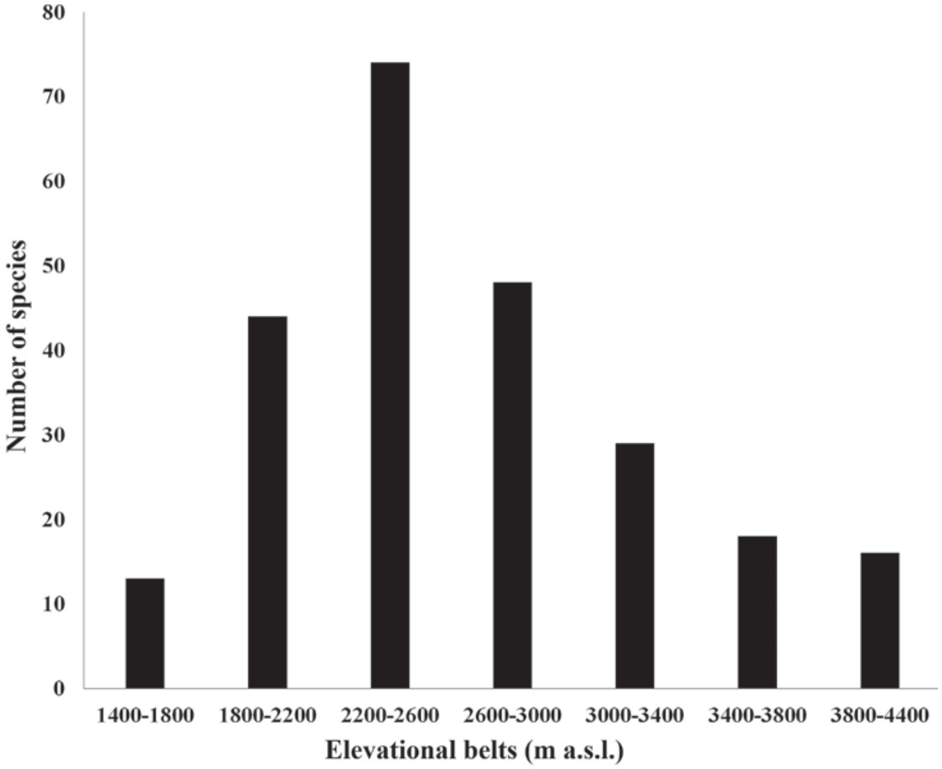

Figure 7. Number of endemic species in different elevational belts in Dena Mts. High number of endemics are concentrated in mid-elevational belts.

Table 2. List of species reaching the subnival zone of Dena Mts (elevation above 4100 m a.s.l.). Al: Alborz; Az: Azerbaijan Plateau; Ke: Yazd-Kerman; Ko: Kopet Dagh-Khorassan; Za: Zagros.

Taxon	Family	Distribution range	Type from Dena Mts
Semenovia dichotoma (Boiss.) Manden.	Apiaceae	Iran (Za)	Kotschy 1842
Crepis heterotricha DC.	Asteraceae	Iran (Az, Al, Za, Ke)	
Erigeron daenensis Vierh.	Asteraceae	SE Anatolia, Iran (Za)	Kotschy 1842
Myopordon persicum Boiss	Asteraceae	Iran (Za)	Kotschy 1842
Psychrogeton amorphoglossus (Boiss.) Novopokr.	Asteraceae	Irano-Anatolia to C Asia	Kotschy 1842
Arnebia euchroma (Royle) I. M. Johnst.	Boraginaceae	Iran (Za, Ke) to Himalaya	
Didymophysa aucheri Boiss.	Brassicaceae	Iran (Za, Az, Al)	
Dielsiocharis kotschyi Boiss.	Brassicaceae	Iran (Za, Az, Al, Ke)	
Draba aucheri Boiss.	Brassicaceae	Iran and C Asia	
Graellsia saxifragifolia (DC.) Boiss.	Brassicaceae	Iran, Hindu Kush	
Physoptychis gnaphalodes Boiss.	Brassicaceae	Iran (Za, Al, Az, Ke, Ko)	
Pseudocamelina aphragmodes (Boiss.) N. Busch	Brassicaceae	Iran (Za)	
Zerdana anchonioides Boiss.	Brassicaceae	Iran (Za, Ke)	
Arenaria balansae Boiss.	Caryophyllaceae	Anatolia and Iran	
Arenaria persica Boiss.	Caryophyllaceae	Iran (Za, Ke)	
Arenaria minutissima Rech. f. & Esfand.	Caryophyllaceae	Iran (Za, Ke)	
Minuartia sublineata Rech.f.	Caryophyllaceae	Iran (Za, Az)	
Silene daenensis Melzh.	Caryophyllaceae	Iran (Za)	
Chenopodium foliosum Asch.	Chenopodicaceae	Casmopolite	
Euphorbia aucheri Boiss.	Euphorbiaceae	Irano-Anatolia region, Hindu Kush	
Astragalus melanodon Boiss.	Fabaceae	Iran (Za)	Kotschy 1842
Astragalus zerdanus Boiss.	Fabaceae	Iran (Za)	
Onobrychis cornuta (L.) Desv.	Fabaceae	SW Asia	
Vicia ciceroidea Boiss.	Fabaceae	Iran (Za, Al, Az)	Kotschy 1842
Nepeta lasiocephala Benth.	Lamiaceae	Iran (Za)	Kotschy 1842
Scutellaria multicaulis Boiss.	Lamiaceae	Iran (Za, Al, Ke)	
Stachys obtusicrena Boiss.	Lamiaceae	Iran (Za, Ke)	
Gagea cf. alexeenkoana Micsz.	Liliaceae	Caucasus, Iran	
Acantholimon tomentellum Boiss.	Plumbaginaceae	Iran (Za)	
Bromus frigidus Boiss. & Hausskn.	Poaceae	Iran (Za)	Kotschy 1842
Elymus longearistatus (Boiss.) Tzvelev	Poaceae	Irano-Anatolian region	
Piptatherum laterale (Regel) Roshev.	Poaceae	From Anatolia to Central Asia and Himalaya	
Polygonum serpyllaceum Jaub. & Spach	Polygonaceae	Iran, Hindu Kush	Kotschy 1842
Potentilla flaccida Th.Wolf ex Bornm.	Rosaceae	Iran (Za, Al)	
Asperula glomerata (M.Bieb.) Griseb. subsp. *filiformis* (Bornm.) Ehrend. & Schönb.-Tem.	Rubiaceae	Iran (Za, Ke)	
Galium pseudokurdicum (Ehrend.) Schönb.-Tem.	Rubiaceae	Iran (Za) , Iraq	Kotschy 1842
Rubia pauciflora Boiss.	Rubiaceae	Iran (Za)	
Scrophularia subaphylla Boiss.	Schrophulariaceae	Iran (Za, Al, Az, Ke) , Iraq	Kotschy 1842
Veronica kurdica Benth. subsp. *filicaulis* (Freyn) M. A. Fischer	Scrophulariaceae	Iran (Za, Ke)	

taxa endemic to the Dena Mts, five have a mean elevational distribution between 1600 and 2500 m a.s.l., 12 taxa between 2500 and 3500 m a.s.l., and five taxa above 3500 m a.s.l.

The subnival vegetation types are dominated by scree and rocks and are very open, the vegetation having a maximum cover of 20%. Most of the 38 taxa reaching the subnival zone of Dena Mts (elevations above 4100 m a.s.l.) are endemics of the Iranian Plateau (68%), and from those, 42% are endemic of Zagros and Yazd-Kerman, and 21% are endemic of Zagros (Table 2). As only ca. 10% of the plant taxa recorded from Dena Mts (1200 taxa; Jafari Kokhedan 2003) are endemic to Zagros, the high rate of endemism for the subnival flora confirms previous findings that the rate of endemism is considerably higher in alpine and subnival habitats compared to lower elevations (Irl et al. 2015; Steinbauer et al. 2016; Noroozi et al. 2019b).

Description of new sytaxonomic units

We recorded a total of 33 species in 19 plots. The species richness ranged from 3 to 11 species per plot. The two clusters of the first TWINSPAN division level were considered as associations embedded in a new alliance that is proposed for Central and Southern Zagros. Based on the DCA ordination diagram (Figure 8), the associations are well separated from each other. We describe two new associations under a new alliance.

***Galion pseudokurdici* all. nov.** (Table 3)

Type (holotypus hoc loco): *Zerdanetum anchonioidis* ass. nov. (see below)

Character species: *Astragalus melanodon* (Figure 5A), *Bromus frigidus* (Figure 5B), *Galium pseudokurdicum* (Figure 5D), *Stachys obtusicrena* (Figure 5F).

This alliance is only known from the subnival zone of Dena Mts. Most of the character species of this unit are distributed in South and Central Zagros and in the Yazd-Kerman mountains. *Astragalus melanodon* is restricted to Central and Southern Zagros, *Bromus frigidus* and *Galium pseudokurdicum* are endemics of Zagros, and *Stachys obtusicrena* is an endemic of Zagros and Yazd-Kerman mountains. Therefore, this alliance could likely

Table 3. Relevés of scree vegetation of the subnival zone classified in *Didymophyso aucheri-Dracocephaletea aucheri* (character species highlighted in brown). The two associations *Aethionemetum umbellati* ass. nov (character species in cells with blue shading) and *Zerdanetum anchonioidis* ass. nov. (character species in cells with green shading) are classified in the alliance *Galion pseudokurdici* all. nov. (character species in cells with violet shading). Two last columns are the synoptic table (syn. Tab.) presenting the constancy (in %) and fidelity (phi value × 100) of the species in each association.

Class	***Didymophyso aucheri-Dracocephaletea aucheri* Noroozi et al. 2014**																			**Syn. Tab.**	
Alliance	***Galion pseudokurdici* all. nov.**																			**Constancy (Fidelity)**	
Association	**Ass. 1 *Aethionemetum umbellati* ass. nov.**										**Ass. 2 *Zerdanetum anchonioidis* ass. nov.**									**1**	**2**
Relevé Nr.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
Elevation (m)	4084	4084	4094	4103	4106	4280	4278	4291	4249	4013	4280	4226	4218	4190	4189	4171	4164	4165	4162		
Aspect	SW	SW	SW	SW	SW	SW	SW	S	NE	S	NE	N	N	NE	NE	NE	E	NE	N		
Slope (°)	35	35	35	35	40	30	30	30	25	40	30	15	20	30	10	25	15	15	10		
Vegetation cover%	15	20	15	15	10	10	5	2	15	20	15	10	10	25	15	15	20	20	35		
Scree%	85	80	85	80	90	90	90	90	85	80	70	40	30	60	70	35	80	70	40		
Soil%	-	-	-	-	-	-	5	5	-	-	15	-	-	10	5	-	-	-	10		
Rock%	-	-	-	5	-	-	-	-	-	-	-	50	60	5	10	50	-	10	15		
Species richness	8	11	8	7	6	6	3	3	7	9	6	9	10	4	6	11	10	6	9		
Aethionema umbellatum		+	+			+	+	+		+										60 (66)	
Nepeta lasiocephala			+	1	1	1	1	2	1	1										80 (82)	
Silene daenensis	+	+	+	+	+				+	2							+			70 (60)	11
Zerdana anchonioides												1	1		+	1		+			56 (62)
Erigeron daenensis												+	+			+					33 (45)
Myopordon persicum															2			1			22 (35)
Astragalus zerdanus											+		+						+		33 (45)
Veronica kurdica subsp. *filicaulis*												+	+								22 (35)
Arenaria persica																1	2		2		33 (45)
Piptatherum laterale									1			1	+	1	+	+	1		+	10	78 (68)
Bromus frigidus	1	1	2	+	+	1			2		1	+	1	+		+	+		2	70	78 (9)
Galium pseudokurdicum	2	2	1	1	1	+	+		1	1		1	1	1		1	+	+		90 (28)	67
Astragalus melanodon	1	2								2	1						+	1	+	30	44 (15)
Stachys obtusicrena	+		+												1		+	+		20	33 (15)
Physoptychis gnaphalodes	+	+			1					2			+	2	1	1	2	2	1	40	78 (38)
Elymus longearistatus	+	1	1	2	1			+	1	2					+		+			80 (58)	22
Euphorbia aucheri		+	1	+						1										40 (50)	
Psychrogeton amorphoglossus				+								+				+				10	22 (17)
Potentilla flaccida						+			+										+	20 (12)	11
Dielsiocharis kotschyi												+				+					22 (35)
Scrophularia subaphylla																+					11 (24)
Arnebia euchroma																	+				11 (24)
Crepis heterotricha											2										11 (24)
Chenopodium foliosum		+																		10 (23)	
Draba aucheri													r						+		22 (35)
Gagea cf. *alexeenkoana*						+													1	10	11 (2)
Arenaria minutissima																+					11 (24)
Onobrychis cornuta												+	+								22 (35)
Polygonum serpyllaceum		+									1									10	11 (2)
Pseudocamelina aphragmodes										1										10 (23)	
Rubia pauciflora											+										11 (24)
Scutellaria multicaulis		+																		10 (23)	
Acantholimon tomentellum	+																			10 (23)	

be found in similar habitats of Zagros as a whole and of the Yazd-Kerman mountains.

This alliance fits well under the class *Didymophyso aucheri-Dracocephaletea aucheri* Noroozi et al. 2014 (Tables 3, 4). This class was described from the high alpine and subnival scree vegetation types of Alborz and mountains of NW Iran, together with two orders and three alliances (Table 4): *Didymophysetalia aucheri* (with one alliance, *Didymophysion aucheri*) and *Physoptychio gnaphalodis-Brometalia tomentosi* (with two alliances, *Erigerontion venusti* and *Elymo longearistati-Astragalion macrosemii*). Additional data and studies from other parts of the Zagros and Yazd-Kerman mountains are needed to clarify if our newly described alliance belongs to one of the mentioned orders, or if a new order should be described. Ecological characters like elevational range, steepness, the composition of soil, screes and stones, and also physiognomy of the communities and species richness in the new alliance are closer to *Didymophysion aucheri* from Central Alborz (see Noroozi et al. 2014).

***Aethionemetum umbellati* ass. nov.** (Figure 9; Table 3)

Type relevé (holotypus hoc loco): Table 3, relevé 10

Character species: *Aethionema umbellatum* (Figure 9A), *Nepeta lasiocephala* (Figure 9B), *Silene daenensis* (Figure 9C).

Differential species: *Euphorbia aucheri* (Figure 5C).

This unit can be found on steep slopes (with an average inclination of 33°, and a range of 24–40°) that are mostly south- to west-exposed. The ground is mostly covered

Table 4. Synoptic table of the scree communities in N Iran and Dena Mts. Values are percentage constancies. The constancy values of character species of syntaxa are shaded, and the constancy values of character species of the class present in the newly described alliance are given in bold.

Mountains	**Alborz and NW Iran**			**Dena**
Alliance number	**All1**	**All2**	**All3**	**All4**
Number of relevés	23	69	63	19
***Didymophysion aucheri* (All1)**				
Achillea aucheri	39	.	2	.
Veronica aucheri	26	.	2	.
Galium aucheri	52	.	.	.
Veronica paederotae	30	.	.	.
Senecio vulcanicus	22	.	.	.
Erysimum elbrusense	30	.	5	.
Cerastium purpurascens	39	.	5	.
***Erigerontion venusti* (All2)**				
Draba bruniifolia	.	29	.	.
Alopecurus aucheri	.	22	.	.
Nepeta menthoides	.	25	.	.
Tripleurospermum caucasicum	.	33	.	.
Sesleria phleoides	.	22	.	.
Galium hyrcanicum	.	41	.	.
Erigeron caucasicus	.	62	.	.
Pedicularis caucasica	.	25	.	.
Minuartia glandulosa	.	26	.	.
Koeleria eriostachya	.	38	.	.
Festuca alaica	4	75	3	.
***Elymo longearistati-Astragalion macrosemii* (All3)**				
Nepeta racemosa	.	.	24	.
Astragalus macrosemius	.	.	57	.
***Galion pseudokurdici* all. nov. (All4)**				
Bromus frigidus	.	.	.	74
Galium pseudokurdicum	.	.	.	79
Astragalus melanodon	.	.	.	37
Stachys obtusicrena	.	.	.	26
Didymophyso-Dracocephaletea				
Physoptychis gnaphalodes	**1**	**16**	**17**	**58**
Euphorbia aucheri	**4**	**.**	**24**	**21**
Elymus longearistatus	**.**	**.**	**60**	**53**
Didymophysa aucheri	96	32	.	.
Dracocephalum aucheri	48	35	32	.
Bromus tomentosus	13	70	78	.
Alopecurus textilis	22	32	.	.
Asperula glomerata	30	.	40	.
Ziziphora clinopodioides	.	49	25	.
Poa araratica	4	49	37	.
Helichrysum psychrophilum	4	32	8	.

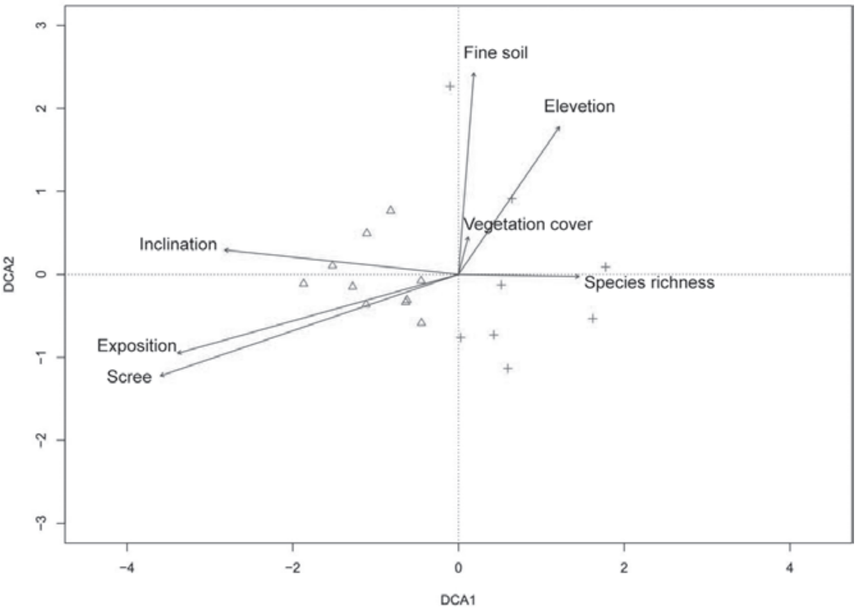

Figure 8. DCA ordination of the plots with environmental variables and vegetation features. *Aethionemetum umbellati* (triangle), *Zerdanetum anchonioidis* (square).

by scree and gravel (ca. 85%) and the vegetation cover is accordingly sparse (ca. 13%). The species richness of this association ranges from three to 11 (on average seven) species per relevé. This association is endemic to Dena Mts. *Aethionema umbellatum* and *Nepeta lasiocephala* are local endemics, whereas *Silene daenensis* is an endemic of the Zagros mountain range.

Zerdanetum anchonioidis **ass. nov.** (Figure 10; Table 3)

Type relevé (holotypus hoc loco): Table 3, relevé 13

Character species: *Astragalus zerdanus* (Figure 10A), *Erigeron daenensis* (Figure 10B), *Myopordon persicum* (Figure 10C), *Veronica kurdica* subsp. *filicaulis*, *Zerdana anchonioides* (=*Sterigmostemum anchonioides*; Figure 10D).

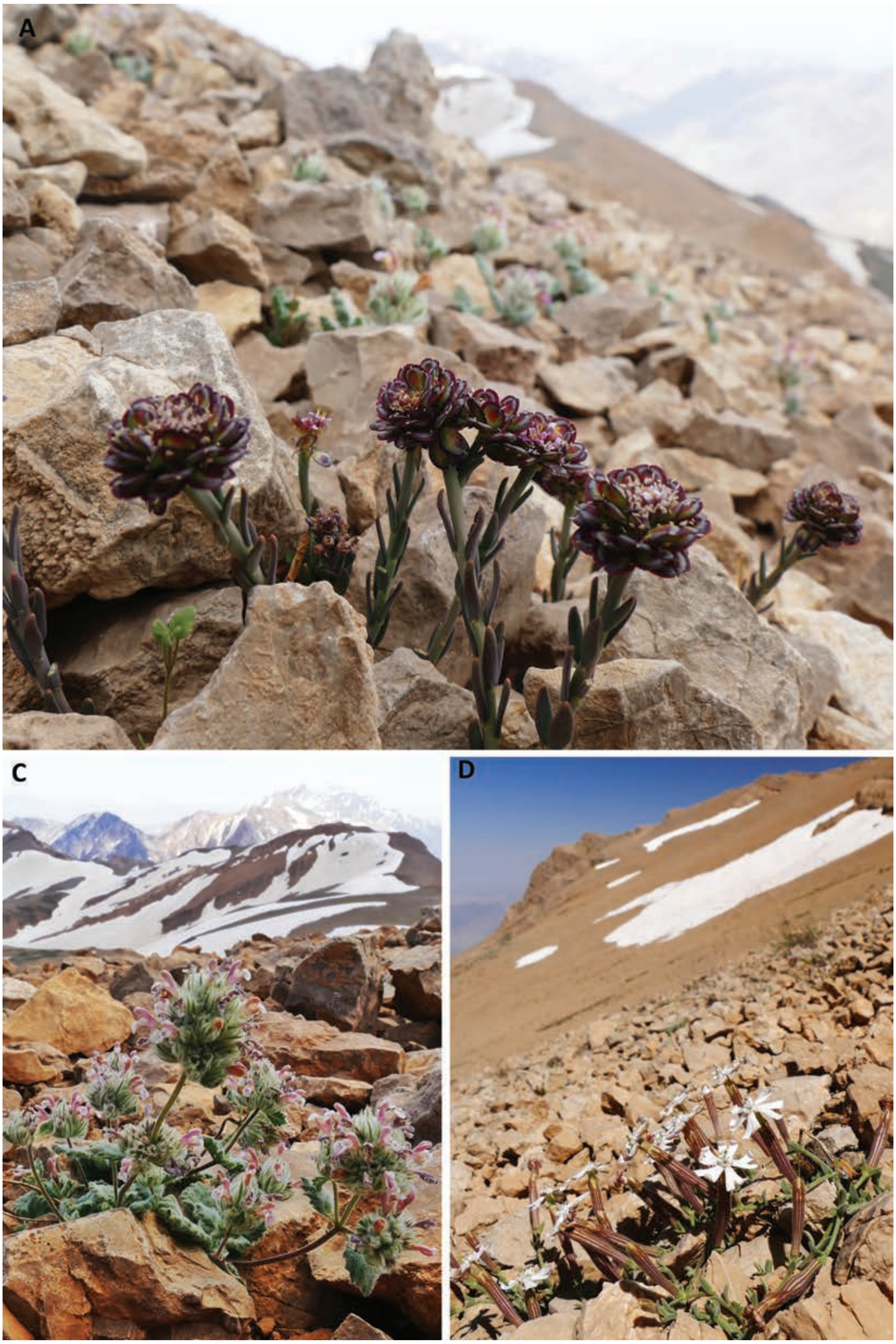

Figure 9. New association *Aethionemetum umbellati* and its character species. **A)** *Aethionema umbellatum* (4200 m a.s.l.). **B)** *Nepeta lasiocephala* (4300 m a.s.l.). **C)** *Silene daenensis* (4200 m a.s.l.).

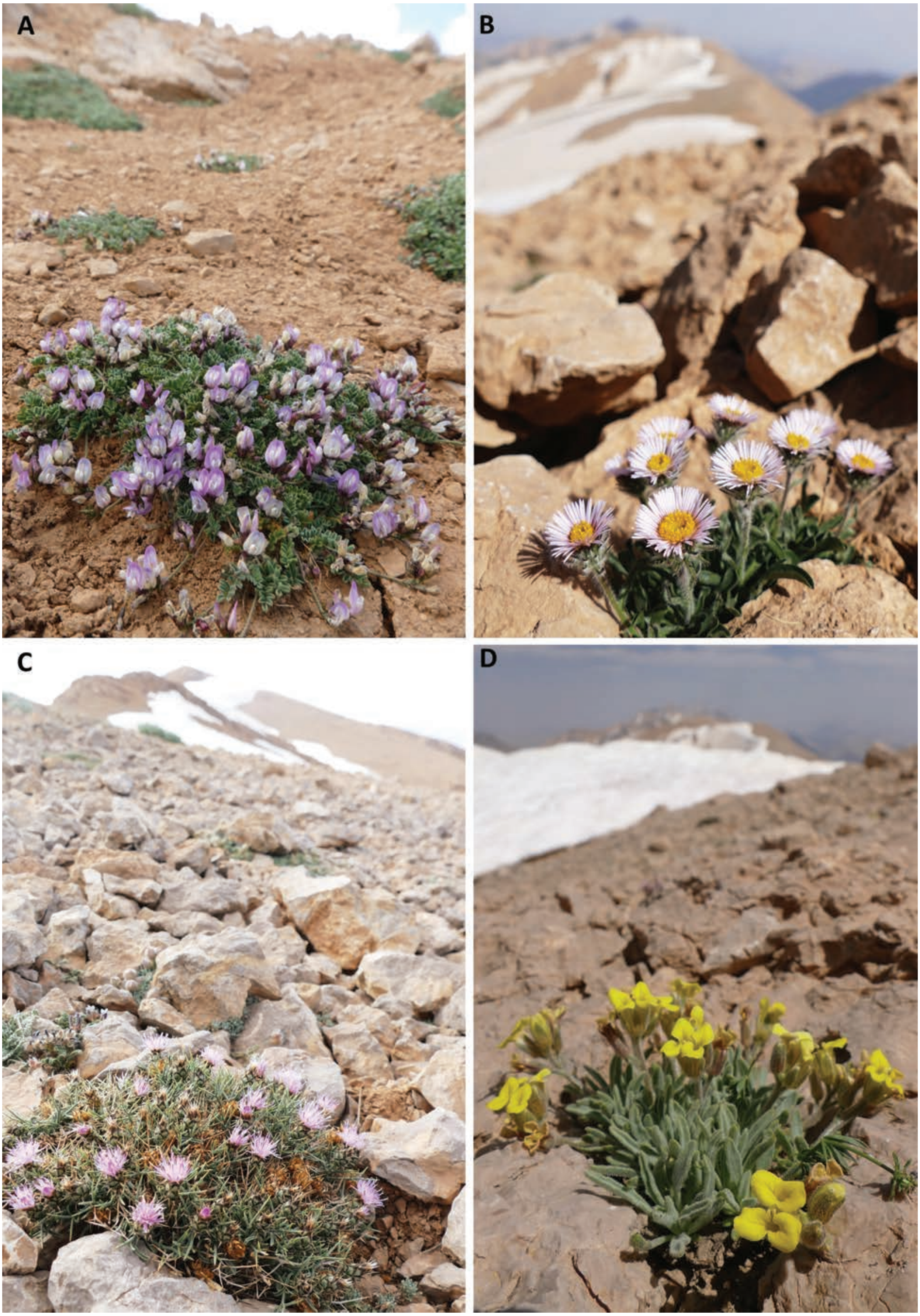

Figure 10. New association *Zerdanetum anchonioidis* and its character species. **A)** *Astragalus zerdanus* (4150 m a.s.l.). **B)** *Erigeron daenensis* (4250 m a.s.l.). **C)** *Myopordon persicum* (4200 m a.s.l.). **D)** *Zerdana anchonioides* (4300 m a.s.l.).

Differential species: *Arenaria persica*, *Piptatherum laterale*.

This unit is mostly found on north- to north-eastern-exposed slopes with an average inclination of ca. 20° (range from 10 to 30°). This association occurs on stony and scree grounds with, compared to the previous community, a lower proportion of scree (ca. 55%) and a higher proportion of rocks (on average 28%) and open soil (ca. 10%). The average vegetation cover of the association is ca. 20% and species richness ranges from four to 11 (average of eight) species per relevé. *Zerdana anchonioides* is an endemic of Southern Zagros and the Yazd-Kerman mountain range. *Astragalus zerdanus*, *Erigeron daenensis* and *Myopordon persicum* are endemic elements of Zagros. *Veronica kurdica* subsp. *filicaulis* is an endemic taxon of Zagros and Yazd-Kerman. Based on the distribution of the characteristic species, the geographic extent of this association is expected to cover the subnival zone of Southern and Central Zagros.

Conservation concerns

Dena Mts harbor a high amount of endemic species. Although the number of endemic species is also high in mid-elevational belts, the proportion of endemics increases with increasing elevation. Consequently, our newly described communities of the subnival zone harbor a high number of range-restricted species. Shrinking of alpine and subnival habitats and the loss of cold-adapted species of the high mountains have been recorded, and also have been predicted in biodiversity scenarios for the 21st century as the result of a general upward shift of plant species under a warmer climate (Chen et al. 2011; Engler et al. 2011; Pauli et al. 2012). The subnival zone, with a very high proportion of endemic and range-restricted species in South-West Asia (Noroozi et al. 2011; Noroozi et al. 2019b), may be the most fragile habitat under the impact of ongoing climate change due to the absence of alternative habitats for the cold-adapted species to move into. Therefore, subnival species of Dena Mts, which are already restricted to habitats near the summits of the mountain range (in a narrow elevation belt above 4100 m a.s.l. with small area size), are at high risk of population size reduction or even extinction. Moreover, like other high mountains of Iran, overgrazing is a big problem for the natural vegetation types of the high mountains. Most of the big herds of the lowlands and montane zone move to the high elevations in summertime and concentrate in small areas of alpine habitats. Usually, the size of the herds exceed the capacity of these vegetation types, and the natural species composition and range-restricted species are highly endangered (Noroozi et al. 2008; Bagheri et al. 2022). Dena Mts have the highest summit of the entire Zagros and are attractive for mountaineering and tourism. Although Dena Mts lie within a protected area, this will not prevent shrinking of alpine habitats due to the ongoing global warming, or degradation of these ecosystems due to overgrazing or tourism. Consequently, strong attention to increase the efficiency of the protection and to reduce other anthopogenic activities in high elevations of this mountain system in particular and of the entire South-West Asian mountains in general is highly recommended.

Data availability

All data are presented in the paper.

Author contributions

J.N. planned the research, conducted the field sampling, identified the species, and analyzed the data, A.T. identified the species and contributed to data analyzing, M.S. contributed to fieldwork and data collection, and G.M.S. contributed to writing and editing. All authors have read and agreed to the published version of the manuscript.

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RESEARCH PAPER NEOTROPICAL VEGETATION

Plant communities of high-Andean *bofedal* wetlands across a trans-Andean transect in southern Peru

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Abstract

Aims: Ecosystems of the Tropical Andes include plant communities above 4,000 m in elevation, associated with wetlands known as *bofedales*. To enhance our understanding of them, we surveyed *bofedal* plant communities in the Peruvian Andes. **Questions:** Which are the most common *bofedal* plant communities, and what are their main characteristics? **Study area:** An east-to-west 68 km megatransect in Ayacucho and Huancavelica departments in Peru, the area of influence of a gas pipeline. **Methods:** We surveyed 127 (1 m × 1 m) permanent plots annually between 2017 and 2019 to assess plant communities, calculated diversity metrics, and applied non-parametric hypothesis testing analysis of similarities and multivariate analyses to the data. **Results:** We identified 13 plant communities with 3.5 to 11.7 mean species richness. Only seven were statistically different; the other six were rare and require additional surveys to define their status as independent communities. The *Distichia muscoides*-dominated community was found in most sites (90%), plots (55%), and along the entire elevational range we studied. *D. muscoides*, *Plantago tubulosa*, and *Rockhausenia pygmaea* were the most frequent species in the studied *bofedales* (in 30 of 31 sites). These species are usually cushion or carpet forming, so average plant cover was high in most plant communities where they occurred (89–98%). The seven plant communities (dominated by *D. muscoides*, *R. pygmaea*, *Plantago tubulosa*, *P. rigida*, *Lachemilla diplophylla*, *Aciachne pulvinata* and *Juncus stipulatus*) were consistent in their structural and compositional characteristics and maintained differences between them during our three-year study. **Conclusions:** We show that *bofedal* plant communities in the southern Peruvian Andes are more heterogeneous than the four broad types previously reported. This heterogeneity occurs at local site levels but also at landscape and regional scales. We highlight the importance of considering this heterogeneity when discussing and implementing management, restoration, and conservation actions in *bofedales*.

Taxonomic reference: WFO (2024)

Keywords

Alpine vegetation, Andes, *bofedal*, diversity, peatland, Peru, wetland

Introduction

The tropical Andes, a global biodiversity hotspot, contain diverse ecosystems and habitats (Young et al. 2007). A major factor contributing to this diversity is the east–west humidity gradient in the Central Andes, reflected in the differentiation of the humid Puna towards the eastern flanks and the dry Puna (Josse et al. 2009) facing the Pacific slopes (Killeen et al. 2007; Espinoza et al. 2015).

Within this gradient, the Central Andes contain plant communities above 4,000 m a.s.l. which are associated with wetlands and water-saturated soils. These communities are known by several local names ("turbera" in Colombia and Ecuador; *bofedal* in Ecuador, Peru and Bolivia, "vegas" or "mallines" in Chile and Argentina, Hergoualc'h et al. 2022). These wetlands are patchy and island-like in nature and are usually surrounded by large swards of grasslands and drylands. At the local level, they have a consistent and characteristic set of plant species, but at regional levels, plant abundances and composition are influenced by environmental factors such as elevation, topography, hydrology, geology, and wildlife grazing (Ruthsatz 2012; Valencia et al. 2013; Salvador et al. 2014; Oropeza 2019; Portal-Quicaña 2019; Izquierdo et al. 2020; Domic et al. 2021; Monge-Salazar et al. 2022). In addition to these natural factors, human uses of the *bofedales* (e.g., grazing areas for native and introduced livestock, water use, peat extraction) have also been deemed important in influencing their ecological processes and plant community composition (Ruthsatz 2012; Maldonado-Fonkén 2014; Chimner et al. 2019; Yager et al. 2019; Navarro et al. 2023).

According to the National Institute for Research on Glaciers and Mountain Ecosystems (INAIGEM), the *bofedales* in Peru include four major types of plant formations, named after the life-form(s) of the dominant and most conspicuous species: cushions (formed by e.g. *Distichia muscoides*, *Oxychloe andina*, *Plantago rigida*), carpets (e.g. *Plantago tubulosa*, *Rockhausenia pygmaea*), grasses and graminoids (e.g. *Festuca* spp., *Calamagrostis* spp., *Carex* spp., *Eleocharis* spp., *Phylloscirpus* spp.), and mosses and shrub wetlands (formed by e.g. *Sphagnum* spp., *Andicolea* spp.). *Bofedales* dominated by cushions are the most frequent type, especially in central and southern Peru. INAIGEM highlighted the heterogeneity of these ecosystems at vegetation and hydrological levels. Still, little information is available on grass- and graminoid-dominated and carpet *bofedales*, as well as on *bofedales* subjected to strong seasonal water availability (saturated only in the rainy season; INAIGEM 2023).

The INAIGEM classification, the first of its kind at national level, is based on previously published information for *bofedales* vegetation in Peru (Cooper et al. 2010; Ruthsatz 2012; Maldonado-Fonkén 2014; Salvador et al. 2014; Maldonado-Fonkén 2018; Polk et al. 2019; Portal-Quicaña 2019), expert consultations and ongoing studies. Similar plant formations have been described for Colombia, Ecuador, Bolivia, and Argentina (Ruthsatz 2012; Benavides and Vitt 2014; Loza Herrera et al. 2015; Ruthsatz et al. 2020; Domic et al. 2021; Izquierdo et al. 2022; Suarez et al. 2022). Several plant communities or even mixed communities within a single site have also been reported (Ruthsatz 2012; Maldonado-Fonkén 2014). Nevertheless, most of these studies focused on the dominant species and physiognomy of the plant communities, so a more comprehensive description is needed.

Within the framework of the Biodiversity Monitoring and Assessment Program (BMAP), a collaboration between the Smithsonian Institution and the PERU LNG company set in the southern Andes of Peru (Dallmeier et al. 2013), we studied the vegetation of the high-Andean wetlands along an east to west 68 km-long megatransect from Ayacucho to Huancavelica departments.

This contribution aims to identify and characterize the most common *bofedal* plant communities along the megatransect. In doing so, we attempt to answer the following guiding questions: Is *Distichia muscoides* the only dominant species, as commonly treated? How do patterns of diversity, structure, and composition of plant communities change along the megatransect? Are the diversity and vegetation cover values high or low compared with other reports? Can selected environmental factors, such as soil moisture and water table depth, explain floristic and plant community patterns?

Study area

Our study area corresponds to the area of influence of the PERU LNG pipeline (LNG: liquified natural gas, Figure 1, Table 1), encompassing a variety of habitats between 4,200 and 4,900 m a.s.l. along 68 km from the southwest to the northeast of the Central Andes, in the departments of Ayacucho and Huancavelica in Peru. Precipitation follows a seasonal pattern, with 60–90% of total rainfall between December and March (Langstroth et al. 2013). For the evaluation sites the total annual precipitation values according to PISCO (Peruvian Interpolated data of SENAMHI's Climatological and hydrological Observations), range from 480 mm to 817 mm, with site KP 164 + 500 reaching 1232 mm (Aybar et al. 2019). Average monthly precipitation in the dry season (June–August) ranges from 3.3 to 12.2 mm, and in the wet season (January–March) from 107 to 130 mm (Aybar et al. 2019). Mean air temperatures range from 9.7 °C to 19.7 °C, with minimum temperatures reaching values below 0 °C at night (Valencia et al. 2013). The study area overlaps with several rural Andean communities, where traditional husbandry of alpacas, lamas, and sheep (introduced) is common.

Methods

We surveyed plant communities of 31 *bofedales* along our study transect, located between 4,265 and 4,855 m a.s.l. According to previous studies using satellite images (PERU LNG, not published), *bofedales* were reported to have sizes between 1.25 and 43.98 ha, although we observed sites smaller than 1 ha in the field. We did the assessments annually during the austral dry season (June–July) from 2017 to 2019. In 2017, we set up randomly

Table 1. *Bofedal* study sites in the southern Peruvian Andes.

No.	Site ID	UTM Coordinates (WGS84, 18L)		Elevation (m a.s.l.)	Number of plots	Monitoring wells
		E	N			
1	132+850	-74.50292135	-13.28192729	4,301–4,304	4	-
2	138+000	-74.54629416	-13.28596879	4,573–4,575	5	1
3	140+880	-74.57035634	-13.29443795	4,566–4,581	3	1
4	145+340	-74.60595285	-13.30802288	4,665–4,668	3	-
5	147+308	-74.62303259	-13.30278615	4,687–4,699	4	1
6	149+270	-74.63785065	-13.29687591	4,707–4,716	6	
7	150+800	-74.64953935	-13.29020998	4,489–4,507	4	-
8	152+800	-74.66311571	-13.27994714	4,528–4,537	6	-
9	153+000	-74.66438133	-13.27932488	4,537–4,561	2	1
10	153+170	-74.6658498	-13.27888374	4,594–4,605	2	-
11	154+099	-74.67328382	-13.27710299	4,660–4,666	3	-
12	154+372	-74.67505366	-13.27911266	4,647–4,648	3	-
13	154+700	-74.67834744	-13.28062693	4,672–4,673	4	-
14	158+470	-74.70899211	-13.29287104	4,818–4,826	7	-
15	162+365	-74.74256575	-13.29731089	4,848–4,850	3	1
16	163+760	-74.75422408	-13.29975484	4,798–4,802	3	-
17	164+250	-74.75856181	-13.30140472	4,745–4,758	4	-
18	164+700	-74.76191007	-13.30472645	4,727–4,735	4	1
19	165+500	-74.7673449	-13.3082309	4,801–4,810	3	-
20	167+640	-74.78545257	-13.30631175	4,825–4,829	4	-
21	168+250	-74.78972555	-13.30850359	4,777–4,778	4	-
22	168+500	-74.7918393	-13.30922873	4,745–4,752	3	-
23	168+750	-74.79468335	-13.30891456	4,715–4,718	3	-
24	170+100	-74.80589219	-13.309059	4,686–4,687	5	-
25	171+100	-74.81293477	-13.31202117	4,721–4,726	4	-
26	195+500*	-74.98609111	-13.37539601	4,531–4,547	5	1
27	198+000	-74.98406711	-13.39648287	4,596–4,605	5	2
28	4SI	-74.52708698	-13.28360093	4,265–4,299	6	-
29	6SIad	-74.76143284	-13.30177817	4,722–4,728	4	1
30	6SI	-74.75980718	-13.3024729	4,733–4,736	5	2
31	NC12	-74.79573822	-13.30617555	4,661–4,666	6	1

*: this was the only site with a rock fence.

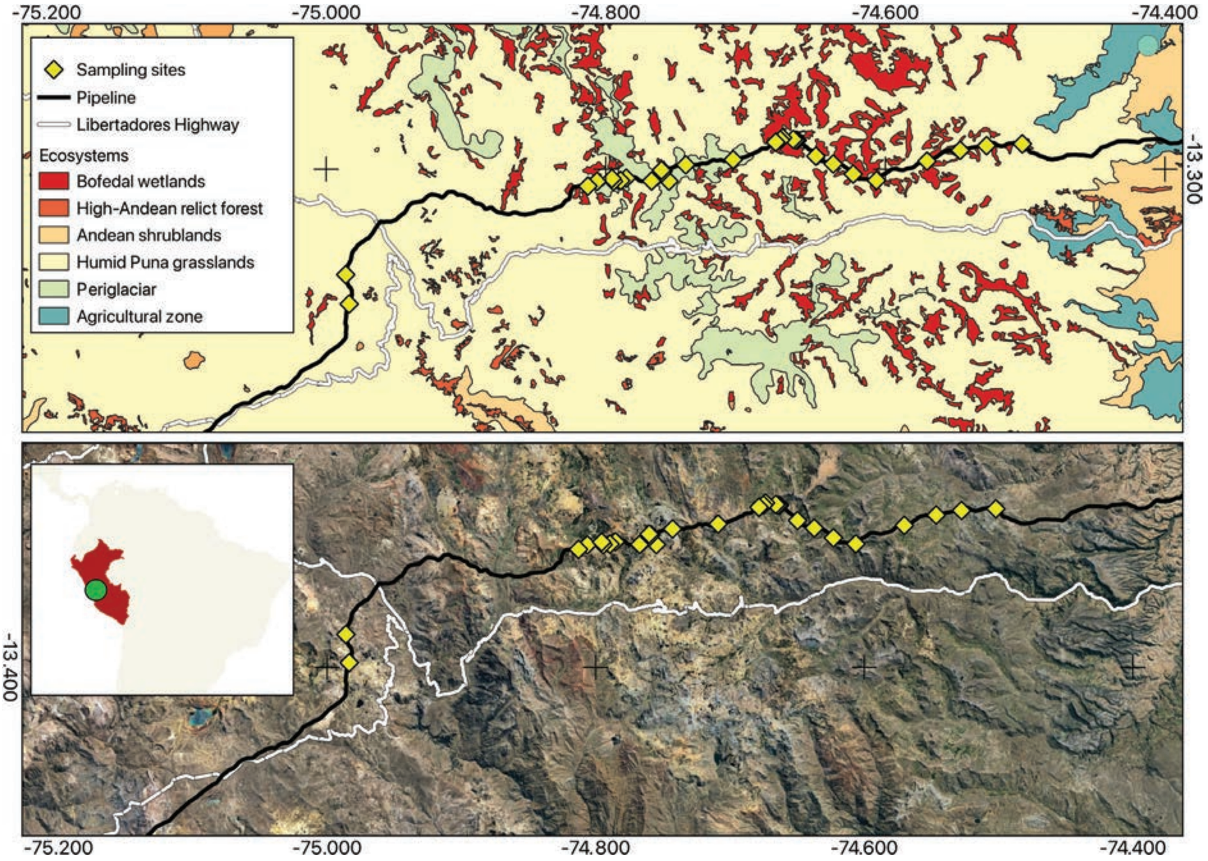

Figure 1. Location of *bofedales* and main ecosystems in the study area. The map inset shows the position of Peru within South America and the approximate study area, indicated by a green dot. The ecosystems shapefiles used are from Peru's Ecosystem Map (MINAM 2019).

distributed 1 m × 1 m permanent plots in homogeneous patches of the dominant vegetation to characterize the plant communities in each *bofedal*. Per *bofedal*, we surveyed between two and seven plots (Table 1). The number was established considering the surface area of the *bofedal*, its heterogeneity (different plant communities), and the resources available for research. 378 plots were surveyed in the three years, 127 in 2017 and 2019, and 124 in 2018 (the missing plots could not be relocated).

We surveyed plant cover (per species) and ground cover with the point intercept method using a grid quadrat frame (Bonham 2013), considering 100 points (crossing points of the thread from the quadrat) per plot. The percentage cover for each species will equal the number of points in which the species was recorded. In subsequent years, we returned to each plot using coordinates and photographs (Suppl. material 1) and recorded the same plot area during each survey (Suppl. material 2; Linares-Palomino and Maldonado-Fonkén 2023).

We recorded cover estimates of several strata (ground cover) as useful proxies of degradation and potential habitat preferences of plant communities and species. We used the following categories: vegetation (vascular plants), moss, bare soil (or peat), dead vegetation, wildlife and livestock dung, rock, and water.

We used information on soil moisture and water table depth from the BMAP. We measured soil moisture (only in 2017) in 71 plots (2–3 records per plot) of ten plant communities (Table 2), with a ML3 ThetaProbe Soil Moisture Sensor from Delta-T Devices (UK), configured for organic soils. The water table monitoring wells were located at 11 sites (Table 1) and in six plant communities (Table 2). Using a peat sampler from Royal Ejelkamp (The Netherlands) we made a 50.8 mm diameter hole, where we inserted a PVC tube of the same size. Water table measurements were taken between July 2017 and December 2019, every one or two months in the first two years, and only in January and December of the last year. The number of sites, plots, soil moisture measurements, and monitoring wells per plant community are presented in Table 2.

We collated a list of species and morphospecies based on field collections and surveys done by the BMAP since 2009 (Valencia et al. 2013). We followed APG IV (The Angiosperm Phylogeny Group et al. 2016), and scientific names and authorship followed The World Flora Online (WFO 2024). Species were primarily identified in the field by a team of experienced *bofedal* botanists and ecologists (MM, HC). However, when plant material was fragmentary and/or lacked fertile structures, we collected and photographed samples and checked them against specialized literature (Tovar 1993; Gonzáles 2015; Sylvester et al. 2016) or referred them to specialists. We used the morphospecies concept on collections that were difficult to identify at the species level but otherwise had morphological characters that unequivocally differed from all the other material already identified in the area.

Since *bofedal* communities are associated with water-logged conditions, some species thrive in moist or saturated soils (hydrophytes and others). These were defined as moisture indicators (Suppl. material 3) based on our field observations and literature (Kahn et al. 1993; Tovar 1993; Gonzáles 2015; Meneses et al. 2015).

Data analyses

To determine whether plant communities differed in composition and abundance (cover), we performed a one-way Analysis of Similarities (ANOSIM) on a plot × species matrix using the Bray-Curtis index (Bray and Curtis 1957) with PAST 4.12b (Hammer et al. 2001). We identified the species with the highest cover and the most frequent companion species for each plant community. To further describe each community, we calculated their species richness, Pielou's evenness (Pielou 1966) and estimated the percentage of each ground cover type per community.

We used a non-parametric Analysis of Variance with the Kruskal-Wallis test (Kruskal and Wallis 1952) with InfoStat version 2019 (Di Rienzo et al. 2019), to identify significant statistical differences ($p < 0.050$) in richness, evenness, vegetation cover, cover of moisture indicators, soil moisture and water table depth between plant communities.

We applied a Hellinger transformation on the raw plant cover values of a plot × species matrix across years (2017–2019) to visualize the variability in species composition and abundance through non-metric multidimensional

Table 2. Number of sampling units per plant community: vegetation, soil moisture, and monitoring wells. 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2. Soil moisture measurements were done with the vegetation assessment in 2017. Water table measurements (monitoring wells) were taken in five months of 2017 (July, September, October, November, and December), four in 2018 (February, May, July, and September), and two in 2019 (January and December).

Number of		**Plant communities**													**Total**
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	
Sites		28	13	8	7	5	1	1	1	1	1	1	1	1	**31**
Vegetation plots per year	2017	69	23	10	9	6	2	2	1	1	1	1	1	1	**127**
	2018	69	22	10	9	5	2	1	1	1	1	1	1	1	**124**
	2019	69	23	10	9	6	2	2	1	1	1	1	1	1	**127**
Soil moisture (2017)	n	121	38	18	6	6	6	6	-	3	3	-	3	-	**210**
	plots	41	13	6	2	2	2	2	-	1	1	-	1	-	**71**
Monitoring wells (2017–2019)	n	5	4	2	-	-	1	-	-	-	-	-	-	1	**13**
	N° sites	4	3	2		-	1	-	-	-	-	-	-	1	**11**

scaling (NMDS) using a dissimilarity matrix of Bray-Curtis distances (Legendre and Gallagher 2001). We complemented the characterization of the plant communities by calculating and plotting sample-based rarefaction curves based on Hill numbers (q = 0, species richness) using incidence data (frequency) from the complete species pool of each surveyed plot (combined data from 2017–2019). We then used a Principal Component Analysis (PCA) to explore how the identified communities were distributed according to five community descriptors: plant cover, bare soil, species richness, Pielou's evenness, and cover of moisture indicators. To perform the PCA, we calculated the mean value of those descriptors for each plant community in a given year. We used the "vegan" package (Oksanen et al. 2022) for both the NMDS and PCA analyses, and the "iNEXT" package for rarefaction curves (Hsieh et al. 2016).

Results

Bofedal plant communities in southern Andean Peru

Based on the species' dominance (i.e. plant cover) and compositional patterns, we identified 13 plant communities (Figure 2) with mean species richness between 3.5 to 11.7 (Table 3). In most cases, they have one clearly dominant species (mean cover 40–70%, Figure 3), but two were mixed communities in which at least two species shared dominance (each species with cover values of 10–22%). Seven of these communities (Group 1) differed statistically (ANOSIM, Bray-Curtis, $p < 0.050$, Table 4, Suppl. material 4). The other six communities (Group 2) were rare (one plot per year each) and did not have statistical

Table 3. General characteristics of *bofedal* plant communities in the southern Peruvian Andes. $^{+}$: Mean; *Other ground cover categories reached more than 10% in two communities. *Aciachne pulvinata* (dead vegetation: 11.33±4.03) and Mixed community 2 (bare soil 33±12.7%). **Total richness is correlated with sampling effort (Table 2). Water table measurements are negative. 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2.

		Plant communities												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Environmental variables														
Elevation (m)		4,292–4,850	4,299–4,798	4,374–4,726	4,265–4,801	4,284–4,718	4,722–4,733	4,531–4,533	4277	4749	4826	4301	4825	4850
Soil moisture (%)$^{+}$		79.1±1.9	62.6±2.6	55.3±4.8	100	68.6±12.9	63.9±6.1	76±7.9	-	45.1±15.2	100	-	19.7±0.9	-
Water table (cm)	Mean	8.6±3.3	30.9±5.1	43.4±9.9	-	-	47.6±12.8	-	-	-	-		-	19±10.4
	Max	87	95	200	-	-	140	-	-	-	-		-	94
Other characteristics														
Vegetation cover (%)$^{+}$		95.2±0.5	93.7±0.6	92.2±1.6	91.7±1.4	93.6±1.2	74.8±8.1*	91.4±4.7	98±1	89±1	95.3±2.2	89.7±3.3	89.3±0.9	66.3±12.1*
Cover of moisture indicators (%)$^{+}$		94.1±0.6	92.3±0.7	91.2±1.9	89±1.7	92.8±1.3	72.8±8.9	91.4±4.7	97.3±0.3	89±1	95.3±2.2	88.7±3.7	71.7±7.7	64.7±10.7
Richness per plot	Total**	55	38	20	32	26	18	10	9	9	11	15	18	13
	Range	1–12	5–15	1–7	5–13	3–12	3–13	6–8	5–6	3–9	5–9	10–11	11–13	6–10
	Mean	6.5±0.2	8.2±0.3	3.6±0.3	8.4±0.4	7.4±0.6	8±1.8	6.8±0.4	5.7±0.3	5.7±1.8	7.3±1.2	10.7±	11.7±0.7	8±1.2
Pielou index		0.53	0.70	0.38	0.69	0.61	0.58	0.75	0.54	0.63	0.76	0.78	0.86	0.71

Table 4. Cover of dominant species (dark grey background) including those with more than 15% in at least one plant community. Plant communities with different superscripts differ significantly (ANOSIM Bray Curtis, $p < 0.05$). Values are mean percentage cover from annual survey data (2017–2019). Plant community names correspond to those of the dominant species: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2.

	Plant community (cover per species in %)												
	1^{a}	2^{b}	3^{c}	4^{d}	5^{e}	6^{f}	7^{gi}	8^{h}	9^{h}	10^{h}	11^{h}	12^{h}	13^{hi}
Dominant species in one or more community													
Aciachne pulvinata	7.0	2.0	3.5	2.1	1.0	44.2	-	-	-	-	-	4.0	2.0
Calamagrostis chrysantha	3.5	-	-	-	-	-	-	-	54.0	-	-	-	-
Calamagrostis rigescens	4.4	4.3	-	6.6	7.0	2.0	17.6	70.3	12.0	-	2.3	1.0	-
Calamagrostis vicunarum	3.2	2.1	7.5	5.1	1.5	3.0	-	-	-	-	-	22.5	-
Distichia filamentosa	-	-	-	-	-	-	-	-	-	40.3	-	-	-
Distichia muscoides	66.2	10.3	1.8	7.8	5.8	4.7	-	-	12.0	-	1.0	9.3	17.0
Eleocharis albibracteata	3.0	8.3	1.0	8.6	8.2	14.0	-	5.0	-	-	15.0	1.0	21.3
Juncus stipulatus	1.6	1.3	-	-	3.7	3.5	40.4	7.0	-	-	4.0	-	-
Lachemilla diplophylla	10.4	5.7	-	13.0	54.4	1.3	11.2	-	7.7	-	3.0	10.3	5.3
Lobelia oligophylla	6.2	3.0	1.0	6.9	7.1	5.0	1.5	1.5	-	-	40.3	-	1.0
Plantago rigida	4.9	4.6	79.4	6.7	-	-	-	-	-	-	-	-	-
Plantago tubulosa	7.0	16.4	2.5	46.3	10.6	3.0	1.7	11.0	5.0	4.0	4.0	10.3	9.0
Rockhausenia pygmaea	3.5	43.6	1.0	8.3	11.2	13.3	2.5	1.0	1.0	6.0	2.0	7.3	2.0
Other species													
Phylloscirpus cf. *acaulis*	3.6	10.2	-	4.0	3.6	1.3	-	-	-	24.0	1.0	-	5.5
Zameioscirpus muticus	9.8	2.0	-	-	-	-	-	-	-	21.7	-	-	-

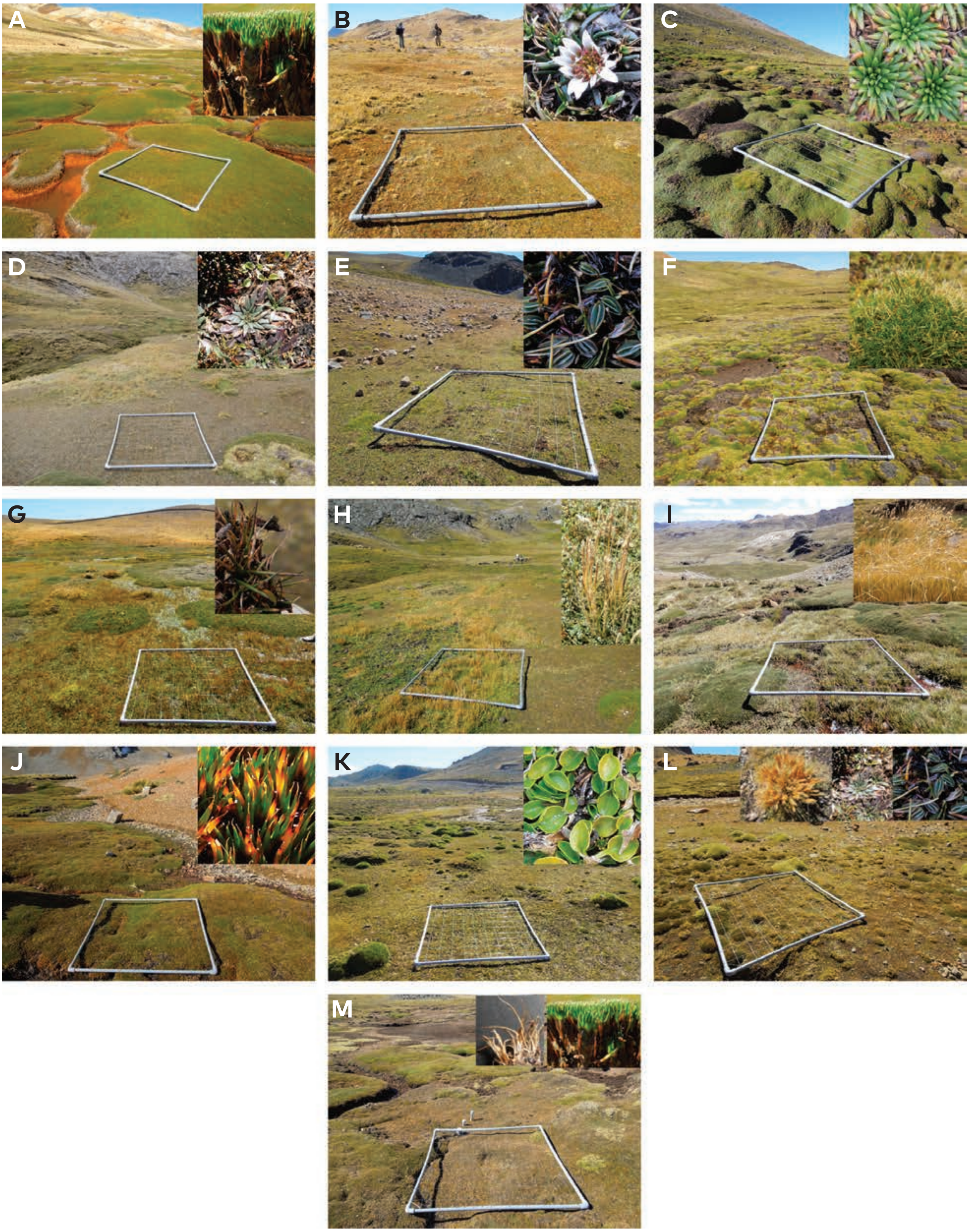

Figure 2. *Bofedal* plant communities in the southern Peruvian Andes. Plant communities: A: *Distichia muscoides*, B: *Rockhausenia pygmaea*, C: *Plantago rigida*, D: *Plantago tubulosa*, E: *Lachemilla diplophylla*, F: *Aciachne pulvinata*, G: *Juncus stipulatus*, H: *Calamagrostis rigescens*, I: *Calamagrostis chrysantha*, J: *Distichia filamentosa*, K: *Lobelia oligophylla*, L: Mixed community 1 (*Calamagrostis vicunarum*, *Plantago tubulosa*, *Lachemilla diplophylla*), M: Mixed community 2 (*Eleocharis albibracteata*, *Distichia muscoides*). The pictures also include the quadrat frame used for the point intercept grid-quadrat method.

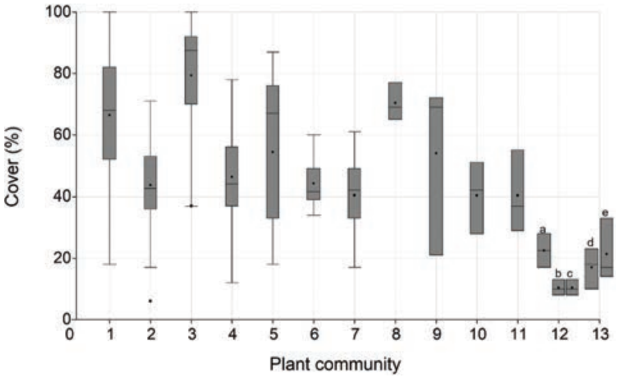

Figure 3. Box plots of the cover of dominant species per plant community. Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1 (a: *Calamagrostis vicunarum*, b: *Lachemilla diplophylla*, c: *Plantago tubulosa*), 13: Mixed community 2 (d: *Distichia muscoides*, e: *Eleocharis albibracteata*).

support (ANOSIM, Bray Curtis $p > 0.050$), sharing similarities with at least five other communities.

Environmental variables (elevation, soil moisture, water table depth) and other characteristics (vegetation cover, cover of moisture indicators, species richness, Pielou index) per community are presented in Table 3 and Figure 4. The cover of dominant species, including those with more than 15% cover in at least one plant community, is presented in Table 4. Frequent companion species are presented in Table 5. Detailed information per plant community, including all the species and their frequencies, is available in Suppl. material 3.

Communities are presented from the most to the least common, according to their frequency in the study area. Plant communities were named after dominant species. The ones outlined below, correspond to the seven well defined communities (Group 1):

1. *Distichia muscoides* community: A cushion-type community usually with pools, high soil moisture values, and a shallow mean water table depth. It was widely distributed in the study area, occurring in the

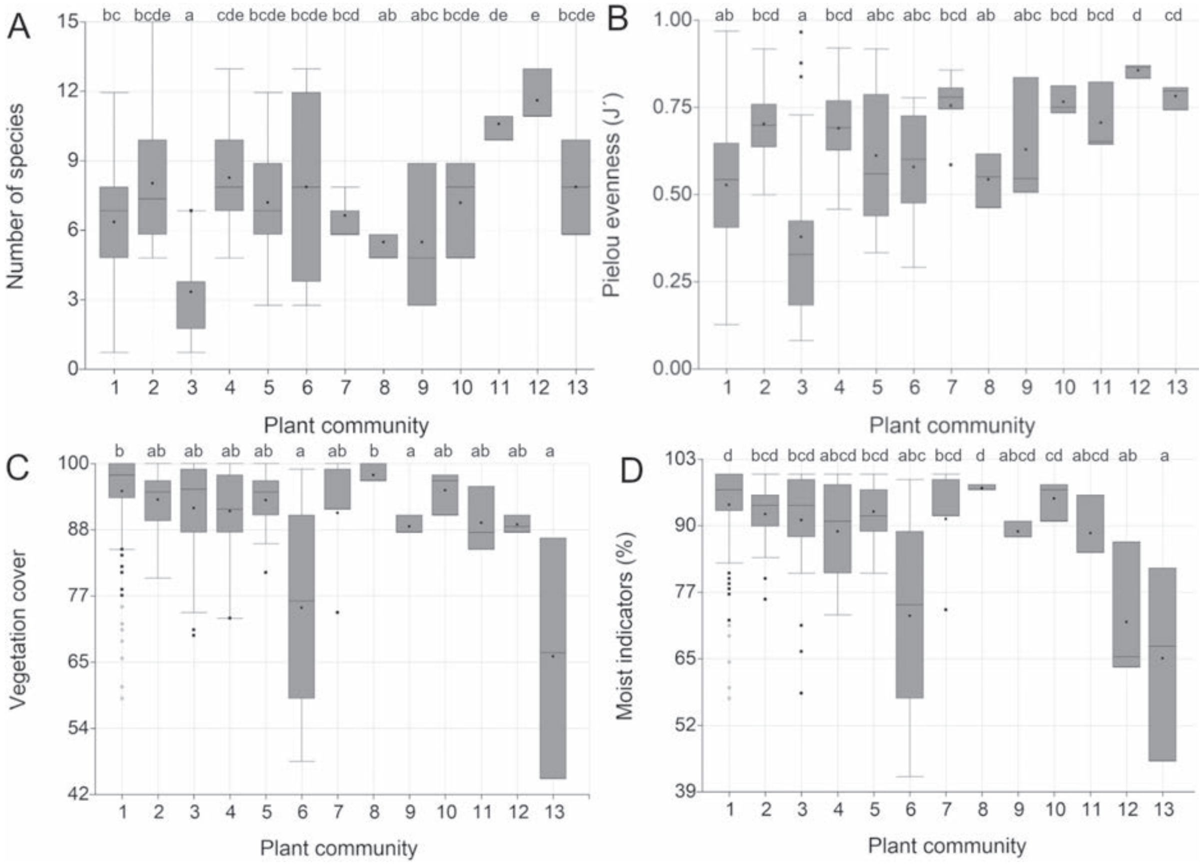

Figure 4. Box plots of A) number of species, B) Pielou's evenness, C) vegetation, and D) moisture indicators cover per square meter in each plant community. Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2. Communities with a common letter are not significantly different (Kruskal Wallis Test, $p > 0.050$). Inside each box, horizontal line and dot represent the median and mean values, respectively.

Table 5. Species with highest frequency (%) per plant community. Includes dominant species (dark grey background) and frequent companions (in bold). Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2.

Species	**Plant community (frequency per species in %)**												
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Aciachne pulvinata	9	22	40	30	12	100	-	-	-	-	-	33	33
Calamagrostis chrysantha	2	-	-	-	-	-	-	-	100	-	-	-	-
Calamagrostis rigescens	22	21	-	30	59	17	**100**	100	67	-	**100**	33	-
Calamagrostis spicigera	30	50	**50**	37	-	-	-	-	-	67	-	67	-
Calamagrostis vicunarum	9	16	13	26	12	50	-	-	-	-	-	67	-
Carex sp.	18	22	10	41	6	33	-	67	-	67	-	**100**	-
Cotula mexicana	5	4	-	19	47	-	**100**	67	33	-	100	-	-
Distichia muscoides	100	56	17	44	29	50	-	-	**100**	-	67	**100**	100
Distichia filamentosa	-	-	-	-	-	-	-	-	-	100	-	-	-
Eleocharis albibracteata	15	**90**	3	**63**	**65**	33	-	67	-	-	**100**	67	100
Hypochaeris taraxacoides	21	53	33	**67**	24	-	-	-	-	-	**100**	-	33
Juncus stipulatus	5	4	-	-	18	33	100	33	-	-	-	-	33
Lachemilla diplophylla	48	66	-	48	100	50	**100**	-	**100**		67	100	**100**
Lilaeopsis macloviana	4	4	-	11	29	33	**100**	-	-	-	-	-	-
Lobelia oligophylla	31	31	7	52	47	**100**	40	67	-	-	100	-	33
Plantago tubulosa	**63**	**97**	13	100	**88**	50	60	**100**	33	33	**100**	100	**100**
Plantago rigida	4	7	100	11.11	-	-	-	-	-	-	-	-	-
Rockhausenia pygmaea	**57**	100	7	**85**	53	50	40	33	33	**100**	67	100	67
Rockhausenia solivifolia	12	6	-	-	-	-	-	-	-	**100**	-	-	-
Zameioscirpus muticus	30	1	-	-	-	-	-	-	-	**100**	-	-	-

largest number of sites, plots, and elevational ranges. Its mean richness per square meter (7) was significantly higher than that of the *Plantago rigida* community (4) but lower than in the *Lobelia oligophylla* (11) and in the Mixed community 1 (12) (Figure 4a). The mean evenness was 0.5 (Figure 4b). It had one of the highest vegetation (95%, Figure 4c) and moisture indicators cover values (94%, Figure 4d).

2. *Rockhausenia pygmaea* community: A flat, firm cushion community formed by a dense aggregation of *Rockhausenia pygmaea* individuals, but not hummock forming. We did not observe pools close to it, but the soil surface was usually wet to the touch (soil moisture above 60%), and the third shallowest mean water table depth was recorded here. It was the second most common plant community. The mean richness per square meter was 8 (Figure 4a), and the evenness 0.70 (Figure 4b). Vegetation cover was 93%, while moisture indicators cover was 92% (Figure 4c, d). *Plantago tubulosa* and *Eleocharis albibracteata* were frequent companion species.
3. *Plantago rigida* community: A hard cushion community formed by densely aggregated *P. rigida* individuals devoid of pools. The surface was usually dry. The mean water table depth was close to the one in the *Aciachne* community, but *P. rigida* had the deepest record (-200 cm) in this study. The mean richness per plot (4) was the lowest among the thirteen communities. It was not significantly different only from the *Calamagrostis rigescens* (6) and *Calamagrostis chrysantha* (6) communities (Figure 4a). The mean evenness value of 0.38 was also the lowest among all communities (Figure 4b). Vegetation (92%) and moisture indicators (91%) cover were still high (Figure 4c, d).
4. *Plantago tubulosa* community: This flat, hard cushion community without pools has a usually wet surface with the highest record of soil moisture. Its mean richness per plot (8) and evenness values (0.69) were similar to those in most other communities (Figure 4a, b). Vegetation (92%, Figure 4c) and moisture indicators cover (89%, Figure 4d) were high.
5. *Lachemilla diplophylla* community: An herbaceous community, usually in sites with a water layer above the soil or with a very wet soil surface. The soil moisture was higher than in the *R. pygmaea* and *P. rigida* communities, but lower than in the *D. muscoides* community. The mean richness per plot was 7 (Figure 4a). Its evenness (0.61) was significantly lower than the one in Mixed community 1 (Figure 4b). The vegetation (94%, Figure 4c) and moisture indicators (93%, Figure 4d) cover were high.
6. *Aciachne pulvinata* community: A soft-cushion community. Cushions formed by *A. pulvinata* have usually a yellowish or light green color (the latter when plants are young), with sharp-pointed fruits that can produce pain (prick) when touched. The soil surface was always dry, without pools close to it. Nevertheless, soil moisture was close to those registered in some previous communities. The mean water table was the deepest recorded. The mean richness per plot was 8, while the evenness was 0.58 and only significantly lower than that of the two mixed communities. The vegetation and soil moisture indicators cover had lower values than most other communities, usually below 75% (Figure 4c, d).
7. *Juncus stipulatus* community: A rush (*Juncaceae*) community in permanently waterlogged areas (with water on the surface throughout the year). The soil

moisture was comparable with values observed in the *D. muscoides* community. The species richness per plot was relatively constant (Figure 4a), as well as the evenness which was high (0.75, Figure 4b). The vegetation and soil moisture indicators cover were high (91%, Figure 4c, d).

The following descriptions correspond to six potential communities we initially identified in our analyses (Group 2). To confirm the results, additional surveys and more plots from these communities will be required (currently, all have been recorded in one single plot, sampled annually).

8. *Calamagrostis rigescens* community: This community is dominated by a short tussock. The soil surface can be wet or dry. The mean richness per plot was one of the lowest (6), and the records were relatively constant in the surveyed period (Figure 4a), while the evenness was close to 0.5 (Figure 4b). Vegetation (98%) and moisture indicators (97%) cover were very high and constant (Figure 4c, d).
9. *Calamagrostis chrysantha* community: This community was dominated by a tall tussock, usually with a wet soil surface. The dominant species was commonly recorded growing in pools. The mean richness per plot was one of the lowest (6, Figure 4a). Vegetation and moisture indicators cover were high, and with low variability (89%, Figure 4c, d).
10. *Distichia filamentosa* community: This cushion community exhibits predominantly wet soil surfaces with pools close to it and was present in close proximity to a cryoturbated zone, i.e. subjected to a sequence of ice and thawing. It exhibited the highest soil moisture record together with *Plantago tubulosa* community. The mean richness per plot was 7 (Figure 4a), while the evenness was 0.76, one of the highest (Figure 4b). Vegetation, and moisture indicators cover indicators were very high (95%, Figure 4c, d).
11. *Lobelia oligophylla* community: This is an herbaceous community, usually with a wet surface. It had one of the highest records of mean richness per plot (11, Figure 4a) and evenness (0.78, Figure 4b). Vegetation (90%, Figure 4c) and moisture indicators (89%, Figure 4d) cover were high.
12. Mixed community 1: An herbaceous community with small tussocks of *Calamagrostis vicunarum*, some patches of herbaceous species (like *Lachemilla diplophylla*), and flat hard cushions of *Plantago tubulosa*. The soil surface was usually wet. Nevertheless, the soil moisture was the lowest recorded. The mean richness (12) and evenness (0.86) per plot were the highest recorded (Figure 4a, b). In this case, the cover of moisture indicators (72%) was much lower than the vegetation cover (89%), showing the presence of species that grow in drier areas.
13. Mixed community 2: An herbaceous community with sedges (*Eleocharis albibracteata*) and hard cushions of *Distichia muscoides*. The soil surface was usually wet, with a mean water table depth above -20 cm, but with its deepest record comparable to values found in the *R. pygmaea* community. The mean richness per plot was 8 (Figure 4a), and the evenness was high (0.71, Figure 4b), but not as much as in Mixed community 1. The vegetation (66%) and moisture indicators (65%) cover had the lowest records among all communities and were as variable as in the *Aciachne pulvinata* community (Figure 4c, d).

Patterns of diversity, structure, and composition of *bofedal* plant communities

We recorded 68 species belonging to 15 families and 45 genera (Suppl. material 3). The most species-rich family was *Poaceae* (24 species), followed by *Asteraceae* (10 species).

Group 1 communities' composition and dominance patterns remained stable and without significant statistical differences when assessed between years (Suppl. material 5, Figure 5, left panel). This pattern was also observed at the site (*bofedal*) level, where the identified communities showed an overall small contrast between years (Suppl. material 6). In contrast to the group 1 communities, group 2 displayed more variability in plant composition between the 2017 and the 2018–2019 surveys (Suppl. material 6).

The *Distichia muscoides* community was found in most of the sites (90%), plots (55%), and almost along the entire elevational range of our study (4,292–4,850 m a.s.l.). Other common plant communities were dominated by *Rockhausenia pygmaea* (42% of the sites, 18% plots), *Plantago rigida* (26% of the sites, 8% plots) and *Plantago tubulosa* (23% of the sites, 7% plots). The other nine plant communities were found in fewer than 17% of the sites and 12% of the plots (Table 2).

The communities with the highest mean richness were Mixed community 1 (12) and *Lobelia oligophylla* community (11), while *Plantago rigida* community (4) had the lowest values. Most communities had similar mean richness (7–8, Table 3), usually with no significant differences (Figure 4a). The species richness per plot ranged from 1 to 15. Nevertheless, 75% of the 1 m^2 plots had only 1–8 species; this included 79% of the *D. muscoides* community' plots and 100% of the *P. rigida*, *J. stipulatus* and *C. rigescens* communities' plots. Rarefaction curves showed consistent patterns; the *Plantago rigida* community displayed lower species richness compared to others. In contrast, these other communities exhibited similar species richness at lower sample sizes (Suppl. material 7). We highlight that communities shared most of their species (85–100%, Suppl. material 3). The Pielou index attained values between 0.38 (in *P. rigida* community) and 0.78 (*L. oligophylla* community, Table 3).

The species present in most *bofedales* (30 of 31 sites) were *D. muscoides*, *P. tubulosa* and *R. pygmaea*. Four species were most frequent per plot during our three-year

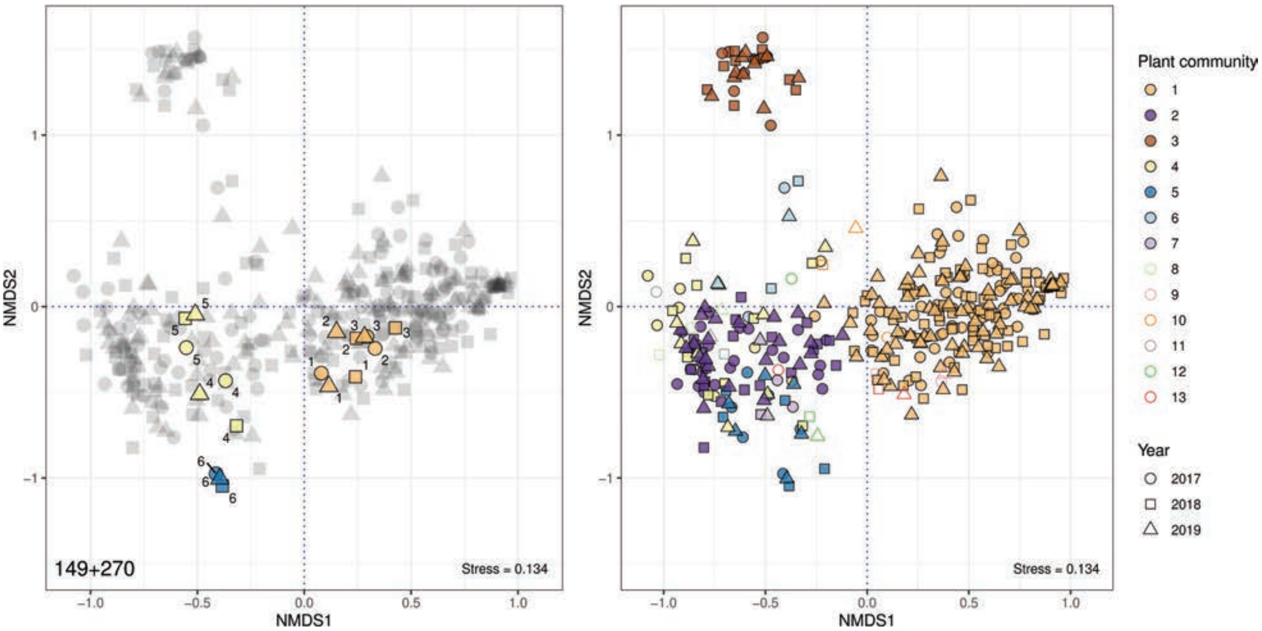

Figure 5. Species composition variability of the thirteen plant communities identified. NMDS based on Hellinger-transformed vegetation cover dissimilarities (Bray-Curtis distance) between 2017–2019. Left panel: Example of variation in plant composition of three plant communities present at 149+270 *bofedal*. Number indicates the same sampling location. Right panel: Variability of species composition across years. Filled symbols represent plant communities significantly different from each other. Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2.

study: *Distichia muscoides* (occurred in 74% of all plots), *Plantago tubulosa* (69%), *Rockhausenia pygmaea* (63%) and *Lachemilla diplophylla* (51%). They were common companion species in most plant communities when they were not dominant (Table 4, Suppl. material 3).

Average plant cover was high in most plant communities (89–98%). The lowest values were recorded in the *Aciachne pulvinata* community (75%) and the Mixed community 2 (66%). The former had the highest values of dead cushions (11%), and the latter had the highest values of bare soil surfaces (33%, Table 2). These two cover types (dead cushions and bare soil) had cover values below 6% in all other plant communities. Other types of ground cover (water, mosses, dead plants, rock fragments, dung) had values below 9% and were thus considered less important in the study area.

Considering the data per year (Suppl. material 8), the variability of *bofedales* communities (PCA component 1) is defined by the cover of moisture indicator species (IH%, eigenvalue +0.54), overall plant cover (eigenvalue +0.52), and percentage of bare soil (eigenvalue -0.49). This first component clearly separates *Aciachne*, *Lobelia*, and mixed communities 1 and 2 from all other communities. The second component is defined by the species richness per plot (S, +0.68) and Pielou's evenness (J', +0.58), grouping the *P. rigida*, *C. chrysantha*, *C. rigescens*, *D. muscoides*, *Lachemilla diplophylla* and *A. pulvinata* communities.

Plant composition and abundance across *bofedales* and years showed a major dispersion in variability for *D. muscoides*, *R. pygmaea* and *P. tubulosa* communities, with a distinctive and less variable floristic assemblage for the *P. rigida* community (Figure 5, right panel). However, interannual variability is less evident within the same *bofedal*, for almost all identified communities (Figure 5, left panel, Suppl. material 6).

Soil moisture mean values per community were usually above 55%. The lowest values were recorded in the Mixed community 1 (20%) and in *Calamagrostis chrysantha* (45%); while *Plantago tubulosa* and *Distichia filamentosa* communities exhibited the highest values (100%). A Kruskal–Wallis test revealed only significant differences between the driest (Mixed community 1) and those over 60% of soil moisture (*Distichia muscoides*, *Rockhausenia pygmaea*, *Plantago tubulosa*, *Lachemilla diplophylla*, *Juncus stipulatus* and *Distichia filamentosa*). All other communities had overlapping values (Figure 6).

The months with the deepest water table record were September (-59±5 cm) and October (-55±9 cm). While the months with the shallowest water table were February (-5±1 cm) and December (-12±5 cm). The water table was deeper than 90 cm in the dry season, in at least one year in four of the five communities, with the only exception of *D. muscoides* community (Table 2). Mixed community 2 and *D. muscoides* had the shallowest mean water table depth (-19 cm). *P. rigida* (-43 cm) and *A. pulvinata* (-47 cm) communities had the deepest water table level. The water table reached depths greater than 130 cm in the dry season (Figure 6).

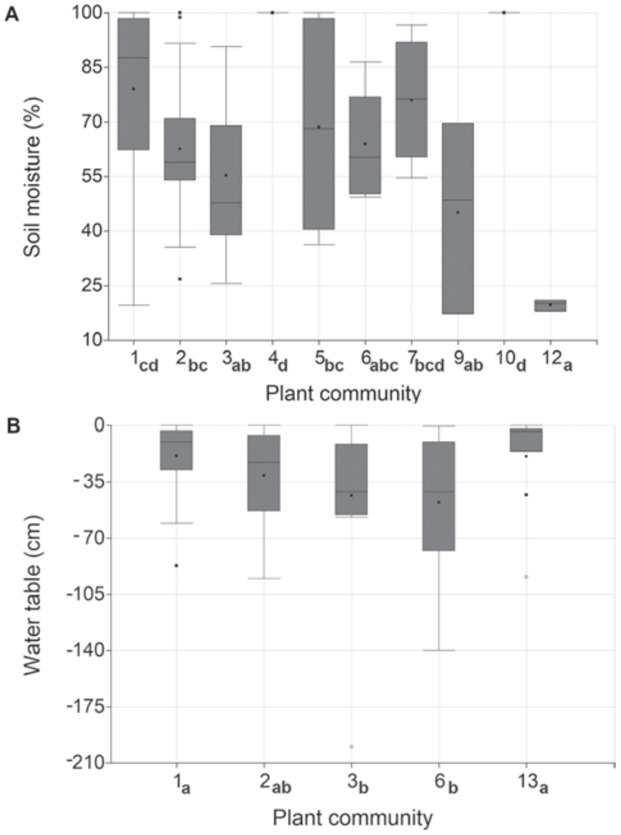

Figure 6. A) Soil moisture and B) water table depth per plant community. Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2. Communities with a common letter are not significantly different (Kruskal Wallis Test, $p > 0.05$). Inside each box, horizontal line and dot represent the median and mean values, respectively.

Discussion

The *bofedal* plant communities we characterize here along a southern Peruvian east–west Andean transect are heterogeneous as reported in studies across the Andes from Colombia (Cleef 1981; Benavides and Vitt 2014), Ecuador (Suarez et al. 2022), Peru (Cooper et al. 2010; Maldonado-Fonkén 2014; Salvador et al. 2014; Maldonado-Fonkén 2018; Polk et al. 2019; Portal-Quicaña 2019), Bolivia (Ruthsatz 2012; Loza Herrera et al. 2015; Domic et al. 2021), Chile (Squeo et al. 2006) and Argentina (Ruthsatz et al. 2020; Izquierdo et al. 2020; Izquierdo et al. 2022).

The seven plant communities (group 1) we identified (*Distichia muscoides*, *Rockhausenia pygmaea*, *Plantago rigida*, *Plantago tubulosa*, *Lachemilla diplophylla*, *Aciachne pulvinata* and *Juncus Stipulatus*) were consistent in their structural and compositional characteristics and maintained differences between them during our three-year study. The remaining six potential communities or group 2 (*Calamagrostis rigescens*, Mixed community 1, *Calamagrostis chrysantha*, *Distichia filamentosa*, *Lobelia oligophylla*, Mixed community 2) require additional surveys to resolve their status as independent communities. We include them here as some have been described previously with similar structural or compositional characteristics, such as communities of *Distichia filamentosa* in Bolivia (Ruthsatz 2012) or communities with either *Lobelia oligophylla* or *Calamagrostis tarmensis* in northern Peru as co-dominant species (Cooper et al. 2010).

All the dominant or co-dominant species of the thirteen plant communities we describe here, have been previously reported as key components in *bofedales* throughout South America, as will be discussed below, although not necessarily by being the most abundant or frequent species in the community.

The *Distichia muscoides* hard cushion community has been reported throughout Peru (INAIGEM 2023), including in areas close to our study sites (Maldonado-Fonkén 2014, 2018; Portal-Quicaña 2019). This community is found in South America following the wide geographical distribution of its distinctive species from Colombia to northern Argentina (Ruthsatz 2012). Nevertheless, it is not the only dominant species in *bofedales*, as shown in our study and other works in Colombia (Cleef 1981; Benavides and Vitt 2014), Ecuador (Suarez et al. 2022), Peru (Cooper et al. 2010; Maldonado-Fonkén 2014; Salvador et al. 2014; Polk et al. 2019; Portal-Quicaña 2019), Bolivia (Ruthsatz 2012; Loza Herrera et al. 2015), Chile (Squeo et al. 2006) and Argentina (Ruthsatz et al. 2020; Izquierdo et al. 2022). This community is present in sites rarely affected by saline stress (electrical conductivity 19–713 $\mu S\ cm^{-1}$), droughts, or frost (Salvador et al. 2014). The number of species previously reported per site in Bolivia and Peru was between 16–39 (Ruthsatz 2012), while we reported 3–28 species. The lowest species richness was found in sites with almost exclusive dominance of *D. muscoides*, with pools retaining considerable water even in the dry season and usually with soil moisture over 80%. Since *D. muscoides* is an aquatic plant (Leon and Young 1996), a shallow water table (and consequently, high soil moisture) could limit the development of other species with less tolerance for saturated conditions. High water tables favor peat accumulation enabling increased carbon capture and storage compared to sites with lower water tables. *D. muscoides* is dominant under very stable hydrological conditions and with a water level close to the surface, not deeper than 50 cm (Oyague 2021). Our study confirmed this, as this community had the shallowest mean water table, only three monitoring wells had values that exceeded 50 cm of depth in September 2017 or 2018.

Rockhausenia pygmaea is distributed from Venezuela to Argentina (Salvador et al. 2014) and is considered a characteristic species of *bofedales* (Ruthsatz 2012; Ruthsatz et al. 2020). It is a peat-forming species (Benavides and Vitt 2014) that grows forming carpets (Salvador et al. 2014), low-firm cushions to hummocks (Aubert et al. 2014). It was identified as a potential dominant species in the

Rockhausenia pygmaea–Pernettya prostrata assemblages in Ancash (Polk et al. 2019) and in the *Plantago tubulosa–Oreobolus obtusangulus–Rockhausenia pygmaea* assemblages in Cajamarca (Cooper et al. 2010), both in northern Peru. We recorded it as a dominant species and forming a recognizable community in 42% of the sites, being the second most common community after *Distichia muscoides*. Our records of soil moisture and water table suggest that it can thrive in drier conditions than *D. muscoides*.

Plantago rigida communities have been reported in Peru (Salvador et al. 2014), Ecuador (Suarez et al. 2022), and Colombia (Cleef 1981). According to Ruthsatz (2012), this species also grows at the edge of *bofedales* and in drier environments, and our results showed that it can thrive in drier conditions than *D. muscoides*. Nevertheless, Cleef (1981) reported it in wet depressions. In our study, it was the species with the highest abundance in its community and usually with fewer (less than five) companion species that can grow in the rare small openings between the leaves of this species or on the outside border of the cushions.

Plantago tubulosa is distributed along the Andes from Central America to Argentina (Cooper et al. 2010; Salvador et al. 2014) and is also considered a common species in *bofedales* (Ruthsatz et al. 2020). *P. tubulosa* communities have been reported from northern to southern Peru (Cooper et al. 2010; Salvador et al. 2014; Maldonado-Fonkén 2018), extending to Bolivia (Loza Herrera et al. 2015). However, it is most referred to as a co-dominant species in mixed communities with *Distichia muscoides* (Salvador et al. 2014) and *Oreobolus obtusangulus* (Polk et al. 2019), or in the *Plantago tubulosa–Oreobolus obtusangulus–Rockhausenia pygmaea* assemblage (Cooper et al. 2010). In our study, communities heavily dominated by *P. tubulosa* were found in 23% of the sites. This species also occurred as co-dominant with *Calamagrostis vicunarum* and *Lachemilla pinnata* in the Mixed community 1. Soil moisture was high and less variable than in the *D. muscoides* community; nevertheless, considering the lack of pools, we recommend additional studies about its water requirements.

Aciachne pulvinata was previously reported only as a companion species in *bofedales* in Peru (Cooper et al. 2010; Salvador et al. 2014) and Bolivia (Ruthsatz 2012). This species, associated with overgrazing (Salvador et al. 2014; Cochi Machaca et al. 2018), was present in eight of the 13 communities but was dominant only in one site with a low plant cover (75%) and the highest percentage of dead cushions (11%) recorded among the communities. Maldonado-Fonkén (2018) described a related community characterized by the sister taxon *Aciachne acicularis* in Ayacucho, where the percentage of litter and bare soil were at least 10% each, while the plant cover was 73%. We reported similar values in this study, despite the differences in survey methods. This community, together with *P. rigida*, had low water requirements. According to our observations, *A. pulvinata* increases its coverage in *bofedales* where the water level is decreasing.

Distichia filamentosa is distributed in Peru, Bolivia, and Chile (Ramirez 2011). This community has also been reported in those countries, growing at the upper growth limit of other cushion species (Squeo et al. 2006; Ruthsatz 2012; Loza Herrera et al. 2015). It has also been recorded in overgrazed areas in Bolivia (Cochi Machaca et al. 2018). We observed similar conditions in the only site where we identified this community: *D. filamentosa* was found at the extreme edge of the *bofedal*, next to a cryoturbated area, surrounded by *D. muscoides* cushions. Its water requirements seem to be high (soil moisture in dry season), but we recommend additional studies (water table measurements) in more sites. *Lobelia oligophylla* is distributed from Colombia to Bolivia and Chile (Cooper et al. 2010) and is considered a typical species of *bofedales* (Ruthsatz 2012). It was identified as a co-dominant species with the moss *Drepanocladus longifolius* in seasonally flooded areas in *bofedales* in Cajamarca (Cooper et al. 2010), and it is widely distributed in the peatlands of the Argentinean Puna (Izquierdo et al. 2020). In this study, we found it in a flat wet area but without any adjacent depressions or evidence of water courses that would indicate a potential to become a seasonally flooded area during the rainy season.

Juncus stipulatus, *Calamagrostis rigescens*, *Calamagrostis chrysantha* and *Lachemilla diplophylla* have been previously reported only as companion species in *bofedales* in Bolivia (Ruthsatz 2012) and Peru (Salvador et al. 2014). *C. rigescens* is also reported as a typical species of *bofedales* in Argentina (Ruthsatz et al. 2020) and is associated with overgrazing (Cochi Machaca et al. 2018). Species of the same genera, like *Juncus arcticus* or *Calamagrostis tarmensis*, have been previously described as co-dominant in *bofedales* communities in northern Peru (Cooper et al. 2010). In the case of rushes, they were found bordering lakes and ponds (Cooper et al. 2010). In our study, the *Juncus stipulatus* community was found in permanently waterlogged places but devoid of nearby pools. In contrast, the *Lachemilla diplophylla* community was usually found on wetter surfaces and moister areas, even recording the highest abundance of soil moisture indicators cover.

We encourage further study of the six preliminary communities (Group 2) to determine whether they result from local anthropogenic processes (e.g., overgrazing and draining) that increase the dominance of certain species or if more complex factors come into play (e.g., changes in water temperature and quality, regional climatic changes, etc.).

In most studies on *bofedales* vegetation, total species richness or mean richness per site is reported. These results are strongly influenced by the area assessed and sampling methods, which makes comparisons per area or sampling unit (e.g. square meter) difficult and shows an knowledge gap. Salvador et al. (2014) reported 56 species (vascular plants) in 24 sites, while Portal-Quicaña (2019) reported 85 species in one *bofedal* close to our study area. Our results (68 species in 27 sites) are similar to both studies. Other reports included 102 species in 36 sites (Cooper et al. 2010) and 119 species in 47 sites (Izquierdo et al. 2020). The number of species per 1 m^2 we found (1 to 15) is similar to what was reported in Argentina (1–13, Izquierdo et al. 2020). As reported in previous studies, *Poaceae* and *Asteraceae* were the families with the most species (Maldonado-Fonkén 2018). Nevertheless, studies in Argentina, northern and central Peru included *Cyperaceae* as a third important family (Cooper et al. 2010; Polk et al. 2019; Izquierdo et al. 2020), which is much less conspicuously represented in our study.

Water table measurements per plant community in *bofedales* are uncommon, and this is the first report of soil moisture values. Although mentioned, details of the water table are usually not provided in published studies (e.g. Cooper et al. 2010). According to the recent classification proposed by INAIGEM (2023), the *bofedales* where we installed monitoring wells are considered seasonal because the water table is deeper than 20 cm for several months of the year. This suggests that water availability in our sites is strongly influenced by rainfall seasonality. This applies to 13 of 31 sites and five communities (*A. pulvinata*, *D. muscoides*, Mixed community 2, *P. rigida* and *R. pygmaea*). However, rainfall seasonality is probably not the only water source of these *bofedales*. Hillslope groundwater flowing from lateral moraines, talus, colluvium, or bedrock aquifers can also be a source (Cooper et al. 2019), especially because streams, lakes, and glaciers are uncommon in the area. Further hydrological studies are required to clarify the main water source of these *bofedales*.

Even though *bofedales* can be hydrologically seasonal, the dominant plants are perennial. Some have deep roots (e.g., *Distichia* spp., *Plantago* spp.) and can withstand periods without much water. In addition, the high content of organic matter or peat facilitates water storage. Therefore, the plant cover usually does not change over time significantly. Species richness could be more sensitive. If water is unavailable (too deep) for longer periods than the species can withstand, permanent changes can occur in the plant communities (e.g., dominant species, plant cover, etc.). A La Niña event (November 2017 to March 2018; IGP 2023), usually associated with droughts in southern Peru, provided an opportunity to test this. Our results showed this was not the case within our sites, with stable values over time. Furthermore, we learned that assessing the communities in the dry season (when resources are limited for plants), can give better information of their condition over time.

The concept of *bofedales* necessarily includes a set of several distinctive plant communities that respond to microenvironmental site characteristics (Cooper et al. 2010; Ruthsatz 2012; Salvador et al. 2014; Polk et al. 2019). We show that the heterogeneity in plant communities occurs at local site level, and also at landscape and regional scales, with 84% of our studied sites having 2–3 plant communities. Recognizing this vegetational heterogeneity is important for conservation, ecosystem management and/or restoration activities since it allows the establishment of reasonable goals according to the diversity, structural and compositional characteristics of the sites. Given the scarcity of regional-level surveys in Peru, our results constitute the first steps towards identifying useful indicators of vegetation characteristics for biological baseline development and monitoring. These indicators are essential for setting achievable and site-specific restoration goals and distinguishing relevant contributions of ecosystem services such as carbon storage, water regulation or grazing. To achieve this, we identified three key gaps in *bofedales* knowledge in Peru that need to be addressed in the short to medium term. First, we need to characterize the floristic variation across latitudinal and longitudinal gradients. We believe that there are several local studies describing the floristic composition of *bofedales* in several regions in Peru that make it possible to attempt an initial comprehensive analysis of plot-based studies at the national scale. Second, we need to improve the accuracy of remote-based sensor mapping of *bofedales*. Although the currently available official map of Peru's *bofedales* represents an important milestone, it inadequately describes the distribution and area of several bofedales in our study area. Some are misrepresented in terms of size or location, while others are not included at all. Third, the most complex challenge lies in understanding the various factors to which different *bofedales* plant communities respond, particularly those that define the structure and functioning of these unique ecosystems in a context of rapid land-use and climatic changes.

Data availability

Yearly plot-based species cover data have been deposited at Figshare and are publicly available (https://doi.org/10.25573/data.24512719). All other data used and mentioned in the manuscript are provided as Suppl. materials 1–8.

Author contributions

Conceptualization: M.M.F. and R.L.P.; methodology, formal analysis, writing-original draft preparation: M.M.F. and H.C.; data curation, field assessment: M.M.F.; writing-review and editing: M.M.F., R.L.P., H.C. and B.V. All authors have read and agreed to the published version of the manuscript.

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Supplementary material

Supplementary material 1
Examples of permanent plots (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl1

Supplementary material 2
Plot data (xlsx-file)
Link: https://doi.org/10.3897/VCS.115726.suppl2

Supplementary material 3
Information per plant community (xlsx-file)
Link: https://doi.org/10.3897/VCS.115726.suppl3

Supplementary material 4
Results (*p* and *R* values) of the One-way Analysis of Similarities (ANOSIM) between plant communities with Bray-Curtis index (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl4

Supplementary material 5
Results (*p* and *R*-values) of the One-way Analysis of Similarities (ANOSIM) between plant communities per year with Bray-Curtis index (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl5

Supplementary material 6
NMDS based on plant cover of the thirteen plant communities for each peatland evaluated between 2017–2019 (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl6

Supplementary material 7
Sample-based rarefaction curves (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl7

Supplementary material 8
Principal Component Analysis (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl8

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EDITORIAL

NEOTROPICAL VEGETATION

Vegetation classification in the Neotropics – Novel insights from Latin America and the Caribbean

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Abstract

Our editorial introduces a Special Collection of scientific articles on current vegetation research in the most biodiverse of all biogeographic realms, the Neotropics. It contains nine scientific contributions dedicated to vegetation data, description and classification. Four research papers provide new vegetation classifications of important Neotropical biomes, namely the Arid Chaco in Argentina, Mexican temperate forests, and Andean wetlands in the Argentine Puna and southern Peru. Furthermore, one study provides a novel bioclimatic-vegetation classification approach applied to Mexican vegetation, while another proposes a new synthesis of the South American terrestrial biomes as geocomplexes. Finally, three vegetation databases are presented in the Special Collection: *ArgVeg – Database of Central Argentina* (GIVD ID: SA-AR-002), *CACTUS – Vegetation database of the Dutch Caribbean Islands* (GIVD ID: SA-00-004) and *VegAndes: the vegetation database for the Latin American highlands* (GIVD ID: SA-00-005). The Special Collection provides fundamental data and tools to better understand the diversity and complexity of Neotropical vegetation.

Abbreviations: GIVD = Global Index of Vegetation-Plot Databases, IAVS = International Association for Vegetation Science, IAVS-LACS = IAVS Regional Section for the Latin America and the Caribbean, VCS = Vegetation Classification and Survey

Keywords

Andes, Argentina, classification, database, Dutch Caribbean Islands, geocomplex, Mexico, Peru, vegetation formation

Background

The Neotropics extend from Mexico to Tierra del Fuego and contain around 85,000 vascular plant species, making it the most phytodiverse biogeographic realm on Earth (Ulloa Ulloa et al. 2017). The Neotropics encompass several renowned global biodiversity hotspots, including Mesoamerica, the Caribbean islands, the Tropical Andes, the Atlantic Forest and the Cerrado (Mittermeier et al. 2011; Peyre 2021). They also play a crucial part in maintaining essential ecosystem services that are vital to humanity and help uphold planetary boundaries (Rockström et al. 2009; Díaz et al. 2020). One primary example is global climate regulation through major carbon sinks in tropical rainforests and mountain ecosystems such as páramos (Brienen et al. 2015; Thompson et al. 2021). Moreover, by comprising the Mayan, Amazonian and Andean forests, the Neotropics ought to be considered the most diverse and extensive germplasm bank worldwide. The Neotropics have remained relatively preserved compared to other realms, partly due to their low population density and vast inhospitable landscapes. It is of the utmost importance to assess and predict human impacts to ensure our sustainable coexistence with nature in the future (Kobayashi et al. 2019).

The Neotropical realm was first described and classified according to its biogeographic regions by Wallace (1876), leading to numerous subsequent classifications based on plants and/or animals up to the present (e.g., Cabrera and Willink 1973; Morrone 2017). For instance, Rivas Martinez et al. (2011) recognized 50 biogeographic provinces, which they classified into 11 regions: Caribbean-Mesoamerica, Neogranadian, Guyanan-Orinoquian, Amazonian, Brazilian-Paranaense, Chacoan, Tropical South Andean, Hyperdesertic Tropical Pacific, Pampean, Middle Chilean-Patagonian, Valdivean-Magellanian (see Navarro et al. 2023, for a novel classification). Although there is still no clear consensus today, researchers are increasingly compiling information and producing useful phytoregionalizations, vegetation classification and vegetation pattern analyses. At a finer scale, the vegetation diversity in the Neotropics (Figure 1) can be associated with its unique biogeography, the complex evolution of its orogeny and soils, the immense floristic cradle, and more recently, human interactions. For example, the Andean páramo, covering 25,000 km^2 of tropical alpine habitats, harbors more than 500 plant communities alone (Rangel-Churio 2000; Peyre et al. 2021).

Despite the substantial body of research already published, the vegetation of the Neotropical realm remains poorly documented compared to others such as the

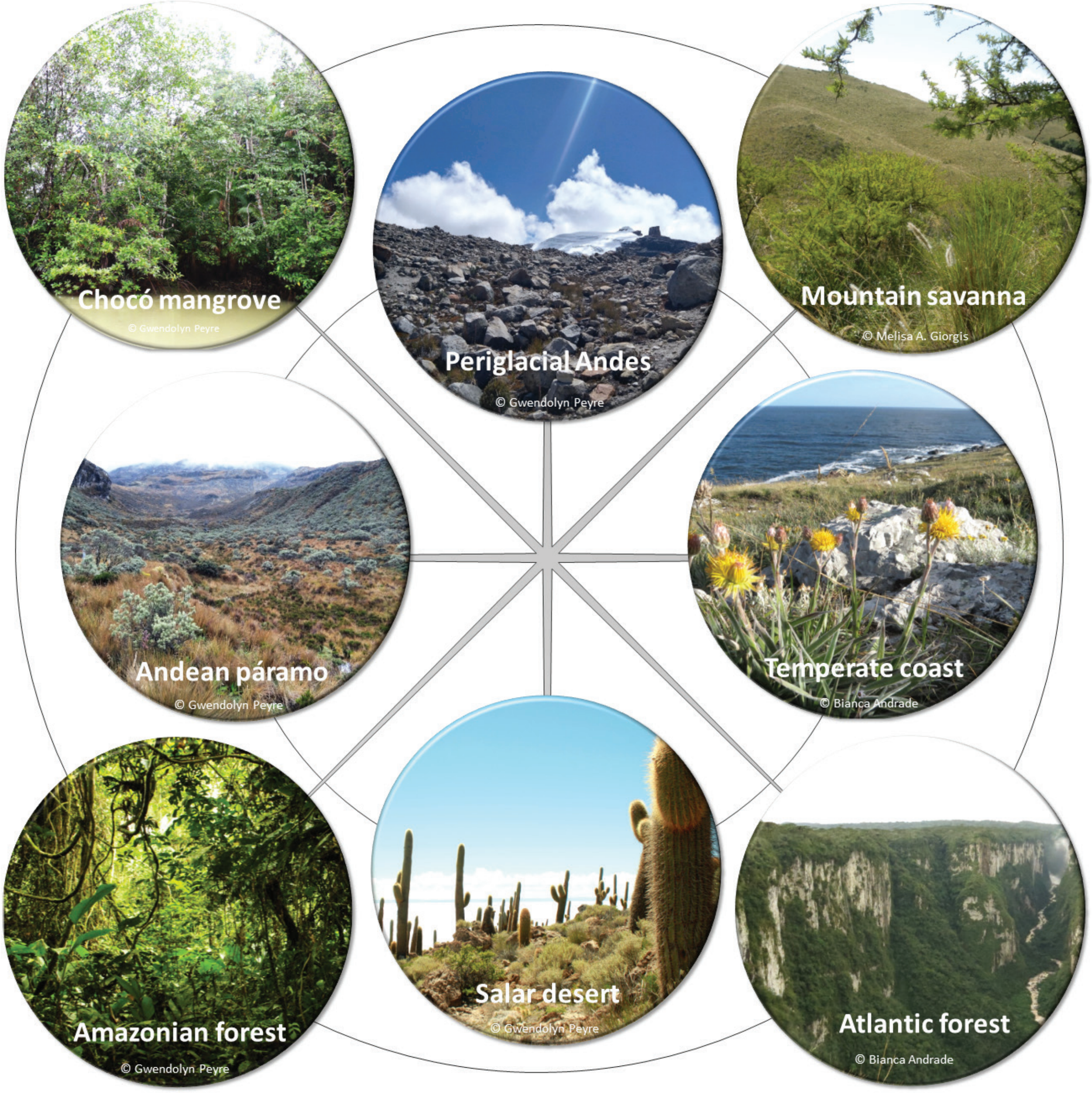

Figure 1. Neotropical vegetation types in Latin America and the Caribbean (creation: Gwendolyn Peyre).

Palaeartic, Nearctic, Australasian or Oceanian realms (Sabatini et al. 2021). Several factors contribute to this lack of information and we would like to highlight a few key ones. First, political instability and limited economic resources allocated to science are significant obstacles (Casas and Mercado 2015). For instance, in 2020, Latin America and the Caribbean invested 0.62% of their regional income in science, compared to 3.32% in North America and 2.28% in the European Union (Banco Mundial 2020). Second, the immense Neotropical biodiversity is challenging to synthesize due to the lack of integrated taxonomic studies and a high proportion of missing diversity. For example, Ecuador and Peru could harbor up to 30% of the total missing species worldwide, across all taxa, which can hinder our ability to conduct representative and comprehensive biological studies (Joppa et al. 2011). Additionally, other barriers such as data availability, data access and language barriers can also interfere with efforts to compile large repositories of neotropical vegetation information (but see the Special Collection for a few examples).

In 2022, Vegetation Classification and Survey (VCS) and the Latin American and Caribbean Section of the International Association for Vegetation Science (IAVS-LACS) partnered to launch this Special Collection dedicated to "Neotropical vegetation". This Special Collection aims to provide new insights into vegetation classification-related research across the Neotropical biogeographic realm. It focuses on vegetation classification/typology and/or ecoinformatics from three perspectives, (1) vegetation data, distribution, representativeness and access; (2) vegetation description, analysis and classification; and (3) vegetation management and conservation.

Content of the Special Collection

The VCS Special Collection comprises nine articles, including five Research Papers, one Review and Synthesis, and three Long Database Reports. We introduce the studies as follows:

Zeballos et al. (2023) provide an integral classification of the vegetation types of the Arid Chaco in Central-Western Argentina. The authors investigated the main vegetation types of the Arid Chaco, characterized their flora, endemism, chorotypes, and life forms, and associated them with environmental gradients. Based on 654 relevés, they identified nine vegetation types, with xerophytic shrublands being dominant. They highlighted the effects of historical and present land-use, conferring a clear Chaquenian identity to this area.

Ávila-Akerberg et al. (2023) conducted extensive work on the classification and nomenclature of temperate forest types in Mexico. The authors provide a comprehensive analysis and synthetic update of the nomenclature of sub-humid and temperate forests in Mexico. Through their research, they found that vegetation classification proposals tend to standardize criteria and nest hierarchical integrations at various levels based on physiognomic, climatic, phenological and floristic attributes. They established that physiognomy was a primary divider at a broader scale, whereas floristics typically divided at finer scales. Their work calls for a complete inventory of the phytosociological associations of temperate forests in the country.

Casagranda and Izquierdo (2023) contributed a novel study on modelling the potential distribution of floristic assemblages of high Andean wetlands dominated by *Juncaceae* and *Cyperaceae* in the Argentine Puna. Their aim was to model the potential distribution of *vegas*, high Andean wetlands, and their flora. Their models predicted that *Juncaceae*-dominated *vegas* were chiefly distributed in the Northern region, at high elevation, and in humid, cold conditions. In contrast, *Cyperaceae*-dominated *vegas* were mostly predicted in the southern region, at lower elevation and in drier, hotter conditions. The authors provided planning tools to better understand *vega* distribution under changing environmental conditions.

Gopar-Merino et al. (2024) provide a coupled cartographic approach between bioclimatology and vegetation formations of Mexico. This study represents a first attempt to unravel the intricate interplay between climate and vegetation and to unify a system for depicting Mexican vegetation patterns. Using a combined geobotanical and bioclimatological approach, the authors identified 13 distinct bioclimatic classes. When combined with physiognomic types, these classes depicted 11 forest, three shrubland and three herbaceous biomes. Their method can be used for classification and conservation initiatives focused on vegetation.

Maldonado-Fonkén et al. (2024) classified the plant communities of high-Andean *bofedal* wetlands across a trans-Andean transect in southern Peru. The authors sampled a nearly 70 km long transect in southern Peru and characterized its plant communities and flora. They identified seven different plant communities, often forming cushion and mat vegetation, dominated by *Distichia muscoides*, *Werneria pygmaea*, *Plantago tubulosa*, *Plantago rigida*, *Lachemilla diplophylla*, *Aciachne pulvinata* and *Juncus stipulatus*. Their findings highlight the *bofedal* diversity in the region and suggest new lines of research and management initiatives.

From a systematic angle, **Navarro et al. (2023)** have proposed an innovative synthesis titled "South American terrestrial biomes as geocomplexes: a geobotanical landscape approach". They associate vegetation units at the landscape level, showing how these units interact with each other and are conditioned by climatic, topographic and edaphic gradients within a geographic area. Based on this premise, the authors establish a conceptual framework that views the biome as a landscape complex (geocomplex), which includes vegetation geoseries that, in turn, comprise geomorphologically linked zonal and azonal vegetation series. Applying this framework to South America, they identified and synoptically characterized 33 geocomplex biomes and 16 macrobiomes. The results will be summarized in a dataset for the scientific community.

The VCS Special Collection also promotes three new vegetation data initiatives for the Neotropical realm. **Giorgis et al. (2022)** have contributed "ArgVeg – Database of Central Argentina". This novel dataset, GIVD ID: SA-AR-002, includes 1,092 vegetation-plot records, containing 1,184 valid native and non-native vascular plant species (September 2022). The database covers the main vegetation types of the Chaco, Espinal and Pampa in central Argentina. It fills in an important data gap and highlights the outstanding plant diversity of central Argentina. The authors call for further contributions and networking towards a better understanding, conservation and management for these endangered ecosystems.

Janssen et al. (2023) present the repository "CACTUS – Vegetation database of the Dutch Caribbean Islands". The database, GIVD ID: SA-00-004, compiles vegetation-plot records from the Dutch Caribbean Islands, and currently contains 2,701 of these. The database can be used for vegetation classification in an undersampled and underrepresented region, tracking vegetation change over time, to assist in the planning of vegetation surveys, as a source for plant species distribution maps, and to inform nature conservation and policy.

Finally, **Peyre et al. (2022)** promote the novel dataset "VegAndes: the vegetation database for the Latin American highlands". VegAndes, registered under GIVD ID: SA-00-005, is an extensive dataset for georeferenced and standardized information on vascular plants in the Latin American highlands. The database compiles 5,340 vegetation plots sampled in 11 Latin American countries, with 5,804 taxon names, and spans over seven decades. Because the VegAndes data support multi-scale studies in botany, ecology and biogeography, it makes a significant contribution to biodiversity research and management in Latin America, especially considering the impacts of climate change on vulnerable tropical mountains.

Future perspectives

The diverse research featured in this VCS Special Collection suggests significant potential for collaboration among vegetation scientists from Latin America and the Caribbean and the IAVS journals, Journal of Vegetation Science, Applied Vegetation Science and Vegetation Classification and Survey. In 2019, the IAVS-LACS was launched, aiming to connect researchers dedicated to vegetation science in Latin America and the Caribbean. It is expanding rapidly due to its broad regional interest and outreach. Currently, the IAVS-LACS group is conducting an extensive bibliometric review on regional works, as an invited contribution to the Journal of Vegetation Science. This new initiative will help to identify knowledge, geographical and topical gaps and promote new initiatives and collaborations within and beyond the community. The growing need for understanding the impacts of global change on spatial and temporal variations in vegetation is particularly relevant for the Neotropics, and it calls for urgent measures to improve data availability and research.

Author contributions

GP planned and drafted this editorial, while all other authors contributed, revised and approved it.

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RESEARCH PAPER

CLASSIFICATION OF EUROPEAN FORESTS

Compositional and ecological diversity of Cansiglio forest (Friuli Venezia Giulia, Italy)

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Abstract

Aim: The aim of this study is to describe the compositional and ecological diversity of the Natura 2000 Site 'Cansiglio Forest' (IT3310006). **Study area:** The study area is located in the South-Eastern Prealps between the Venetian-Friulian plain and the Cansiglio plateau, a typical karstic system. **Methods:** A total of 25 vegetation relevés, each of 250 m^2, were sampled in the LIFE SPAN (LIFE19 NAT/IT/000104) project plots and were subjected to cluster analysis (Bray-Curtis, Ward) and NMDS ordination. Variables such as Ellenberg Indicator Values, environmental parameters, life forms, chorotypes, and phytosociological units were tested using ANOVA and the Kruskal-Wallis test to assess significant differences between clusters. The *indicspecies* package was applied to study the association between species patterns and combinations of clusters. **Results:** We distinguished three clusters. Cluster A, characterized by several species, including *Chaerophyllum hirsutum* and *Phegopteris connectilis*, shows higher EIVs for moisture, acidic soil reaction and lower temperature, a more open canopy and mainly Circumboreal and Euro Asian species of *Vaccinio-Piceetea*. Cluster B1, a mixed forest of *Fagus sylvatica* and *Abies alba* with *Circaea alpina*, has intermediate EIVs, a closed canopy, low herbaceous layer cover, and higher cover of SE-European species. Cluster B2, a pure *Fagus sylvatica* forest with *Lathyrus venetus*, has lower EIVs for humidity and higher for temperature, and mainly Central European species of *Carpino-Fagetea*. **Conclusion:** The anthropogenic spruce forest is developing in the Cansiglio plateau and is favored by thermal inversion. It could be identified with *Senecioni cacaliaster-Piceetum*, but further study is needed to confirm. The mixed forest of *Fagus sylvatica* and *Abies alba* and the pure beech forest represent two facies of the *Cardamino pentaphylli-Fagetum fagetosum*, with the first one dominating on the coldest slopes and the second one on the highest and warmer belt. This community can be included in the *Aremonio-Fagion* alliance.

Taxonomic reference: Euro+Med PlantBase (2023).

Syntaxonomic references: Mucina et al. (2016) for classes, orders and alliances; Willner et al. (2017) for suballiances.

Abbreviations: ANOVA = analysis of variance; EIV = Ellenberg indicator value; FVG = Autonomous Region of Friuli Venezia-Giulia; HSD = honestly significant difference; NMDS = non-metric multidimensional scaling.

Keywords

Abies alba, *Fagus sylvatica*, Illyrian species, karstic morphology, *Picea abies*, South-Eastern Prealps, thermal inversion

Introduction

The Cansiglio Forest spans two regions in North-Eastern Italy, Veneto and Friuli Venezia Giulia, and is known for its historic forest management, which began in 1548 by the Republic of Serenissima of Venice for the manufacture of boat oars (Cassol et al. 2013). Following the establishment of the Autonomous Region of Friuli Venezia Giulia (FVG) in 1966, ownership of the forest was divided between the two regions.

The Cansiglio plateau is a typical karstic system, known as a *polje* (from Slavic languages "field"), which appears as a vast plain bordered by a crown of mountains with squared and very steep sides. The entire system emerges from the Venetian-Friulian plain, in the orographic unit of the South-Eastern Prealps. In the bottom of the Cansiglio plateau the *Picea abies* forest develops, while climbing along the rugged slope of the Friulian side the *Fagus sylvatica* forest mixed with *Abies alba* occurs, and, still proceeding upward until the subalpine plane is the terminal pure *Fagus sylvatica* forest (Figure 1) (Mayer and Hofmann 1969; Del Favero et al. 1998). Among the hypotheses explaining this inverted vegetation series, the most noticeable phenomenon is thermal inversion, which results in a stagnation of cold moist air favoring *Picea abies* at the bottom (Busato and Lorenzoni 1973; Pignatti 1998).

Another peculiar element of this forest is its marginal position on the boundary of the Friulan-Venetian plain, which exposes the higher parts to the moisture currents, setting up a distinctly oceanic climate that is the optimum for *Fagus sylvatica*. Further inland, decreasing precipitation and increasing continentality favor the presence of *Abies alba* and *Picea abies*, a phenomenon that seems to be more important than the increase in elevation, as occurs in the North of the Alps (Poldini and Vidali 1993).

The South-Eastern Prealps saw the growth of the *Picea abies* population in the late glacial period, which then spread to the inner Central Alps and later to the Western Alps (Magri et al. 2006). Previous studies carried out in the Palughetto mire report the presence of forests with *Picea abies* in the Cansiglio plateau since 14,600 years BP (Vescovi et al. 2007). Concerning the recent history of the forest communities at the valley bottom, silvicultural treatments favoring *Picea abies* have been quite intensive (Vitale and San Martini 1914; Hofmann 1931) and, as in the case of the inner Alps (Gafta 1994), have led to the formation of an anthropogenic forest which is difficult to fit into a syntaxonomic scheme (Poldini and Bressan 2007).

Regarding *Fagus sylvatica* forests, studies carried out in the Palughetto mire suggest that *Fagus sylvatica* was present in the Cansiglio Forest since at least the early Holocene, but it became more abundant only during the

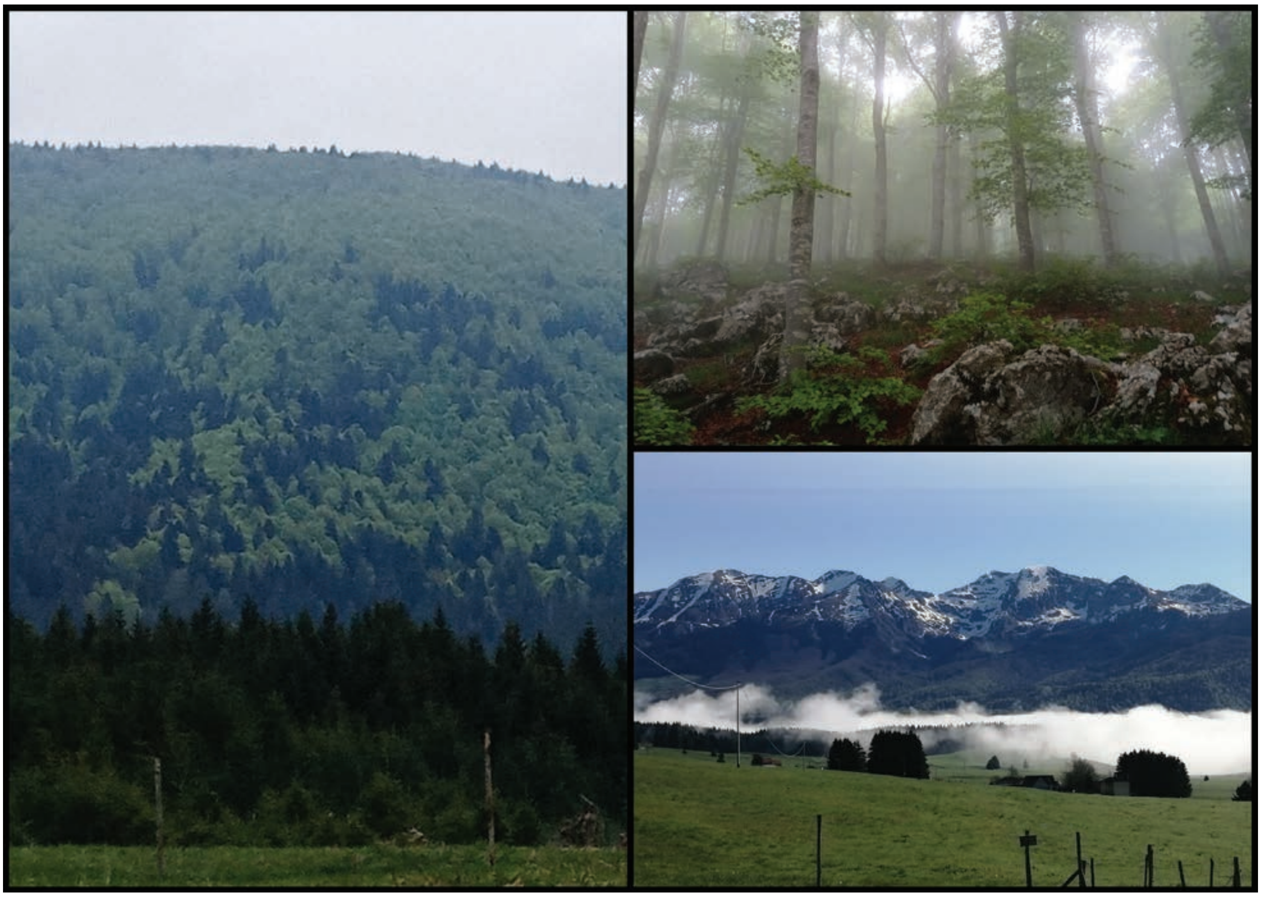

Figure 1. Panoramic photograps of Cansiglio Forest. **Left side**: vegetation belt (from the bottom) *Picea abies*, mixed *Fagus sylvatica* and *Abies alba*, pure *Fagus sylvatica* communities. **Top-right**: moist air on the top of Cansiglio forest. **Bottom-right:** stagnation of cold moist air in the Cansiglio plateau.

mid-Holocene (Vescovi et al. 2007). The increase in *Fagus sylvatica* abundance during the mid-Holocene is thought to be related to the cooling and moistening of the climate, which favored the expansion of beech forests in the European Alps (Tinner and Lotter 2006).

The Cansiglio Forest is part of a larger region that extends from the Northern Apennines to the North-Eastern Dinaric mountains and is characterized by a high diversity of *Fagus sylvatica* forests (Willner et al. 2009). The Southern-Eastern Alps likely represent a migration route from Northern Apennines and the Dinaric Alps refugia during the last glacial period (Magri et al. 2006; Willner et al. 2009).

The presence of Illyrian species, which are endemic or subendemic to the Illyrian region (Trinajstić 1992; Poldini and Galizia Vuerich 1997), has led some authors to frame this community within the suballiance *Saxifrago rotundifoliae-Fagenion* and the alliance *Aremonio-Fagion* (Marinček et al. 1993; Poldini and Nardini 1993; Poldini and Vidali 1993; Marinšek et al. 2013). This hypothesis would also be supported by the analysis of the degradation stages of the submontane, montane, and subalpine horizons, which lead to replacement herbaceous associations that also fall within Illyrian syntaxa (Chiapella Feoli and Poldini 1993). It must be said that some authors do not consider the Illyrian species to be sufficient for framing these communities within the *Aremonio-Fagion*, instead placing them in the more central *Fagion sylvaticae* (Pignatti and Pignatti 2016). Another aspect that is not yet completely clear at the syntaxonomic level is the identification of the communities of *Fagus sylvatica* mixed with *Abies alba*, which are known among foresters as '*Abieti-Fagetum*'. Some authors frame this community as an association in its own right as *Cardamino pentaphylli-Abietetum* Mayer 1974 (Gafta 1994; Poldini and Bressan 2007), while others consider it to be a facies of *Cardamino penthaphylli-Fagetum* (Poldini and Nardini 1993).

The aim of this study is to contribute to the knowledge of the compositional and ecological diversity of forest plant communities, with some suggestions on syntaxonomy, of the Natura 2000 Site 'Cansiglio Forest' (IT3310006).

Methods

Study area

The study area (Figure 2) is located in the 'Foresta del Cansiglio', mainly in the Natura 2000 Site (IT3310006) (https://eunis.eea.europa.eu/sites/IT3310006) in North-Eastern Italy. The reserve covers approximately 2,713 ha, 88% of which is forest, and is managed by the FVG (Cassol et al. 2013).

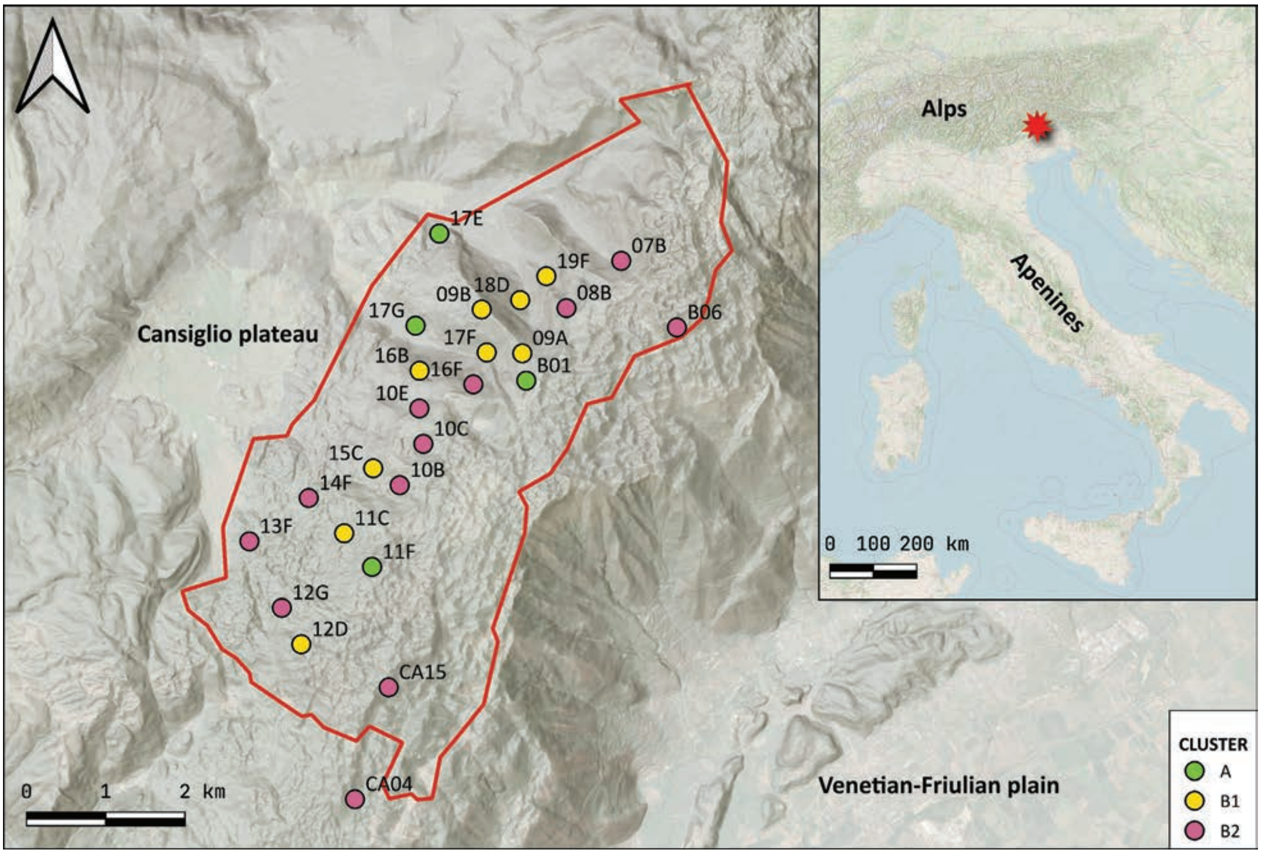

Figure 2. Study area. Perimeter of Foresta del Cansiglio Natura 2000 Site (IT 3310006) in red line and location on Nord East of Italy. Dots in the maps represent the relevés locations, colors according to clusters: **A** *Picea abies* community. **B1** *Fagus sylvatica* with *Abies alba* community. **B2** *Fagus sylvatica* community. Maps based on OpenStreetMap (OpenStreetMap contributors 2015)

The bedrocks consist of limestone and marl of the Monte Cavallo formation (Mantovani et al. 1976), which were deposited in the marine environment of a carbonate reef during the Middle-Upper Cretaceous. The inner plateau of Pian del Cansiglio develops in a Northeast-Southwest direction at an average altitude of about 1000 m a.s.l., while the surrounding mountain crown culminates in Monte Pizzoc (1565 m a.s.l.) and Millifret (1581 m a.s.l.) to the South-West and in Monte Croseraz (1694 m a.s.l.) and the Monte Cavallo group (2250 m a.s.l.) to the North-East. The karst phenomena create numerous cavities, caves, and sinkholes, and they do not allow the development of a superficial hydrographic network. Only in some sinkholes does waterproofing due to the accumulation of clay minerals cause water stagnation.

For climate data, we refer to a historical series from the years 1994 to 2022 from the weather station of 'Cansiglio-Tramedere (TV)' operated by ARPAV (2023) and located at 1022 m a.s.l. on the Cansiglio plateau (Figure 3).

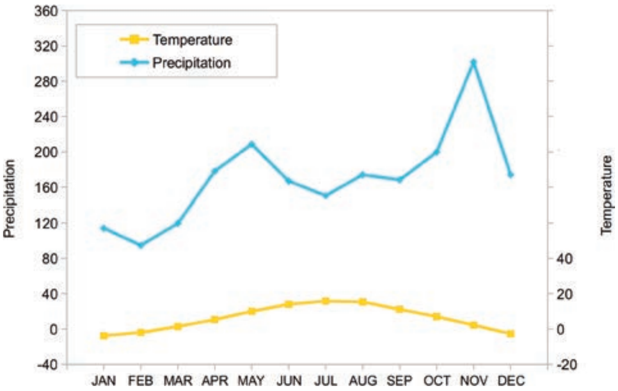

Figure 3. Average monthly temperatures as Celsius degree and precipitation as mm for the years 1994–2000 of Cansiglio – Tramedere station, Veneto, Italy.

The average annual precipitation recorded for the period is 2050 mm, with an average annual temperature of 6.1 °C. The precipitation data show a maximum in November and two other attenuated peaks in May and August. In the Cansiglio plateau, thermal inversion is a common phenomenon in which cold, denser air from the marginal reliefs gets trapped in the valley floor, which has an average altitude of 1015 m. This phenomenon is attributed to the higher elevation of the Crosetta (1120 m) and Campon (1050 m) passes, which hinder air from exiting the plateau. Consequently, this can result in negative temperature peaks of -30 °C during the winter season, causing prolonged snow cover and frequent fog formation (Cassol et al. 2013).

Regarding the edaphic conditions (Garlato and Borsato 2016), the plateau is characterized by Cutanic Alisols (FAO 2006) with an A-EB-Bt horizon sequence, in which clays undergo a translocation process from surface to deep horizons. The very low reaction (pH 4.5–5.4) of these soils is due to the removal of carbonates and bases by infiltrating water. On steep wooded slopes, where rocky outcrops are often widespread, very thin soils of the Epileptic Phaeozems (Calcaric) (IUSS 2007) can be found. These soils are characterized by a high skeleton and organic matter content in the A horizon. On moderately steep wooded slopes characterized by evident karst phenomena, soils with an A-Bt-R profile are present. These soils are thicker than the previous ones but do not exceed 75 cm in any case.

Dataset

We used 25 relevés collected by the authors between 2021 and 2023. All the relevés were carried out according to the 7-step version of the cover-abundance scale of Braun-Blanquet (1964), which was transformed into central class percentage values (r=0.1%, +=0.5%, 1=3%, 2=15%, 3=37.5%, 4=62.5%, 5=87.5%) for statistical analysis. The location of the plots was chosen based on the experimental plots of the LIFE SPAN project, which selected 25 forest plots randomly distributed within the forest and reachable via forest roads. The plot is composed of five circular subplots with a radius of 4 m, strategically positioned: one at the center of the plot and the others placed 12 m apart (center to center) in the directions of 45°, 135°, 225°, and 315°. The total area sampled is approximately 250 m^2. Details of relevés data are presented in Suppl. material 1.

The dataset is composed of three types of matrices: floristic (25 relevés × 94 species), environmental parameters (6 variables × 25 relevés), and indicators matrix (8 variables × 94 species). The environmental parameters matrix comprises variables collected in the field, such as altitude, aspect, slope, percentage of surface rockiness, percentage of tree layer and herbaceous layer cover. The indicators matrix includes Ellenberg indicator values (EIVs) for light, temperature, moisture, soil reaction, and nitrogen (Tichý et al. 2023) and other categories such as phytosociological units at class level (Mucina et al. 2016), chorotypes (Pignatti et al. 2017), and life forms (Dřevojan et al. 2023).

The syntaxonomic reference for diagnostic species of beech forests follows Willner et al. (2017).

Data analysis

Initially, we calculated the average of EIVs weighted on species cover, and the relative percentage cover of each phytosociological unit, chorotype and life-form for each relevé.

The different communities were identified by performing an agglomerative cluster analysis on a Bray-Curtis (Faith et al. 1987; Ricotta and Podani 2017) dissimilarity matrix using Ward's algorithm (Murtagh and Legendre 2014) with the *stats* package (R Core Team 2022). We applied a nonmetric multidimensional scaling (NMDS) ordination (*vegan* package, Oksanen et al. 2016) and identified the gradients of variables involved using the *envfit* function, which fits supplementary variables on ordination scores using multiple regression. Significance of each variable was tested using a permutation test (n = 999) and only significant variables have been plotted (p-value < 0.05). The *indicspecies* package (De Cáceres and Legendre

2009) was used to determine the fidelity between species and clusters by Pearson's *phi* coefficient of association (Chytrý et al. 2020). We applied the phi coefficient equalizing clusters size (Tichý and Chytrý 2006) after transforming our floristic matrix to presence-absence data. A species was determined as diagnostic if it had phi > 0.5, a statistically significant association with a particular cluster (*p*-value < 0.05), and a constancy value equal to or higher than 30%. (Suppl. material 2)

Finally, in order to compare the means of variables between clusters, we performed one-way ANOVA and multiple pairwise-comparisons by Tukey HSD on the variables, respecting the assumptions of normality by Shapiro-Wilk test and homogeneity by Levene's test. When assumptions were not accomplished, we applied the Kruskal-Wallis rank sum test and multiple pairwise-comparisons by Dunn's test with Bonferroni correction for *p*-value.

All analyses and graphics were performed using R software (R Core Team 2022).

Results

The results of the cluster analysis carried out on the floristic matrix show two main groups of relevés (Figure 4a): the first cluster (A) represents the *Picea abies* community, while the second cluster represents the *Fagus sylvatica* forest and is divided into two sub-clusters. The first sub-cluster (B1) is the mixed *Fagus sylvatica* and *Abies alba* community, while the second (B2) is the almost pure *Fagus sylvatica* community.

In the NMDS diagram (Figure 4b), the three clusters do not overlap, and the projections of variables by *envfit* function show several significant correlations with the ordination axes. The first axis is mainly correlated with EIVs of light, temperature, and moisture, as well as with the *Carpino-Fagetea sylvaticae* and *Vaccinio-Piceetea* classes. It is also weakly correlated with altitude, with Central European, Euro-Asian, and Circumboreal chorotypes, as well as with Hemicryptophyte life form.

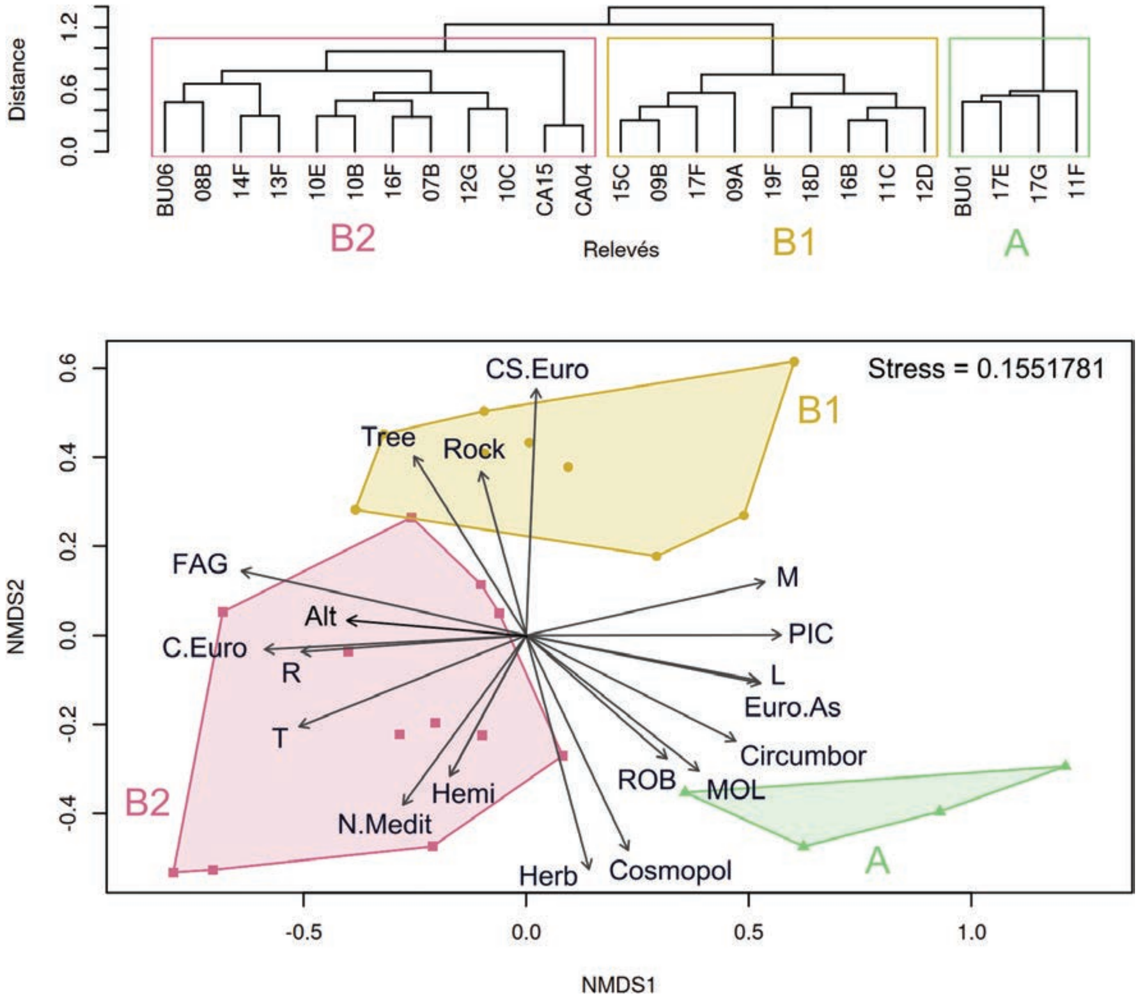

Figure 4. a) Dendrogram of relevés resulting from Ward's minimum variance clustering, with Bray-Curtis distance and **b)** NMDS ordination diagram. Cluster **A** *Picea abies* community. Cluster **B1** *Fagus sylvatica* with *Abies alba* community. Cluster **B2** *Fagus sylvatica* community. Overlaid vectors represent the following variables: EIVs **L** light, **T** temperature, **M** moisture, **R** soil reaction, **FAG** *Carpino-Fagetea sylvaticae*, **PIC** *Vaccinio-Piceetea*, **MOL** *Molinio-Arrhenatheretea*, **ROB** *Robinietea*, **C.Euro** Central European, **Euro.As** Euro-Asian, Circumboreal, **CS.Euro** Central-South European, **N.Medit** North-Mediterranean, **Cosmopol** Cosmopolite, **Hemi** Hemicriptophyte, **Tree** tree layer cover, **Herb** herb layer cover, **Rock** rockiness, **Alt** altitude.

The second axis is mainly correlated with Central-South European and Cosmopolites chorotypes, as well as with the percentage of tree layer, herb layer, and rockiness. It is also weakly correlated with the North-Mediterranean chorotype and *Molinio-Arrhenatheretea* and *Robinietea* phytosociological classes.

From the ordination, the effect of thermal inversion is clearly visible, which places the relevés of A at the lower altitude, with higher EIV of moisture, and the relevés of B2 with higher EIV of temperature, at the top. Another gradient is the phytogeographical one, which orders the relevés according to three directions: in cluster A they are predominantly Circumboreal and Euro-Asian chorotypes, rich in *Vaccinio-Piceetea* species, while in sub-cluster B1 they comprise the Central-South European chorotype and in sub-cluster B2 the Central European chorotype with *Carpino-Fagetea sylvaticae* species and thermophile species from the North of Mediterranean.

Description of clusters and communities

Details of cluster species composition are presented in Suppl. material 2.

Cluster A: Picea abies community (Figure 5)

Diagnostic species of herb layer: *Alchemilla xanthochlora*, *Chaerophyllum hirsutum*, *Hypericum montanum*, *Maianthemum bifolium*, *Myosotis sylvatica*, *Phegopteris connectilis* and *Scrophularia nodosa*.

In the first cluster, *Picea abies* reaches the highest cover and frequency. These relevés are located at an average altitude of 1135 m a.s.l., with relevés 17E and 17G on the edge of the Cansiglio plateau where this community mainly develops, while relevés 11F and B01 are found inside the forest in areas with spruce afforestation. Cluster A is characterized by the lowest EIVs of temperature and soil reaction, and the highest values of moisture and light (Figure 6).

The tree layer is more open, and the herbaceous layer has the maximum cover percentage and the largest number of species, with most of them being Hemicryptophytes. Regarding the chorological spectrum, Circumboreal, Euro-Asian, South-East European, and Cosmopolite species reach the highest values, while Central European and Central-South European species have the lowest values (Table 1).

One of the most frequent diagnostic species is *Chaerophyllum hirsutum*, which, together with mosses, forms a carpet favoured by high moisture. These conditions also favour the growth of *Alchemilla xanthochlora*, *Maianthemum bifolium*, *Myosotis sylvatica*, and *Phegopteris connectilis*, which prefers this acidic substrate. Where the canopy is even more open or towards the fringes, *Hypericum montanum* and *Scrophularia nodosa* occur, especially in the areas often used by ungulates to forage or breed (relevés 17E, 17G). Although in this community *Vaccinio-Piceetea* species reach the highest frequency, the higher abundances correspond to *Carpino-Fagetea sylvaticae* species; furthermore, *Molinio-Arrhenatheretea* and *Robinietea*

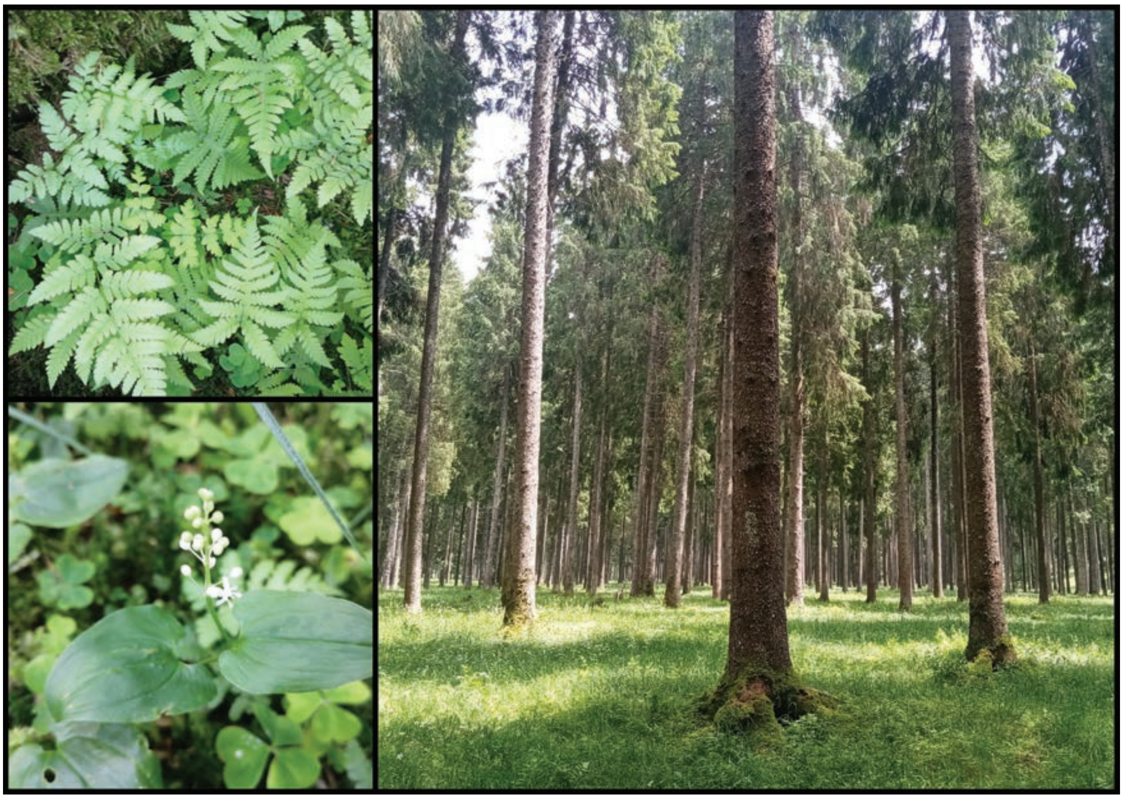

Figure 5. *Picea abies* community. **Top-left**: *Phegopteris connectilis* **Bottom-left**: *Maianthemum bifolium*. **Right side:** relevé 17E on the bottom of Cansiglio plateau.

Table 1. Means and standard deviation of environmental parameters and relative cover as percentage of phytosociological units, chorotypes and life forms. **A** *Picea abies* community. **B1** *Fagus sylvatica* with *Abies alba* community. **B2** *Fagus sylvatica* community. Chi-squared resulting from Kruskal-Wallis test and the letters express the significance of the differences between group means from pairwise comparisons by Dunn test. Only variables with values > 1 for at least one cluster are displayed.

Cluster	**A**		**B1**		**B2**			
Number of sampling sites	**4**		**8**		**13**			
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	***chi*-squared**	***p*-value**
Environmental parameters								
Altitude (m a.s.l.)	1134.5	226.0	1195.1	98.8	1218.9	110.5	0.26734	0.875
Aspect (°)	285.5	42.4	217.8	105.5	230.4	103.6	1.3819	0.501
Slope (°)	18.8	13.1	30.0	8.9	27.7	8.1	1.7814	0.410
Tree cover layer (%)	55.8 a	12.3	97.9 b	12.4	79.6 a	8.8	16.048	0.000 ***
Herb cover layer (%)	85.8 b	17.9	25.0 a	24.8	52.5 ab	22.7	10.774	0.005 **
Rockiness (%)	0.0 a	0.0	10.0 b	7.5	4.4 ab	4.1	9.8493	0.007 **
Phytosociological units								
Carpino-Fagetea sylvaticae	47.3 b	20.03	81.5 a	18.76	93.0 a	6.22	17.08	0.000 ***
Molinio-Arrhenatheretea	10.7 a	7.66	0.0 b	0.02	0.2 b	0.51	11.201	0.004 **
Robinietea	5.4 a	7.78	0.1 b	0.17	1.2 ab	1.23	4.267	0.027 *
Vaccinio-Piceetea	34.0 a	23.36	16.9 ab	19.20	4.5 b	5.52	6.773	0.005 **
Chorotypes								
Central South European	0.00 a	0.00	28.17 b	18.46	3.63 a	6.53	15.109	0.001 ***
Circumboreal	27.9 b	8.93	8.7 a	9.37	6.9 a	6.53	11.29	0.000 ***
Cosmopolite	11.03 a	8.12	0.54 b	0.65	4.05 ab	3.99	10.93	0.004 **
Euro Asian	25.02 b	10.85	10.56 a	12.15	4.53 a	4.19	8.903	0.001 **
Euro Central	8.66 a	12.41	37.31 ab	23.20	55.40 b	12.41	12.59	0.000 ***
Nord Mediterranean	0.00	0.00	0.00	0.00	3.72	8.10	3.0064	0.222
Orophite South European	1.58	2.98	0.48	0.96	0.10	0.35	2.5707	0.277
Paleotemprate	1.05 b	1.03	0.22 a	0.57	0.07 a	0.23	8.0099	0.018 *
South East European	20.00	12.84	8.54	4.83	15.16	10.92	2.0572	0.358
South European	0.01	0.02	3.33	5.04	2.08	4.35	1.4934	0.474
South West European	4.49	2.55	1.81	2.53	3.77	5.39	2.1573	0.340
Life forms								
Geophyte	0.23 a	0.42	5.13 ab	4.58	12.03 b	9.87	10.473	0.005 **
Hemicryptophyte	70.28 b	8.64	19.45 a	5.22	26.91 a	6.75	11.038	0.004 **
Phanerophyte	29.44 a	11.76	74.78 b	15.12	60.06 ab	9.83	13.51	0.001 **

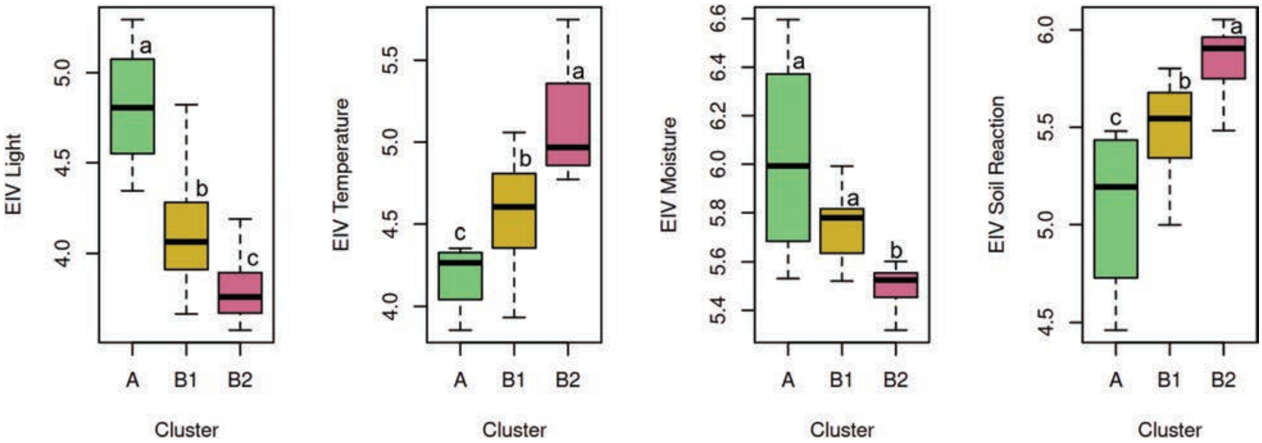

Figure 6. EIVs for light, temperature, moisture and soil reaction for each cluster. Y-axis: values of the EIVs. X-axis: A *Picea abies* community, B1 *Fagus sylvatica* with *Abies alba* community, B2 *Fagus sylvatica* community. Box plots of median, interquartile range and range with different letters express the significance of the differences between group means at $p < 0.05$ according to Tukey's test following a significant ANOVA.

species also occur, due to the position of these relevés close to the grasslands and to the most anthropized part of the study area (Table 1).

Finally, we looked for cluster differences concerning the number of diagnostic species of beech forests indicated by Willner et al. (2017). We found that there are very few species diagnostic of *Aremonio-Fagion*, including the suballiance *Lonicero alpigenae-Fagenion*; however, the number of meso-basiphytic beech forest species remains similar to that of cluster B (Figure 7).

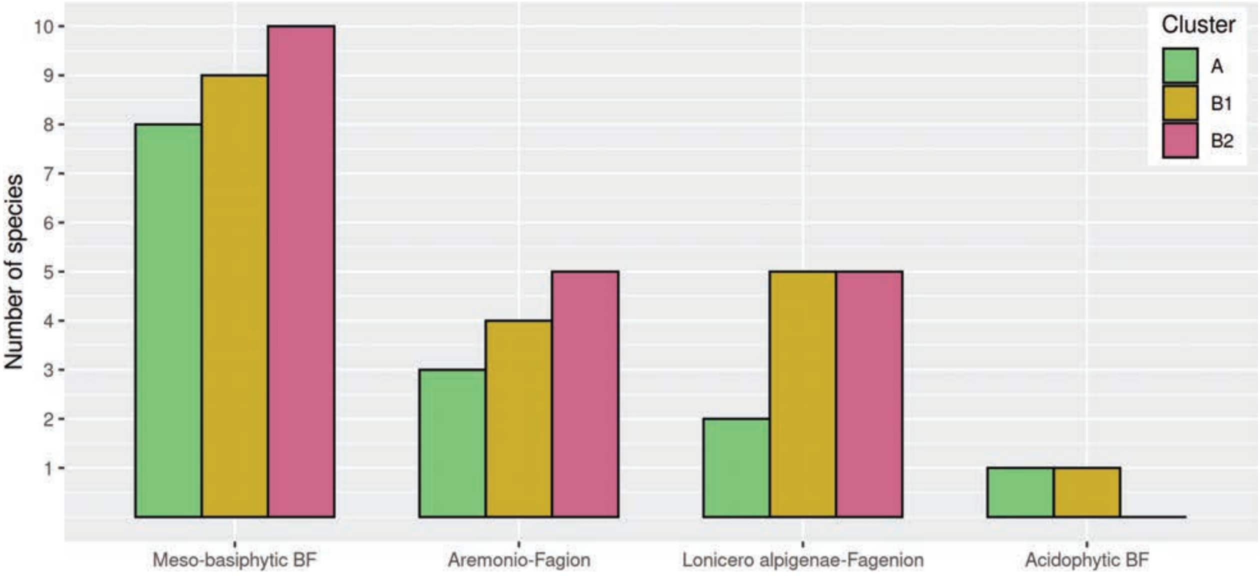

Figure 7. Number of beech diagnostic species according to Willner et al. (2017). X-axis: main groups of diagnostic species for each cluster. Cluster A *Picea abies* community. Cluster B1 *Fagus sylvatica* with *Abies alba* community. Cluster *B2 Fagus sylvatica* community.

Cluster B1: Fagus sylvatica with Abies alba community (Figure 8)

Diagnostic species of herb layer: *Circaea alpina*.

The second cluster consists of eight relevés in which the tree layer is a mixture of *Fagus sylvatica*, *Abies alba*, and sometimes *Picea abies*. These relevés show a greater closure of the canopy and a lower cover of the herbaceous layer in which *Cardamine trifolia* and *Anemone trifolia* achieve the greatest cover and frequency and resulting in *Circaea alpina* being diagnostic. The relevés are positioned mainly on the steepest and rockiest slopes at an average altitude of 1185 m a.s.l. EIVs are intermediate between the other two groups, with significant differences in light, temperature and reaction (Figure 6). Central European species represent the main chorotype, followed by the Central-South European and Euro-Asian ones. The preponderant phytosociological group is the *Carpino-Fagetea*, as for sub-cluster B2, while the species of the *Vaccinio-Piceetea* decrease to about 17% (Table 1).

Cluster B2: pure Fagus sylvatica community (Figure 9)

Diagnostic species of herb layer: *Lathyrus venetus*.

The last cluster is composed of 13 relevés of almost pure *Fagus sylvatica* stands, where *Cardamine pentaphyllos*, *C. enneaphyllos* and *Geranium nodosum* reach maximum cover and frequency. *Lathyrus venetus* occurs as a diagnostic, but it reaches low frequency (31%). This community is present mainly at the top of the massif at an average altitude of 1228 m a.s.l., on Western facing slopes. EIVs for temperature and soil reaction reach the highest values but are lower for moisture and light (Figure 6). The chorological spectrum shows that Central European species predominate, followed by the South-Eastern, then less the Circumboreal, Cosmopolite and the other European species. As for the phytosociological groups, it is almost entirely *Carpino-Fagetea*, with a small percentage of *Vaccinio-Piceetea* (Table 1).

Discussion

Although *Vaccinio-Piceetea* species are most abundant in the *Picea abies* community, the most represented phytosociological group remains the *Fagetalia*. This is common in the *Picea abies* forests of the mountain belt of the Alps. Many of these forests in Friuli originated from beech forests that were converted to spruce forests through silvicultural practices (Poldini and Bressan 2007), although thermal inversion may suggest a natural component in the case of Cansiglio (Pignatti 1998). This results in a difficult syntaxonomic classification, particularly in higher syntaxonomic levels where these montane communities, particularly in areas supporting *Galium odoratum*, are sometimes attributed to the order *Fagetalia* (Leuschner and Ellenberg 2017). The presence of *Milium effusum*, *Ranunculus lanuginosus*, *R. platanifolius*, *Saxifraga rotundifolia*, *Senecio cacaliaster*, and *Stellaria nemorum* could lead to the classification of this community as the association *Senecioni cacaliaster-Piceetum* described by Poldini and Bressan (2007) for the forests of Friuli. These are the mountain spruce forests, particularly rich in megaforbs, that are distributed mainly in the calcareous and dolomitic bedrocks of Carnic Alps (Poldini 1989) on acidic Distric Cambisol and arenitic substrates. Further surveys are needed to investigate the soil features in detail.

The mixed *Fagus sylvatica* with *Abies alba* community mainly develops on the cooler inner Northern slope characterised by stone blocks that favour cold ventilation. The herb layer is poor and characterised by the high frequency of *Oxalis acetosella* and enriched by Illyrian species such as *Anemone trifolia* and *Cardamine trifolia*. A diagnostic species of this mixed forest is *Circaea alpina*, transgressive from the *Vaccinio-Piceetea*, and indicated as a local differential species of the *Abieti-Piceion* by Poldini and Nardini (1993), which attests to its fresh character compared to the pure *Fagus sylvatica* forest, confirmed by EIVs differences.

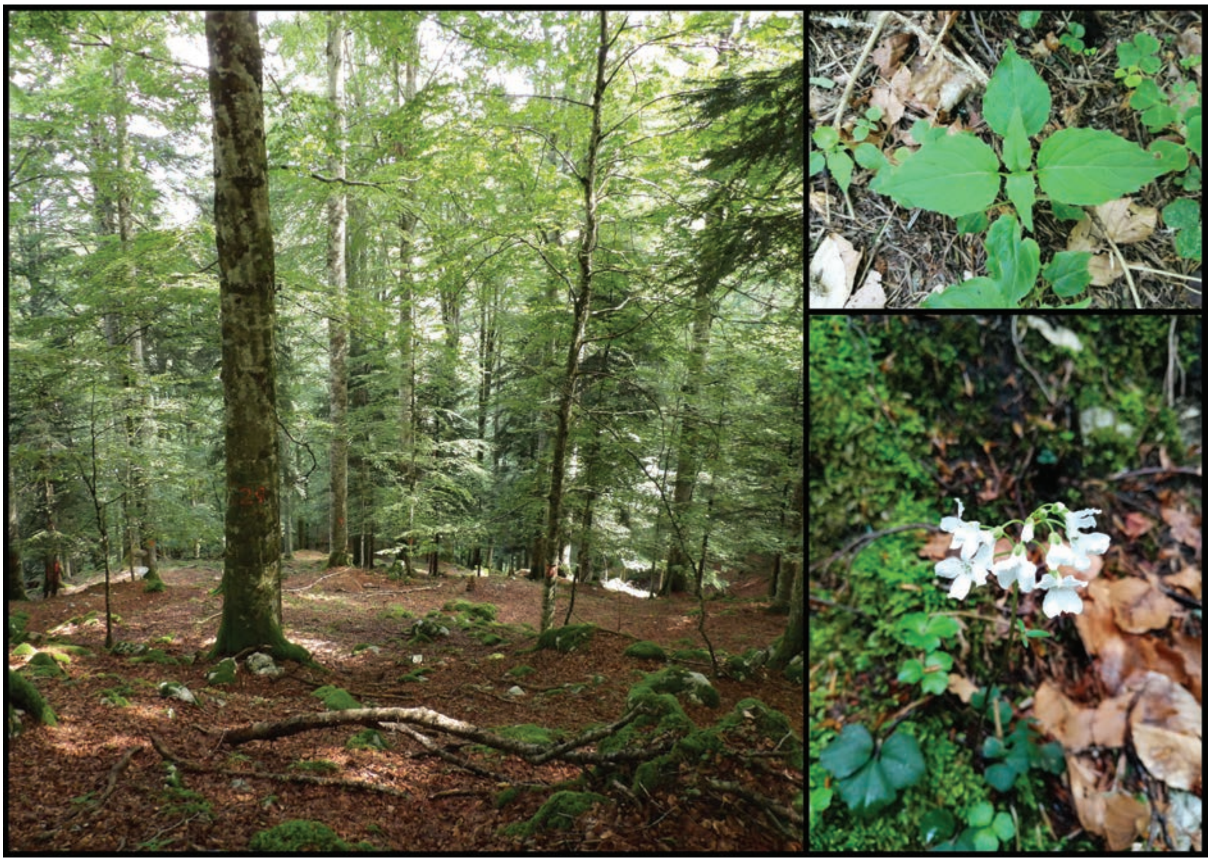

Figure 8. Mixed *Fagus sylvatica* with *Abies alba* community. **Left side:** relevé 16F on the steepest side of Cansiglio forest. **Top-right**: *Circaea alpina*. **Bottom-right**: *Cardamine trifolia*.

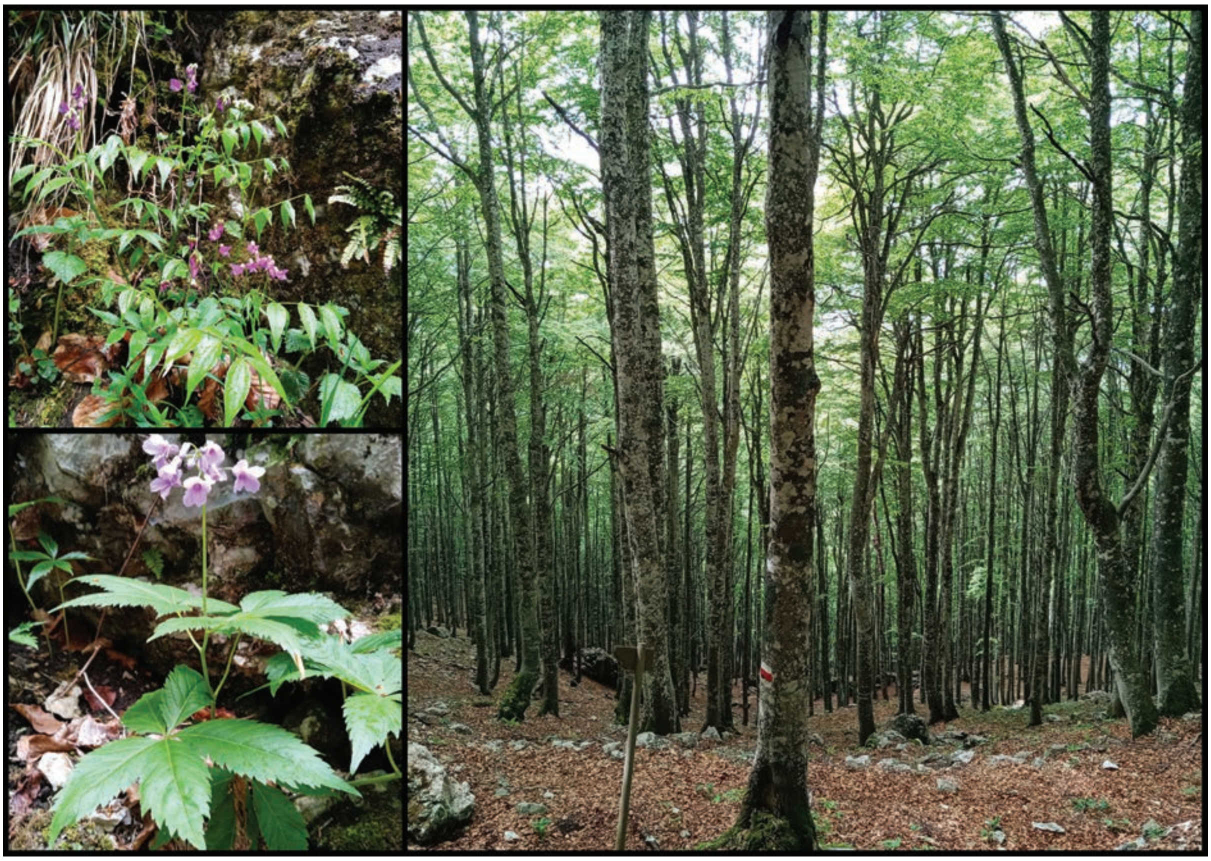

Figure 9. Pure *Fagus sylvatica* community. **Top-left**: *Lathyrus venetus*. **Bottom-left**: *Cardamine pentaphyllos*. **Right side:** relevé 7B on the top of the Cansiglio forest.

Finally, the pure *Fagus sylvatica* community is found in the highest belt, where the influence of warm and humid currents from the Friulan-Venetian plain favours optimal growing conditions for the beech. This community can be identified as the formerly so-called 'high-mountain beech forest with *Dentaria* spp.' (Poldini and Nardini 1993) which is established on deep soils rich in organic matter and skeleton, and is mainly characterised by the presence of mesophilic and hygromorphic species, transgressive from megaforb formations. The herb layer is almost entirely composed of beech forest species, including Illyrian species such as *Cardamine enneaphyllos*, *C. pentaphyllos*, *Geranium nodosum*, and *Lamium orvala*.

Considering the similarity of the floristic composition and the scarcity of diagnostic species, we may consider the mixed silver fir-beech forest as a facies expressing an ecological differentiation of the *Cardamino pentaphylli-Fagetum* Mayer and Hofmann 1969 *fagetosum* Poldini and Nardini 1993, rather than a separate association such as *Cardamino pentaphylli-Abietetum* Mayer 1974, as described for Cansiglio by Gafta (1994) and reported by Poldini and Bressan (2007) for FVG.

At the syntaxonomic level, both the pure beech forest and the silver fir-beech mixed forest can be placed within the meso-basiphytic beech forests, according to the ecological subdivision of European beech forests by Willner et al. (2017), due to the presence of *Actaea spicata*, *Cardamine bulbifera*, *Carex sylvatica*, *Galium odoratum*, *Geranium robertianum*, *Impatiens noli-tangere*, *Lamium galeobdolon*, *Paris quadrifolia*, and *Scrophularia nodosa*. Considering the importance of the phytogeographical and evolutionary issues which characterise the communities in the Eastern side of the Alps and Prealps, in this case, we choose to adopt the phytogeographical subdivision in Willner et al. (2017) and attribute this community to the *Aremonio-Fagion* alliance, thanks to the presence of Illyrian species such as *Adenostyles alpina*, *Anemone trifolia*, *Aposeris foetida*, *Cardamine enneaphyllos* and *Cyclamen purpurascens*. Regarding the suballiance, the presence of *Asplenium viride*, *Cardamine trifolia*, *Homogyne alpina*, *Lonicera nigra*, *Petasites albus*, *Rosa pendulina* and *Veronica urticifolia* places them within the *Lonicero alpigenae-Fagenion*, which includes the *Saxifrago rotundifoliae-Fagenion* proposed by Marinšek et al. (2013) for calcareous soils and described by Poldini and Nardini (1993) for Friuli-Venezia Giulia.

Conclusion

The vegetation of the Cansiglio forest has distinctive characteristics due to various factors, such as karst geomorphology, geographic location, evolution of glacial cover since the last glaciation, and human intervention. The most striking aspect is the karst geomorphology, which is characterized by a closed inner plateau surrounded by a steep mountain crown, resulting in a phenomenon of thermal inversion. This causes a stagnation of cold, moist air, which favours the growth of *Picea abies* at the bottom, although the long history of forest management has also contributed to the establishment of this community. This community could be identified as the *Senecioni cacaliaster-Piceetum* first described by Poldini and Bressan (2007) for the forests of FVG but, due to the scarcity of relevés for this group, further surveying is needed to deepen the knowledge of this community.

Pure and mixed beech stands can be identified as the *Cardamino pentaphylli-Fagetum fagetosum*, with an *Abies alba* facies on cool, Northern slopes, which takes on the physiognomy of the '*Abieti-Fagetum*'. Willner's flexible syntaxonomic approach (Willner et al. 2017) allows us to give importance to the phytogeographical and evolutionary issues and to include these communities in the *Aremonio-Fagion* alliance and the *Lonicero alpigenae-Fagenion* suballiance.

Data availability

Data are included in the electronic appendices.

Author contributions

B.D., F.F., P.C. and F.S. planned the research, F.S. conducted the field sampling, performed the statistical analyses and wrote the text, while all authors critically revised the manuscript.

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Supplementary material

Supplementary material 1
Dataframe of relevés (*.xlsx)
Link: https://doi.org/10.3897/VCS.118821.suppl1

Supplementary material 2
Synoptic table of relevés (*.xlsx)
Link: https://doi.org/10.3897/VCS.118821.suppl2

VEGETATION CLASSIFICATION
AND SURVEY

International Association for Vegetation Science (IAVS)

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LONG DATABASE REPORT

ECOINFORMATICS

IranVeg – the Vegetation Database of Iran: current status and the way forward

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Abstract

Iran, situated in Southwest Asia, showcases a diverse landscape, including three phytogeographical regions and two global biodiversity hotspots. This diversity is attributed to its intricate geology, mountainous terrain, wide altitudinal range, and heterogeneous climate, fostering a rich flora characterized by a significant proportion of endemism. We present an updated version of the Vegetation Database of Iran (IranVeg) (GIVD ID AS-IR-001), comprising 13,411 plots spanning six major habitat types. These encompass deciduous forests (18.0%), woodlands and shrublands (5.6%), steppes and other grasslands (52.0%), saline depressions (9.3%), wetlands (12.2%), and anthropogenic habitats (2.9%), derived from 100 published and unpublished resources, comprising 3,919 plant species, belonging to 961 genera and 147 families. The vegetation data of Iran have been assigned to 31 valid and invalid phytosociological classes. The oldest plots were recorded in 1936 in the Alborz Mountains in northern Iran, while more than 60% of all plots were collected after 2010. Plot sizes vary from less than 1 m^2 to 10,000 m^2 with the highest species richness of 101 species recorded in a 25 m^2 montane grassland plot. IranVeg stands as the first national vegetation database in Iran, promising valuable insights into biodiversity patterns and facilitating the assessment of future environmental and anthropogenic changes. It remains open to further development through a collaborative network of vegetation scientists. This comprehensive database holds significant potential for advancing vegetation classification and survey efforts in Iran and beyond.

Taxonomic reference: World Flora Online (WFO 2024).

Keywords

biodiversity, Iran, macroecology, phytogeography, phytosociology, relevé, Southwest Asia, vegetation-plot database

GIVD Fact Sheet: Vegetation Database of Iran (IranVeg)

GIVD Database ID: AS-IR-001 **Last update:** 2024-09-30

Vegetation Database of Iran (IranVeg) **Web address:**

Database manager(s): Alireza Naqinezhad (anaqinezhad@gmail.com); Jalil Noroozi (jalil.noroozi@univie.ac.at); Soghra Ramzi (s.ramzi91@gmail.com)

Owner: Consortium of the Vegetation Database of Iran (IranVeg Consortium). Individual datasets are owned by the data authors, lists of whom are available within the database.

Scope: IranVeg is a national database from Iran. This database provides 13,411 vegetation plots from various habitats and vegetation types across the whole country.

Abstract: Iran, encompassing a vast territory spanning 1,648,195 km2, features altitudes ranging from 26 m b.s.l. to 5,671 m a.s.l. at Mount Damavand. The country exhibits a diverse range of climatic conditions, from arid regions with less than 50 mm of precipitation in central deserts to areas in the north receiving over 2,000 mm of precipitation annually. This ecological diversity gives rise to various ecosystems and vegetation types across Iran.

The IranVeg database represents a significant initiative aimed at creating a comprehensive repository of Iran's vegetation. This database, which is both geographically and floristically representative at the national level, holds immense value for analyzing biodiversity patterns and forecasting future changes in the region. Its growth is anticipated through the continuous addition of new data contributed by vegetation scientists. The database currently comprises 13,411 vegetation plots. These plots represent a wide array of vegetation types found in Iran, including deciduous forests (18.0%), woodlands and shrublands (5.6%), steppes and other grasslands (52.0%), saline depressions (9.3%), wetlands (12.2%), and anthropogenic habitats (2.9%).

Availability: according to a specific agreement **Online upload:** no **Online search:** no

Database format(s): TURBOVEG, Excel **Export format(s):** TURBOVEG, Excel, CSV file, plain text file

Plot type(s): normal plots, nested plots **Plot-size range (m^2):** 0.0001 to 10000

Non-overlapping plots:	**Estimate of existing plots:**	**Completeness:**	**Status:**
13411	20000	67%	completed and continuing

Total no. of plot observations:	**Number of sources (biblioreferences, data collectors):**	**Valid taxa:**
13411	100	3919

Countries (%): IR: 100

Formations: Forest: 18% = Terrestrial: 18% // Non Forest: 82% = Aquatic: 3%; Semi-aquatic: 9%; Terrestrial: 70% (Arctic-alpin: 8%; Non arctic-alpin: 62% [Natural: 59%; Anthropogenic: 3%])

Guilds:

Plot size categories (%): < 1 m2: 24.3%; 1-10 m2: 17.7%; 10-100 m2: 28.8%; 100-1000 m2: 19.9%; 1000-10000 m2: 1.0%; >= 10000 m2: 0%; unknown: 8.3%;

Environmental data (%): altitude: 80; slope aspect: 50; slope inclination: 60; microrelief: 9; surface cover other than plants (open soil, litter, bare rock etc.): 38; other soil attributes: 21; soil pH: 29; land use categories: 16; other attributes: organic matter (21), nitrogen (22), phosphorus (13), potassium (14), calcium carbonate (11), electrical conductivity (17), sand (25), silt (25), and clay (25)

Performance measure(s): presence/absence only: 10.8%; cover: 89.2%

Geographic localisation: GPS coordinates (precision 25 m or less): 70.6%; political units or only on a coarser scale (above 10 km): 29.4%

Sampling periods: before 1920: 0%; 1920-1929: 0%; 1930-1939: 0.2%; 1940-1949: 0%; 1950-1959: 0.1%; 1960-1969: 0.1%; 1970-1979: 5.3%; 1980-1989: 1.1%; 1990-1999: 6.4%; 2000-2009: 25.7%; 2010-2019: 58.9%; after 2020: 2.1%; unknown: 0%

Information as of 2024-10-01; further details and future updates available from http://www.givd.info/ID/AS-IR-001

Introduction

Iran, located in Southwest Asia and spanning over 1,648,000 km^2 between 25° and 40° northern latitude and 44° and 63° eastern longitude, features a diverse topography with approximately 62% of its terrain situated above 1,000 m a.s.l. (Noroozi et al. 2019a). The country has been called a country of extremes in SW Asia (Akhani 1998) and elevation varies from 26 m b.s.l. on the southern Caspian Sea shores to 5,671 m a.s.l. at the summit of Mt. Damavand, the highest summit in SW Asia. The country encompasses three macrobioclimatic zones – temperate, mediterranean and tropical – yielding ten bioclimates defined by temperature and precipitation (Djamali et al. 2011). Annual precipitation ranges from below 30 mm in the desertic Dasht-e-Lut, in southern Iran, to above 2,000 mm in the Hyrcanian deciduous forests of the north (Akhani et al. 2010; Gholizadeh et al. 2020). Mean temperatures of the coldest and warmest months vary from -13.3 °C in Firuzkuh (Alborz Mts) to 47.5 °C in the Kerman deserts (Djamali et al. 2011). Furthermore, Iran's geological structure is intricate, characterized by formations of diverse origin (plutonic, volcanic, sedimentary, and metamorphic), age (Precambrian to Quaternary) and composition (Stöcklin 1968; Berberian and King 1981).

The huge climatic, topographic and edaphic variation lead to a rich floral history and high evolutionary potential (Klein 1990; Akhani 1998). The country lies at the interface of three phytogeographical regions: the "Euro-Siberian" along Caspian Sea shores in the north, the "Irano-Turanian" covering most of the country, and the "Saharo-Sindian" along the Persian Gulf and the Oman Sea in the south (Zohary 1973; Léonard 1981–1989). This environmental and phytogeographical diversity fosters a rich floristic diversity of the country embracing more than 8,000 vascular plant species, 32% of which are endemics (Noroozi et al. 2019a). Notably, Iran hosts two global biodiversity hotspots (Caucasian and Irano-Anatolian; Mittermeier et al. 2011) and five areas of endemism, i.e. Zagros, Alborz, Azerbaijan Plateau, Kopet Dagh-Khorassan, and Yazd-Kerman (Noroozi et al. 2019a, 2019b).

The northern slopes of the Alborz Mountain range, extending from the Caspian Sea shores up to 2,800 m a.s.l., are covered by temperate deciduous Hyrcanian forests, a UNESCO World Heritage Site (World Heritage Convention 2019). These forests preserve the phylogenetic heritage of the late Tertiary period, housing endemic Arcto-Tertiary floristic elements (Bobeck 1951; Browicz 1989; Frey et al. 1999; Gholizadeh et al. 2020; Ghorbanalizadeh and Akhani 2022). In the Zagros Mts, the largest mountain range of Iran, the "Kurdo-Zagrosian oak steppe-forest" (*sensu* Zohary 1973) is dominated by diverse *Quercus* species distributed throughout (Sabeti 1976; Sagheb Talebi et al. 2014; Ambarlı et al. 2018, 2020). While the mountains harbor the bulk of Iran's flora and endemics, the central plateau is characterized by low species richness (Zohary 1973; Frey and Probst 1986; Léonard 1991–1992; Noroozi et al. 2019a, 2019b). The harsh and dry conditions prevailing in this region due to low rainfall and high evaporation rates, support primarily xerophytic species. Dominant vegetation types include xerophytic pistachio-almond forest-steppes, *Artemisia* steppes, psammophytic vegetation and halophytic vegetation in saline depressions (Zohary 1973; Frey and Probst 1986; Léonard 1991–1992; Ghahreman and Attar 1999; Asri 2003; Akhani 2004). Moreover, steppes and grasslands including thorn-cushion and dwarf shrubland vegetation predominantly cover the vast mountain ranges of Iran (Zohary 1973; Noroozi 2020). The presence of two distinct coastal regions, along the Caspian Sea in the north and bordering the Persian Gulf and Oman Sea in the south, further enriches Iran's biodiversity. These coastal habitats, characterized by specific vegetation and habitat types, face various threats, as noted by Tirgan et al. (2022) for the south Caspian coastline. The coastal regions on the Persian Gulf are characterized by *Acacia* and *Prosopis* semidesert shrublands and mangroves (Frey and Probst 1986; Léonard 1991–1992; Akhani and Ghorbanli 1993; Akhani and Samadi 2015).

Despite its location in the arid region of Southwest Asia, Iran boasts 26 internationally recognized Ramsar wetland sites, covering approximately 1% of its total surface area, as reported by the Ramsar Organisation (Convention on Wetlands Secretariat 2024). Moreover, montane wetlands, including fens, bogs, riverine, and spring types, are dispersed across the steppe-covered mountains of Iran, and play a vital role in biodiversity conservation. Many of them exist as isolated, patchy, and remote habitats within the broader arid environment, functioning as ecological oases. These spot-like wetlands support highly unique and specialized ecosystems, providing refuge for rare and endangered flora and fauna (Kürschner and Djamali 2008; Djamali et al. 2009; Naqinezhad et al. 2019; Fensham et al. 2023). Studies by Jalili et al. (2014) and Naqinezhad et al. (2021) emphasize their significance, underlining the crucial role these habitats play in preserving biodiversity, despite their limited and fragmented distribution.

The history of botanical surveys in Iran is rich, with contributions from distinguished publications such as Boissier (1867–1888), Parsa (1943–1980), Rechinger (1963–2015), Assadi et al. (1988–2024) and Ghahreman (1976–2007). Subregional floras complement national efforts, including for example "Flora of Ilam" (Mozaffarian 2008), "Flora of Gilan" (Mozaffarian 2019), "Illustrated Flora of Golestan National Park" (Akhani 2005, 2023), "Illustrated Flora of Alborz Mountain Range Iran" (Noroozi and Talebi 2023) and many others.

Pioneering efforts in vegetation description, classification and mapping using physiognomic-ecological approach by Bobeck (1951), Zohary (1963, 1973), Mobayen and Tregubov (1970), Probst (1972, 1981), Frey and Probst (1977, 1986), Frey and Kürschner (1979), Frey (1980) and Frey et al. (1999) laid the foundation for subsequent research. In a paper entitled "On the geobotanical structure of Iran", Zohary (1963) was the first to tentatively describe 54 associations from 26 classes in all parts of the country using a physiognomic/ecologic survey. However, all these associations are considered as "nomina nuda" due to inappropriate descriptions of associations and vague lists of associated species (Léonard 1993; Theurillat et al. 2021). Phytosociological studies further elucidated specific habitat types, including forests and woodlands (Djazirei 1964, 1965; Mossadegh 1971; Dorostkar and Noirfalise 1976; Assadollahi 1980; Rastin 1980, 1983; Akhani and Ziegler 2002; Hamzeh'ee et al. 2008; Ravanbakhsh et al. 2018; Gholizadeh et al. 2020; Karami-Kordalivand et al. 2021; Esmailzadeh and Soofi 2022), alpine and montane steppes (Gilli 1939; Klein 1984, 1987; Klein and Lacoste 1994, 1999; Noroozi et al. 2010, 2014, 2017; Akhani et al. 2013; Mahdavi et al. 2013; Naqinezhad and Esmailpoor 2017), lowland steppes, inland and coastal dunes (Léonard 1991–1992; Asri 2003; Naqinezhad 2012a; Mahdavi et al. 2017; Tirgan et al. 2022), wetlands (Asri and Eftekhari 2002; Asri and Moradi 2006; Asri et al. 2007; Naqinezhad et al. 2009, 2021; Kamrani et al. 2011), and halophytic and saline vegetation (Carle and Frey 1977; Akhani and Ghorbanli 1993; Asri and Ghorbanli 1997; Asri 1999; Alaie 2001; Akhani 2004, 2006; Ghorbanalizadeh et al. 2020; Ghorbanalizadeh 2022). In addition to phytosociological studies, some research endeavors aimed to assess various elements of biodiversity along environmental gradients (Rahmanian et al. 2020, 2023; Talebi et al. 2021) and to implement biodiversity monitoring, examining the impacts of various management regimes (Valadi et al. 2022; Sanaei et al. 2023; Bashirzadeh et al. 2024).

Vegetation-plot databases play a pivotal role in large-scale analyses such as vegetation classification and mapping, floristic diversity studies, habitat management, biogeographical analysis and biodiversity assessment and monitoring (Wiser 2016; Chytrý et al. 2020; Loidi et al. 2021; Sabatini et al. 2022). Accessing data sources becomes crucial particularly when conducting synthetic analyses to tackle overarching ecological challenges within macroecological objectives (Madin et al. 2007). Over the years, millions of vegetation plots have been meticulously recorded and partially digitized for specific local purposes (Dengler et al. 2011; Bruelheide et al. 2019). To address deficiencies in vegetation survey data and bridge the gap between community ecology and macroecology, it is imperative to amalgamate individual vegetation datasets into comprehensive databases that span expansive geographic regions (Dengler et al. 2011, 2018; Wiser 2016; Sabatini et al. 2021).

Iran's vegetation data, collected since the 1930s through extensive fieldwork, have now been consolidated into the IranVeg database, representing an important national effort to catalog and organize the country's diverse plant communities. This comprehensive resource aims not only to provide a platform for advancing vegetation ecology research but also to address critical questions related to biodiversity conservation, ecosystem services, and climate change resilience. The IranVeg database offers a wealth of information for researchers, conservationists, and policymakers alike, facilitating large-scale analyses of vegetation patterns, species distributions, and habitat dynamics across Iran's varied landscapes. By integrating decades of field observations with modern analytical tools, it paves the way for interdisciplinary studies, fostering collaborations between community ecology, macroecology, and conservation biology. This paper offers a detailed overview of the IranVeg Vegetation Database, highlighting its foundational objectives, methodological framework, and the transformative potential it holds for future ecological research and sustainable development in Iran and beyond. With this database, we hope to inspire and empower vegetation scientists and ecologists to explore new frontiers in understanding vegetation and plant biodiversity in arid and semi-arid regions of Western Asia and beyond.

Database development, structure and management

The Vegetation Database of Iran (IranVeg) was unveiled during the 9th International Meeting on Vegetation Databases at Hamburg University, Germany, in February 2010. At the meeting, the Global Index of Vegetation-Plot Database (GIVD) was launched (Dengler et al. 2010), and a total of 2,000 plots were registered in GIVD as the "Vegetation Database of Iran" (ID AS-IR-001). This dataset was described in a special volume of "Biodiversity and Ecology" dedicated to the meeting (Naqinezhad 2012b). Additionally, three smaller datasets were also registered in GIVD, namely the "Vegetation database of mountain wetlands" (ID AS-IR-002; Naqinezhad 2012c), the "Vegetation database of the Hyrcanian area" (ID AS-IR-003; Naqinezhad 2012d) and the "Alpine Vegetation of Iran" (ID AS-IR-004). By 2015, these datasets were consolidated into a unified national database, retaining the GIVD ID AS-IR-001, comprising a total of 2,335 plots.

IranVeg is a self-governed consortium in which every data contributor becomes a member. The Custodian and a Deputy Custodian were provisionally elected to coordinate the database, with A. Naqinezhad the current Custodian and J. Noroozi and S. Ramzi the Deputy.

Since January 2022, we have initiated a comprehensive work plan to update the Vegetation Database of Iran and add newer data. This involved conducting a thorough survey of all available vegetation literature and collaborating with authors. Consequently, our database consists of data from published resources by either digitizing old literature or access to direct stored excel spreadsheets/TURBOVEG xml files of the authors (68%) and unpublished data (32%) (Suppl. material 1).

Management of the database is done with TURBOVEG (Hennekens and Schaminée 2001). All data have been sourced directly from the original references. In addition to the comprehensive list of plant species, some plots also contain recorded environmental data such as altitude, slope, aspect, and physical and chemical soil characteristics. Coordinates have been meticulously handled. While some were directly reported with GPS precision, others were derived from the central point of the study area (county, city, village, specific site, etc.) using Google Earth engine with a precision of 5 km. To ensure consistency, all coordinates have been standardized and are presented in decimal degrees throughout the dataset. The species nomenclature was standardized using the *U.Taxonstand* package in R (Zhang and Qian 2023), and harmonized with the World Flora Online database (WFO 2024).

Finally, we assigned the plots in IranVeg to six major habitat types to better describe them. This classification was not based on statistical analysis but was rather a descriptive grouping. However, since phytosociological classification analyses have been performed on most of the sources from which the plots were extracted, we were able to assign these plots with greater accuracy. Species richness was also reported within these predefined groups. Given that plot size is an important driver of biodiversity, we excluded plots with sizes outside the central 95% percentile when reporting area/species richness relationship in each habitat.

Database content

The updated edition of the "Vegetation Database of Iran (IranVeg)" now comprises 13,411 plots spread across Iran, averaging 0.8 plots per 100 km^2, with a notable concentration in the northern regions (Figure 1). The plots in IranVeg in question likely account for approximately 67% of all plots surveyed in Iran, exhibiting substantial overlap with 392 plots in GIVD ID: AS-IR-005 (Mahdavi and Akhani 2015) and 1,597 plots in GIVD ID: AS-IR-006 (Gholizadeh et al. 2019). The majority of the recorded plots have been collected through vegetation surveys based on the phytosociological approach, while the remainder consists of biodiversity and monitoring plots, including 209 series of nested plots spanning various habitat types.

Out of 13,411 plots compiled in IranVeg, 7,375 have already been included in the emerging version 4.0 of the global database sPlot (https://www.idiv.de/en/sdiv/working-groups/wg-pool/splot/splot-database.html; see Bruelheide et al. 2019) and 2,875 in the Palaearctic database GrassPlot, version 2.00 (Dengler et al. 2018; Biurrun et al. 2019).

The predominant methods of vegetation survey employed by vegetation ecologists working in Iran were the 7-step and 9-step versions of the Braun-Blanquet cover-abundance scales, derived from the Zurich-Montpellier

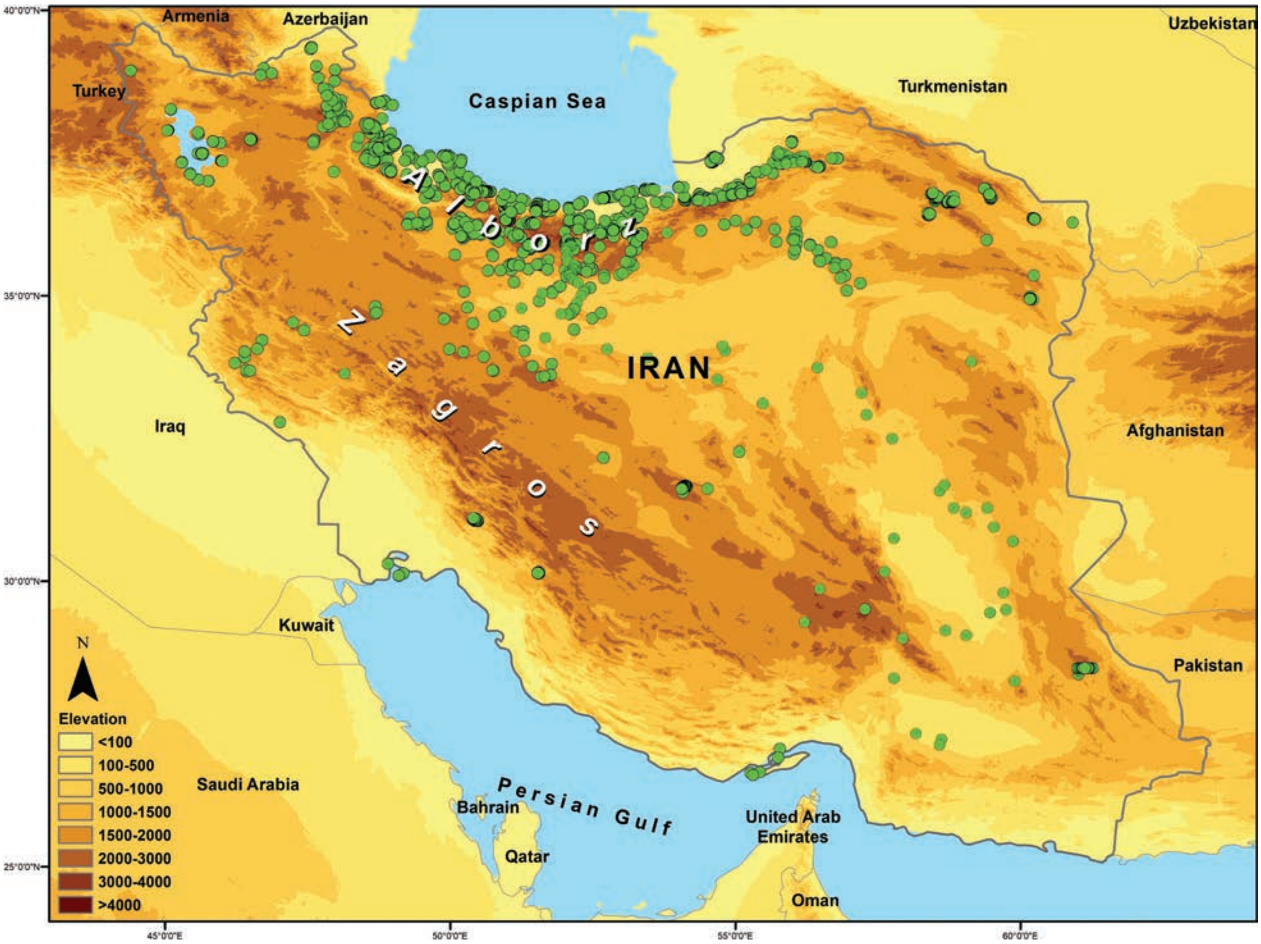

Figure 1. Topographic map of Iran showing the spatial distribution of IranVeg plots across the country.

School (Braun-Blanquet 1964). As a result, the majority of the registered plots (58.9%) have been collected utilizing these scales. Additionally, the vegetation cover of 27.1% of plots was represented in direct percentage (see Dengler and Dembicz 2023), 10.8% as presence/absence, 2.3% with the van der Maarel scale (van der Maarel 1979) and 1.0% on the Londo scale (Londo 1976).

Plot sizes varied wildly from less than 1 m^2 to 10,000 m^2, while in 8.4% of the plots size was not reported (Fact Sheet, Figure 2). The oldest plots were recorded in the 1930s (1936) in the high regions of the Alborz Mountains in northern Iran (Gilli 1939). Notably, there were no additional reports in the 1940s, and more than 60% of plots were recorded after 2010 (Fact Sheet, Figure 3). About 71% of plots were georeferenced with GPS coordinates at a precision of 25 m or less, while the coordinates for others were derived from the central point of the study area (county, city, village, specific sites, etc) using Google Earth engine with a precision of 5 km (Fact Sheet).

The dataset encompasses several crucial environmental variables. The most frequently recorded variables are altitude, slope, and aspect recorded in 80%, 60%, and 50% of the plots, respectively. Furthermore, some plots have documented edaphic factors from which pH (28.7%), and physical soil characteristics such as the proportions of sand, silt, and clay (25%) constitute the most recorded soil data (Table 1).

IranVeg comprises records of 3,912 species of vascular plants and seven species of bryophytes, distributed across 961 genera and 147 families. The dominant families include *Asteraceae*, *Fabaceae* and *Poaceae*, with *Astragalus* being the most species rich genus in the database. Species richness within the stored plots varies, ranging from 1 (in plots of 4, 16 and 25 m^2) to 101 (in 25 m^2), with approximately two-thirds of the plots containing fewer than 20 species.

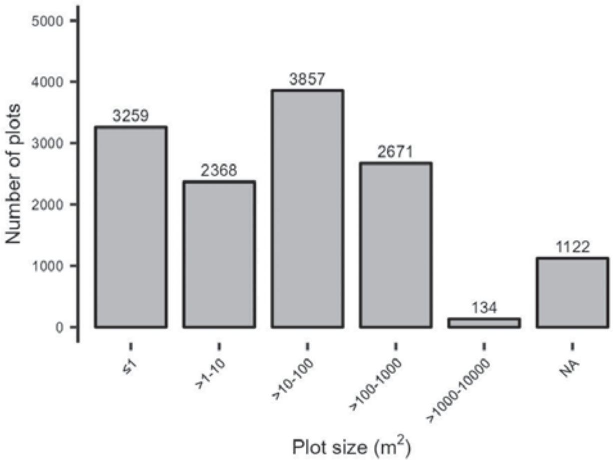

Figure 2. Plot size distribution in the IranVeg database. NA: plots without size information.

Table 1. Environmental variables recorded in the IranVeg database.

Variable	Measurement unit	Availability in the database (%)	Min.	Max.	Mean	Median
Altitude	m a.s.l.	80	-26	4799	2019	2100
Slope	°	60	0	85	23	22
Slope aspect	°	50	0	360	142	140
Total cover	%	32	0.2	165	64	70
Microrelief	cm	9	0	400	48	30
Organic matter	%	21	0.03	47.7	7	6.2
pH	-	29	2.7	8.8	7	6.9
N	%	22	0	5.3	0.4	0.4
P	ppm	13	0	122	16	4.4
K	ppm	14	3.9	4022	470	346
$CaCO_3$	%	11	0.5	37.5	2	6.2
Electrical conductivity	µS/cm	17	0.15	4280	242	112
Sand	%	25	0	99.7	50	54.9
Silt	%	25	0.06	66.7	24	24
Clay	%	25	0	71	18	14.6

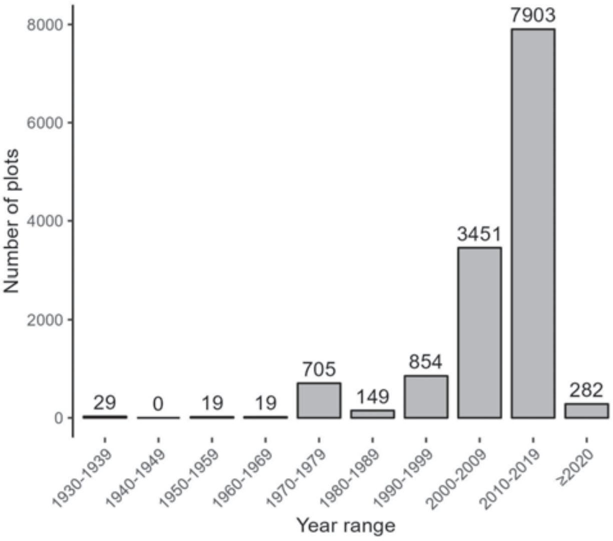

Figure 3. Temporal distribution of vegetation plots included in the IranVeg database (1936–2023).

Major habitat types

Given that the compilation of Iranian vegetation data is an ongoing project and still far from completion, any classification of habitats or large physiognomic vegetation types should be grounded in the plots collected thus far. Currently, based on the available plot data, six major habitat types can be distinguished in IranVeg.

1) Deciduous forests: The deciduous temperate forest in northern Iran represents 18.0% of the plots in the database (Figures 4, 5). These plots are characterized by notable species richness, typically containing 20 to 40 species per plot, with sizes ranging from 20 to 400 m², with an average size of 371 m² (Figure 6). Hyrcanian forests are generally categorized into four main elevational zones: lowland, submontane, montane and upper-montane (see Gholizadeh et al. 2020). Dominant tree species in these forests include *Fagus orientalis*, *Carpinus betulus*, *Quercus castaneifolia*, *Q. macranthera*, *Parrotia persica*, *Alnus glutinosa*, *A. subcordata*, *Populus caspica* and *Pterocarya fraxinifolia* (Akhani et al. 2010; Sagheb Talebi et al. 2014) (Figures 7a–c).

Recent comprehensive phytosociological surveys of the Hyrcanian forests identified eight alliances and 26 associations belonging to five orders and four classes, namely *Alnetea glutinosae*, *Alno glutinosae-Populetea albae*, *Carpino-Fagetea sylvaticae* and *Quercetea pubescentis* (Gholizadeh et al. 2020; Karami-Kordalivand et al. 2021; Esmailzadeh and Soofi 2022). A large number of plot data used in the datasets were extracted from old doctoral theses and related publications carried out by some European institutions (Djazirei 1964, 1965; Mossadegh 1971, 1981; Dorostkar 1974; Dorostkar and Noirfalise 1976; Assadollahi 1980; Rastin 1980, 1983; Assadollahi et al. 1982; Klein and Lacoste 1989).

2) Woodlands and shrublands: Woodlands and shrublands account for 5.6% of all plots in the current database (Figures 4, 5). Species richness in most plots of this major habitat type ranges from 1 to 20 species per plots, with sizes ranging from 2 to 400 m² and an average of 180 m², with the highest recorded richness being 87 species in a plot of 16 m² (Figure 6). This major habitat type comprises plots accommodated in various drought-adapted "forest/shrubby steppes" dominated by oak, juniper, pistachio-almond and *Acacia-Prosopis* in the Irano-Turanian and Saharo-Sindian regions of Iran (Frey and Probst 1986; Erdős et al. 2018; Noroozi et al. 2020; Ambarlı et al. 2020). Along the Zagros Mountain ranges, the climax vegetation is an open xerophytic cold-resistant deciduous oak woodland steppe which dominates between 1,000 and 2,000 m a.s.l. and accounts for almost 40% of Iran's forests/woodlands (Sagheb Talebi et al. 2014) (Figure 7d). Zohary (1973) described this formation as "Kurdo-Zagrosian oak steppe-forest" which forms a rather broad belt in western and southwestern Iran to Iraq. *Quercus brantii*, *Q. infectoria*, and *Q. libani* are dominant species in these habitats. Moreover, the arid and semi-arid gentle slopes of the mountains of Iran are mainly covered by open xerophytic scrub/shrub communities. These communities were named

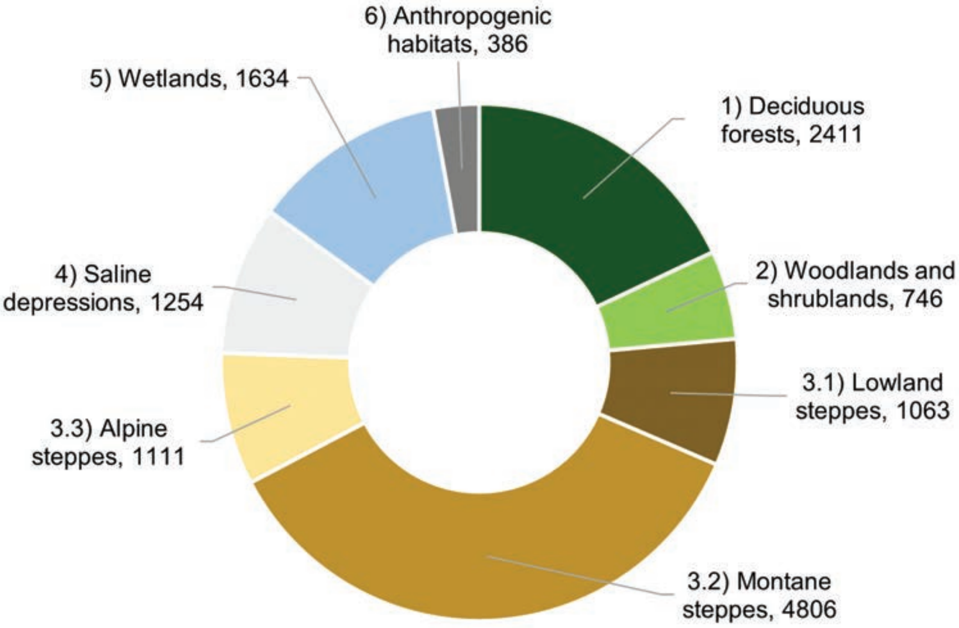

Figure 4. Distribution of vegetation plots in the IranVeg database across major habitat types.

"Pistazien-Mandel-Ahorn-Trockenwald" by Bobeck (1951) and "*Juniperus-Pistacia-Amygdalus*-steppe scrub" by Zohary (1973). This pistachio-almond shrub steppe is generally characterized as a transitional community located on rather gentle slopes between lowland *Artemisia*-dominated desert steppe areas and thorn-cushion formations of montane steppe, and is characterized by *Pistacia atlantica*, *P. khinjuk* and *Prunus scoparia* as the main species (Figure 7e). Long-term land use and overgrazing have degraded these woodlands (Djamali et al. 2008, 2011), leading to their replacement by thorn-cushion montane steppes at higher altitudes and *Artemisia* steppes at lower altitudes (Djamali et al. 2011). Our vegetation database also embraces plots from juniper woodlands in the montane and subalpine zones of the Iranian mountains up to 3,000 m a.s.l. (Zohary 1973; Frey and Probst 1986; Ravanbakhsh et al. 2016). These woodlands, which range from sparsely distributed to dense forest-like, occur almost at the same elevation band of montane thorn-cushion steppes and are intermixed with such communities (Memariani et al. 2016). The main species on the dry southern slopes are *Juniperus polycarpos* and associated species (see Memariani et al. 2016; Hojjati et al. 2018) which are different from the carpet-like formations of *J. communis* and *J. sabina* that cover the subalpine zone of the northern humid slopes of the Alborz Mts (Figure 7f). Moreover, the relict Mediterranean woodland community of *Cupressus sempervirens* on the northern slopes of Alborz Mts, can be added to this group (Zohary 1973; Frey and Probst 1986) (Figure 7g). The group of woodlands and shrublands also includes extremely xeromorphic savanna-like woodlands in the Saharo-Sindian region of southern Iran, where *Vachellia tortilis*, *V. oerfota*, *V. flava*, *Prosopis cineraria*, *P. koelziana*, *Ziziphus spina-cristi* and *Haloxylon salicornicum* are the dominant species (Frey and Probst 1986; Hamzeh'ee 1999; Nadjafi Tirehe-Shabankareh et al. 2006; Akhani and Samadi 2015) (Figure 7h).

The syntaxonomic classification of this habitat type is still far from complete. There are 10 validly published associations from this habitat, belonging to four alliances, four orders and three classes, namely *Pistacietea verae* (Nowak et al. 2024a), *Junipero-Pistacietea* (Zohary 1963) and *Quercetea brantii* Zohary 1963 (Ravanbakhsh et al. 2016; Hamzeh'ee 2017).

3) Steppes and other grasslands: Over half (52.0%) of the available plots encompass a diverse array of habitats broadly categorized as steppes and other grasslands. The term "steppe and other grasslands" is used as a broad sense (see Zohary 1973; Akhani 1998) and includes a variable array of physiognomy encompassing mesophytic to xerophytic, non-arboreal vegetation types covered by very dense to very sparse dwarf-shrubs, thorn-cushions or hemicryptophytes (excl. forests, woodlands, wet grasslands and halophytic communities) (see Akhani 1998; Ambarlı et al. 2018, 2020; Noroozi 2020; Talebi et al. 2021). This major habitat ranges from lowland arid/semi-arid playas up to 4,200 m a.s.l. in the alpine zone. We also included snowbed vegetation and other patchy montane mesophytic meadows/grasslands into this definition. Despite the presence of numerous transitional zones in the dataset and some azonal habitats such as chasmophytic vegetation, we propose three broad classes of steppes in Iran meeting general elevational gradients and main physiognomic-ecologic features.

3.1) Lowland steppes (7.9% of all plots; Figures 4, 5): This category sometimes called "*Artemisia* steppes" (see Zohary 1973; Akhani 1998; Ambarlı et al. 2018) comprises desertic and semi-desertic steppes of plains and undulating gentle slopes of vast areas of Iran and generally occurs below 1,200 m a.s.l. Lowland steppes are predominantly characterized by *Artemisia* spp., which are herbs or dwarf-shrubs of the *Asteraceae* family and typically have an aromatic and bluish-silvery appearance (Ambarlı et al. 2020) (Figure 7i). The density and floristic composition of these steppes are influenced by various factors, including edaphic conditions, annual precipitation, duration of the

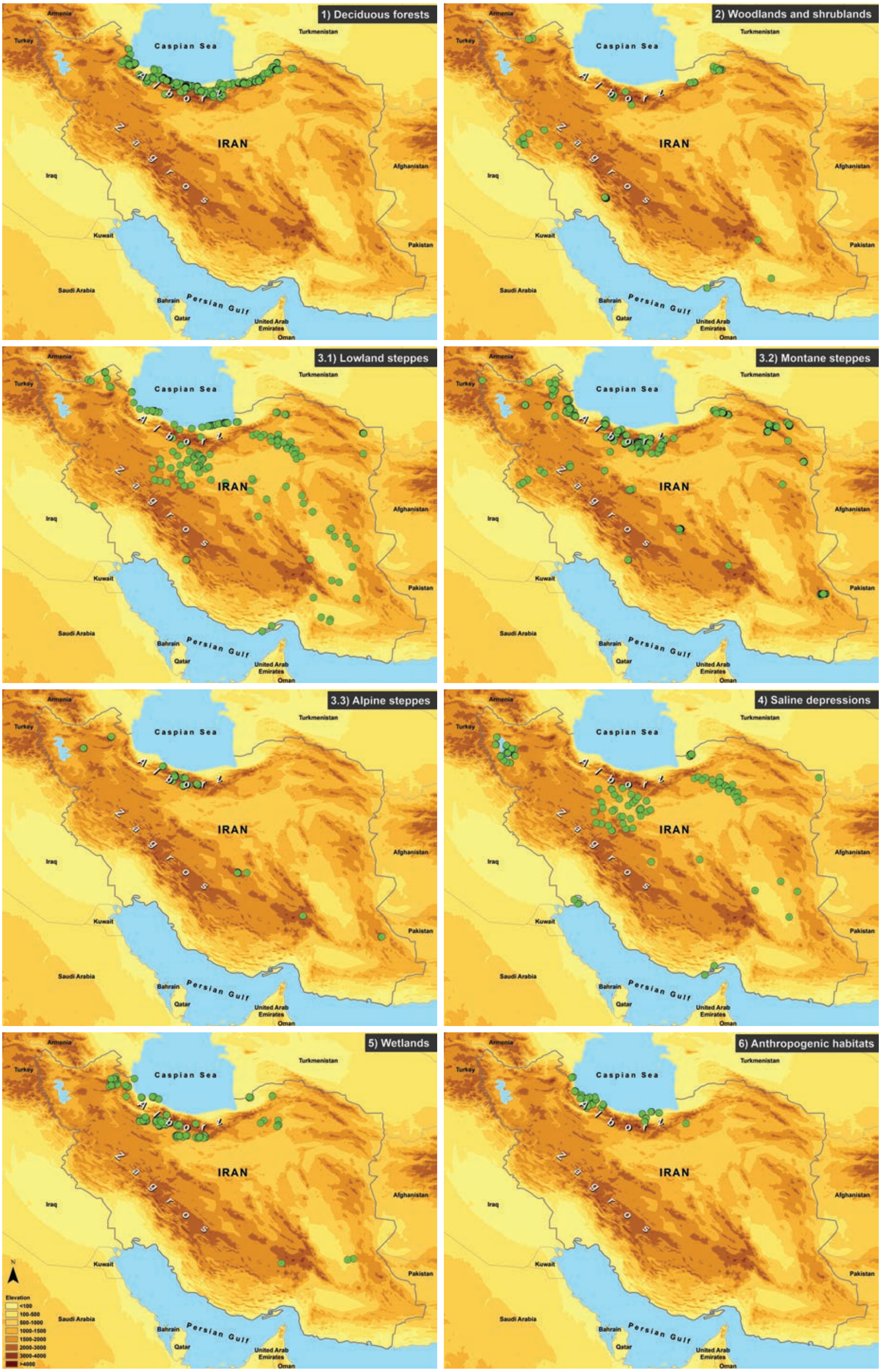

Figure 5. Spatial distribution of IranVeg plots across the major habitat types.

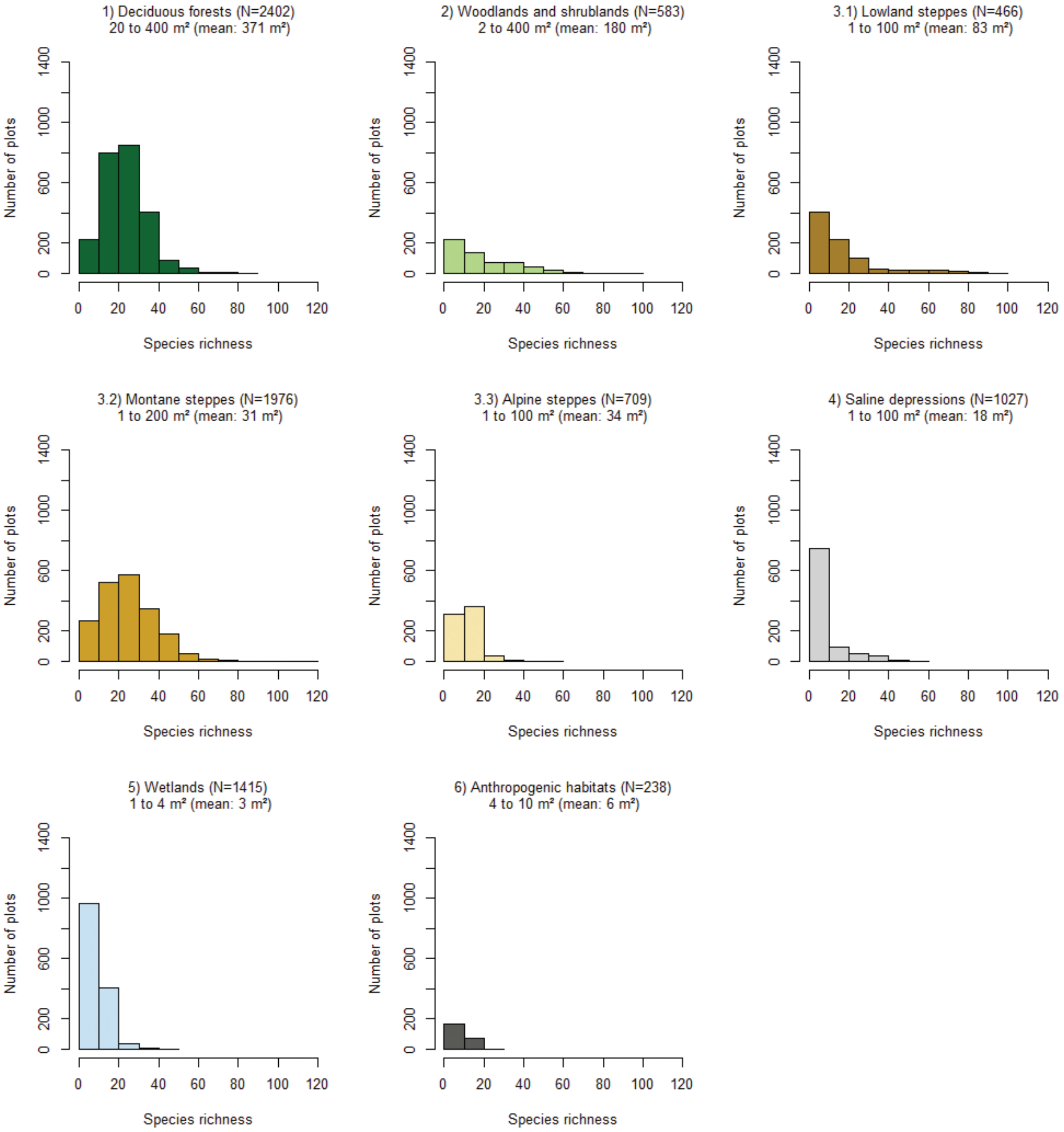

Figure 6. Frequency distribution of species richness across the major habitat types. Vegetation plots outside the central 95% percentile in size were excluded. N: Total number of plots.

dry season, altitude, and erosion (Frey and Probst 1986). However, this group of steppes received the lowest amount of precipitation (<100 mm to 300 mm) (see Assadi 1989; Akhani 1998). This habitat type also includes vast sand dune hills covered by a group of inland psammophytic vegetation of central Iran. Furthermore, coastal dune vegetation of southern Caspian shore including *Punica granatum* dwarf-shrublands are also included in this habitat type. Since there were only a limited number of central Iranian sand dune plots in our dataset, we included this kind of vegetation within lowland steppe (Figures 7j–l). Most plots of this group have a species richness ranging from 1 to 20 species per plot within areas of 1 to 100 m^2 with an average size of 83 m^2 (Figure 6), while a maximum of 86 species was found in a plot of 25 m^2.

Syntaxonomic classification of this habitat type is not fully dealt with. However, two main invalid phytosociological classes, *Artemisietea fragrantis anatolica* (Zohary 1973) and *Artemisietea sieberi*, including several valid and invalid associations, have been proposed from the lowland desertic steppes (see Zohary 1963, 1973; Asri 2003; Hamzeh'ee 2018). Furthermore, inland and coastal sand dunes were classified into three different classes, *Cakiletea maritimae*, *Artemisietea lerchianae* and *Stipagrostietea pennatae* (Zohary 1963; Asri 2003; Mahdavi et al. 2017).

3.2) Montane steppes (35.8% of all plots; Figures 4, 5): This category encompasses steppes and grasslands found within an altitude range of 1,200–3,500 m a.s.l. with comparatively higher precipitation (up to 400 mm). Among the studied plots, this habitat type possesses the highest species richness. The maximum richness level is reported from this group with 101 species in one plot of 25 m^2. Approximately half of the plots show species richness ranges between 20–40 while plot sizes vary from 1 to 200 m^2, with an average of 31 m^2 (Figure 6). This group includes subalpine tall herb communities of *Stipa* spp. and thorn-cushion dwarf shrub communities such as *Astragalus* spp., *Artemisia* spp., *Acantholimon* spp. and *Acanthophyllum* spp. (Figures 8a–b). Additionally, this group comprises plots from rocky and outcrop habitats (Figure 8c).

Notably, Klein (2001) and Noroozi et al. (2010, 2017) proposed a total of 38 valid associations, 11 alliances and four orders belonging to two classes, *Oxytropidetea persicae* (Klein 1982) and *Astragalo microcephali-Brometea tomentelli*, from this habitat type in their intensive phytosociological studies on montane and alpine zones of the Iranian mountains.

3.3) Alpine steppes (8.3% of all plots; Figures 4, 5): This group is distinguished by the high altitude, exceeding 3,500 m a.s.l., dominated by thorn-cushion grasslands, extending into the subnival zone and snowbed vegetation (Figure 8d–f). Hemicryptophytes dominate in the subnival zone and snowbed vegetation, while chamaephytes struggle to thrive due to the shortened growth period (Noroozi et al. 2010, 2014). Characterized by a notable proportion of endemic species, this habitat represents a unique ecosystem (Noroozi et al. 2010). Over 90% of the plots in this group demonstrate species richness varying from 1 to 20, covering plot sizes ranging from 1 to 100 m^2, with an average of 34 m^2 (Figure 6).

Valid syntaxa for the alpine steppes in northern and northwestern Iran have been proposed by Klein (1982) and Noroozi et al. (2010, 2014, 2017), including 14 associations, four alliances, three orders, and the class *Didymophyso aucheri-Dracocephaletea aucheri* (Noroozi et al. 2014).

4) Saline depressions: Saline and sabkha ecosystems, comprising 9.3% of all compiled plots, are mainly located at low and medium altitudes in coastal and inland salt depressions and playas in northern, southern and central Iran (Figures 4, 5). The plots often represent low species richness with fewer than 10 species per plot in sizes ranging from 1 to 100 m^2, with an average of 18 m^2 (Figure 6). This major habitat type includes the central Iranian great deserts "Dasht-e Kavir" and "Kavir-e Lut", the salt flats and salt marshes of the Urmia lake, the SE Caspian Sea, the Khuzestan Plain and coastal parts of the Persian Gulf and Oman Sea (Akhani 2004; Akhani and Samadi 2015) (Figure 8g–i). The formation of these saline habitats in Iran is attributed to several factors, including the recycling and accumulation of salts in the soil due to low rainfall, river flow, salt spray in littoral and marsh zones, as well as geological origin (Akhani 2004). Salinity and moisture are two significant ecological drivers shaping zonation patterns in halophytic vegetation in these areas (Akhani 2004, 2006). Saline depressions are characterized by structurally uniform plant communities with low species diversity (Asri 2003; Akhani 2004, 2006; Mehrabian et al. 2009; Ghorbanalizadeh et al. 2020). Genera such as *Anabasis*, *Atriplex*, *Climacoptera*, *Halothamnus*, *Limonium*, *Salsola* and *Suaeda* are among the most important halophytic genera in the saline habitats of Iran (Akhani and Ghorbanli 1993; Asri and Ghorbanli 1997; Akhani 2004). Several plant communities have so far been proposed for the saline depressions of Iran belonging to the classes *Thero-Salicornietea*, *Kalidietea foliati*, *Salicornietea fruticosae*, *Molinio-Arrhenatheretea*, *Tamaricetea arceuthoidis* and *Caroxylo-Climacopteretea* (e.g. Akhani and Mucina 2015; Ghorbanalizadeh et al. 2020).

5) Wetlands: A total of 12.2% of the compiled plots belong to wetland habitats (Figures 4, 5). Most plots show poor richness with fewer than 10 species per plot in sizes ranging from 1 to 4 m^2, and an average size of 3 m^2. The maximum richness recorded was 38 species in a plot of 4 m^2 (Figure 6). We use the term "wetlands" for a wide range of habitats, from freshwater lakes, rivers and riparian habitats with open water to montane mires and springs as well as wet meadows with inundated soil (see Sharifi et al. 2013; Jalili et al. 2014; Naqinezhad et al. 2021) (Figure 8j–l). One of the outstanding features of the dry Irano-Turanian montane steppes is that they embrace "green islands" of mires/springs in their matrix. These wet patches are important areas to be considered for conservation because they are refugia for many endemics/near endemics and are diagnostic species in these habitats. These include *Cerastium persicum*, *Cirsium glaberrimum*, *Deyeuxia parsana*, *Eleocharis palustris* subsp. *iranica*, *Ligularia persica*, *Myosotis sylvatica* subsp. *rivularis*, *Ranunculus amblyolobus*, *R. kotschyi*, and *Swertia longifolia* (Naqinezhad et al. 2009, 2021; Kamrani et al. 2011). The only valid publication of syntaxa from this group is by Naqinezhad et al. (2021) on mires and spring habitats of the Alborz Mountains, reporting 11 associations, three alliances, three order and three classes, *Montio-Cardaminetea*, *Scheuchzerio-Caricetea nigrae* and *Molinio-Arrhenatheretea*. There are plots of open water habitats characterized by aquatic floating and submerged plants (e.g. *Nelumbo nucifera*, *Myriophyllum spicatum*, *Najas minor*, *Ceratophyllum demersum*, *Potamogeton* spp. and *Lemna* spp.) and emergent plants (e.g. *Phragmites australis*, *Schoenoplectus litoralis* and *Typha* spp.) from the phytosociological classes *Lemnetea*, *Potamogetonetea* and *Phragmito-Magnocaricetea* (Asri and Eftekhari 2002; Asri and Moradi 2006; Asri et al. 2007; Maghsoudi et al. 2015; Hamedani et al. 2017).

6) Anthropogenic habitats: This major habitat type encompasses all plots collected from habitats strongly modified by humans, including arable fields and urban green spaces, currently accounting for 2.9% of plots (Figures 4, 5). The sizes of the plots were 4 or 10 m^2 and more than 50% of the plots of this group contained fewer than 10 species. The maximum richness of 18 species was recorded in 10 m^2 of an urban ruderal community (Figure 6). Both native and alien ruderal species are frequent in this group of plots (Figure 8m). From a phytosociological point of view, most of the syntaxa proposed for this group have been invalidly proposed, and further studies are needed to explore the syntaxonomic position of these habitats in Iran. However, one valid class of *Bidentetea tripartitae* (Asri and Eftekhari 2002) and three invalid classes *Panicetea segetalis*, *Secalinetea iranica* and *Ruderetea* (Zohary 1963) were proposed for this type of vegetation.

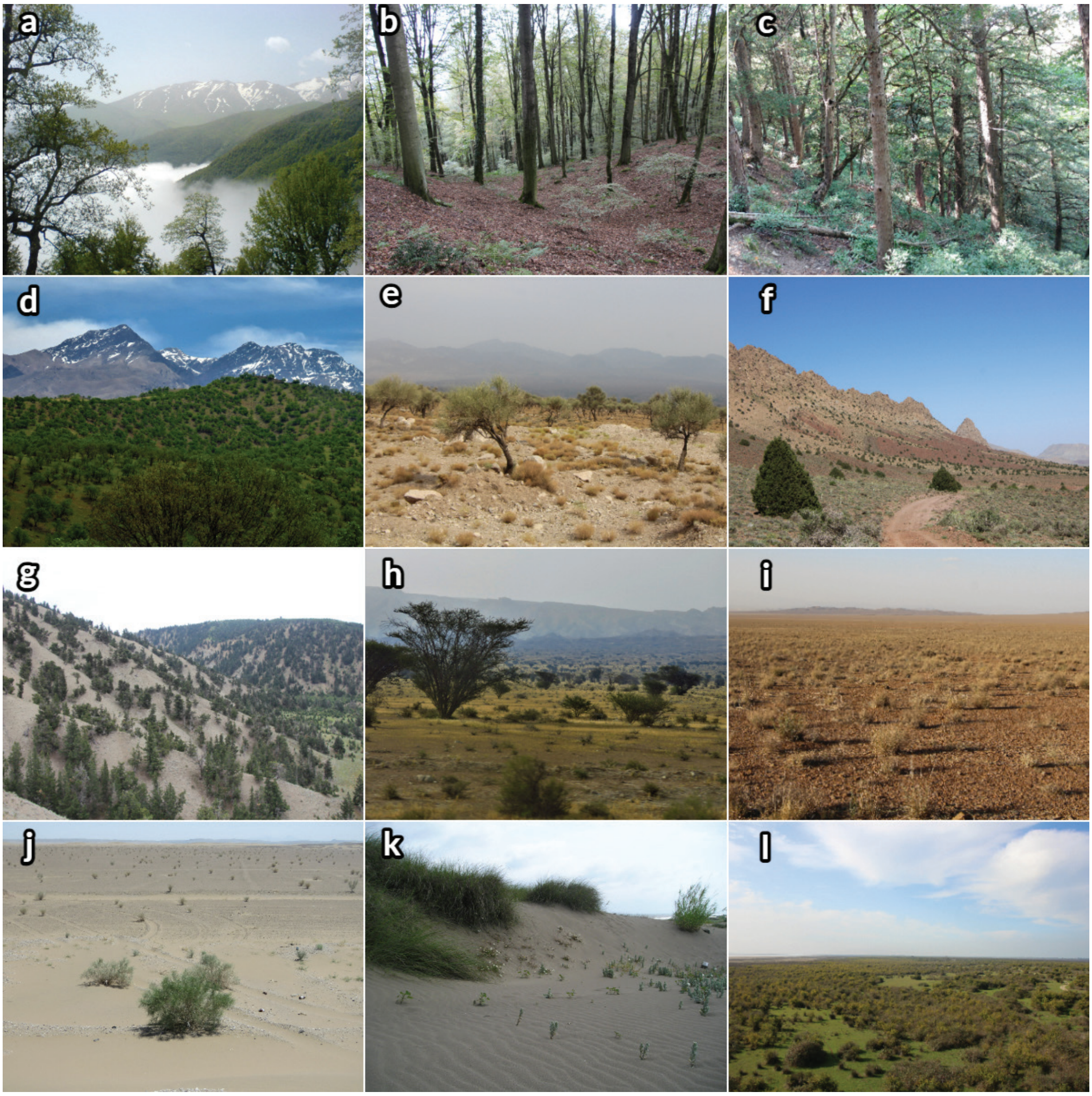

Figure 7. Photos of the major habitat types of Iran. Deciduous forests: a) Hyrcanian forest landscape, northern Iran; b) beech forests of the Hyrcanian ecoregion, northern Iran; c) unique yew (*Taxus baccata*) stand in the Hyrcanian forest, northern Iran; woodlands and shrublands: d) *Quercus* steppe woodlands in Zagros, western Iran; e) pistachio-almond steppe shrublands in Kerman, southern Iran; f) *Juniperus polycarpos* woodlands in Semnan, northern Iran; g) *Cupressus sempervirens* woodlands in Hassanabad-Chalus, northern Iran; h) savanna-like woodlands, southern Iran; lowland steppes: i) *Artemisia* community in central Iran; j) inland sand dunes in central Iran; k) coastal dunes in Miankaleh Biosphere Reserve, northern Iran; l) *Punica granatum* coastal shrublands in Miankaleh Biosphere Reserve, northern Iran. Photos by A. Naqinezhad (a–b, d–g, i, k–l); A. Talebi (h, j); O. Esmailzadeh (c).

Conclusions and future perspectives

The IranVeg database stands as a vital repository, not only providing a snapshot of Iran's current and past vegetation but also laying the groundwork for future ecological research and conservation endeavors. While certain vegetation types and regions have received considerable attention, others remain poorly studied or are completely absent from our dataset. For instance, extensive areas across the Alborz Mountain range, particularly near the capital city, Tehran, have been extensively sampled due to their proximity to research centers, resulting in relatively well studied vegetation types in these regions. Conversely, vast stretches of land (see Figures 1, 5) lack even a single plot, highlighting significant gaps in our understanding of certain habitats and regions.

Several factors contribute to this disparity in data coverage. Challenges such as limited funding and logistical difficulties in remote areas are particularly prevalent, especially for oak woodland communities in the massive mountains of Zagros and savanna-like grasslands in the

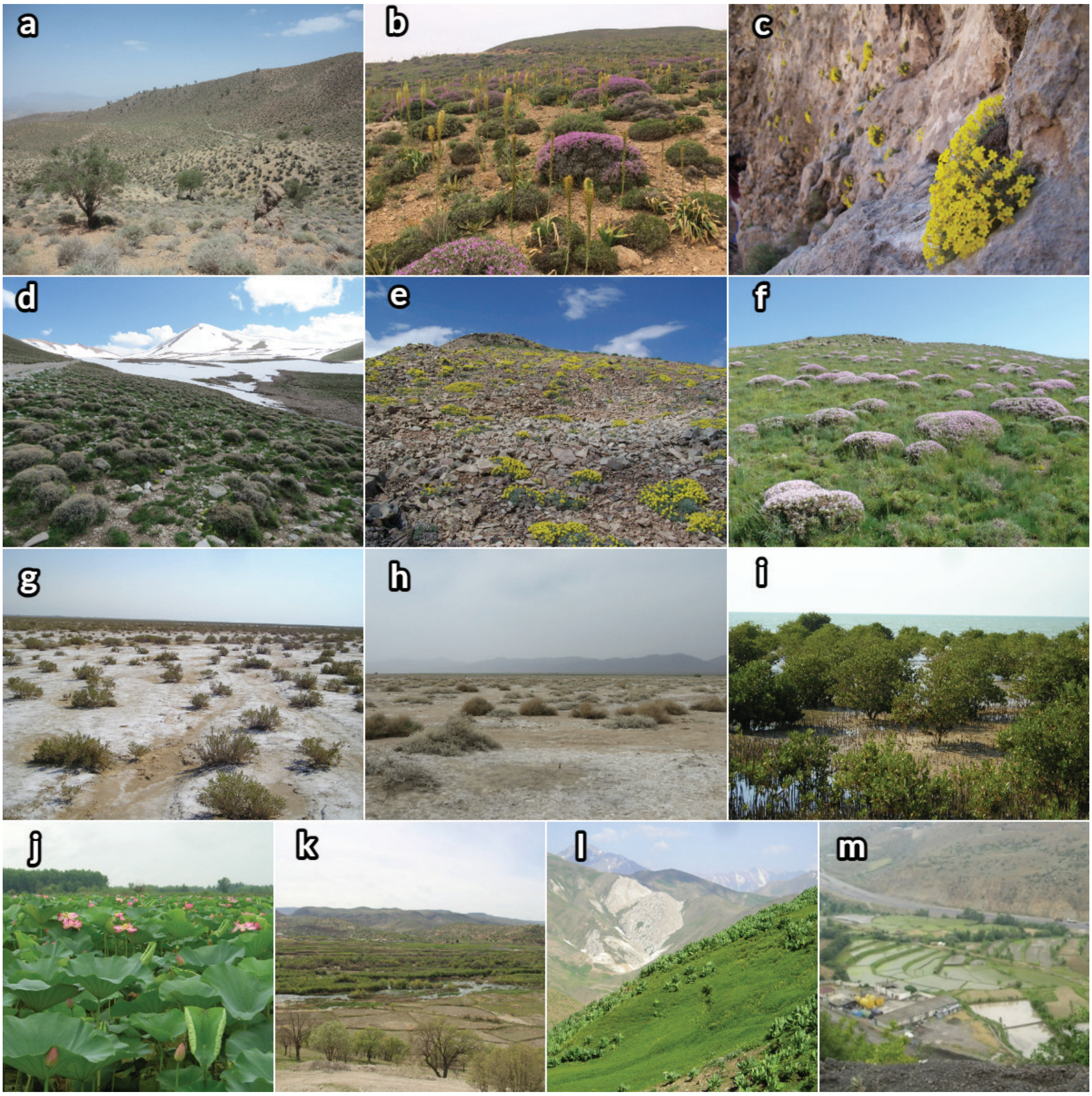

Figure 8. Photos of the major habitat types of Iran. Montane steppes: a) montane steppe in Taftan Mts., southeastern Iran; b) thorn-cushion grasslands in Baharkish Mts., eastern Iran; c) rock vegetation of *Dionysia* in Zagros Mts, western Iran; alpine steppe: d) alpine vegetations of Sahand Mts., northwestern Iran; e) alpine-subnival screes in Tuchal Mts., central Alborz, northern Iran; f) thorn-cushion grasslands in alpine zone in Bozgush Mts., northwestern Iran; saline depressions: g) *Halocnemum strobilaceum* communities in Mond Protected Area, Bushehr, southern Iran; h) *Halocnemum-Siedlitzia* communities of southern Iran; i) mangrove forests in Bushehr, southern Iran; wetland: j) *Nelumbo nucifera* community in the Anzali Ramsar Site, northern Iran; k) riparian habitats in Kohgiluyeh and Boyer Ahmad, western Iran; l) montane mires in the Alborz Mountains, northern Iran; anthropogenic habitats: m) rice fields of northern Iran. Photos by A. Naqinezhad (a, g, i–m); J. Noroozi (c–f); A. Talebi (h); S. Rahmanian (b).

subtropical Saharo-Sindian regions of southern Iran. Furthermore, decreasing interest among scholars in vegetation ecology topics has hindered comprehensive vegetation studies in Iran. Additionally, barriers such as insufficient incorporation of vegetation data in land use planning and limited emphasis on vegetation ecology in university curricula further exacerbate the situation.

To address these challenges, it is imperative to emphasize the importance of vegetation data, both nationally and internationally. Expanding and enhancing vegetation data from Iran is essential for several reasons. Locally, such data are invaluable for diversity analyses, vegetation classification, landscape planning, land management, biodiversity conservation, and ecosystem restoration efforts. Internationally, Iran's diverse vegetation serves as a crucial component of global biodiversity and ecosystem function. Thus, better understanding and documenting Iran's vegetation contribute not only to national conservation goals but also to broader global biodiversity conservation efforts. These kinds of datasets play a pivotal role in fostering macroecological investigations on a continental or global scale. Notably, selected datasets from this Iranian repository have already been utilized in macroecology research through opt-in projects registered in sPlot (Bruelheide et al. 2019; Sabatini et al. 2021) and GrassPlot (Dengler et al. 2018, 2020; Biurrun et al. 2019, 2021; Dembicz et al. 2021a, 2021b; Zhang et al. 2021; Ulrich et al. 2022) as well as other large scale regional analyses (Loidi et al. 2021; Naqinezhad et al. 2021, 2022; Nowak et al. 2024a, b; Novák et al. 2023; Gallou et al. 2023; Sękiewicz et al. 2024).

A total of 31 phytosociological classes, along with numerous subordinate syntaxa, have been proposed for the vegetation types in Iran. However, only a small fraction of these proposed syntaxa have been validly published. Considerable effort is still required to complement and validate the remaining syntaxa. The slow progress in the syntaxonomic classification of Iran can be attributed to several factors. Primarily, the standardization of phytosociological work in the country has lagged behind the international pace. Moreover, many Iranian authors are reluctant to follow standard phytosociological nomenclature, believing that without comprehensive surveys and further data collection, any decision regarding the validation of proposed syntaxa would be premature. Consequently, many of these proposed syntaxa have been regarded as provisional. In this paper, we do not aim to validate these syntaxa, as that would require a separate and extensive effort, particularly given the complex vegetation structure and vast geographical scope of Iran.

While our database represents a significant achievement, it is important to acknowledge its limitations. We cannot claim to have digitized 100% of all relevant data to date. Indeed, a considerable portion of vegetation data likely remains undocumented in publications, theses, and personal notebooks. To provide a more accurate assessment, future efforts should aim to estimate the fraction of existing data captured in our database compared to data available elsewhere. Moreover, it is essential to recognize other major databases in the region, such as those for Turkey (Kavgaci 2016; Uğurlu 2016; Uğurlu and Isik 2020; Güler 2023) and Middle Asia (Nowak and Nobis 2019; Nowak et al. 2024b), which may have larger datasets covering smaller areas. Acknowledging and collaborating with these initiatives can foster a more comprehensive understanding of vegetation across Southwest and Middle Asia.

In conclusion, IranVeg represents a collaborative effort toward understanding and conserving Iran's botanical heritage. Moving forward, continued collaboration among researchers and the development of a cooperative network are crucial for further enhancing the database and addressing the complex ecological challenges facing Iran and the broader region. Researchers holding relevant vegetation data are encouraged to contribute to IranVeg, while those seeking to utilize the database for research purposes are welcome to submit proposals to the custodians. The proposal could be submitted by one or a group of leading researchers who are responsible for collected data. The most important benefits of contributing plots into this national database are opt-in options to the papers extracted from this collective national database and also own access of the contributing authors to the full database as this is the case in other collaborative databases such as GrassPlot (Dengler et al. 2018, 2020; Biurrun et al. 2019) or sPlot (Bruelheide et al. 2019; Sabatini et al. 2021). By leveraging shared knowledge and resources, we can advance our understanding of Iran's vegetation and contribute to global conservation efforts.

Data availability

Access to the database is restricted; however, interested researchers may obtain the data by submitting a formal request to the database manager.

Author contributions

AN, JN and PM perceived the idea and registered the preliminary dataset. AN, JN and SR coordinate the IranVeg Consortium as Custodian and Deputy Custodian, respectively. SR aggregated new datasets, performed analysis and prepared the draft with main contribution by AN. SST aggregated data. JN, HG, BH, YA, and AT read and approved the final version of the article. The other co-authors have collected the field data and read/modified the final version.

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Supplementary material

Supplementary material 1
Data sources utilized in the IranVeg database (*.pdf)
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VEGETATION CLASSIFICATION AND SURVEY

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REPORT   PHYTOSOCIOLOGICAL NOMENCLATURE

Report 3 of the Committee for Change and Conservation of Names (CCCN)

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Abstract

We report the decisions made by the Assembly of the Group of Phytosociological Nomenclature (GPN) in 2023 on previous recommendations of the Committee for Change and Conservation of Names (CCCN). Further, we discuss eight Requests for a binding decision and nine nomenclatural Proposals. Recommendations on acceptance or rejection of these Proposals are provided. We recommend the conservation of the following names: *Mesobromion erecti* (Braun-Blanquet et Moor 1938) Zoller 1954, *Galio sylvatici-Carpinetum betuli* Oberdorfer 1957, *Lithospermo-Carpinetum betuli* Oberdorfer 1957, *Nanocyperetalia* Klika 1935, *Isoetetalia* Braun-Blanquet 1936 and *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967.

Abbreviations: CCCN = Committee for Change and Conservation of Names; GPN = Working Group for Phytosociological Nomenclature; ICPN = International Code of Phytosociological Nomenclature; VCS = Vegetation Classification and Survey.

Keywords

binding decision, *Isoetetalia*, *Mesobromion*, *Nanocyperetalia*, nomenclature, *nomen conservandum*, phytosociology, syntaxonomy

Introduction

The Committee for Change and Conservation of Names (CCCN) is a Topic Committee of the Working Group for Phytosociological Nomenclature (GPN) established in accordance with the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021). Its task is to evaluate requests for binding decisions on controversial or ambiguous cases in the interpretation of the Code, and proposals for the conservation or rejection of syntaxon names. In the last report of the Committee (Willner et al. 2021) we announced the next one for the year 2022. However, as usual, most of the nomenclatural cases turned out to be quite complicated, and the progress of our discussions was slower than expected. In fact, several Proposals touched on very fundamental questions of interpretation of the ICPN, and some of them also revealed ambiguities that should be addressed in the next edition of the Code. This, together with the other obligations of each committee member, led to a delay of two years. Nevertheless, we are pleased to present the third Report of the CCCN.

In May 2022, the GPN Steering Committee co-opted Massimo Terzi to the CCCN. It now consists of six members, namely: Wolfgang Willner (chair), Andraž Čarni, Federico Fernández-González, Jens Pallas, Massimo Terzi and Jean-Paul Theurillat.

Authors wishing to submit a Proposal or a Request for a binding decision on a syntaxon name are asked to consult Appendices 2 and 6 of the International Code of Phytosociological Nomenclature (ICPN), respectively (Theurillat et al. 2021). It is highly recommended to consult previously published Proposals and Requests. All Proposals and Requests published in Vegetation Classification and Survey (VCS) are automatically processed by the CCCN according to the ICPN rules. Concerning the submission itself, there are two possibilities. Proposals and Requests can be submitted as independent articles using the VCS submission system. In this case, article processing charges may apply, depending on your country and status. Alternatively, you can submit a Proposal or a Request with the same structure by e-mail to the first author of this report. In the latter case, the Proposals and the Requests will be published in the next CCCN Report (the authors of each Proposal will be indicated). Publication of nomenclatural Proposals and Requests as part of the CCCN Report is free of charge.

Our report is structured into three main sections: In the first section, we report the final decisions made by the GPN Assembly on previous recommendations of the CCCN. In the second section, we discuss new Requests for binding decisions, and in the third one, we discuss new Proposals for the conservation or rejection of syntaxon names. Our recommendations remain provisional until approved by the GPN Assembly. The final decisions on the new recommendations will be presented in the next CCCN Report.

Decisions by the GPN Assembly

In spring 2023, the members of the GPN were asked to vote on the recommendations published in the last CCCN Report (Willner et al. 2021). The voting was done per e-mail and took place from 10 March to 10 April 2023. Members were asked whether they agreed or disagreed with the CCCN recommendations. The results were as follows [an asterisk (*) after the proposal number indicates that the recommended version of the proposal differs from the original one]:

(17*) To conserve the name *Berberidion* Braun-Blanquet 1950 with a conserved type and against *Prunion spinosae* Soó 1931 (recommended). Vote: 22 yes, 0 no.

(20) To conserve the name *Aceretalia pseudoplatani* Moor 1976 against *Tilietalia* Moor 1973 (recommended). Vote: 23 yes, 0 no.

(21) To conserve the name *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 against *Festucetalia* Soó 1940 (not recommended). Vote: 12 yes, 6 no.

(21*) To conserve the name *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 with a conserved type and against *Festucetalia* Soó 1940 (recommended). Vote: 21 yes, 0 no.

All recommendations (positive and negative ones) have been accepted. Therefore, the following entries are to be added to Appendix 3 of the ICPN (Theurillat et al. 2021):

(17) *Berberidion* Braun-Blanquet 1950 nom. et typus cons. [Braun-Blanquet 1948–1950, part 6: 349]
(=) *Prunion spinosae* Soó 1931 [Soó 1931: 294]
Typus conservandus: *Berberido-Rosetum* Braun-Blanquet 1961 [Braun-Blanquet 1961: 189].

(20) *Aceretalia pseudoplatani* Moor 1976 nom. cons. [Moor 1976: 330, 336]
(=) *Tilietalia* Moor 1973 [Moor 1973: 128–129]
Holotypus: *Lunario-Acerion* Moor 1973 [Moor 1973: 128]

(21) *Festucetalia valesiacae* Braun-Blanquet et Tüxen ex Braun-Blanquet 1950 nom. et typus cons. [Braun-Blanquet 1948–1950, part 3: 312]
(=) *Festucetalia* Soó 1940 [Soó 1940: 32]
Typus conservandus: *Festucion valesiacae* Klika 1931 [Klika 1931: 376]

Recommendations on Requests for a binding decision

During the reporting period, the CCCN examined four published Requests for a binding decision. They are numbered from (1) to (4) in the following section, as in the original publications. In addition, several *ad hoc* Requests arose during the discussion of Proposals. These are numbered (A1), (A2), etc., in the order in which they were discussed.

(1) Name-giving taxon in the name *Isoeto longissimae-Cicendietum* Br.-Bl. 1967 nom. corr. Request by Silva and Molina (2021). Suggested completion of the name: *Isoeto longissimae-Cicendietum filiformis*. Vote: 6 pro, 0 contra (recommended).

The members of the CCCN see no problem with the proposed choice of the name-giving *Cicendia* species and therefore recommend that the Request be accepted. However, we noticed that the nomenclature of the corresponding alliance '*Cicendion* (Rivas Goday in Rivas Goday et Borja 1961) Br.-Bl. 1967' (form of the name in Mucina et al. 2016) needs a thorough revision, which will be published elsewhere.

(2) Name-giving taxon in the name *Gnaphalio-Verbenetum supinae* Rivas Goday 1970 nom. invers. Request by Silva and Molina (2021). Suggested completion of the name: *Gnaphalio luteoalbi-Verbenetum supinae*. Vote: 6 pro, 0 contra (recommended).

While the CCCN supports the proposed name-giving *Gnaphalium* species, there was a discussion about the legitimacy of the inversion of the name. Both *Gnaphalium luteoalbum* and *Verbena supina* belong to the herb layer, so only the second paragraph of Art. 10b applies. The inversion is based on the lectotype where *Verbena supina* has a higher cover than *Gnaphalium luteoalbum*. However, considering the original diagnosis as a whole (table 8 in Rivas Goday 1970), *G. luteoalbum* has a higher cover in six out of ten relevés, *V. supina* has a higher cover in three relevés, and in one relevé both species have the same cover. While Art. 42 clearly states that the nomenclatural type is relevant to determine the correct order sequence of the name-giving taxa, there is no reference to the type in Art. 10b. This creates some ambiguity that should be addressed in the next edition of the Code.

(3) Valid publication of the names *Xerobromion* and *Mesobromion* in Zoller 1954. Request by Terzi et al. (2021). Recommendation: Both names are valid (6 pro, 0 contra).

Braun-Blanquet and Moor (1938) proposed the two suballiances *Xerobromenion* and *Mesobromenion* within the alliance *Bromion* Koch 1926 to separate the xerophilous associations from the meso-xerophilous ones. At that time, however, the same termination *-ion* was used for both the alliance and the suballiance rank (i.e., *Xerobromion* and *Mesobromion*, respectively). Thus, the use of the names without an explicit indication of the rank was ambiguous. Zoller (1954) adopted the names *Xerobromion* and *Mesobromion*, stating that these two units were so different from each other that they could only be united under a single alliance *Bromion* by force ("mit Zwang"; Zoller 1954, p. 36), and therefore such a concept was not followed in his work. However, this rejection of the alliance *Bromion* alone can not by itself be accepted as a valid change of rank of the previously published suballiances, also because Zoller mentioned "characteristic species of the suballiance *Xerobromion*" in two tables. Fortunately, the new rank is explicitly mentioned at a few places ("*Xerobromion*-Verband": p. 50, p. 52; "*Mesobromion*-Verband": p. 253), a fact that was only discovered after the publication of the Request. Therefore, it is clear that the names *Xerobromion* (Braun-Blanquet et Moor 1938) Zoller 1954 and *Mesobromion* (Braun-Blanquet et Moor 1938) Zoller 1954 can be accepted as validly published.

The requirement of explicitly using the name at the new rank – in this case with the explicit indication of the rank, as the termination *-ion* is ambiguous – is analogous to the rule for changing the position of a subassociation (Art. 4b): the new combination (association name plus subassociation epithet) must be used explicitly; the mere expression of the change of position is not sufficient.

(A1) Valid publication of the names *Carpinetum* and *Alno-Carpinetum* in Issler 1924. Request by W. Willner (CCCN). Recommendation: Both names are valid (4 pro, 1 contra, 1 abstention).

During the discussion of Proposals 24 and 25 (Novák 2019, see below) it became necessary to decide on the validity of the association names published by Issler (1924) in the first part of his study of the forests of the southern Vosges mountains and the adjacent Rhine plain. In the original Proposals (Novák 2019), the names *Carpinetum* and *Alno-Carpinetum* were considered as not validly published in Issler (1924), because the diagnoses consist only of synoptic species lists, where for each species a range of cover values found in the individual relevés is given. However, the majority of the CCCN members concluded that this is a sufficient diagnosis in the sense of Art. 7, as it can be seen as an indication of mean cover values.

(A2) Name-giving taxon in the name *Lithospermo-Carpinetum betuli* Oberdorfer 1957. Request by Novák (2019). Suggested completion of the name: *Lithospermo purpurocaerulei-Carpinetum betuli* Oberdorfer 1957. Vote: 6 pro, 0 contra (recommended).

This Request was part of Proposal 24 (see below). *Lithospermum purpurocaeruleum* is mentioned as a character species of the association with constancy IV, while *L. officinale* is listed as a class species with constancy II. Although *L. purpurocaeruleum* may have been intended as the name-giving taxon, there is no information in the original diagnosis that this was the case. The CCCN voted unanimously to accept the choice of *L. purpurocaeruleum* as the name-giving species.

(A3) Name-giving taxon in the name *Nanocyperetalia* Klika 1935. Request by J.-P. Theurillat (CCCN). Suggested completion of the name: *Nanocyperetalia flavescentis*. Vote: 5 pro, 1 abstention (recommended).

The holotype of this order is the alliance *Nanocyperion flavescentis* Koch 1926 [see Proposal 26 (Fernández-González et al. 2021) for details]. However, while the name-giving taxon of the alliance is clear, because the specific epithet was added in the original diagnosis, this is not the case for the order name, which was published without epithet. As there is more than one *Cyperus* species present in the original diagnosis of the alliance (and therefore the order), a binding decision must be made. We propose to select the same name-giving taxon as for the alliance, namely *Cyperus flavescens* L. (Sp. Pl. 1: 46. 1753).

(A4) Name-giving taxa in the names *Isoetetalia* Braun-Blanquet 1936 and *Isoetion* Braun-Blanquet 1936. Request by J.-P. Theurillat (CCCN). Suggested completion of the names: *Isoetetalia durieui* and *Isoetion durieui*. Vote: 5 pro, 1 abstention (recommended).

Both names were published without a specific epithet and are mostly used without epithet in the literature. However, since the type association of the *Isoetion* is the *Isoetetum* *durieui* Braun-Blanquet 1936 (Brullo and Minissale 1998), we propose *Isoetes durieui* Bory 1844 as the name-giving taxon of both the alliance and order names. See also Proposal 27 (Fernández-González et al. 2021) below.

(4) Name-giving taxon in the names *Molinio arundinaceae-Quercetum* Samek 1962 and *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967. Request by Slezák et al. (2021). Suggested completion of the names: *Molinio arundinaceae-Quercetum roboris*. Vote: 5 pro, 1 abstention (recommended).

This request was submitted together with Proposal 28 (Slezák et al. 2021, see below). The two names in question refer to hygrophytic oak forests where the dominant oak species is usually *Quercus robur* (Roleček 2013). The CCCN recommends accepting the choice of *Q. robur* as the name-giving species in both association names.

Recommendations on published Proposals

The Proposals are numbered as in the original publication. An asterisk (*) after the number of the Proposal indicates that the recommended version of the Proposal differs from the original one.

(22) To conserve the name *Mesobromion erecti* (Braun-Blanquet et Moor 1938) Oberdorfer 1957 against the name *Bromion erecti* Koch 1926. Proposed by Theurillat et al. (2017). Following the conclusions on Request 3 for a binding decision on the validity of the alliance name *Mesobromion erecti* published in Zoller (1954) (see above), the Proposal was modified accordingly (see Proposal 22*). No vote.

(22*) To conserve the name *Mesobromion erecti* (Braun-Blanquet et Moor 1938) Zoller 1954 against the name *Bromion erecti* Koch 1926. Modified version of the Proposal by Theurillat et al. (2017). Vote: 3 pro, 2 contra, 1 abstention (recommended).

Although the CCCN did not reach a unanimous decision, a majority voted in favour of this Proposal. The main reasons are as follows: (i) The name *Bromion erecti* is potentially confusing for people unfamiliar with phytosociological nomenclature. *Mesobromion* and *Xerobromion* are names with well-defined contents, whereas *Bromion* has been used in at least three different ways: (a) in the sense of the *Mesobromion* (e.g., Mucina et al. 1993, 2016; Chytrý 2007), (b) in the sense of the *Xerobromion* (Oberdorfer 1957; Korneck 1974) and (c) for a unit comprising both (Braun-Blanquet and Moor 1938; Braun-Blanquet 1948–1950). (ii) Braun-Blanquet and Moor (1938) clearly considered the *Xerobromion* as the typical core of the *Bromion*. As noted by Zoller (1954), about half of the alliance character species listed by Braun-Blanquet and Moor are more or less restricted to the *Xerobromion*. Therefore, the decision of Oberdorfer (1957) to maintain the name *Bromion* for the *Xerobromion* is completely understandable from a historical point of view, although not in accordance with the ICPN (which had not yet been published in 1957). (iii) For a long period, the name *Bromion* was not in common use. It was restored when authors started to follow the ICPN and realised that the type of the name *Bromion* was the *Mesobrometum erecti* Koch 1926. However, conservation of names was not possible at that time. Nevertheless, several authors continued to use the name *Mesobromion* instead of *Bromion* (Weeda et al. 2002; Aeschimann et al. 2004; Bardat et al. 2004; Delarze et al. 2015; Willner et al. 2019).

There was also a lively discussion in the CCCN about the type of the name *Mesobromion erecti* (Braun-Blanquet et Moor 1938) Zoller 1954. The *Mesobrometum erecti* was validly published for the first time in Koch (1926). However, because of the absence of complete bibliographic references in Braun-Blanquet and Moor (1938), Theurillat et al. (2017) concluded that the type of the basionym *Mesobromenion erecti* Braun-Blanquet et Moor 1938 is a later homonym of Koch's name, the '*Mesobrometum erecti* Scherrer ex Braun-Blanquet et Moor 1938'. In the meantime, further considerations led to the conclusion that the volumes of the *Prodrome of Plant Communities* (*Prodromus der Pflanzengesellschaften*, *Prodrome des groupements végétaux*) published between 1933 and 1940, of which Braun-Blanquet and Moor (1938) is the 5th part, should be considered as a single work, including the *Bibliographia Phytosociologica* (Tüxen and Prügel 1935; De Leeuw 1935; Braun-Blanquet and Diemont 1936). A reference to the published volumes of the *Bibliographia* is given on the back cover of each volume of the *Prodrome*, and a generic reference is also given in the first volume (Braun-Blanquet 1933: 4). Thus, the name *Mesobrometum* in Braun-Blanquet and Moor (1938) is not a later homonym, because there is a sufficient indirect reference to Koch (1926): on p. 40 and 41, under the *Mesobrometum typicum*, Braun-Blanquet and Moor (1938) refer to Tüxen (1928), and the full bibliographical details can be found in the *Bibliographia Phytosociologica*, Fasc. 1 (Tüxen and Prügel 1935). Tüxen (1928), describing the *Mesobrometum* of NW Germany, provided an unambiguous reference to Koch (1926).

Another question is the correct author citation of the *Mesobrometum erecti*. Koch (1926) referred the name to "Braun-Blanquet, Max Scherrer". As shown by Terzi et al. (2016), the (invalid) subass. "*Brometum bromosum*" of Scherrer (1925) is part of the original diagnosis of Koch's *Mesobrometum*. According to Scherrer (1925), Braun-Blanquet suggested the name "*Meso-Brometum*" for this mesophilous type of the *Brometum*, but this name was not definitely adopted by Scherrer. Moreover, Scherrer provided unambiguous references to the *Xero-Brometum*, which he considered as another subassociation of the *Brometum*. However, by using the name *Mesobrometum*, Koch clearly excluded the *Xero-Brometum* from his association. One could say that Koch raised Scherrer's invalid subassociation '*Brometum bromosum*' to the rank of association. However, as the name *Mesobrometum* was proposed by Braun-Blanquet, and not by Scherrer, it is recommended to cite the name as *Mesobrometum* Braun-Blanquet ex Koch 1926, and not as *Mesobrometum* Scherrer ex Koch 1926, but *Mesobrometum* Braun-Blanquet et Scherrer ex Koch 1926 could be an alternative. This is, in fact, a matter of taste and has no nomenclatural consequences.

(23) To conserve the name *Galio sylvatici-Carpinetum betuli* Oberdorfer 1957 against *Querco pedunculatae-Carpinetum betuli* Klika 1928. Proposed by Novák (2019). Vote: 5 pro, 1 contra (recommended).

The name *Galio sylvatici-Carpinetum betuli* is widely used for the oak-hornbeam forests of Central Europe, except in the more Atlantic west, where the name-giving *Galium sylvaticum* and some other diagnostic species do not occur and the *Galio-Carpinetum* is replaced by the *Stellario-Carpinetum* (Oberdorfer 1992; Leuschner and Ellenberg 2017). Some authors (e.g., Willner and Grabherr 2007; Novák et al. 2020) exclude the moist oak-hornbeam forests from the *Galio-Carpinetum* and include them in a broader *Stellario-Carpinetum* (see also Proposal 25). Regardless of this syntaxonomic question, all authors agree that the typical *Galio-Carpinetum* occurs on relatively dry soils, and that the co-dominant oak species on such sites is usually *Quercus petraea*. Before 1957, all the oak-hornbeam forests of Central Europe were grouped into a single broad association *Querco-Carpinetum*, but this name has not been used in any major reference work for decades.

The first author who described a *Querco-Carpinetum* was Klika (1928). In fact, Klika (1928, p. 34ff) described two associations of oak-hornbeam forests: a '*Quercetum pedunculatae-Carpinetum*' on drier soils and a '*Carpinetum*' on more mesic soils. While the latter is an illegitimate homonym of the *Carpinetum* Issler 1924 (see also Proposal 24*), the '*Quercetum pedunculatae-Carpinetum*' (recte: *Querco roboris-Carpinetum* nom. corr.) is a legitimate name that would have priority over the name *Galio sylvatici-Carpinetum* Oberdorfer 1957. As mentioned above, the co-dominance of *Quercus robur* is rather atypical for dry oak-hornbeam forests, and Klika (1928) even says that it is probably a result of forestry. Thus, the name *Querco roboris-Carpinetum* Klika 1928 nom. corr. would not only replace a well-established name in current use, but would also be misleading with regard to the natural tree species composition of this community. Moreover, another *Querco roboris-Carpinetum* was described independently of Klika by Tüxen (1930). However, the '*Querceto-Carpinetum*' [recte: *Querco roboris-Carpinetum*] Tüxen 1930 corresponds syntaxonomically to the *Stellario-Carpinetum* Oberdorfer 1957 (see, e.g., Preising et al. 2003). Although both *Q. robur* and *Q. petraea* are present in the original diagnosis of Tüxen's name (with *Q. robur* being by far the more frequent one), the '*Querceto-Carpinetum*' is in fact a later homonym to Klika's '*Quercetum pedunculatae-Carpinetum*' because on the first page of his paper, Tüxen (1930) writes "Assoziation von *Quercus robur* und *Carpinus betulus* = *Querceto-Carpinetum*". So it is clear that *Q. robur* is the name-giving oak species in Tüxen's '*Querceto-Carpinetum*'.

In view of all these facts, it is obvious that the reintroduction of the name *Querco roboris-Carpinetum* Klika 1928 nom. corr. would be a continuous source of error, and the conservation of the name *Galio sylvatici-Carpinetum* Oberdorfer 1957 is recommended.

(24) To conserve the name *Lithospermo-Carpinetum betuli* Oberdorfer 1957 against *Carpinetum betuli* Issler 1925. Proposed by Novák (2019). Following the conclusions on Request A1 for a binding decision (see above), the Proposal was modified accordingly (see Proposal 24*). No vote.

(24*) To conserve the name *Lithospermo-Carpinetum betuli* Oberdorfer 1957 against *Carpinetum betuli* Issler 1924. Modified version of the Proposal by Novák (2019). Vote: 4 pro, 1 contra, 1 abstention (recommended).

The *Lithospermo-Carpinetum betuli* Oberdorfer 1957 [or *Lithospermo purpurocaerulei-Carpinetum betuli* if Request A2 is accepted, see above] includes thermophytic oak-hornbeam forests in SW Central Europe (Boeuf et al. 2014; Novák et al. 2020). According to the principle of priority, the name *Carpinetum betuli* Issler 1924 should be adopted for this unit. However, this name has not been used in any major reference for almost a century. We therefore recommend that the Proposal be accepted.

Oberdorfer's name *Lithospermo-Carpinetum betuli* is a nomen superfluum for the *Carpinetum betuli* Issler 1924 (Art. 29b), and is therefore automatically typified by Issler's earlier name (Art. 18b). For the *Carpinetum betuli* Issler 1924, we select relevé 2 in table 3 in Issler (1926) as the neotypus hoc loco, which was the relevé proposed by Novák (2019) as the conserved type for the *Lithospermo-Carpinetum*. However, since the *Carpinetum betuli* Issler 1924 is validly published, no conserved type is necessary.

(25) To conserve the name *Stellario holosteae-Carpinetum betuli* Oberdorfer 1957 against *Alno glutinosae-Carpinetum betuli* Issler 1926. Proposed by Novák (2019). Following the conclusions on Request A1 for a binding decision (see above), the Proposal was modified accordingly (see Proposal 25*). No vote.

(25*) To conserve the name *Stellario holosteae-Carpinetum betuli* Oberdorfer 1957 against *Alno glutinosae-Carpinetum betuli* Issler 1924. Modified version of the Proposal by Novák (2019). Vote: 1 pro, 3 contra, 2 abstentions (not recommended).

The name *Stellario-Carpinetum* was coined by Oberdorfer (1957) for subatlantic oak-hornbeam forests lacking the diagnostic species of the more subcontinental *Galio-Carpinetum* (see Proposal 23). Oberdorfer (1957) distinguished five subassociations: *typicum* (on mesic sands), *agrostietosum* (on drier sands), and *allietosum*, *ficarietosum* and *caricetosum brizoidis* (all three on wet, gleyic soils). More recently, the *Stellario-Carpinetum* has been extended to include also the wet subassociations of the *Galio-Carpinetum* (e.g., Willner and Grabherr 2007; Chytrý 2013; Novák et al. 2020). However, the oldest name for wet oak-hornbeam forests in Central Europe is *Alno glutinosae-Carpinetum* Issler 1924. This name has rarely been used in the Central European literature, but it was recently adopted by Boeuf et al. (2014).

In contrast to Proposals 23 and 24, it can hardly be argued that the reintroduction of the name *Alno-Carpinetum* for wet oak-hornbeam forests would be a continuous source of error, even though it would be a change of a name commonly used in some countries. However, during the discussions in the CCCN, serious doubts arose as to whether the names *Alno-Carpinetum* Issler 1924 and *Stellario-Carpinetum* Oberdorfer 1957 really refer to the same association. As mentioned above, three of Oberdorfer's subassociations are wet oak-hornbeam forests similar to the *Alno-Carpinetum* (although Oberdorfer did not mention this name), but the *Stellario-Carpinetum typicum* is not one of them. It is therefore possible that the *Stellario-Carpinetum* is actually the correct name for the *Poo chaixii-Carpinetum* sensu Novák et al. (2020), while the *Stellario-Carpinetum* sensu Novák et al. (2020) should be named *Alno-Carpinetum*. In conclusion, there was no majority in favour of the Proposal, and it is not recommended.

Since the original diagnosis of the *Alno-Carpinetum* only contains a synoptic table, we select a neotype from Issler (1926), i.e. from the relevés on which the synoptic list of Issler (1924) is based upon. We select relevé 3 in table 2 of Issler (1926) as the neotypus hoc loco of the *Alno-Carpinetum* Issler 1924. This is the same relevé as the superfluous lectotype (Art. 19c) of the '*Alno-Carpinetum typicum* Issler 1926' selected by Boeuf et al. (2014, p. 158).

(26) To conserve the name *Nanocyperetalia* Klika 1935 against *Nanocypero-Polygonetalia* Koch 1926. Proposed by Fernández-González et al. (2021). Vote: 5 pro, 1 abstention (recommended).

The name *Nanocypero-Polygonetalia* Koch 1926, which to our knowledge has never been used since its first publication, was considered as invalid in Mucina et al. (2016). However, as shown by Fernández-González et al. (2021), it is in fact valid and legitimate, thus threatening the well-established name *Nanocyperetalia*. This Proposal aims to avoid this inappropriate change of a commonly used name. The CCCN recommends its acceptance.

(27) To conserve the name *Isoetetalia* Braun-Blanquet 1936 with a conserved type. Proposed by Fernández-González et al. (2021). Vote: 5 pro, 1 abstention (recommended).

According to its original diagnosis in Braun-Blanquet (1936), the name *Isoetetalia* is a superfluous name of the *Nanocypero-Polygonetalia* Koch 1926, since the order *Isoetetalia* includes the alliance *Nanocyperion* Koch 1926 in addition to the new alliance *Isoetion*. In the previous edition of the Code, it was not clear whether Art. 18b (ruling the type of superfluous names) would take precedence over Art. 20 in cases where the application of both articles leads to contradictory results. This has been clarified in the 4th edition by explicitly stating that Art. 20 does not apply to superfluous names. Therefore, since the order *Isoetetalia* includes, in addition to the new alliance *Isoetion*, the alliance *Nanocyperion* Koch 1926, which is the type of the *Nanocypero-Polygonetalia* Koch 1926, the name *Isoetetalia* Braun-Blanquet 1936 is a superfluous name of the *Nanocypero-Polygonetalia* Koch 1926 and automatically gets the *Nanocyperion flavescentis* Koch 1926 as its type. Consequently, a new syntaxon name would be needed for the traditional concept of the *Isoetetalia*. To avoid such an inappropriate change of a commonly used name, Fernández-González et al. (2021) proposed to conserve the name *Isoetetalia* Braun-Blanquet 1936 with the *Isoetion* Braun-Blanquet 1936 as conserved type. The CCCN recommends that this Proposal be accepted.

(28) To conserve the name *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967 against *Molinio arundinaceae-Quercetum* Samek 1962. Proposed by Slezák et al. (2021). Vote: 5 pro, 1 abstention (recommended).

The name *Molinio arundinaceae-Quercetum* is used for hygrophytic Central European acidophilous oak forests (Pallas 1996; Moravec 1998; Valachovič et al. 2021). However, there are two independent homonyms, of which the earlier one (*Molinio arundinaceae-Quercetum* Samek 1962) is problematic because its type relevé does not fully fit the traditional concept of this association. To avoid the change of a commonly used name, Slezák et al. (2021) proposed to conserve the later homonym *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967. The CCCN sees no problem with this Proposal and therefore recommends its acceptance. Moreover, a binding decision should be made to clarify the name-giving oak species in both names (see Request 4 above).

(29) To conserve the name *Omphalodo nitidae-Coryletum avellanae* Amigo, G. Azcárate et Romero 1994 with a conserved type. Proposed by Rodríguez-Guitián and Amigo Vázquez (2022). Vote: 2 pro, 4 contra (not recommended).

This name was coined by Amigo et al. (1994) for a mesophytic woodland community of the north-western Iberian Peninsula, mostly dominated by *Corylus avellana*, a tall shrub that occasionally reaches 10 m in height but is mostly confined to the (upper) shrub layer. However, the selected type relevé is dominated by the tree *Quercus robur* and, as stated by Rodríguez-Guitián and Amigo Vázquez (2022), represents "an oak forest [...], overshadowing an understory of *Corylus avellana*". Thus, the name *Omphalodo nitidae-Coryletum avellanae* is illegitimate because no name-giving taxon belongs to the highest of the dominant strata (Art. 29b). In the following years, the *Omphalodo-Coryletum* was interpreted as a seral community and accepted in syntaxonomic checklists of Spain and Portugal (Rivas-Martínez et al. 2001; Costa et al. 2012). The Proposal aims at preserving this current use of the name by means of a conserved type representing a hazel woodland without *Quercus robur*.

During the discussion of the Proposal, a contradiction between Art. 29b, Example 5 and Art. 53 was detected. On the one hand, the mentioned Example suggests that a name being illegitimate due to a physiognomically "untypical" type can be preserved by a conserved type. On the other hand, Art. 53 states that names rejected according to Art. 29b are not eligible for getting a conserved type. There was no agreement among the CCCN members whether this contradiction is absolute (and therefore could only be resolved by an amendment to the Code) or merely bad wording that could be resolved by appropriate interpretation (i.e., conservation is acceptable if the conserved type eliminates the violation of Art. 29b and at the same time preserves the current use of the name).

An important difference between the present Proposal and Example 5 of Art. 29b is the fact that the holotype of the *Omphalodo nitidae-Coryletum avellanae* was not selected by accident but fully intentionally. Indeed, Amigo et al. (1994) describe it as "one of our best examples of *Omphalodo-Coryletum*", and they classified the association within the alliance *Carpinion betuli*. This and the mentioned statement in Art. 53 led the majority of the CCCN to vote against the Proposal. A new name should be published for the hazel woodlands of the NW Iberian Peninsula.

(30) To conserve the name *Polysticho setiferi-Fraxinetum excelsioris* (Tüxen et Oberdorfer 1958) Rivas-Martínez ex Díaz et Fernández Prieto 1994 with a conserved type. Proposed by Loidi et al. (2022). Vote: 2 pro, 3 contra, 1 abstention (not recommended).

This case is similar to the previous one in that it concerns the name of a woodland in the Atlantic part of the Iberian Peninsula, supposedly dominated by *Quercus robur* in its most mature stage, but more often represented by seral stages dominated by *Fraxinus excelsior* and *Corylus avellana* due to human land use. However, in contrast to the *Omphalodo nitidae-Coryletum avellanae*, the name-giving *Fraxinus excelsior* is a tree of similar size as *Quercus robur*. The name *Polysticho setiferi-Fraxinetum excelsioris* is a nomen novum for the illegitimate name *Corylo-Fraxinetum cantabricum* Tüxen et Oberdorfer 1958. However, in the lectotype selected by Díaz and Fernández Prieto (1994) *Quercus robur* (without layer) has only a +, *Fraxinus excelsior* (tree layer) a 2 and *Fagus sylvatica* (tree layer) a 4 (relevé 139 in table 87 in Tüxen and Oberdorfer 1958). Thus, although selected from the "typical" subassociation, the lectotype represents a transitional stand towards beech forests. Unfortunately, the second relevé of the typical subassociation is also problematic, as it is a shrubby stage dominated by *Corylus avellana*, having a tree layer cover of just 10% ("Kronenschluss 0.1", with *F. excelsior* being the only species in the tree layer). Indeed, Tüxen and Oberdorfer (1958) wrote that the abundance of the tree species in both relevés was untypical, although they considered them to be relatively close to the "typus" of the association in terms of species composition. Moreover, they described relevé 139 as "*Fazies, die dem Fagetum nahesteht*" (facies close to the *Fagetum*). For the other relevé, they noted that it was "*durch Ausholzung etwas gestört*" (slightly disturbed by logging). In conclusion, both relevés do not correspond exactly to the named syntaxon in the author's opinion, and they should not be selected as lectotype (Art. 19a).

Loidi et al. (2022) published a relevé strongly dominated by *Quercus robur* as neotype for the *Polysticho setiferi-Fraxinetum excelsioris* (≡ *Corylo-Fraxinetum cantabricum*) and, at the same time, they proposed this relevé as the conserved type. However, as shown above, the lectotypification by Díaz and Fernández Prieto (1994) must be rejected because the two relevés in the original diagnosis of the typical subassociation were considered atypical by the authors (Art. 19a, 21). Therefore, the establishment of a neotype was necessary, and the first publication of a neotype must be followed, unless it can be shown that it was based on a misinterpretation of the original diagnosis (Art. 21). Loidi et al. (2022) argue that it was due to the scarcity of forests dominated by *Q. robur* throughout the surveyed territory that Tüxen and Oberdorfer (1958) preferred to use *Fraxinus excelsior* as the name-giving tree species of the association instead of *Quercus*. However, a closer inspection of the original description gives a somewhat different picture. On p. 284, Tüxen and Oberdorfer (1958) write (translation from German): "Only ash (*Fraxinus excelsior*) and – in the shrub layer – hazel (*Corylus avellana*) occur constantly and often predominantly in all forms of this Atlantic forest community and are therefore best suited to denominate the association, especially as they differentiate it well against the oak-hornbeam forests of the Central European *Querceto-Carpinetum*. We did not use the oaks in the name because they (*Quercus petraea* and predominantly *Quercus robur*, but also *Quercus pubescens* and *Quercus ilex*) are not represented, let alone dominate, across the entire breadth of the association."

Before proceeding to neotypification, the authors of the proposal should have considered whether forests dominated by *Fraxinus excelsior* and those dominated by *Quercus robur* could be considered as different associations, in which case a new association should be described for the latter, and a neotype with a dominance – or at least co-dominance – of *F. excelsior* in the tree layer should be selected for the former. However, this is a syntaxonomic question that is beyond the mandate of this Committee. In any case, there is no immediate need to conserve the name *Polysticho setiferi-Fraxinetum excelsioris* with a conserved type, and therefore the proposal is not recommended.

Data availability

No data used.

Author contributions

All authors are members of the CCCN and participated in the evaluation and discussion of the Proposals and the Requests. WW planned the report and wrote the first draft, which was commented and revised by all authors.

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RESEARCH PAPER

Floristics of Virginia's Northern and Central Piedmont grasslands

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Abstract

Aims: The grasslands of the North American Piedmont host diverse communities of sun-loving plants, but more than 90% of these grasslands have been lost across the region. Grasslands of the northern and central Piedmont of Virginia have received little formal study, but they are likely to be as diverse and threatened as they are in other parts of the eastern United States. To conserve the remaining Piedmont grasslands, we need to characterize floristic communities, identify the edaphic factors and disturbance regimes that drive their persistence, and develop methods to restore degraded grasslands. **Study Area:** Northern and Central Virginia Piedmont, USA. **Methods:** We surveyed plant communities and collected soil samples in 132 grasslands in old fields, powerline clearings, and roadsides. We used cluster analysis, indicator species analysis, and non-metric multidimensional scaling overlaid with soil and environmental variables to identify community groups. **Results:** We identified 695 plant taxa (87% of which are native) including 13 species that are rare in Virginia, two of which are globally critically imperiled (*Pycnanthemum clinopodioides* and *P. torreyi*). Six of our study sites contained 100 or more species with a maximum of 114 species in a single plot, making them among the most species-rich 100 m^2 plots recorded in the United States. Cluster analysis and ordination indicated four community groups, which we refer to as the Northern Prairies, Central Prairies, Savanna/Woodlands, and Wet Grasslands. **Conclusions:** The descriptions of these community groups can be used as reference information to inform grassland restoration in Virginia. Virginia's Piedmont grasslands are threatened by fire suppression, development, invasive species, and inappropriate management by utility companies. Swift action to conserve high quality grasslands and restore degraded ones is required to save these diverse plant communities.

Taxonomic reference: Weakley et al. (2012).

Abbreviations: NMDS = non-metric multidimensional scaling; PERMANOVA = permutational multivariate analysis of variance.

Keywords

biodiversity, cluster analysis, floristics, grassland, ordination, Piedmont grasslands, savanna, Southeastern grasslands, Virginia, woodland

Introduction

Temperate grasslands are the most threatened biome globally, with high rates of habitat loss and low levels of protection (Hoekstra et al. 2005). Worldwide, an estimated 45.8% of temperate grasslands have been lost to development or converted to agricultural land, and 49% of all grasslands have experienced degradation due to human activities and climate change (Hoekstra et al. 2005; Gang et al. 2014; Bardgett et al. 2021). The remaining temperate grasslands receive little conservation effort, in part due to the perception that they represent degraded forests and the assumption that grasslands can recover quickly after degradation (Veldman et al. 2015a, 2015b; Dudley et al. 2020; Buisson et al. 2022). This bias has led some scientists and organizations to misclassify extant grasslands as areas for potential reforestation, which would create forests at the expense of historic grasslands (Veldman et al. 2015b). To address this, conservation ecologists have called for increased recognition, restoration, and protection of grassland ecosystems during and beyond the United Nations Decade on Ecosystem Restoration (2020–2030) (Veldman et al. 2015b; Dudley et al. 2020; Török et al. 2021).

Grasslands host an array of plant and animal species, and their conservation and restoration can help address the 53% decline in North American grassland bird populations since the 1970s (Rosenberg et al. 2019). In addition to their conservation value, grasslands provide resources for livestock production and a range of ecosystem services, including water supply regulation, erosion control, and pollination (Bengtsson et al. 2019). In the face of global climate change, grasslands account for up to 34% of the global terrestrial carbon storage, the majority of which is in underground root and soil stores that are less susceptible to release by fire than the carbon stored above-ground in forest vegetation (White et al. 2000).

Among the temperate grasslands in need of increased recognition and study are the grasslands of the southeastern United States. These often-overlooked yet old ecosystems range from open tallgrass prairies to extensive savannas to open woodlands, glades, and barrens, all of which were historically common across the South (Barden 1997; Juras 1997; Noss 2013; Noss et al. 2015; Hanberry et al. 2020; Hanberry and Noss 2022; Krings et al. 2023; Szakacs et al. 2024). The savannas, open woodlands, and grasslands across the Piedmont uplands were maintained in part by relatively frequent, low-intensity fires originating from both dormant-season lightning strikes and early spring cultural burns conducted by Native American peoples to prepare land for hunting and agriculture (Spooner et al. 2021). Though we have lost most of these grasslands to modern-day agricultural expansion, land development, fire suppression, and forest encroachment, those that remain include some of the most endemic-species-rich habitats in eastern North America with higher native plant diversity than the tallgrass prairies of the American Great Plains (Noss 2013; Noss et al. 2015, 2021). In the remaining grasslands and rocky outcrops in the Virginia Piedmont, this species richness includes 52 globally and/or state-listed rare plant species, including microendemics such as *Phemeranthus piedmontanus* (Piedmont fameflower), *Marshallia legrandii* (tall Barbara's-buttons), and *Dichanthelium harvillii* (Harvill's panic grass), state-listed rare species such as *Buchnera americana* (American bluehearts) and *Solidago rigida* var. *rigida* (stiff goldenrod), and the federally endangered *Echinacea laevigata* (smooth coneflower) and *Rhus michauxii* (Michaux's sumac) (Townsend and Ludwig 2020; Fleming and Patterson 2021; Townsend 2023).

Despite their endemic species richness and previous widespread distribution, southeastern grasslands, including those of Virginia's Piedmont, have lost an estimated 90% of their former range (Noss et al. 2021). Those that remain face continued habitat loss and fragmentation, the disruption of natural disturbance regimes, invasive species pressure, and changes in temperature and precipitation due to climate change (Tompkins 2019; Noss et al. 2021). For example, the Piedmont grasslands of Virginia have been nearly extirpated and persist largely as semi-natural communities maintained by human disturbance, such as grazing or mowing, that keep woody canopies from shading out heliophytic grassland species (Townsend and Ludwig 2020; Fleming and Patterson 2021). The only remaining examples of significant size (>2000 ha) are within the frequently burned military base training areas of Fort Barfoot and Quantico Marine Base (Fleming et al. 2001; Fleming and Patterson 2021).

To conserve the remaining Piedmont grasslands and to provide a target reference state for grassland restoration efforts, we need to determine the distribution of these grasslands and characterize grassland floristic groups. The Virginia Department of Conservation and Recreation currently classifies the grasslands of the Piedmont as a subtype of the Piedmont Oak-Hickory Woodlands, Savannas, and Grasslands Group, and this subtype description is based on just six open grassland locations and eleven savanna/woodland sites (Fleming and Patterson 2021). Fifty-four other woodland, bald, glade, and savanna sites have been surveyed by the Virginia Department of Conservation and Recreation, and an additional open woodland protected area in Halifax County has been shown to contain many rare plant species (Townsend and Ludwig 2020; Fleming and Patterson 2021; Szakacs et al. 2024). Aside from these limited studies, native grasslands, open woodlands, and savannas in the Virginia Piedmont have not been surveyed and their species compositions, distribution, and conservation statuses unknown.

To address these knowledge gaps, we located and surveyed high-quality grassland fragments across the northern and central Virginia Piedmont. We predicted that some sites would host diverse plant communities that included rare species. We also predicted that native plant communities would differ across various substrates based on field observations that suggested that soil factors, notably pH and base cation content, may be drivers of grassland persistence, diversity, and variability. Based on these predictions, we aimed to define general vegetation community groupings that can guide future floristic, conservation, and restoration work.

Study area

Our study was conducted within a 17-county region within the Piedmont physiographic province in northern and central Virginia (Figure 1). The Piedmont is characterized by its gently rolling topography and is bound by the Blue Ridge Mountains to the west and the Fall Line to the east. It extends from Virginia's northern border with Maryland to its southern border with North Carolina. It is underlain by a complex assemblage of metamorphic and igneous rock, which have been deeply weathered by the humid climate.

Methods

Site selection

We identified a pool of potential grassland fragments across the northern and central Virginia Piedmont through a combination of systematic inspections of satellite imagery, structured driving surveys, and consultations with regional botanical experts. From the grassland fragments initially identified, 132 species-rich sites with a predominance of native, helophytic species were selected for vegetation surveys (Figure 1). We chose to survey the highest-quality grassland fragments we could find to define a reference state to inform future grassland conservation and restoration efforts.

Most of the remaining grasslands on the Virginia Piedmont occur in areas with soils that are unsuitable for agriculture and histories of human management or disturbance that enable heliophytic species to persist. Therefore, many of our sites were located in powerline corridors, old fields (e.g. former pastures mowed every 1–3 years, historical battlefields maintained as parks), and roadside rights-of-ways. We did not sample actively hayed or grazed sites, sites known to be planted with native wildflower seed, or sites containing non-native species indicative of commercially available meadow seed mixes such as *Echinacea purpurea* (purple coneflower) or *Coreopsis tinctoria* (plains coreopsis).

Vegetation surveys

We sampled the vegetation at each site between June and November with modified Whittaker plots using a method adapted for sampling small, fragmented grasslands (Miller et al. 2015). We established one to three 100-m^2 study plots at each site based on their size, with more study plots in larger fragments to capture local community variability. All survey plots were placed so that there were no adult trees within the plot and minimal tree canopy cover. We iden-

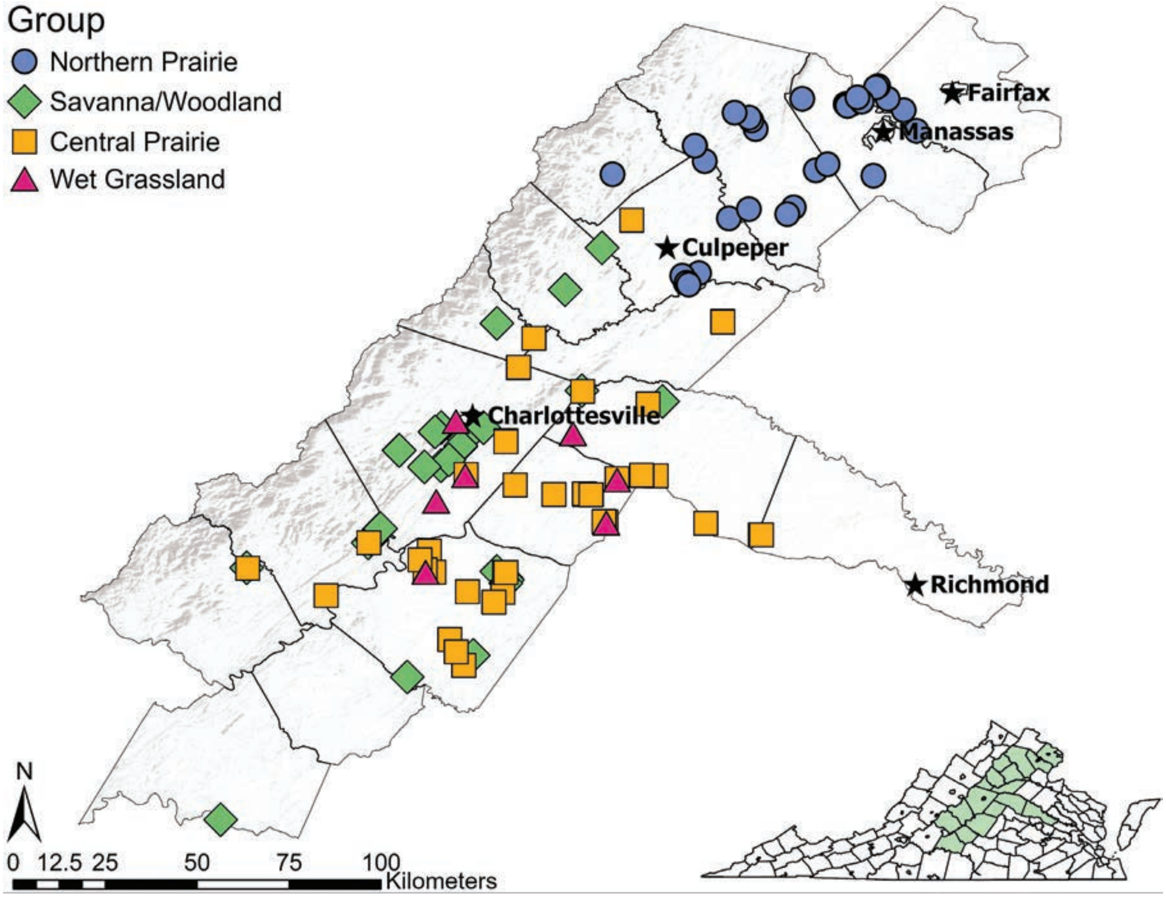

Figure 1. 129 of the 132 grassland sites surveyed in the northern and central Virginia Piedmont. Sites are colored according to their floristic community group as determined by this study. Three survey sites were excluded from analyses and are not included on the map.

tified all woody and herbaceous plants within each plot to the lowest taxonomic level possible using the dichotomous keys in the *Flora of Virginia* (Weakley et al. 2012). We collected voucher specimens of plants that could not be identified to the species level in the field for later identification.

For the first surveys conducted in the northern Piedmont in 2020, the survey plots were 2 × 50 m (100 m^2), and we estimated percent cover within five 1 m^2 quadrats evenly spaced every ten meters along the 50 m edge of the plot. Any species found within these plots but outside the quadrats were included in the plot species list. In subsequent surveys conducted in the Central Piedmont in 2021, the survey plots were modified to 4 × 25 m (100 m^2), and we estimated percent cover across the entire plot. To standardize the percent cover estimates from within quadrats in 2020 and across the entire plot in 2021, we calculated the average percent cover of each species across all five quadrats in the 2020 data. We converted percent cover into an ordinal cover class variable with ten possible values: 0 = absent, 1 < 0.1%, 2 = 0.1 to 1%, 3 = 1 to 2%, 4 = 2 to 5%, 5 = 5 to 10%, 6 = 10 to 25%, 7 = 25 to 50%, 8 = 50 to 75%, and 9 = 75 to 100%. This cover class scale follows methods used to determine formal floristic types in forests by the Virginia Department of Conservation and Recreation, though we adapted these methods to include a cover class of 0 in this study (Fleming 2007). Species found within the 100 m^2 plot but outside the quadrats in the 2020 surveys were assigned a cover class value of 1 in accordance with the treatment of incidental species recorded in surveys by the Virginia Department of Conservation and Recreation (Fleming 2007).

Soil sampling

To assess relationships between soil attributes and plant community composition, we aggregated at least five soil cores that were 15 cm deep and 5 cm in diameter. These cores were taken from locations distributed evenly throughout each study plot to create a single soil sample for each study site. We sent these soil samples to Brookside Laboratories, Inc. to analyze for pH, Mehlich III extractable micronutrients, total cation exchange capacity, percent organic matter, estimated nitrogen release, and bulk density (soil testing methods detailed in Suppl. material 1).

GIS data

We supplemented our field-collected data with soil unit characteristics and topographic information compiled from publicly available databases using the ArcGIS Pro Spatial Analyst package (Version 3.2.0, Esri Inc., Redlands, CA, US). We derived flood frequency and soil drainage class information from the dominant condition data for each soil unit underlying a site in the USDA Soil Survey Geographic Database (Soil Survey Staff 2022).

We obtained the elevation of each site in meters from the 30 m National Elevation Dataset (U.S. Geological Survey 2022). We calculated the slope of each site in degrees from the digital elevation model using the Spatial Analyst Slope tool. We calculated a simplified topographic position index for each site by subtracting the average elevation within a 10-cell circular radius of a site from the site's elevation (Weiss 2001). In the resulting index, positive values represent areas higher than their surroundings, like peaks, and negative values represent areas lower than their surroundings, like valleys.

Data preparation and transformation

We conducted all statistical analyses in R using RStudio (R Version 4.4.1 R Core Team 2024, RStudio Version 2024.09.0+375 Posit Team 2024). If a species could not consistently be identified to the subspecies or variety level in our surveys, all records of that species were reclassified to the species level. We created a matrix of the average cover class code for each species for each site. We used this species matrix to calculate the species richness, the inverse Simpson's Diversity Index, and the average cover classes of woody, graminoid, and forb taxa for each site. To reduce noise, we removed species that occurred at less than 1% of the 132 sites before conducting multivariate analyses (McCune et al. 2002). Removed species occurred in 75 of the 132 sites, only nine of which had more than five removed species, with a maximum of eight removed species at a single site. These removed species were included in the presented species lists and in the calculation of species richness and diversity values for all sites.

Three sites with an average Bray-Curtis dissimilarity from all other sites greater than 2.5 standard deviations from the mean were considered outliers and were removed prior to multivariate analysis to avoid distortions in the ordination (McCune et al. 2002). Plant species recorded at these outlying sites are included in Table 1 and Suppl. material 2, but these sites were not included in the cluster analysis, ordination, or indicator species analysis. Bray-Curtis dissimilarity was chosen to emulate the methods used to determine formal floristic types in forests by the Virginia Department of Conservation and Recreation (Fleming 2007). Bray-Curtis dissimilarity is widely used in vegetation studies due to the relatively equal weighting it gives to both dominant and rare species in analyses (Bray and Curtis 1957). The remaining 129 sites were used in the cluster analysis and non-metric multidimensional scaling (NMDS) ordination.

To prepare the ArcGIS data for analysis, we converted the categorical variable for soil drainage class to a numeric ordinal variable with higher values corresponding with increasingly poorer drainage. Flood frequency was similarly transformed, with higher values corresponding to more frequent flooding. These ordinal variables were converted to interval-scaled variables for analysis. The distributions of the continuous soil and geological variables were examined and transformed to linear distributions if necessary to correct for strong positive or negative skew. The variables estimated soil N release (#N/acre), soil bulk density (g/cm^3), and relative forb cover were squared. The variables slope, soil P content (mg/kg), soil K content (mg/kg), soil Mg content (mg/kg), soil Zn content (mg/kg), soil

Table 1. Species of conservation concern and the number of study sites at which they were recorded. A rank of S3 indicates that a species is uncommon in Virginia (20–50 sites state-wide), a rank of S2 indicates that a species is rare in Virginia (5–20 sites state-wide), while a rank of S1 indicates that a species is critically rare in Virginia (1–5 sites state-wide) (Townsend 2023).

Scientific Name	Common Name	State Rank	Global Rank	Number of Sites	Average Cover Class
Symphyotrichum ericoides var. *ericoides*	white heath aster	S3	G5T5	10	3.00
Pycnanthemum torreyi	Torrey's mountain-mint	S2	G2	6	3.00
Pycnanthemum clinopodioides	basil mountain-mint	S1	G1G2	3	4.33
Gymnopogon brevifolius	short-leaf beard grass	S3	G5	2	5.50
Agrostis scabra	rough bentgrass	S3?	G5	1	3.00
Asclepias purpurascens	purple milkweed	S3	G5?	1	1.00
Baptisia australis	blue wild indigo	S3	G5	1	3.00
Desmodium canadense	showy tick-trefoil	S1	G5	1	1.00
Dichanthelium annulum	ringed panicgrass	S3	G4	1	4.00
Dichanthelium ravenelii	Ravenel's rosette grass	S3	G5	1	2.00
Hexastylis lewisii	Lewis' Heartleaf	S3	G3	1	4.00
Solidago rigida var. *rigida*	stiff goldenrod	S2	G5T5	1	1.00
Tragia urticifolia	nettle-leaf noseburn	S3	G5	1	4.00

Mn content (mg/kg), and soil Ca content (mg/kg) were natural-log-adjusted. The variables relative woody cover and relative graminoid cover were square-root-adjusted. The variables elevation (m), soil pH, soil organic matter content (%), soil Al content (mg/kg), and total cation exchange capacity (meq/100g) were cube-root-adjusted. The variables soil Na content (mg/kg), soil Cu content (mg/kg), soil S content (ppm), soil Fe content (mg/kg), and soil B content (mg/kg) were arctangent adjusted.

Cluster analysis

To classify sites into plant community groups, we conducted a hierarchical, agglomerative cluster analysis using the R package cluster function agnes() using Bray-Curtis dissimilarity and a flexible linkage method using par.method = 0.625 (Maechler et al. 2023). This linkage method corresponds to a Lance-Williams flexible linkage formula with $\beta = -0.25$ by assigning $\alpha = 0.625$ and $\beta = 1 - (2 \times \alpha)$ to approximate Ward's linkage method, which is incompatible with Bray-Curtis dissimilarity (McCune et al. 2002). We pruned the resulting dendrogram at a height of 1.4 based on visual inspection to obtain smallest number of groups with the greatest between-group dissimilarity, resulting in four groups. We conducted permutational multivariate analysis of variance (PERMANOVA) of these groups using the R package vegan function adonis2() with a Bray-Curtis dissimilarity matrix and 9,999 permutations (Oksanen et al. 2024).

Indicator species analysis

Following cluster analysis, we conducted indicator species analysis to identify characteristic species within each grassland group. Analysis was run using the R package indicspecies function multipatt() with the IndVal.g test statistic based on the Indicator Value index of Dufrêne and Legendre (1997) and 999 permutations (De Cáceres and Legendre 2009). This analysis produces a list of species associated with each group ranked by an Indicator Value test statistic that is the product of a site specificity value, *A*, and a fidelity value, *B*. The specificity value measures the probability that a site containing the species is part of the group, with an *A* value of 1.0 indicating that a species is found only at sites within in the given group. The fidelity value measures the probability of finding a species across all sites in a group, with a *B* value of 1.0 indicating that a species is found at all sites within the group. Therefore, species with high Indicator Values are found in most of the sites within a given group but are uncommon in sites from other groups.

Ordination

To examine the separation of the grassland groups produced by the cluster analysis, we visualized the groups in multivariate space using non-metric multidimensional scaling (NMDS) ordinations of our species matrix. We created all NMDS ordinations with the R package vegan function metaMDS using Bray-Curtis dissimilarity and 100 random starts (Oksanen et al. 2024). To select an optimal solution that balances the need for a low stress value with the ability to visually interpret ordination results, we ran NMDS using 1 through 6 axes and built a scree plot of the number of axes run versus their stress values to determine the smallest number of axes needed to obtain a stress value less than 0.2 (Suppl. material 3: figure S3.1, McCune et al. 2002).

To assess which soil and environmental gradients correlated with the results of the NMDS ordination, we projected soil and environmental variable gradients onto our selected ordination using the R package vegan function envfit() with 100 permutations (Oksanen et al. 2024). We projected 23 variables: species richness, relative woody cover, relative graminoid cover, relative forb cover, elevation (m), slope (degrees), topographic position index, flood frequency class, drainage class, pH, soil organic matter content (%), estimated soil N release (#N/acre), soil P content (mg/kg), soil K content (mg/kg), soil Na content (mg/kg), soil Al content (mg/kg), soil Fe content (mg/kg), soil Mn content (mg/kg), soil Zn content (mg/kg), soil Cu content (mg/kg), soil B content (mg/kg), soil cation exchange capacity (meq/100g), and soil bulk density (g/cm^3). Species diversity, soil Ca content and soil Mg content, and soil S content had co-linearity values > 0.65 with species richness, soil cation exchange capacity, and soil Al content, respectively, so they were omitted from analysis. We removed 19 sites with missing data for at least one soil or environmental variable from all environmental variable analyses.

Results

Floristics

We identified 695 species, subspecies, and varieties of plants across all study sites (Suppl. material 2). Of these, 604 (86.9%) were native, 66 (9.5%) were introduced, 20 (2.9%) were invasive, and 5 (0.7%) were of uncertain status in Virginia (Weakley et al. 2012; Suppl. material 2). Only 23 taxa were found at 50% or more study sites while 518 taxa were found at 10% or fewer study sites, indicating that the communities varied greatly across our study region. The three most frequently recorded native taxa were *Rubus flagellaris* (northern dewberry), *Schizachyrium scoparium* var. *scoparium* (little bluestem), and *Dichanthelium acuminatum* (tapered rosette grass), all of which were found at 70% or more of our study sites. The most common non-native taxa, *Lonicera japonica* (Japanese honeysuckle) and *Kummerowia striata* (Japanese clover), were the only non-native taxa found at more than 50% of our study sites. Our surveys identified 13 state or globally rare species, including the globally critically imperiled mountain-mints *Pycnanthemum torreyi* (Torrey's mountain-mint) and *Pycnanthemum clinopodioides* (basil mountain-mint) (Table 1, NatureServe 2024; Townsend 2023). In addition, *Buchnera americana* (American bluehearts), which is rare to critically rare in Virginia, was found outside of the bounds of the 100 m^2 study plots at a site in the northern Piedmont and is therefore not reflected in our study results.

Compositional groups

Cluster analysis indicated four broad grassland community groups (PERMANOVA $P < 0.001$, $R^2 = 0.19$, Figure 2, Suppl. material 4). Based on our interpretation of the floristic composition, indicator species, and best-fitting environmental variables of these groups as detailed in the "Four Piedmont Grassland Groups" section below, we refer to these four groups as the Northern Prairies, Central Prairies, Savanna/Woodlands, and Wet Grasslands in all figures and tables. The number of sites in each group and the average species richness and relative cover classes of graminoids, forbs, and woody plants are listed in Table 2. An example site from each group is illustrated in Figure 2. Full species lists for each group can be found in Suppl. material 5.

Indicator species

The top five indicator species with the highest indicator values for each group are listed in Table 3. A full list of the statistically significant indicator species identified for each group and species associated with combinations of two and three groups can be found in Suppl. material 6.

Ordination and environmental variables

The selected NMDS solution was built on three axes (stress = 0.16, non-metric fit $R^2 = 0.98$, linear fit $R^2 = 0.87$; Figure 3 and Suppl. material 3: figure S3.2). The environmental and soil variables fit to this ordination, their average values for each grassland group, and their fit to the ordination are listed in Table 4. The fit of the soil and environmental variables with R^2 values greater than 0.25 and P values less than 0.05 to the NMDS ordination are illustrated in Figure 3; with the exceptions of slope (degrees) and soil P content (mg/kg) which nearly overlapped in the angle visualized in the figure with relative woody cover and soil organic matter content (%), respectively, to improve figure legibility. Plots that include all environmental and soil variables with P values less than 0.05,

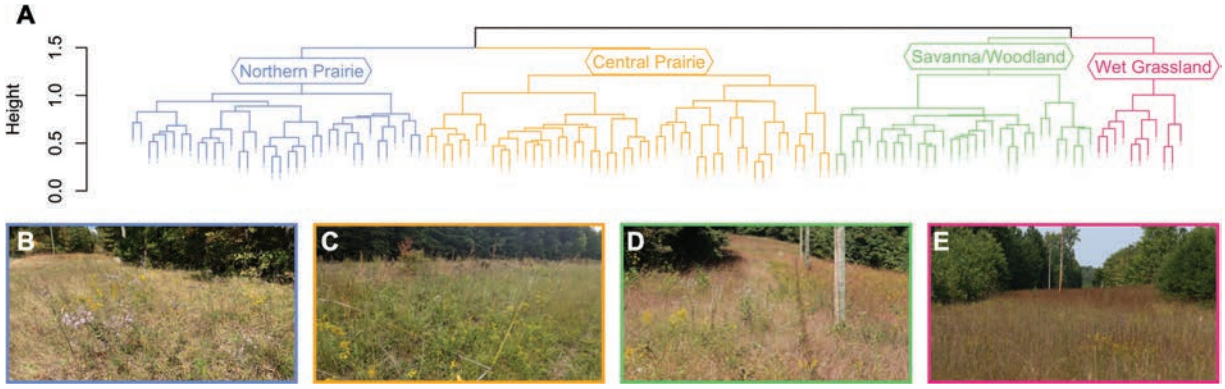

Figure 2. (A) Dendrogram of the four major grassland groups produced by the hierarchical agglomerative cluster analysis of 129 sites. The four major groups were supported by PERMANOVA ($P < 0.001$, $R^2 = 0.19$). (B) Northern Prairie site in Prince William County, VA photographed by JBCH. (C) Central Prairie site in Albemarle County, VA photographed by DF. (D) Savanna/Woodland site in Madison County, VA photographed by DC. (E) Wet Grassland site in Buckingham County, VA photographed by DC.

Table 2. Number of sites and average species richness and relative cover classes for each grassland group.

Group	Number of Sites	Average Species Richness ± Standard Error	Average Relative Graminoid Cover	Average Relative Forb Cover	Average Relative Woody Plant Cover
Northern Prairie	36	61.22 ± 2.18	0.31 ± 0.01	0.50 ± 0.01	0.19 ± 0.01
Central Prairie	50	67.49 ± 2.07	0.30 ± 0.01	0.53 ± 0.01	0.17 ± 0.01
Savanna/Woodland	32	74.25 ± 3.56	0.22 ± 0.01	0.47 ± 0.02	0.30 ± 0.02
Wet Grassland	11	67.55 ± 4.65	0.36 ± 0.02	0.46 ± 0.02	0.18 ± 0.03

Table 3. Top five indicator species for each grassland group.

Group	Scientific Name	Common Name	Specificity	Fidelity	Indicator Value	P Value
Northern Prairie	*Sorghastrum nutans*	Indiangrass	0.60	0.78	0.68	0.001
	Carex bushii	Bush's sedge	0.87	0.50	0.66	0.001
	Poa cuspidata	early bluegrass	0.85	0.44	0.62	0.001
	Chamaecrista fasciculata	partridge pea	0.74	0.39	0.54	0.002
	Strophostyles umbellata	pink fuzzybean	0.79	0.36	0.53	0.005
Central Prairie	*Carex glaucodea*	blue sedge	0.83	0.48	0.63	0.001
	Andropogon gyrans	Elliott's bluestem	0.68	0.52	0.59	0.002
	Andropogon ternarius	splitbeard bluestem	0.76	0.28	0.46	0.015
	Solidago pinetorum	Small's goldenrod	0.90	0.22	0.45	0.013
	Aristida dichotoma	churchmouse threeawn	0.89	0.20	0.42	0.016
Savanna/ Woodland	*Dichanthelium boscii*	Bosc's panicgrass	0.89	0.66	0.77	0.001
	Carya glabra	pignut hickory	0.80	0.66	0.73	0.001
	Prunus serotina var. *serotina*	black cherry	0.67	0.63	0.65	0.001
	Clitoria mariana var. *mariana*	butterfly pea	0.89	0.41	0.60	0.001
	Quercus velutina	black oak	0.66	0.53	0.59	0.004
Wet Grassland	*Eupatorium perfoliatum*	common boneset	0.93	1.00	0.96	0.001
	Dichanthelium microcarpon	branched panicgrass	0.83	0.91	0.87	0.001
	Juncus effusus	common rush	0.89	0.82	0.86	0.001
	Carex lurida	shallow sedge	1.00	0.73	0.85	0.001
	Persicaria sagittata	arrowleaf tearthumb	1.00	0.73	0.85	0.001

the locations of group centroids, and the positions of each species in ordination space can be found in Suppl. material 3: figure S3.2. The ordination indicates that the Central Prairie group has an intermediate species composition among the other three groups. The Northern Prairies diverge in a direction correlated with increased soil Mn content (mg/kg), the Savanna/Woodlands diverge in a direction correlated with increased soil organic matter content (%), higher elevation (m), and higher relative woody plant cover, and the Wet Grasslands diverge in a direction correlated with increased soil Fe content (mg/kg) and higher relative graminoid cover.

Four Piedmont grassland groups

The Northern Prairie group was named for its restriction to the northern Virginia Piedmont. In comparison to the other subgroups, Northern Prairie sites have somewhat more basic soils with notably higher Mn contents. The northern character of this group is reinforced by the presence of *Carex bushii* (Bush's sedge), a sedge that is most frequently found in Northern Virginia, as its second-strongest indicator species.

Likewise, the Central Prairie group was named for its restriction to the central Virginia Piedmont. Though there are indications that this subgroup could extend to the southern Virginia Piedmont as well, this will need to be confirmed by future studies. In contrast to the Northern Prairie group, the strongest indicator species for the Central Prairie group include species such as *Solidago pinetorum* (Small's goldenrod) and *Andropogon ternarius* (splitbeard bluestem) that are common in the central and southern Piedmont but infrequent in the northern Piedmont. Furthermore, the Central Piedmont sites were correlated with intermediate values for many soil and environmental variable gradients in our analyses in comparison to sites from the other three groups.

The Savanna/Woodland group, the group with the highest average species richness of over 74 species per 100 m^2 study plot, was named for the prevalence of woodland and woody species in its indicator species list and the high average relative woody cover classes among its study sites. Though our study plots did not contain adult trees due to the routine mowing of the roadside rights-of-way, powerline corridors, and old fields that comprised the majority of our sites, the herbaceous and shrubby vegetation in these plots contain many species with affinities for woodland habitats despite the lack of woodland structure. Three of the top five indicator species for this group, *Carya glabra* (pignut hickory), *Prunus serotina* var. *serotina* (black cherry), and *Quercus velutina* (black oak) are trees, while another top indicator species, *Dichanthelium boscii* (Bosc's panicgrass), is often found in woodlands and forests. In addition to higher average relative woody cover classes, Woodland/Savanna study sites were correlated with higher elevations, steeper slopes, and had the highest average topographic position index value of 4.69 ± 1.20 among the four groups, indicating that the Woodland/Savanna group grasslands are associated with slopes and uplands.

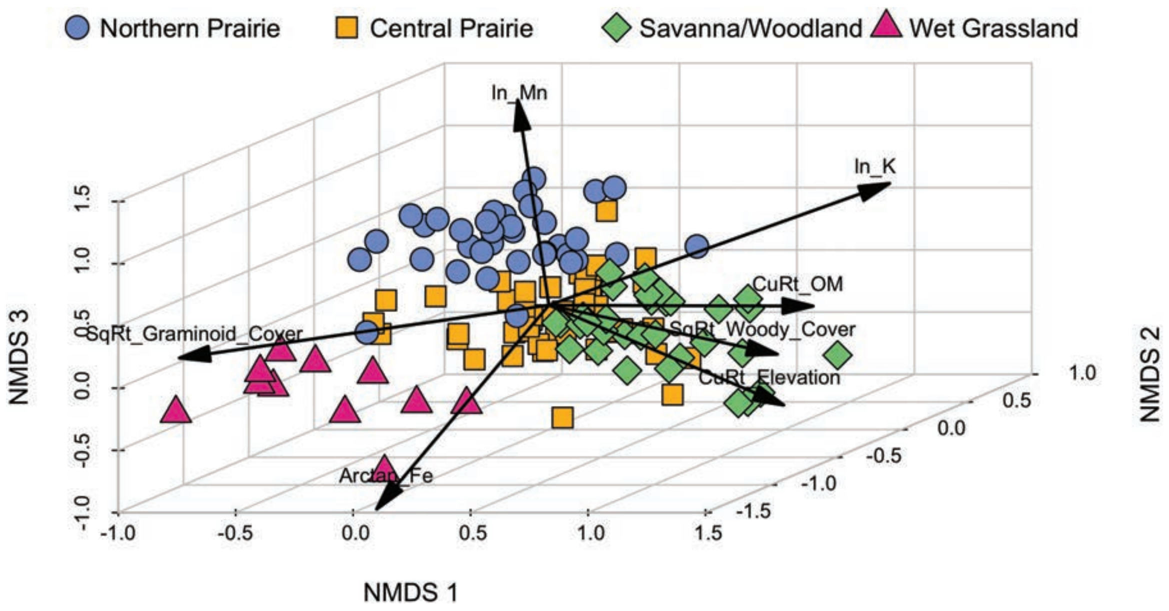

Figure 3. Scatterplot of the NMDS ordination in three dimensions (stress = 0.16, non-metric fit R^2 = 0.98, linear fit R^2 = 0.87). Point shapes and colors indicate the four groups: Northern Prairie, Central Prairie, Savanna/Woodland, and Wet Grassland. Overlaid arrows depict the environmental variables with R^2 values greater than 0.25 and P values less than 0.05, with the exceptions of slope (degrees) and soil P content (mg/kg), which nearly overlapped with relative woody cover and soil organic matter content (%), respectively, were removed for legibility (Table 4).

Table 4. Average values ± standard error and fit of each soil and environmental variable to the NMDS ordination. Group averages were calculated using untransformed data, while variable fitting to the NMDS was performed using transformed data.

Variable	Northern Prairie	Central Prairie	Savanna/Woodland	Wet Grassland	R^2	P Value
Organic Matter Content (%)	4.47 ± 0.27	4.4 ± 0.17	7.57 ± 0.55	5.03 ± 0.96	0.48	0.01
Relative Woody Cover	0.19 ± 0.01	0.17 ± 0.01	0.3 ± 0.02	0.18 ± 0.03	0.46	0.01
Elevation (m)	116.08 ± 9.55	136.98 ± 4.29	176.71 ± 9.21	138.35 ± 7.26	0.44	0.01
Relative Graminoid Cover	0.31 ± 0.01	0.30 ± 0.01	0.22 ± 0.01	0.36 ± 0.02	0.42	0.01
Fe (mg/kg)	139.43 ± 7.96	186.02 ± 10.87	176.91 ± 9.22	367.73 ± 35.67	0.37	0.01
K (mg/kg)	61.43 ± 7.27	69.65 ± 6.51	78.88 ± 6.73	42.45 ± 10.68	0.33	0.01
P (mg/kg)	9.14 ± 2.14	8.04 ± 0.66	14.61 ± 3.17	8.36 ± 1.70	0.32	0.01
Slope (degrees)	2.37 ± 0.38	2.32 ± 0.19	6.49 ± 0.84	3.21 ± 0.59	0.31	0.01
Mn (mg/kg)	129 ± 21.45	65.45 ± 8.72	81.66 ± 12.37	39.73 ± 8.05	0.27	0.01
Bulk Density (g/cm^3)	1.05 ± 0.02	1.00 ± 0.01	0.90 ± 0.02	0.85 ± 0.05	0.24	0.01
Topographic Position Index	1.11 ± 0.53	1.70 ± 0.63	4.69 ± 1.20	-3.26 ± 0.87	0.23	0.01
Al (mg/kg)	709.00 ± 31.10	784.43 ± 29.68	854.22 ± 53.34	605.64 ± 71.01	0.22	0.01
Relative Forb Cover	0.50 ± 0.01	0.53 ± 0.01	0.47 ± 0.02	0.46 ± 0.02	0.21	0.01
Drainage Class	4.47 ± 0.22	3.22 ± 0.09	3.03 ± 0.12	3.30 ± 0.50	0.20	0.01
B (mg/kg)	0.27 ± 0.02	0.35 ± 0.03	0.37 ± 0.03	0.52 ± 0.04	0.19	0.01
Cu (mg/kg)	1.82 ± 0.19	1.33 ± 0.17	1.47 ± 0.20	2.97 ± 1.43	0.19	0.01
pH	5.65 ± 0.11	5.22 ± 0.06	5.26 ± 0.12	5.17 ± 0.10	0.18	0.01
Na (mg/kg)	24.29 ± 3.70	13.37 ± 0.66	13.34 ± 0.9	55.91 ± 36.02	0.13	0.01
Cation Exchange Capacity (meq/100g)	10.73 ± 1.51	7.54 ± 0.56	9.26 ± 0.57	5.94 ± 1.33	0.11	0.02
Flood Frequency Class	1.31 ± 0.15	1.06 ± 0.03	1.09 ± 0.09	1.20 ± 0.20	0.08	0.02
Zn (mg/kg)	4.14 ± 2.27	6.51 ± 1.18	4.30 ± 0.56	16.08 ± 11.06	0.03	0.31
Species Richness	61.22 ± 2.18	67.49 ± 2.07	74.25 ± 3.56	67.55 ± 4.65	0.03	0.42
Estimated N Release (#N/acre)	92.71 ± 2.58	88.22 ± 3.17	91.06 ± 7.22	92.73 ± 4.87	0.02	0.45

Finally, the Wet Grassland group was named for both the prevalence of wet-soil tolerant species in its indicator species list and for the correlation of its sites with characteristics indicative of wet habitats along the soil and environmental variable gradients. All five of its top indicator species are frequently found in or restricted to wet habitats such as floodplains, swamps, wet meadows, and other low habitats. The Wet Grassland group has the only negative average topographic position index of -3.26 ± 0.87, indicating that its sites are found in low-lying areas such as seeps and depressions. Wet Grassland sites also had notably higher soil Fe and Zn content than sites from the other three subgroups.

Discussion

Our study provides an initial synopsis of the floristic composition and variability of Virginia's most diverse and least studied ecological community. In our surveys of grassland fragments across the northern and central Virginia Piedmont, we have documented 604 native taxa in 132 survey sites. Many of these sites have notably high species richness: six of our study sites have 100 species or more within a single 100 m^2 plot, with a maximum of 114 species. We have distinguished four major community groups among our study sites, which we refer to as the Northern Prairies, the Central Prairies, the Savanna/Woodlands, and the Wet Grasslands. Each group has distinctive species composition and edaphic characteristics that should be considered in future conservation and restoration efforts in these threatened habitats.

Piedmont grasslands harbor high species richness

We documented 695 taxa across our study sites, which represent over 21% of the 3,164 species documented in the *Flora of Virginia* (Weakley et al. 2012). This high species richness was present despite the small size and fragmentary nature of our study sites. The severity of human impact on Virginia's grasslands and the lack of documented disturbance history makes it difficult to distinguish the origins or antiquity of many of our grassland sites. However, our observations of repeated patterns in plant community composition across this highly fragmented landscape suggest that some of our study sites were connected in grassland-savanna mosaics in the past. Semi-natural, managed, temperate grasslands in the Czech Republic hold the world record for the highest species richness values at small spatial grains, demonstrating that even small fragments of semi-natural grassland can have high biodiversity value (Wilson et al. 2012). Therefore, it is important to document the floristic variety represented by fragmented grassland communities and recognize their importance for conservation.

Six of our study sites had survey plots containing over 100 species, making these plots some of the most species-rich 100 m^2 plots recorded in the state of Virginia. Furthermore, our six plots may be among the most species-rich 100 m^2 plots recorded across the entire United States: of the 4,773 100 m^2 plots from the United States with publicly available data on VegBank at the time of writing, only six plots contained over 100 species, with a maximum of 129 species (Peet et al. 2013). We found a maximum value of 114 species in a Savanna/Woodland plot in Albemarle County, which had 103 native species. In addition to high native species richness, we have documented populations of 13 state-imperiled species across our study sites, including three potentially new Virginia populations of the globally rare *Pycnanthemum clinopodioides*, which was previously known from fewer than 30 extant populations worldwide (NatureServe 2024).

With their high species richness and the presence of threatened endemic species, our study sites are pockets of biodiversity threatened by a changing climate and landscape (Noss et al. 2021). The value of such fragments to biodiversity conservation are being recognized across the Southeast, and scientific study and conservation efforts in these fragments are increasing. For example, the Southeastern Grasslands Institute, a collaborative biodiversity conservation organization led by Austin Peay State University, has initiated surveys of grassland fragments in roadsides in partnership with the Tennessee Department of Conservation and surveys of powerline rights-of-ways in collaboration with Tennessee Valley Authority, the Electric Power Research Institute, and the Mississippi Entomological Museum (Southeastern Grasslands Institute and Austin Peay State University 2024a). The Piedmont Prairie Partnership, a group of non-profit, state, and federal agencies within the Southeastern Grasslands Institute, is building an interactive map of publicly accessible Piedmont grassland fragments across the Southeast to encourage public awareness and appreciation of native grasslands (Southeastern Grasslands Institute and Austin Peay State University 2024b). Our work in the northern and central Virginia Piedmont is complementary to these research efforts, expanding the area of study into the northern range of the historic Southeastern grassland region.

Grassland groups to inform conservation and restoration

The current community type description for the Piedmont Oak-Hickory Woodlands, Savannas, and Grasslands defined by the Virginia Department of Conservation and Recreation describes the herb layer of these habitats as "highly variable in both density and composition" and notes the presence of *Schizachyrium scoparium* var. *scoparium* (little bluestem), *Sorghastrum* spp. (indiangrasses), *Andropogon* spp. (broomsedges), *Danthonia spicata* (poverty oatgrass), *Desmodium* spp. (tick-trefoils), *Lespedeza* spp. (bush-clovers), *Eupatorium* spp. (thuroughworts), and *Solidago* spp. (goldenrods), particularly *Solidago nemoralis* var. *nemoralis* (gray goldenrod) and *S. juncea* (early goldenrod) (Fleming and Patterson 2021). Our results corroborate this description, listing *Schizachyrium scoparium* var. *scoparium* (little bluestem), *Solidago nemoralis* var. *nemoralis* (gray goldenrod), *S. juncea* (early goldenrod), and *Danthonia spicata* (poverty oatgrass) among the top 10 most common species found across our study sites, and our species list includes four *Andropogon* species, 12 *Desmodium* species, 10 *Lespedeza* species, 16 *Solidago* species, and 13 *Eupatorium* species (Suppl. material 2). However, some species highlighted in the formal description, such as *Erianthus alopecuroides* (silver plumegrass) and *Agalinis purpurea* (purple false foxglove), were found at ten or fewer of our sites, indicating that there is variety in Virginia's grasslands that is not represented by the current community type description.

Our evidence suggests that there are at least four broad grassland community groups in the northern and central

Virginia Piedmont. This expands the current description of Piedmont grasslands as a subtype of the Piedmont Oak-Hickory Woodlands, Savannas, and Grasslands Group defined by the Virginia Department of Conservation and Recreation, whose ability to survey the powerline, roadside, and battlefield sites that comprise the majority of our study has been limited by their designation as Semi-natural/Modified landscapes under the U.S. National Vegetation Classification (Fleming and Patterson 2021). The need to expand the current community type description to include more community groups is supported by the recent characterization of 12 new heliophytic Piedmont community types in southern Virginia and the Carolinas (Szakacs et al. 2024). Once formal vegetation surveys have been conducted across the entire Virginia Piedmont, our general grassland community groups can be further refined into formal community type descriptions based on underlying geology, soil chemistry, and moisture regimes using methods like those used by the Virginia Department of Conservation and Recreation to determine forest community types (Fleming 2007; Fleming and Patterson 2021).

By defining the floristic and environmental variation, our study can provide more accurate guidelines and define more detailed community composition and species richness goals to guide conservationists and restoration practitioners who manage native grasslands across Virginia. In the time since we have conducted our surveys, we have witnessed the degradation of several of our study sites. A population of the state-rare *Solidago rigida* var. *rigida* (stiff goldenrod) was sprayed with herbicide in a powerline clearing in Prince William County, and a population of the globally imperiled *Pycnanthemum torreyi* (Torrey's mountain-mint) was eliminated by the construction of a sidewalk in Albemarle County. These incidents exemplify the threats of habitat loss and degradation faced by grasslands across the Southeast. With habitat loss and destruction rates of 90–100% across their historic range, improving the management of known high quality Southeastern grasslands is an urgent priority (Noss et al. 1995, 2021; Noss 2013). Our experiences in our study sites indicate that limiting herbicide use by utility companies, treating non-native plant invasions, and preventing the conversion of grasslands to other land uses can prevent future losses at a fragment-level scale. Such small-scale efforts led by public land stewards and private landowners, in combination with the efforts of larger conservation organizations across greater Southeastern region such as Southeastern Grasslands Institute to raise public awareness and scientific study of these ecosystems, will be critical to the survival of Southeastern grassland biodiversity.

Conclusion

The native grasslands of the Southeastern United States are among the most diverse and threatened habitats in the country, yet they are understudied and largely unprotected. We need to increase recognition of their ecological value to encourage their conservation and restoration. Through our surveys of species-rich grassland fragments in the northern and central Virginia Piedmont, we have found evidence of at least four grassland community groups in need of further description and documentation. By defining these groups, we can promote the conservation of their endemic biodiversity and create more nuanced reference models for the ecological restoration of degraded Piedmont grassland landscapes.

Data availability

The data and code used in the preparation of this manuscript (with site locations expunged for the protection of rare species) are openly available in the Virginia Tech Data Repository (http://data.lib.vt.edu/) at DOI https://doi.org/10.7294/25267117.

Author contributions

J.B.C.H., D.F., J.L.R., and J.T.C. designed the study; all authors collected field data. J.T.C. compiled supplementary GIS data, conducted analyses, and wrote the first draft of the manuscript. All authors edited the manuscript.

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Supplementary material

Supplementary material 1
Soil analysis methods. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl1

Supplementary material 2
Species list for all study sites. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl2

Supplementary material 3
Scree, stress, and scatter plots for the selected NMDS solution. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl3

Supplementary material 4
Full PERMANOVA results. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl4

Supplementary material 5
Species lists for each of the four grassland types. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl5

Supplementary material 6
Full indicator species analysis results. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl6

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EDITORIAL
AFRICAN VEGETATION STUDIES

African vegetation studies: introduction to a Special Collection

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Abstract

Abstract: This editorial introduces the Special Collection of “African Vegetation Studies”. The collection includes seven research papers from four African countries. One paper examines the impact of traditional agro-ecosystems on plant diversity in Morocco. In Benin, one research paper focuses on vegetation associations in a biosphere reserve, and another is on land cover changes on inselbergs. In Namibia, one paper provides a syntaxonomic description of the Karstveld vegetation, while another models potential vegetation changes along a south-north rainfall gradient. Two papers present research on vegetation classification and descriptions of two natural areas in South Africa, namely the Tankwa Karoo National Park and the Telperion Nature Reserve. The collection demonstrates that there are important classification studies ongoing in different parts of the continent to better understand the diversity and complexity of African vegetation. At the same time our mini-review of the current status of vegetation classification and vegetation-plot databases in Africa highlights that much work remains to be done to achieve a comprehensive and internationally consistent vegetation classification for the countries of Africa, which would be beneficial for land use management, biodiversity conservation and ecological research.

Abbreviations: EVA = European Vegetation Archive; EVS = European Vegetation Survey; GDP = Gross Domestic Product; IAVS = International Association for Vegetation Science; IAVS-AS = IAVS Regional Section for Africa; VCS = Vegetation Classification and Survey.

Keywords

Africa, editorial, International Association for Vegetation Science (IAVS), phytosociology, remote sensing, vegetation classification, vegetation map, vegetation-plot database

Introduction

Africa, the world's second largest continent, is bordered by the Mediterranean Sea, the Red Sea, the Indian Ocean, and the Atlantic Ocean and is almost equally divided by the equator. It covers an area of 30.3 million km^2 (including adjacent islands such as Cape Verde, Madagascar, Mauritius, Seychelles, and Comoros). It is also the second most populous continent after Asia. With 53 countries, Africa has more countries than any other continent in the world.

Africa is characterized by a great diversity of vegetation types and ecosystems. White (1983) classified 16 natural vegetation types mainly based on their physiognomy. These vegetation types include forest, woodland, bushland and thicket, shrub land, grassland, wooded grassland, desert, Afro-alpine vegetation, scrub forest, transition woodland, scrub woodland, mangrove, herbaceous fresh-water swamp and aquatic vegetation, halophytic vegetation, bamboo, and anthropogenic landscape (White 1983; Mengist 2020). However, due to several factors including increasing anthropogenic pressure, climate change, and industrialization, there are vegetation changes over time. These changes have been exacerbated by a rapidly growing human population across the continent, resulting in a high demand for food (and thus agricultural land), construction materials, energy, and other raw materials. These factors led to changes in the various vegetation types, resulting in an update of the vegetation types of Africa by Mayaux et al. (2003), classifying the vegetation into five main types: forest, woodlands and shrublands, grasslands, swamp and mangrove vegetation, and agricultural lands. In any case, all existing classifications of the vegetation of Africa as a whole remain at a very coarse level, hardly suitable for regional planning and conservation prioritization. Fine-scale classification of vegetation does not have a strong academic tradition in Africa except in a few countries.

Although some research on African vegetation has been published, data on the African flora and vegetation remains relatively poorly documented compared to other regions such as Europe and the Americas (Küper et al. 2006). This poor representation of Africa is due to several factors. First, data availability, data access, and language barriers hamper efforts to build databases on African vegetation. Second, low budgetary allocations for science in most African countries are well documented and serve as a major barrier that directly affects research focus and the data availability (Christie 2019; Krishna 2020; Adepoju 2022). For example, in 2006, African Union member states committed to spend 1% of their Gross Domestic Product (GDP) on research and development. But by 2019, the continent's funding was only 0.42% (range of 0.1 to 0.5%) of the GDP, in sharp contrast to the global average of 1.7% and against UNESCO's recommendation of at least 1% (Christie 2019; Krishna 2020; Adepoju 2022). By comparison, in 2020, Latin America and the Caribbean invested 0.62% of their regional income in science, compared to 3.32% in North America and to 2.28 in the countries of the European Union (World Bank 2020). Third, political instability in some regions of Africa also is an obstacle to the sustained and consistent advancement of scientific research. Thus, to better understand the extraordinary diversity of African vegetation and all its habitat types, there is a need to improve vegetation survey techniques, broaden the scope of sampling across the continent and improve collaboration among scientists to address data challenges. This will strengthen communication among vegetation scientists from different regions and provide the scientific basis for national and international nature conservation initiatives and formulation of the best management practices. However, a comprehensive and consistent classification system is still far from being fully realized.

In 2021, the journal Vegetation Classification and Survey (VCS) and the African Section of the International Association for Vegetation Science (IAVS-AS) partnered to launch a Special Collection dedicated to "African Vegetation Studies". The aim of this Special Collection was to provide new case studies of vegetation classifications across the African continent. The vegetation typologies could be of any kind, for example based on vegetation plots or remote sensing data. Likewise, the papers could develop a new classification system for a certain vegetation type in a particular region, or use an existing vegetation typology in applied research, e.g. related to global change. This editorial begins with an overview of the current knowledge on vegetation types in Africa and the available databases, followed by summaries of the articles in the Special Collection, and ends with conclusions and future perspectives.

Current state of vegetation classification in Africa

At the continental scale, only rather coarse physiognomic classifications exist for Africa, namely the one by White (1983). Recently, a remote-sensing based map of even coarser vegetation types was published by Mayaux et al. (2003). Probably the most recent and most detailed global map of biomes is that of Loidi et al. (2022). This study recognized five biomes and nine sub-biomes on the African continent. Based not on vegetation but on vascular plant flora, Linder et al. (2005) classified all of Africa into phytochoria. More recently, Marshall et al. (2021) divided tropical Africa into 19 clusters (floristic provinces). Both sources could also provide a useful framework for vegetation studies.

Studies at finer physiognomic scales, or even at community level based on vegetation plots, exist only in some regions of some countries. Below we provide a rough overview of the current state in four broad regions of Africa where at least one of the authors has some insight. We have excluded Central Africa and Madagascar, where we are not aware of any classification study (except Lebrun 1947 from the Democratic Republic of Congo). This may be our personal bias, but it coincides with the fact that these two regions are also largely without internationally available vegetation plot data (see next section).

Northern Africa

The francophone countries of NW Africa (Morocco, Algeria) have a considerable tradition of phytosociological vegetation classification, mainly carried out by researchers from France, but sometimes also from other European countries. They mostly focused on the climax vegetation, i.e. forests and steppes (e.g. Quézel 1956; Quézel and Barbero 1981, 1986, 1989; Quézel et al. 1987, 1988). In consequence, Morocco is probably the only country in Africa to date that has a comprehensive overview of the syntaxa on its territory (Fennane 2003), but even this is not particularly up to date. The Canary Islands, geographically part of Africa but politically part of the European Union, are probably the best surveyed region of Africa in terms of plant community classification (e.g. Rivas-Martínez et al. 1993). Interestingly, some plot-based vegetation typologies have also emerged in Egypt in recent years, namely for the Sinai (Hatim et al. 2021) and for a mountainous region in the south (Abutaha et al. 2020). Recently, some comprehensive plot-based studies of European vegetation types have also included data from the northernmost (Mediterranean) part of Africa (Marcenò et al. 2018, 2019).

Western Africa

Major vegetation studies conducted in the West African region include the BIOTA (Biodiversity Monitoring Transect Analysis in Africa) West project, the SUN project and the UNDESERT project, which have resulted in numerous publications on the vegetation of West Africa and vegetation databases such as the West African Vegetation (http://www.westafricanvegetation.org/menu/home.aspx) and the West African plants photo guide (http://www.westafricanplants.senckenberg.de/root/index.php). A comprehensive description of the vegetation of West Africa was provided by Hahn-Hadjali et al. (2010), who recognized four vegetation zones and fifteen vegetation types. Several studies have focused on providing descriptions of phytosociological plant communities in specific locations such as the inselberg plant communities of Burkina Faso (Tindano et al. 2024), the woody plant communities of the Comoe-Leraba Reserve (Gnoumou et al. 2020), the occurrence of herbaceous plant communities in West African savannas (Zerbo et al. 2018), among others. Even more specific studies have been conducted, such as a study focused on *Piliostigma* associations (Barthelemy et al. 2015).

Eastern Africa

East Africa does not have a strong tradition of vegetation classification, and we are not aware of any country with a comprehensive overview of fine-scale vegetation types. Recently, however, some specialized studies of wetlands have been published (Alvarez 2017; Behn et al. 2022). Such vegetation has been aligned to classes originally described for Europe as *Phragmito-Magnocaricetea* and *Potamogetonetea*, but now recognized globally. In contrast, the class *Oryzetea sativae*, described for weedy vegetation in rice fields, has also been applied to pioneer vegetation with a likely pantropical distribution. These revisions were based on earlier classifications made by Lebrun (1947) for the vegetation of the Democratic Republic of the Congo. Other work has examined the ecology of plant communities in Afro-montane wetlands in Tanzania (Deil et al. 2016) and forests in the Kenyan Rift Valley (Fujiwara et al. 2014). The systematic collection of data in specialized databases (e.g., Alvarez et al. 2021) and the refinement of new statistical assessments represents important advances toward a general review of vegetation in these regions and elsewhere in Africa.

Southern Africa

For South Africa, Lesotho and Eswatini, a comprehensive and detailed vegetation typology with accompanying maps has been published by Mucina and Rutherford (2006). These maps have been regularly updated and refined since then. However, the work provides the description and distribution of major habitat types with their broad vegetation units but is not based on formal plot-based vegetation classification. There is, however, a long tradition of plot-based Braun-Blanquet-type assessment of vegetation in South Africa, resulting in a significant amount of plot-based vegetation data but formal classifications are largely lacking (Brown and Bredenkamp 2018, but see Luther-Mosebach et al. 2012). There are many local to regional classification and mapping studies, mainly within protected areas of the country, such as in the northeastern South Africa (Bezuidenhout 1993; Brown et al. 1997; Morgenthal and Cilliers 1999; Van Staden et al. 2021), of the more arid western South Africa (Van der Merwe et al. 2008a, 2008b; Luther-Mosebach et al. 2012; Bezuidenhout and Brown 2021), of the central grasslands (Kay et al. 1993; Brand et al. 2011), mountains and inselbergs (Brand et al. 2009; Barret et al. 2024) and of ruderal vegetation in northwestern South Africa (Cilliers and Bredenkamp 1998, 1999a, 1999b).

A similar approach was used for a vegetation map of Namibia by Giess (1971). A country-wide vegetation map for Namibia based on formal vegetation classifications is in progress (Strohbach and Jürgens 2010), and first large-scale approaches have been published (Jürgens et al. 2013). In Botswana, vegetation classifications have mainly been carried out at local scales (e.g. Murray-Hudson et al. 2011; Tsheboeng et al. 2016; Sianga and Fynn 2017; Lori et al. 2019). None of these studies in Botswana, except for Sianga and Fynn (2017), produced a vegetation map but instead described phytosociological plant communities in different localized areas in the Okavango Delta (Murray-Hudson et al. 2011; Tsheboeng et al. 2016) and Khutse Game Reserve (Lori et al. 2019). Currently, there are no published studies on vegetation mapping at a country-wide scale. Therefore, a formal comprehensive vegetation map is still needed in Botswana. Even fewer classification studies are known from Angola, with Revermann et al. (2018) on the forests and woodlands of the Cubango Basin being one of the exceptions.

Databases

Since 1997, several datasets on plant collection records in Africa have been established (Linder 1998, 2001; Lovett et al. 2000; La Ferla et al. 2002). Since 2003, these datasets have been merged with others into a single Biogeographical Information System on African Plant Diversity (BISAP) (Linder et al. 2005; McClean et al. 2005; Küper et al. 2006).

In contrast, the availability of vegetation plots in databases is rather low. When the global vegetation plot database sPlot 2.1 (Bruelheide et al. 2019) was released, the African continent was poorly represented, especially compared to Europe, North America and Australia. Since then, sPlot has made great efforts to increase the data coverage in the Global South (G. Damasceno, pers. comm.). In the current working version of sPlot 4.0, only 45,202 out of a global total of 2,531,784 plots are from African countries (G. Damasceno, pers. comm.). This represents 1.8%, while Africa covers 22.5% of the ice-free surface of the Earth. A total of 30 regional databases contributed vegetation-plot data from 38 African countries, but there is still a considerable number of African countries without a single vegetation plot in sPlot. The spatial coverage of available vegetation plots in the sPlot database largely reflects the pattern of the articles included in this Special Collection (see below) and the state of vegetation studies in Africa summarized in the previous section. The only two countries with relatively good coverage by vegetation plots (in sPlot), both in terms of area and habitat types, are Namibia and Morocco. It is promising that several new regional vegetation-plot databases have emerged in Africa in recent years, such as the Coastal Forests database of Kenya (Fungomeli et al. 2020), SWEA-Dataveg (Alvarez et al. 2021) and the Vegetation Database of Sinai in Egypt (Hatim et al. 2021). South Africa has a National Vegetation Database (NVD) consisting of more than 46,000 plot-based data, curated jointly by the National Botanical Institute and the University of Stellenbosch. The NVD is also registered in the Global Index of Vegetation-Plot Databases (GIVD; Dengler et al. 2011) but has not yet joined sPlot.

Content of the Special Collection

The VCS Special Collection comprises seven articles from four countries in northern, western and southern Africa (Figure 1). The methodological approaches ranged from detailed phytosociological studies based on vegetation plots to coarse vegetation classifications using formations derived from remote sensing. The studies are introduced in the following.

Northern Africa

Chakkour et al. (2023) conducted research on the plant diversity of traditional agroecosystems in mountainous regions of Morocco. The authors placed 94 relevés in six study areas and identified a total of 209 different plant species. The data revealed that the vegetation, although influenced by agricultural activities, showed some affinity to the *Brometalia rubenti-tectorum* order. A total of 46% of the species were agricultural species while 31% were typical of natural and semi-natural areas. Wild grasses showed a high constancy and dominance in all the studied areas. The high number of perennial species present is attributed to the shallow tillage and regular fallow periods while very few introduced (non-native plants) were found. It is also interesting to note that several endemic and rare species were also found within the relevés. The floristic spectrum of these systems is considered typical of the Moroccan flora. The authors conclude that these traditional agroecosystem practices fulfil the criteria of high nature value agriculture. However, should these traditional agroecosystem practices be abandoned in favour of intensive yield-maximizing agriculture, the various segetal species still present, many of which are rare and endemic, will decline necessitating the implementation of policies to ensure that these practices are maintained.

Western Africa

Assèdé et al. (2023) conducted a syntaxonomic analysis of plant associations along different soil types in the Biosphere Reserve Pendjari (BRP) within the Sudanian zone of Benin. A total of 202 phytosociological relevès were sampled according to the Braun-Blanquet approach. The numerical analysis included Detrended Correspondence Analysis through which vegetation patterns were sought. A total of 249 plant species were identified and classified into two major groups belonging to eleven associations all correlated with a moisture gradient along a dryland and wetland continuum. The dryland group being a mixture of woodland and shrub savanna associations was found on rocky and gravelly soils (*Burkeo africanae-Detarietum microcarpi* and *Andropogono gayani-Combretum glutinosi*) and on soils associated with or without fine gravels (*Andropogono gayani-Terminalietum avicennioidis*, *Andropogono gayani-Senegalietum dudgeonii* and *Terminalietum leiocarpae*). The wetland group was characterized by riparian forest associations on sandy-clay soils (*Coletum laurifoliae*, *Borassetum aethiopi* and *Hyparrhenio glabriusculae-Mitragynetum inermis*) and floodplain associations (*Terminalio macropterae-Mitragynetum inermis*, *Brachiario jubatae-Terminalietum macropterae*, *Sorghastro bipennati-Vachellietum hockii*) on silt-clay soils. The authors concluded that soil moisture was a key determinant of plant species establishment and thus the development of plant communities.

Ayeko et al. (2023) studied land cover change in inselbergs and adjacent areas from 2003 to 2018 in a region

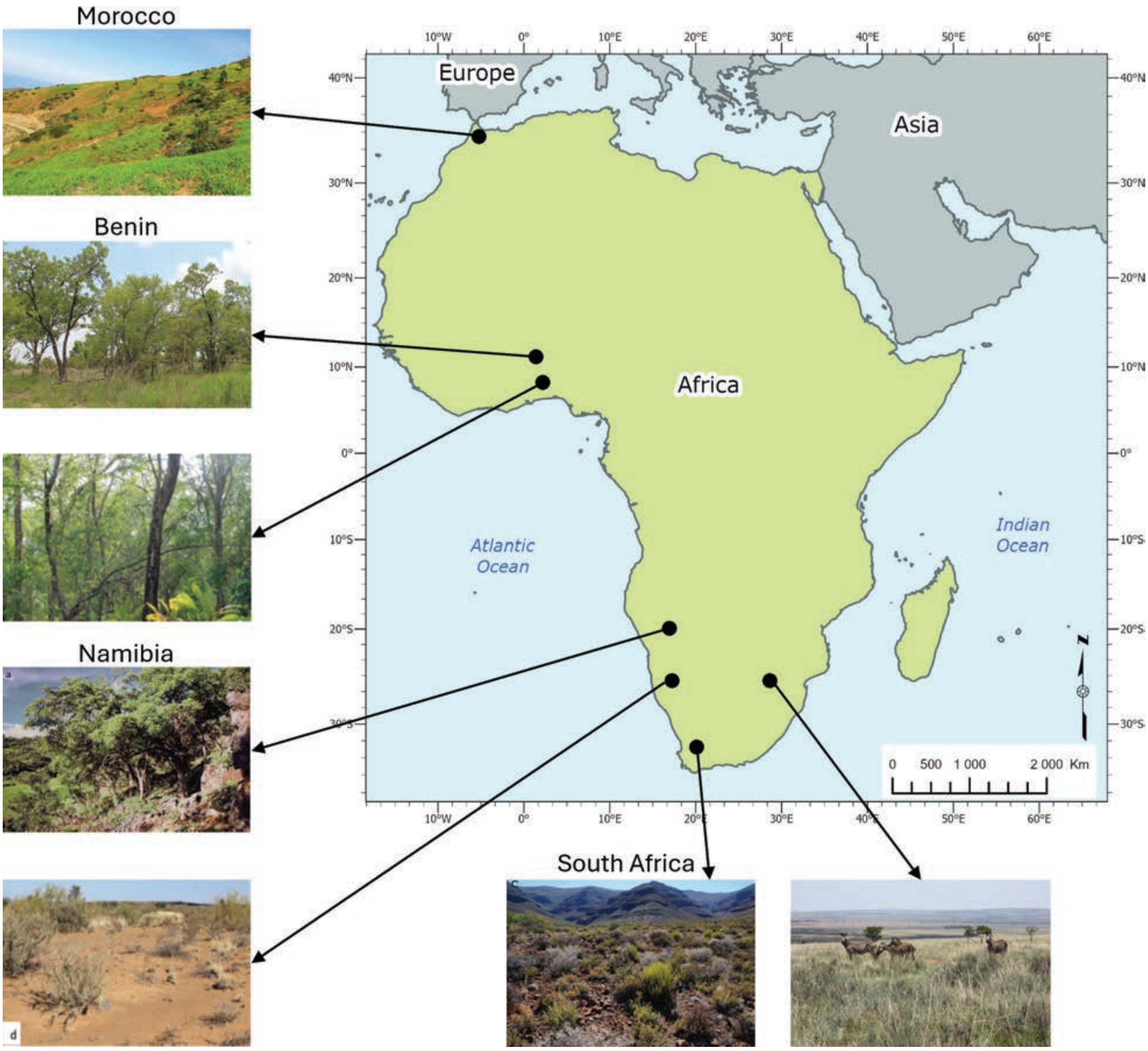

Figure 1. Spatial distribution of the seven articles in the Special Collection "African vegetation studies". The photos stem from the seven studies: Assèdé et al. (2023), Ayeko et al. (2023), Brown et al. (2022), Chakkour et al. (2023), Naftal et al. (2024), Samuels et al. (2023) and Strohbach and Strohbach (2023).

of Benin under anthropogenic pressure, with the aim of assessing dynamics and preserving rare endemic species. The authors used supervised classification of Sentinel-2 and Spot-5 satellite images of inselbergs and adjacent areas at 10-m spatial resolution to analyse different land use land cover classes. Savanna, grassland, field, fallow and plantation areas increased between 2003 and 2018. The results indicate a rapid conversion of natural vegetation in inselbergs and adjacent areas into human-made landscapes, a situation that calls for urgent conservation planning.

Southern Africa

Brown et al. (2022) provide a classification of the vegetation of the Telperion Nature Reserve located within the grassland biome of South Africa. As the second largest biome in southern Africa, grasslands have a high diversity of plants and animals that provide various ecosystem services. The authors provide a detailed description of the different plant communities based on their characteristic species, environmental factors, animal utilization, and topography. Based on 294 relevés, a total of 22 plant communities were identified, grouped into five major communities. The rocky woodland and the mid-plateau grasslands had the highest diversity while a total of 551 different plant species representing 107 plant families were found to be present within the reserve. The study shows that the reserve is a reservoir of plant species making it an important conservation area. This study provides valuable information to enable the management to implement a science-based management plan for the reserve to ensure the long-term functioning and conservation of these grassland ecosystems.

Naftal et al. (2024) used Random Forest models to predict the effect of changing climatic conditions along a south-north rainfall gradient on vegetation within

Namibia. Using 1,986 relevés, the authors classified the vegetation along the gradient into twelve vegetation units. To predict the potential changes in the vegetation composition of these units in 2080, the distribution of the different vegetation classes was modelled using the main climate variables. The results obtained were compared with those of the existing classifications while the model obtained a prediction accuracy of 82%. The results indicate that there will be a higher dominance of broad-leaved and degraded thornbush savannas while units of specific environmental conditions such as the mountain savannas, dwarf shrub savannas and dry thornbush savannas will decrease in area or even disappear. The paper was the Editors' Choice for the second quarter of 2024, for its unique approach of modelling the distribution of vegetation units rather than individual species under future climate conditions.

Samuels et al. (2023) studied three major vegetation types (based on Mucina and Rutherford 2006) along an elevation gradient in the Tankwa Karoo National Park of the arid winter rainfall region of South Africa. The elevation gradient ranged from the lowland plains (338 m a.s.l.) to the escarpment (1147 m a.s.l.). Each vegetation type was sampled at 13–15 sites with 4 m × 100 m linear transects. The authors compared structural and floristic composition, species diversity measures and environmental variables among the three vegetation types. The elevation gradient was identified as a complex gradient that included climatic variables (e.g., increasing aridity with decreasing elevation), soil nutrient and water infiltration status and grazing distribution. Vegetation types were clearly distinguishable in terms of species composition and environmental variables with the strongest separation between the plain and the two upland habitats. Large variations in vegetation variables within the vegetation types were associated with even small variations in environmental variables across the landscape. The study thus concludes that elevation is an important driver of species composition in this system but that, even within vegetation types, environmental variables such as slope and rockiness can result in different states of the vegetation condition.

Strohbach and Strohbach (2023) provide a comprehensive syntaxonomic description of the Karstveld vegetation in Namibia. Based on 889 relevés of 1000 m^2 extracted from the Phytosociological Database of Namibia, the authors distinguished four main vegetation types using TWINSPAN: wetlands and associated grasslands, transitional vegetation between Thornbush savanna and Karstveld, Kalahari type sandy vegetation and true Karstveld vegetation types. Each major vegetation type was further subdivided into more detailed plant communities, 17 of which have been formally described as new plant associations. All associations are clearly defined by diagnostic species. The authors described the true Karstveld vegetation as a new phytosociological class *Terminalietea prunoides*, with eight associations, two new orders and three new alliances. The description of these vegetation units was completed with a comparison of their structure and diversity and with an intuitive visualization of catenas representing their position along topographic gradients. A concluding remark of the authors concerns the high species richness of this region, which is seriously threatened in some areas that are not protected within the Etosha National Park or private nature reserves and conservancies. This study is outstanding because formal syntaxonomic vegetation classification is still rare in Africa as a whole and mostly restricted to the francophone parts of North Africa. Accordingly, it received the Editors' Award of VCS in 2023 (Dengler et al. 2024).

Conclusions and future perspectives

The above review, though certainly not comprehensive and regionally biased, demonstrates that the scientific knowledge of the vegetation of Africa is still extremely incomplete. Continental overviews are very coarse and not particularly up to date. Only a few countries have a comprehensive overview of the vegetation types on their territory, namely Morocco (Fennane 2003) and South Africa, Lesotho and Eswatini (Mucina and Rutherford 2006). In some others, comprehensive regional overviews have been published, such as for Tenerife in the Canary Islands (Rivas-Martínez et al. 1993) or for the Sinai Peninsula in Egypt (Hatim et al. 2021), but beyond that only local studies or studies focused on specific vegetation types exist. The situation is aggravated by the wide variety of methodological approaches used. Furthermore, there is a certain reluctance on the part of African researchers to use formalized phytosociological names for their units according to the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021). The EcoVeg approach, invented in the United States (Faber-Langendoen et al. 2018), seems to be even less used in Africa than the phytosociological approach. In this respect, the seven papers we were able to collect for this Special Collection are not much more than a drop in the ocean. It is also significant that we received contributions from only four countries in three of the major regions of Africa. Nevertheless, together with some other recent classification papers from different African countries and the growing African vegetation plot databases contributing to sPlot, this Special Collection marks a positive development.

We believe that the African Section of the International Association for Vegetation Science (https://www.iavs.org/page/working-groups_africa-section) could play an important role in this regard. To move forward, we consider the following aspects to be crucial:

- To increase the exchange and collaboration between vegetation scientists in the different African countries.
- To use the broad expertise available in IAVS to train African vegetation scientists to implement an Africa-wide sampling approach, to create and manage vegetation databases, and to conduct and publish vegetation classification studies.
- To raise the awareness of a vegetation typology derived from vegetation-plot data being essential for land management and biodiversity conservation.

What can be achieved by a few decades of cross-country cooperation among the vegetation scientists of an entire continent, even in the absence of major funding, can be seen in Europe. There, a few visionary scientists founded the European Vegetation Survey (EVS), like the African Section a subgroup of the IAVS (Mucina et al. 1993). There has been a regular exchange in annual meetings, which has now led to numerous useful and influential products, of which only the most prominent ones are highlighted here: (a) Bohn et al. (2004) produced a rather detailed map of the potential natural vegetation of the continent. (b) Chytrý et al. (2016) launched the European Vegetation Archive (EVA), an integrative vegetation plot database, which now contains more than 2 million plots and has led to numerous high-impact papers. (c) Mucina et al. (2016) published the first comprehensive syntaxonomic overview of the continent's high-rank syntaxa (alliances, orders, classes). (d) Janssen et al. (2016) published the first continent-wide Red List of habitat types, largely based on vegetation typology. (e) Chytrý et al. (2020) released an electronic expert system for the automatic/reproducible classification of vegetation plots into the European system of habitat types (EUNIS). (f) In 2023, no less than three ecological indicator value systems for the vascular plants of Europe were released (Dengler et al. 2023; Midolo et al. 2023; Tichý et al. 2023), which now allow a consistent bioindication across the continent. (g) More recently, also ReSurveyEurope, a database of plots repeatedly sampled over time, has been published as an important source for global change studies (Knollová et al. 2024).

This view of the neighbouring continent does not suggest that Africa should do everything in the same way. Obviously, Africa is a much larger continent and, as mentioned above, currently has far fewer financial resources than Europe. On the other hand, we now have much more advanced IT tools (shared documents in the cloud, large databases, powerful modelling techniques, remote sensing, artificial intelligence) available than at the start of EVS. In addition, African scientists have the advantage of learning what has worked in Europe and what has proved to be a drawback in development. Aiming for methodological standardization at an early stage, rather than reinventing the wheel, would certainly allow things to be done faster and more efficiently than in Europe. The BIOTA approach developed for Africa could provide some elements (Jürgens et al. 2012). A common plot database (EVA; Chytrý et al. 2016) has certainly been one of the cornerstones of the success in Europe. Why should we not be visionary and aim for an African Vegetation Archive (AVA)? There have been some attempts like TAVA (Tropical African Vegetation Archive; see Bruelheide et al. 2019) or SWEA-Dataveg (vegetation database for sub-Saharan Africa; Alvarez et al. 2021), but so far, they could not gain the momentum of EVA, either because of the lack of funding or because many researchers in Africa still focus on regional to national perspectives. Finally, publishing of classification results internationally rather than in regional journals or in grey reports can be very beneficial: (i) it rewards the authors with visibility and citations; (ii) it can motivate others to conduct similar studies; and (iii) it can contribute to a gradual harmonization of approaches. VCS would be pleased to be the publication venue for many of the forthcoming studies.

Author contributions

RTG and LB planned the outline with major inputs by JD. All authors contributed to portions of the draft, improved and approved the manuscript.

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RESEARCH PAPER

CLASSIFICATION OF EUROPEAN FORESTS

Vegetation diversity of *Pinus pinaster* forests in the Italian Peninsula

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Abstract

Aim: To revise *Pinus pinaster*-dominated communities of the Italian peninsula with special regard to central-southern Tuscany, and assess their floristic and ecological differences. **Study area:** Tuscany and Liguria regions, Italy. **Methods:** We classified 251 vegetation plots using the Two-way indicator species analysis method and we explored vegetation patterns through Principal Coordinate Analysis. We then investigated the ecology using Ecological Indicator Values. **Results:** We identified four major groups, primarily distinguished by the substrate of their stands and along a latitudinal gradient. We classified the forests in central-southern Tuscany in the association *Erico scopariae-Pinetum pinastri*. This community includes thermophilous and mesophilous species primarily distributed in the Atlantic and Western Mediterranean regions. Comparison of community means of Ecological Indicator Values revealed significant differences in soil reaction, nitrogen, moisture, and light conditions, but not in temperature, between the central-southern Tuscany forests and the other clusters. We classified the other studied forest communities on acidic substrates within the association *Erico arboreae-Pinetum pinastri*, whereas those found on ultramafic substrates were placed in the *Euphorbio ligusticae-Pinetum pinastri typus cons. propos.*, and in an informal group of secondary vegetation stands. **Conclusions:** Our analyses showed that the *Pinus pinaster*-dominated forests of central-southern Tuscany belong to the association *Erico scopariae-Pinetum pinastri* of the alliance *Genisto pilosae-Pinion pinastri* (class *Pinetea halepensis*). The presence of species of phytogeographical importance in the forest understory, underscores the high biogeographic and conservation value of these pine forests.

Taxonomic reference: Euro+Med (2024-).

Syntaxonomic reference: Mucina et al. (2016), except for the changes proposed by Bonari et al. (2021).

Abbreviations: EVC = EuroVegChecklist; ICPN = International Code of Phytosociological Nomenclature; PCoA = Principal Coordinate Analysis; TWINSPAN = Two-way indicator species analysis.

Keywords

Genisto pilosae-Pinion pinastri, Maritime pine, *Pinetea halepensis*, plant communities, vegetation classification

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Introduction

Mediterranean thermophilous pine forests are a common vegetation type throughout the Mediterranean Basin. These forests are dominated by one of the four Mediterranean thermophilous pines (*Pinus brutia*, *P. halepensis*, *P. pinaster*, and *P. pinea*). They typically occur in extreme climatic or soil conditions, such as on exposed, warm, and dry rocky slopes, on ultramafic bedrocks, marls, dolomites, and limestones (Bonari et al. 2021). Coastal and subcoastal areas of peninsular Italy, as well as Sicily, Sardinia, and other small Mediterranean islands, are characterised by extensive pine forests. These forests occur both naturally and as old or recent plantations established for timber or other tree products. In these forests, *P. pinaster* plays a prominent role in the thermo- and meso-mediterranean belts of the northwestern Tyrrhenian sector of Liguria and Tuscany regions (Central Italy), thriving mostly on siliceous and ophiolitic substrates, often with an understory of thermophilous sclerophyllous species.

Pinus pinaster s.l. (Maritime pine) is a medium-sized tree with a west-Mediterranean Atlantic range, distributed from the Mediterranean area of southwestern Europe to the Atlantic Iberian Peninsula, France, Italy, and northwestern Africa (Barbero et al. 1998; Farjon 2017). The species has a relatively wide ecology, growing in humid and sub-humid climates within a broad range of elevations, from the sea level up to 2000 m a.s.l., and on a variety of substrates, such as schists, serpentines, sandstones, granites, and soils of volcanic origin (Abad Viñas et al. 2016; Farjon 2017; Vázquez-González et al. 2020). It often forms monospecific stands, but also mixed forest stands with *Quercus* spp. or other pines. In Italy, where it is native to Liguria, Tuscany, Sicily, and Sardinia administrative regions, it reaches its eastern native distribution limit in mainland Europe (Pignatti 2017–2019).

From a phytosociological standpoint, *P. pinaster* is an important diagnostic and dominant species of the order *Pinetalia halepensis* belonging to the class *Pinetea halepensis*, which includes all Mediterranean thermophilous pine forests. This class corresponds to the EUNIS habitat type "T3A Mediterranean lowland to submontane *Pinus* forest" and partly also to "N1G Mediterranean coniferous coastal dune forest" (Chytrý et al. 2020).

In Italy, *P. pinaster* forest communities have been studied since the 70s in terms of syntaxonomy (Brullo et al. 1977; Gianguzzi 1999; Biondi and Vagge 2015; Calvia et al. 2022a). Communities on volcanic substrates found in Pantelleria Island and northeastern Sardinia were classified into *Genisto aspalathoidis-Pinetum hamiltonii* Brullo, Di Martino et Marcenò 1977 corr. Gianguzzi 1999 and *Arbuto unedonis-Pinetum pinastri* Calvia, Bonari, Angiolini, Farris, Fenu et Bacch. 2022, respectively (Gianguzzi 1999; Calvia et al. 2022a). Biondi and Vagge (2015) recognised three associations (*Erico scopariae-Pinetum pinastri* Biondi et Vagge 2015, *Erico arboreae-Pinetum pinastri* Biondi et Vagge 2015, and *Buxo sempervirentis-Pinetum pinastri* Biondi et Vagge 2015) distributed in western peninsular Italy, mainly related to acidic substrates with low nutrient content in coastal and inland areas of Liguria and Tuscany regions, currently attributed to the Ligurian and Provençal alliance *Genisto pilosae-Pinion pinastri* of the order *Pinetalia halepensis* (Preislerová et al. 2022). The association *Euphorbio ligusticae-Pinetum pinastri* Hofmann ex Pignatti 1998 *typus cons. propos.* (Pignatti 1998; Furrer and Hofmann 1969) was described for forests in the inner valleys of the Northern Apennines in the Liguria and Piedmont regions (Savona, Alessandria, Genoa, and La Spezia areas). These forests grow on nutrient-poor soils derived from ophiolitic substrates and are characterised by sub-Mediterranean serpentine-adapted species.

Since the recent Mediterranean pine forest classification revision reconsidered the syntaxonomic scheme at the alliance level (Bonari et al. 2021), there is room for the revision of lower syntaxonomic ranks (i.e. association level). Accordingly, it turns out that in some areas of Italy, particularly at the southeastern margin of the natural range of *P. pinaster* in mainland Europe, which is supposedly located in the central-southern Tyrrhenian part of Tuscany (Agostini 1968), lower syntaxonomic levels should be more thoroughly investigated. In this region, local botanists referred the heathlands with *Calluna vulgaris* and *Erica scoparia* to the association *Tuberario lignosae-Callunetum vulgaris* De Dominicis et Casini 1979, neglecting the dominant role of *P. pinaster* that physiognomically shape the forests where this association occurs (Angiolini et al. 2007). Past studies reported the dominance of *P. pinaster* in central-southern Tuscany as a result of intentional introduction in the 19th century for soil improvement and erosion control (Corti 1934; De Dominicis and Casini 1979; Piussi 1982; Mondino and Bernetti 1998; Selvi et al. 2016). Despite this, recent phytogeographical and archival studies suggest that these pine forests may have a natural (autochthonous) origin, in southern Tuscany as well as in many other areas of the Mediterranean region (Figueiral 1995; Martínez and Montero 2004; Gabellini and Saveri 2016; Caudullo et al. 2017; Bonari et al. 2021). Recent studies have also highlighted that these forests are genetically most similar to those in nearby Corsica, and to a lesser extent, to those in Liguria and southern France (Theraroz et al. 2024).

Overall, this paper aims to (i) revise *P. pinaster*-dominated communities of the Italian peninsula with special regard to central-southern Tuscany, and (ii) assess their floristic and ecological differences.

Methods

Study area

The sampling area is situated in central-southern Tuscany, south-west of the city of Siena, on the eastern side of the Colline Metallifere hilly-mountain complex, with elevations ranging from 100 to 800 m a.s.l. (Figure 1). The area falls within the catchment basin of the Farma stream, the main tributary of the Merse river. The

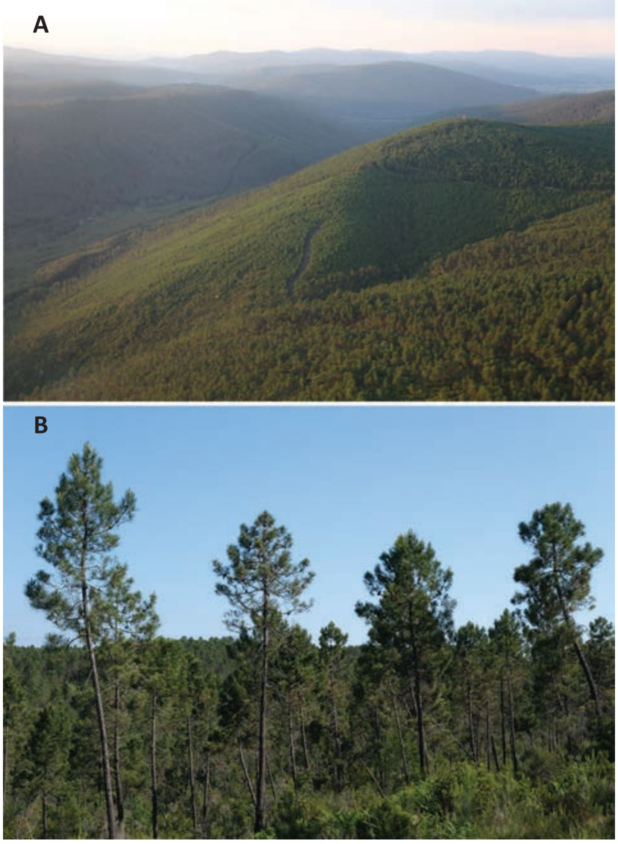

Figure 1. Aerial view (A) and ground view (B) of *Pinus pinaster* forests at their southeasternmost distribution limit in the Italian peninsula (Siena, Italy). Photo credit: G. Bonari, 2016 and 2023, respectively.

lithologies comprise siliceous rocks, mainly composed by the Verrucano Group, silty schists with varying amounts of sandstone, quartzites and anagenites – which give rise to soils of acidic nature, and limited outcrops of karstic limestone and ophiolites (Aldinucci et al. 2008; Carmignani et al. 2013). The area is influenced by a temperate macroclimate, characterised by a strong submediterraneity index, lower mesotemperate thermotype, and upper subhumid ombrotype (Pesaresi et al. 2014). The mean temperature ranges from 5 °C in January to 23.1 °C in July (Landi 2016). Precipitation is seasonal, with autumn (November-December) and winter (January-February) months having a mean of 40 mm/month and summer (July-August) months with a range of 20–40 mm/month (Landi 2016). Within the area, there are significant microclimatic differences with decreasing precipitation moving from the western side to the eastern side of the mountain chain (De Dominicis and Casini 1979), and greater temperature variation on the ridges and thermal inversions in the valley floors (Landi 2016). The study area is included in three Special Areas of Conservation (SACs) of the Natura 2000 network of protected areas (SAC IT5190006 - "Alta Val di Merse"; SAC IT51A0003 - "Val di Farma"; and SAC IT5190007 - "Basso Merse"), which are also part of four Nature Reserves ("Tocchi" Biogenetic Reserve, "Alto Merse" Nature Reserve, "Farma" Nature Reserve and "Belagaio" Nature Reserve).

The main vegetation types in the area include monospecific *P. pinaster* forests, from 8 to 20 m tall, with an understory of thermophilous evergreen shrubs and a sparse herbaceous layer. Other forests include deciduous oak forests dominated by *Quercus cerris*, *Q. petraea*, and *Castanea sativa*, and evergreen sclerophyllous forests with *Quercus ilex*. *Carpinus betulus* forests with relict stands of *Fagus sylvatica* and riparian woods with *Alnus glutinosa* and *Osmunda regalis* of the alliance *Osmundo-Alnion glutinosae* dominate the floors of the humid valleys (Landi and Angiolini 2010). Acidophilous heathlands with *Calluna vulgaris*, *Erica scoparia* and *E. arborea* are widespread in the area (Angiolini et al. 2007). The entire area remains well-preserved, with low human density concentrated in small towns and a complete absence of industrial activities. Olive groves and vineyards occur sparsely in the surroundings.

Data collection and analysis

We sampled 50 10 × 10 m original vegetation relevés subjectively placed all over the study area in May and June 2022, encompassing the major environmental local gradients (see Suppl. material 1: figure S1.1). We recorded the presence and percentage cover of the *taxa*. To compare the surveyed relevés with other *Pinus pinaster*-dominated forests of the Italian peninsula, we retrieved in total 244 published (i.e., Furrer and Hofmann 1969; De Dominicis and Casini 1979; Chiarucci and De Dominicis 1995; Bertacchi et al. 2004; Catalano 2004; Landi et al. 2009; Biondi and Vagge 2015) and unpublished relevés from the north-western part of the Italian peninsula (Liguria and Tuscany regions) from *CircumMed Forest Database* (Bonari et al. 2019b). The resulting dataset (N = 294) was then filtered keeping only relevés where *P. pinaster* had a cover value ≥ 15% and where this species cover was higher than the sum of the broadleaved tree species cover (Bonari et al. 2021), resulting in a final dataset of 251 relevés. The cover threshold of 15% was chosen as it represented a compromise that excluded open vegetation with the presence of pines, but at the same time included plots that represented forests and open pine woodlands (Bonari et al. 2021). Furthermore, our classification analysis supported this choice as it effectively delineated distinct groups. Syntaxonomic nomenclature of Mediterranean pine forests follows the EuroVegChecklist (EVC; https://www.synbiosys.alterra.nl/evc/; Mucina et al. 2016), except for the class and order ranks, which follow Bonari et al. (2021). For phytosociological nomenclature, we followed the fourth edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021). We identified vascular plants and their ecological and adaptive traits using the Flora of Italy and the Flora d'Italia Digitale (Pignatti et al. 2017–2019). The plant names follow Euro+Med PlantBase (Euro+Med 2024-). We also consulted FloraVeg.EU (FloraVeg.EU 2024; Chytrý et al. 2024). All the analyses were performed in the R 4.3.2 environment (R Core Team 2023).

For those relevés from the *CircumMed Forest Database* recorded with the Braun-Blanquet methodology, the cover values of species were transformed into mid-percentage values of individual grades. In all the relevés, the cover values of the same species present in different layers were combined into a single layer, accounting for the possibility of multiple layers overlapping (Tichý and Holt 2006).

We performed TWINSPAN (Hill 1979) to classify the relevés using the '*twinspan*' package (Oksanen and Hill 2023). We used five pseudospecies cut levels (0%, 2%, 5%, 10%, 20%) of species percentage cover.

Then, to explore general patterns of forest communities and to highlight changes in species composition among groups, we ran a principal coordinate analysis (PCoA) of the dataset using the '*vegan*' package (Oksanen et al. 2019). The PCoA model was based on the square-root transformed Bray-Curtis dissimilarity matrix, which was calculated on square-root transformed cover values. Based on the permutation test (p-value ≤ 0.001), we chose the best-fitted species, meaning we projected species showing a correlation coefficient >0.5 with the first two axes and superimposed them in the ordination diagram. To help the interpretation, we also mapped the latitude and longitude of the relevés for each cluster. We defined diagnostic species as those species with a phi coefficient ≥0.3, and constant species as those with a percentage frequency >20%. To compliment this, we used Ecological Indicator Values (EIVs) to better understand their ecological preferences (Pignatti et al. 2017–2019). Ecological Indicator Values inform about the adaptation of a plant species to climatic and edaphic conditions: each species is given values denoting the position at which it reaches peak abundance along environmental gradients (Diekmann 2003). A 9- or 12-point ordinal scale for each of the following parameters is used: temperature, light, soil moisture, soil nitrogen status, soil reaction (pH), continentality, and salinity – the latter two were not used since they are not informative for the vegetation type studied in this paper. To detect differences in unweighted community medians of EIVs among clusters, a Kruskall-Wallis H omnibus test, followed by post-hoc Dunn's multiple comparison test with the Holm correction method to adjust for family-wise Type I error (Holm 1979).

Finally, to investigate the adaptive characteristics of the communities of the clusters, we investigated the life forms and chorotypes spectra by plotting bar charts.

Results

The first TWINSPAN division separated two main pine forest communities, suggesting a distinction that was based on substrates. The TWINSPAN classification was cut at the second level of division, taking into account species composition, geographic distribution, type relevés, and information on their ecology gleaned from the literature (Figure 2).

The same groups can also be distinguished in the ordination PCoA diagram (Figure 3). The clusters were well separated along the two main axes. Axis 1 distinguishes pine forest communities according to a substrate gradient, while axis 2 represents a latitudinal gradient.

The distribution map of the plots is provided in Figure 4. Cluster 1 is concentrated in the eastern Ligurian area, cluster 2 is distributed in central-southern Tuscany and marginally in western Liguria (one relevé), cluster 3 is located in southern Tuscany in a small serpentine area, and cluster 4 is located over the eastern and western Liguria region.

We report an abbreviated synoptic table of diagnostic and constant species across clusters (Table 1). Cluster 1 includes mainly acidophilous species (e.g. *Castanea sativa*, *Pteridium aquilinum*, *Teucrium scorodonia*), cluster 2 encompasses evergreen acidophilous species (e.g. *Arbutus unedo*, *Calluna vulgaris*, *Erica scoparia*), cluster 3 reports a mixture of heavy-metal tolerant species (e.g. *Plantago holosteum*, *Thymus striatus*), and cluster 4 shows a mixture of grassland and garrigue species on serpentine-derived soils (e.g. *Brachypodium phoenicoides*, *Euphorbia spinosa*

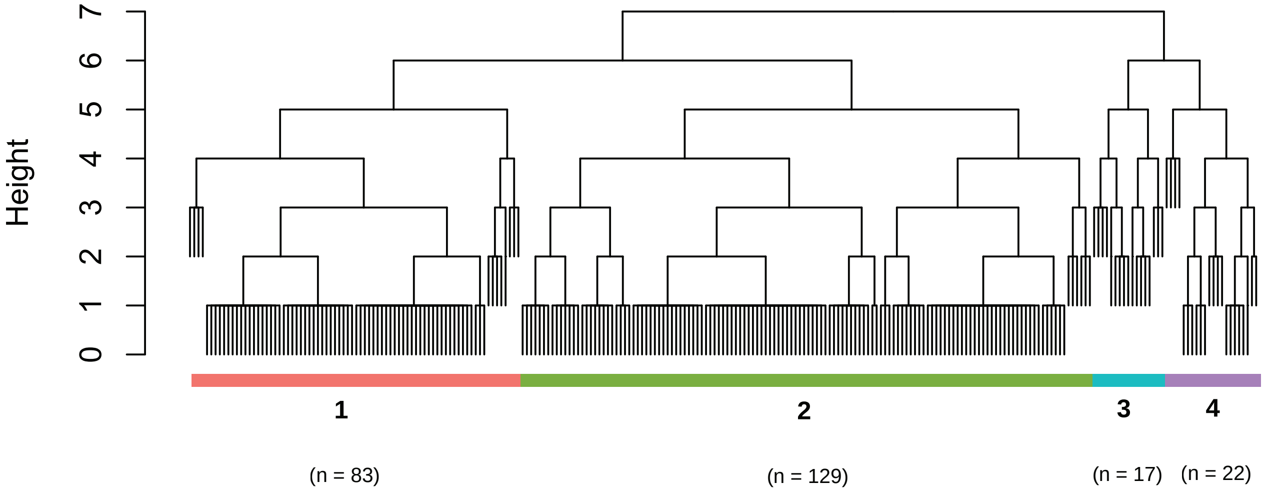

Figure 2. Dendrogram of a TWINSPAN classification based on the species composition of *Pinus pinaster* forest plots. The colours refer to: red - Cluster 1 (Eastern Liguria); green - Cluster 2 (Central-Southern Tuscany and marginally Western Liguria); light blue - Cluster 3 (Southern Tuscany); purple - Cluster 4 (Eastern and Western Liguria). The number of relevés for each cluster is specified in brackets.

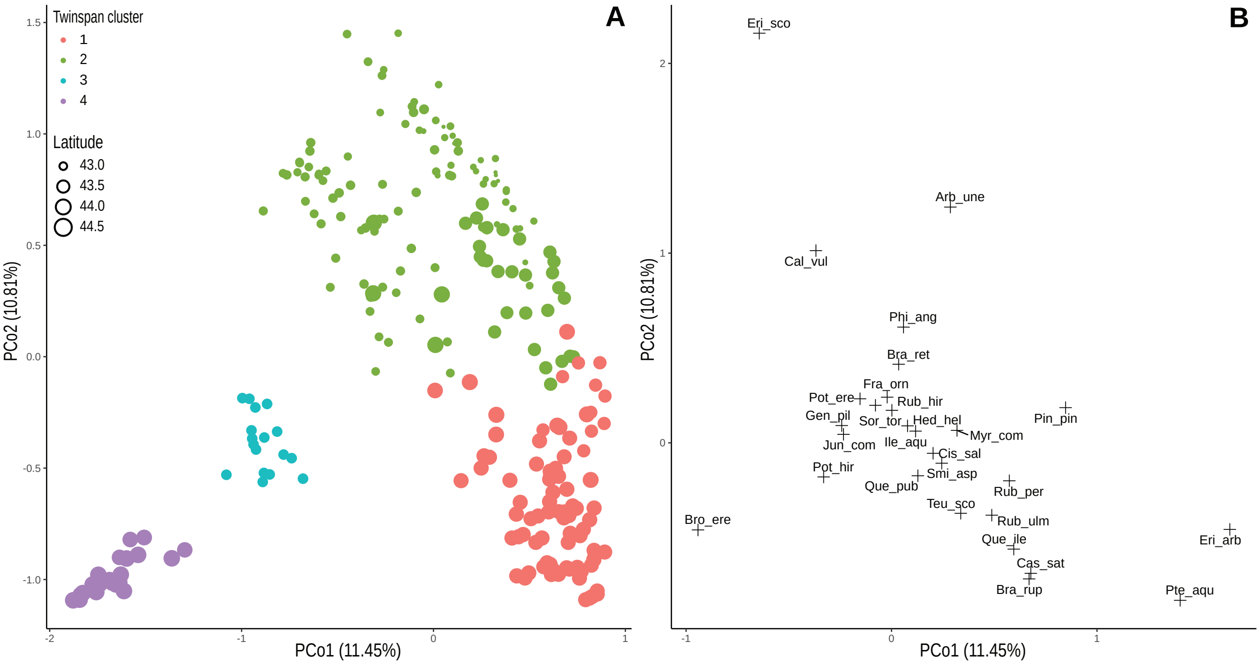

Figure 3. PCoA results showing *Pinus pinaster* forest plots in relation to latitude and clusters (A) and associated species (B). The colours refer to: red - Cluster 1 (Eastern Liguria); green - Cluster 2 (Central-Southern Tuscany and marginally Western Liguria); light blue - Cluster 3 (Southern Tuscany); purple - Cluster 4 (Eastern and Western Liguria). Species showing a correlation coefficient >0.5 with the first two axes have been superimposed to the ordination diagram (B), and are shown with a (+).

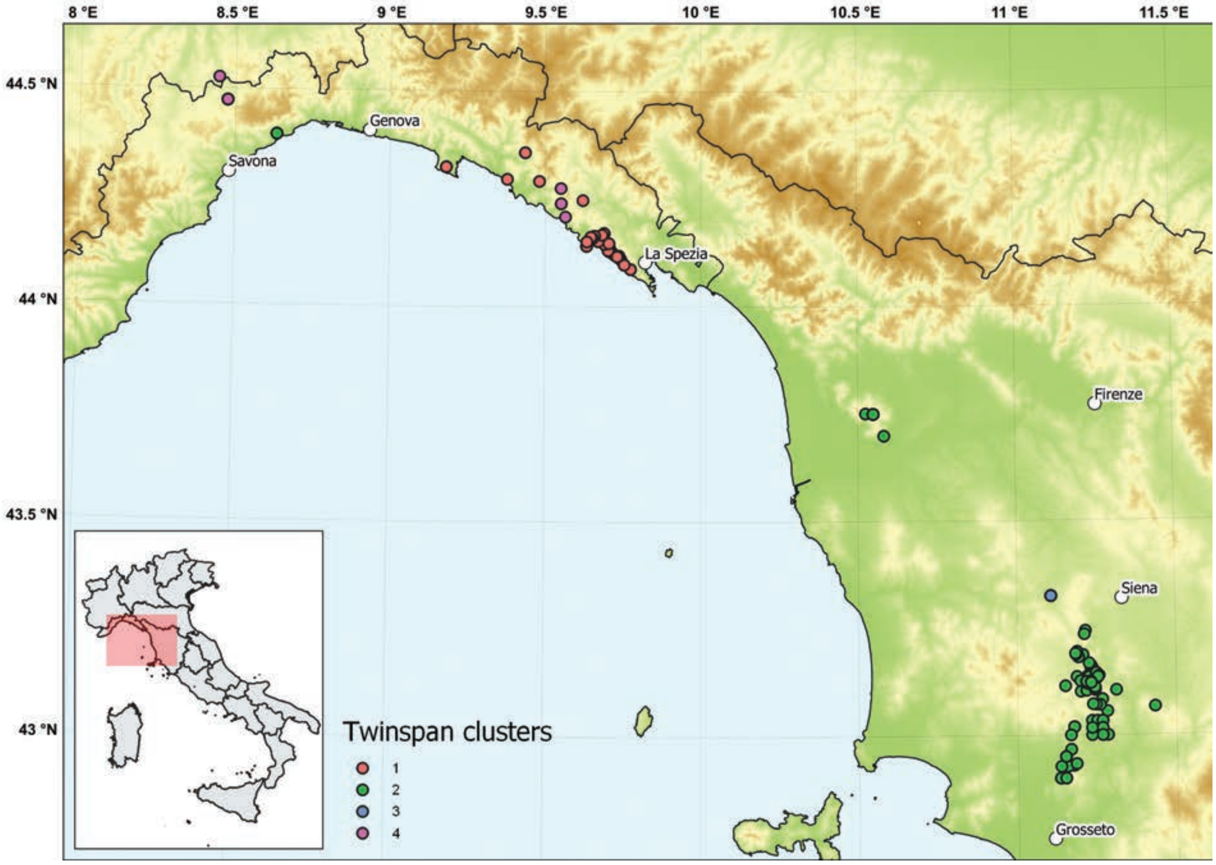

Figure 4. Map showing the distribution of the clusters in relation to the study area. The colours refer to: red - Cluster 1 (Eastern Liguria); green - Cluster 2 (Central-Southern Tuscany and marginally Western Liguria); light blue - Cluster 3 (Southern Tuscany); purple - Cluster 4 (Eastern and Western Liguria). In the upper-right box, the distribution of *Pinus pinaster* in Italy is reported (Caudullo et al. 2017).

Table 1. Abbreviated table of diagnostic and constant species of the clusters resulting from hierarchical cluster analysis (TWINSPAN). For each cluster, only species with a phi coefficient ≥0.45 and constant species with a percentage occurrence frequency >50% are shown. Species are sorted by decreasing phi coefficient for each cluster, but only the percentage frequency is shown. The frequency values >50% are indicated in grey shading. Cluster 1: Eastern Liguria; Cluster 2: Central-Southern Tuscany and marginally Western Liguria; Cluster 3: Southern Tuscany; Cluster 4: Eastern and Western Liguria. See Suppl. material 2: table S2.1 for the full synoptic table and the complete list of species.

Species	**Cluster 1** (n = 83)	**Cluster 2** (n = 129)	**Cluster 3** (n = 17)	**Cluster 4** (n = 22)
Teucrium scorodonia	70	3	.	.
Brachypodium rupestre	67	9	24	.
Pteridium aquilinum	86	41	.	.
Quercus ilex	78	31	18	.
Castanea sativa	69	22	.	9
Rubus ulmifolius	73	30	24	.
Erica scoparia	1	80	76	.
Calluna vulgaris	4	70	.	14
Arbutus unedo	48	88	.	.
Thymus striatus	.	.	100	.
Plantago holosteum	.	.	94	.
Convolvulus cantabrica	.	.	88	5
Festuca robustifolia	.	.	82	.
Genista januensis	4	1	100	.
Koeleria splendens	.	.	76	.
Galium corrudifolium	.	.	71	.
Sanguisorba minor subsp. *balearica*	.	.	65	.
Galatella linosyris	.	.	59	.
Knautia arvensis	.	.	59	.
Stipa etrusca	.	.	53	.
Juniperus oxycedrus	5	3	82	.
Centaurea aplolepa	1	.	100	91
Bromopsis erecta	.	2	94	86
Festuca ovina aggr.	1	.	94	95
Potentilla hirta	.	.	76	91
Brachypodium phoenicoides	.	.	.	100
Plantago maritima subsp. *serpentina*	.	.	.	91
Scabiosa pyrenaica	.	.	.	91
Teucrium montanum	1	.	.	91
Galium purpureum	.	.	.	86
Euphorbia spinosa subsp. *ligustica*	1	2	.	100
Satureja montana	1	1	.	91
Asperula aristata	.	.	.	82
Helictochloa pratensis	.	.	.	82
Scorzonera austriaca	.	.	.	82
Thymus serpyllum	.	.	.	77
Trinia glauca	.	.	.	77
Pilosella piloselloides	.	.	6	77
Carex humilis	2	2	.	86
Sorbus aria	.	2	.	77
Peucedanum oreoselinum	.	2	.	68
Peucedanum cervaria	4	1	.	59
Lotus corniculatus	.	2	6	55
Anthericum liliago	1	11	6	64

subsp. *ligustica*, *Plantago maritima* subsp. *serpentina*, *Thymus serpyllum*). See Suppl. material 2 for the full synoptic table and the complete list of species.

The analysis of Ecological Indicator Values helped to further characterise the ecology of each cluster (Figure 5). Cluster 1 had the highest mean value of soil moisture, temperature (with no significant differences to cluster 2) and the lowest mean value for light (significantly different from clusters 2, 3, and 4). Cluster 2 significantly differed from clusters 3 and 4, having the lowest mean value for soil

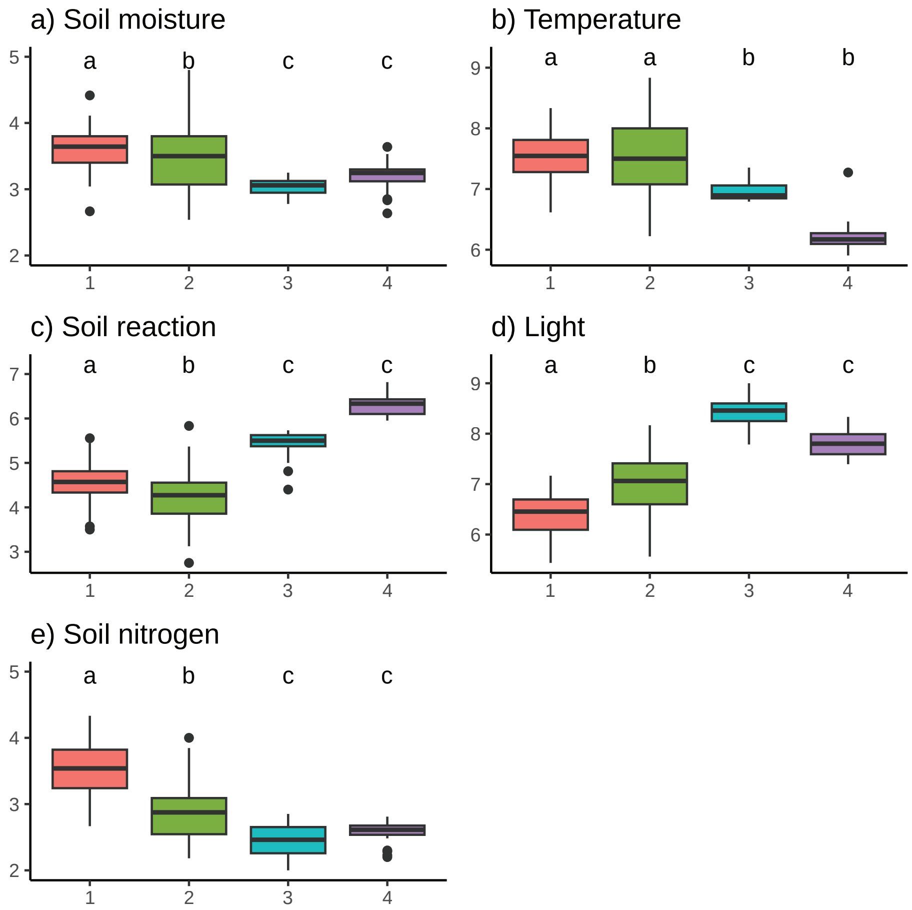

Figure 5. Boxplots of unweighted community means of Ecological Indicator Values showing the results of the post-hoc Dunn's multiple comparison test with Holm correction. The results of pairwise comparisons are indicated using Compact Letter Display method, where different letters between two clusters indicate a statistically significant difference of the test, with $p < 0.05$. The colours refer to: red - Cluster 1 (Eastern Liguria); green - Cluster 2 (Central-Southern Tuscany and marginally Western Liguria); light blue - Cluster 3 (Southern Tuscany); purple - Cluster 4 (Eastern and Western Liguria).

reaction, which indicates an acidophilous plant community. Cluster 3 had the lowest mean value for soil moisture (indicating a markedly xerothermic plant community) and soil nitrogen (with no significant differences to cluster 4) and the highest mean value for light, whereas cluster 4 showed the lowest temperature and the highest soil reaction.

Analysis of life forms (Suppl. material 1: figure S1.2A) showed how the clusters differentiate particularly in the share of phanerophytes and hemicryptophytes, with cluster 2 having the highest percentage of phanerophytes and the lowest of hemicryptophytes. However, the clusters did not differentiate clearly in terms of chorotypes, apart from their share of endemic species to Italy, which was particularly high in cluster 3 (Suppl. material 1: figure S1.2B).

Discussion

The presented analytical comparison of Ligurian-Tuscan *Pinus pinaster* forests highlights the floristic-vegetational diversity of the investigated communities. These forests thrive in diverse edaphic conditions, occurring on both siliceous and ultramafic substrates, and are distributed along a broad climatic gradient encompassing Temperate and Mediterranean areas. Results indicate floristic and ecological similarity of the studied community in central-southern Tuscany to the association *Erico scopariae-Pinetum pinastri* described by Biondi and Vagge (2015) in eastern Liguria and northern Tuscany. This vegetation unit is the type association of the alliance *Genisto pilosae-Pinion pinastri*. The occurrence of taxa such as *Erica arborea*, *E. scoparia*, *Calluna vulgaris*, *Cistus salviifolius*, *Fraxinus ornus*, and *Genista pilosa* confirms that this community belongs to the alliance *Genisto pilosae-Pinion pinastri*. This alliance is classified by the EVC (Mucina et al. 2016) to the order *Quercetalia ilicis* and to the class *Quercetea ilicis*. However, the results of Bonari et al. (2021) supported moving Mediterranean pine forests to the order *Pinetalia halepensis* and class *Pinetea halepensis* based on structure, physiognomy, and diagnostic species. The number of diagnostic species of the class *Pinetea halepensis* is lower if compared to the class *Quercetea ilicis*, but the decision of Bonari et al. (2021) to move low-elevation Mediterranean pine forests to a separate class is based, among other reasons, on diagnostic species analysis (see table 3 in Bonari et al. 2021). Thus, in this paper, we adopted the most recent classification proposed by Bonari et al. (2021) for the nomenclature and positioning of the higher syntaxa.

A significant difference in floristic composition exists between the forests under investigation and the association *Erico arboreae-Pinetum pinastri* of northern Tuscany. Both are characterised by a group of species serving as vicariants (e.g., *Erica scoparia* vs. *E. arborea*, *Genista pilosa* vs. *G. germanica*, *Lonicera implexa* vs. *L. etrusca*, *Brachypodium retusum* vs. *B. rupestre*, *Rubus hirtus* vs. *R. ulmifolius*). In the forests of central-southern Tuscany, the understory is richer in shrubs and chamaephytes, featuring a diverse array of narrow-leaved xerophytes. However, geophytes and therophytes are scarce, even though both vegetation types are species-poor. Since the forest canopy is relatively open, the presence of light-demanding taxa is common (e.g., *Danthonia decumbens*, *Potentilla erecta*, *Serratula tinctoria*, *Tuberaria lignosa*), which is consistent with findings in other Mediterranean pine forests (Bonari et al. 2017, 2018). Furthermore, this *P. pinaster* forest community is closely associated, both spatially and dynamically, with acidophilous *Erica* spp. and *Calluna vulgaris* dominated heathland. This community has been previously classified in the association *Tuberario lignosae-Callunetum vulgaris* (De Dominicis and Casini 1979). The pine forest-relatable scrub vegetation is relevant in this context as a heath scrub transitions into pine forest as pine density increases.

Central-southern Tuscany forests stand out as they host a significant number of Stenomediterranean species, including a notable group with a Eurimediterranean distribution (e.g. *Fraxinus ornus*, *Rubus ulmifolius*, *Sorbus domestica*). Nevertheless, the percentage of European, Eurasian, and Boreal taxa (e.g., *Calluna vulgaris*, *Danthonia decumbens*, *Molinia arundinacea*, *Potentilla erecta*) suggests that there is a substantial influence from the Euro-Siberian region. In particular, the occurrence of *Calluna vulgaris* holds great phytogeographic interest as it marks the southern boundary of its distribution in Italy (Bernetti 1987). In addition, the unique combination of a hyperoceanic climate and dystric cambisols-ferric podzols featuring highly acidic raw humus in this part of Tuscany supports the occurrence of various Atlantic and Mediterranean-Atlantic species, such as *Erica scoparia*, *Genista pilosa*, and *Teucrium scorodonia* (Angiolini et al. 2007). Forests in central-southern Tuscany show clear distinctions from those with similar physiognomy found in Sardinia, where they are classified under the association *Arbuto unedonis-Pinetum pinastri*. While both regions exhibit dominance of sclerophyllous shrubs and vines, along with a sparse herbaceous layer, they differ in terms of a specific set of diagnostic species that are practically absent in the Italian Peninsula (Calvia et al. 2022a).

According to our analysis, the association *Buxo sempervirentis-Pinetum pinastri* seems to be floristically similar to the species composition of the association *Erico arboreae-Pinetum pinastri*. However, we preferred not to synonymize the two associations since the latter was described by Biondi and Vagge (2015) using very few relevés from a small area with siliceous bedrock in the Chiavari inland of central Liguria. We, therefore, preferred to consider this association as doubtful. Further studies are needed to elucidate the syntaxonomic status of this vegetation unit.

Our analysis confirms the floristic autonomy of forests found on ophiolitic substrates in the Liguria region. Along with the occurrence of shrubs like *Juniperus communis*, *Amelanchier ovalis* and *Sorbus aria*, and a xerophilous herbaceous layer featuring, e.g., *Brachypodium phoenicoides*, *Bromopsis erecta*, *Festuca ovina* aggr., and *Teucrium montanum*, several species characteristic of ophiolitic substrates are found, including *Centaurea aplolepa*, *Euphorbia spinosa* subsp. *ligustica*, *Cherleria laricifolia* subsp. *ophiolitica*, *Plantago maritima* subsp. *serpentina* and *Thymus serpyllum*. Hofmann (1960) was the first who provided a detailed description of this forest type from the Deiva State Forest (Savona) under the names "*Euphorbietum spinosae pinetosum pinastri*" ("phytosociological name") and *"Euforbieto-Pinetum"* ("sylvicultural name"). Both names are invalid because they were proposed as provisional (ICPN, Art. 3b), without relevés or a synoptic table with clearly defined frequency classes (Arts. 2b, 7). The subassociation name would also be invalid according to Art. 4a. Some years later, Furrer and Hofmann (1969) validly published the *"Euphorbietum spinosae-ligusticae"* (recte: *Euphorbietum ligusticae*) with a table of 36 relevés from Liguria (Savona, Genoa, Alessandria, and La Spezia). The name is legitimate according to Art. 29b because in all relevés (excepting relevé 8, dominated by *P. pinaster*) the herb and low shrub cover is higher than the cover of shrubs and trees. Indeed, *Euphorbia ligustica* dominates over *Pinus pinaster* in 23 relevés and co-dominates with it in 9 relevés; *Pinus* dominates over *Euphorbia* in 4 relevés, but in two of them the dominant plant is a grass species. Later on, Pignatti (1998: 437, 642) accepted the name "*Euphorbio ligusticae-Pinetum pinastri* Furrer & Hofmann (1960)" citing the "*Euphorbietum spinosae-ligusticae* Furrer & Hofmann (1960)" as a synonym. Despite some inconsistencies in the references that can be interpreted as bibliographical errors (Art. 2b Note 3), it is clear that Pignatti's name "*Euphorbio ligusticae-Pinetum pinastri* Hofmann ex Pignatti 1998" is an incidental later validation of one of Hofmann's names and a superfluous name (Art. 29c) for the *Euphorbietum ligusticae* Furrer et Hofmann 1969. In fact, Pignatti provides a reference to the table of Furrer and Hofmann (1969) excluding four relevés from Genoa in which pine is absent. Pignatti's name has been rarely used, but is a good name for the *P. pinaster* forests on ophiolites from Liguria belonging to the *Genisto pilosae-Pinion pinastri*. Therefore, we propose to conserve the *Euphorbio ligusticae-Pinetum pinastri* Hofmann ex Pignatti 1998 *typus cons. propos.* with the relevé 8 (16th in the table; *Pinus pinaster* cover: 4; *Euphorbia ligustica*: 2) of the table in Furrer and Hofmann (1969) as *typus conservandum* according to Art. 53 of the ICPN. This proposal will be submitted to the CCCN for approval by the GPN Assembly. To fix the syntaxonomic concept of the *Euphorbietum ligusticae* Furrer et Hofmann 1969, we designate as *lectotypus hoc loco* the relevé 12 (3rd in the table; *P. pinaster* cover: 1; *Euphorbia ligustica*: 3) of the table in Furrer and Hofmann (1969). Both relevés come from Savona area, considered by the authors as the most representative of the floristic composition of the association. The *Euphorbietum ligusticae* is currently included in the alliance of scrub vegetation on serpentines *Alyssion bertolonii* E. Pignatti et Pignatti 1977 (Vagge 1997; Mucina et al. 2016; Terzi et al. 2022).

Our classification includes an informal group comprising of pine forest plantations established on ultramafic bedrock in southern Tuscany (Chiarucci 2004). In line with Bonari et al. (2021), we preferred not to describe a formal syntaxon for pine plantations in areas where the pines are clearly planted.

From a habitat perspective, the studied pine forest communities were not included in Annex I of the 92/43/EEC Habitats Directive. On the one hand, this exclusion is due to the extensive use of *P. pinaster* for past reforestation in the surrounding areas, making it difficult to distinguish native sites from artificially established ones. On the other hand, old-established plantations of native pine species can develop an understory of natural species composition that makes these forest communities valuable in terms of nature conservation (Bonari et al. 2017, 2019a, 2020). We suggest, therefore, to attribute these communities to the habitat type 9540 “Mediterranean pine forests with endemic Mesogean pines” included in Annex I of the 92/43/EEC Habitats Directive, and specifically to the subtype no. 42.823 “Franco-Italian Mesogean pine forests: *Pinus pinaster* forests of siliceous lower meso-Mediterranean areas of Provence, of marls and limestones of the upper meso-Mediterranean level of the Maritime Alps and the Ligurian Alps, and of mostly siliceous or clayey soils of the hills of Liguria and Tuscany” (Biondi et al. 2010). This habitat is also featured as “T3A Mediterranean lowland to submontane *Pinus* forests” according to the EUNIS Habitat Classification (Chytrý et al. 2020). These classification systems include old-established plantations within the natural distribution of the pine. We support the extension of the natural distribution of *P. pinaster* into central-southern Tuscany, *sensu* Caudullo et al. (2017), which is also aligned with the observations of Agostini (1968). The presence of these forests in Tuscany is indeed due to the combination of favourable climatic and edaphic conditions that allow this species to thrive in this region. Additionally, the extensive distribution of these forests, though undoubtedly impacted by the establishment of plantations at places (Selvi et al. 2016), can be partly also attributed to the pioneering nature of the pine, which has exhibited a trend of expansion and recovery of natural conditions over the last few decades in southern Europe, including Liguria and Tuscany regions (De Dominicis and Casini 1979; Arrigoni 1997; Gabellini and De Dominicis 2003; Wyse et al. 2019; Santoro et al. 2021; Calvia et al. 2022b).

Conclusions

Our study has expanded the floristic and ecological knowledge of *Pinus pinaster* forests at the southeasternmost margin of their European mainland distribution range and has contributed to their classification by proposing an updated syntaxonomic scheme. We extended the occurrence of the alliance *Genisto pilosae-Pinion pinastri* (class *Pinetea halepensis*) to central-southern Tuscany, beyond the Ligurian-Provençal seaboard. Based on ecological characteristics, diagnostic species, type relevés, and information gleaned from existing literature, we confirmed the associations *Erico arboreae-Pinetum pinastri* and *Erico scopariae-Pinetum pinastri*, distributed from eastern Liguria to southern Tuscany on siliceous soil conditions. Importantly, we identified a syntaxonomic placement for the forests of central-southern Tuscany, which previously lacked classification at the association level, attributing them to the association *Erico scopariae-Pinetum pinastri*. Additionally, we identified two communities on ultramafic substrate: one confined to central Liguria, proposed in our study as association *Euphorbio ligusticae-Pinetum pinastri*, for which we suggest conserving the association name, and another one found in central Tuscany and consisting of introduced plantations. The results of this study underscore the importance of conserving the central-southern Tuscany *P. pinaster* forests, not only because the dominant pine species is situated at the southeasternmost boundary of its distribution on the Italian peninsula, but also due to the presence of species with phytogeographical significance in the forest understory.

Syntaxonomic scheme

Class *PINETEA HALEPENSIS* Bonari et Chytrý in Bonari et al. 2021
  Order *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014
    Alliance *Genisto pilosae-Pinion pinastri* Biondi et Vagge 2015
      Association *Erico arboreae-Pinetum pinastri* Biondi et Vagge 2015 [Cluster 1]
      Association *Erico scopariae-Pinetum pinastri* Biondi et Vagge 2015 [Cluster 2]
        Pinus pinaster secondary plantations on serpentine of southern Tuscany (informal group) [Cluster 3]
      Association *Euphorbio ligusticae-Pinetum pinastri* Hofmann ex Pignatti 1998 *typus cons. propos.* [Cluster 4]
      Association ? *Buxo sempervirentis-Pinetum pinastri* Biondi et Vagge 2015

The question mark “?” refers to the doubtful syntaxonomic status of this vegetation unit.

Data availability

Relevés of this article are available upon request through the *CircumMed Forest Database* (Global Index of Vegetation-Plot Databases, ID: EU-00026).

Author contributions

G.B. planned the research; D.C. and M.M.V. conducted the field sampling with support of M.L.; D.C., M.M.V., M.L., and G.B. identified plant specimens; M.M.V. and K.C. performed the statistical analyses; D.C. and M.M.V. led the writing and review with major contributions of G.B. All authors critically revised the manuscript and approved the final and revised version.

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Supplementary material

Supplementary material 1
Distribution of the relevés, life form and chorotype spectra of individual clusters (.docx file)
Link: https://doi.org/10.3897/VCS.118023.suppl1

Supplementary material 2
Synoptic table with percentage frequency and phi coefficient for each species in the clusters (.docx file)
Link: https://doi.org/10.3897/VCS.118023.suppl2

VEGETATION CLASSIFICATION AND SURVEY

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RESEARCH PAPER

GRASSLANDS OF ASIA

Vegetation of the southern slopes of Mt. Damavand, Iran: a comprehensive phytosociological classification

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Abstract

Aims: To provide the first syntaxonomic scheme of the main natural and semi-natural steppic vegetation types along a 3000-m elevational gradient. **Location**: South-facing slopes of Mt. Damavand, Iran. **Methods**: A dataset of 330 phytosociological plots of 25 m^2 sampled in all main vegetation types of the region was subjected to unsupervised classification with TWINSPAN. After some manual adjustments to maximise the floristic distinctness of clusters, the resulting units were translated into syntaxa at the class, order, alliance and association level. Diagnostic species were determined with phi values as measure of fidelity. The differences in abiotic and vegetation parameters among associations/communities were visualised with boxplots and the environmental gradients associated with the community differentiation via detrended correspondence analysis (DCA). **Results**: We found four main groups that are ecologically well interpretable and considered at the level of phytosociological classes: rocky habitats (*Tanacetalia kotschyi*, class unknown), scree habitats (*Didymophyso aucheri-Dracocephaletea aucheri*), snow-beds (*Salicetea herbaceae*) and grasslands (*Astragalo-Brometea*). We distinguished six orders, nine alliances and 18 association-level communities, which were floristically well separated. Many of these syntaxa were new to science. Elevation was the main driver of species composition and formation of the major vegetation groups. **Conclusions**: This study contributes to advancing the syntaxonomic understanding of the vegetation of Iran. It is particularly valuable as it covers the complete elevational gradient of 3000 m and thus also comprehensively includes the vegetation types of the lower elevations that previously had been rarely studied syntaxonomically in Iran. Furthermore, this study is the first to examine mown (semi-natural) tall herb rich grasslands in Iran, which were assigned to the new alliance *Cousinion petrocauli*. Since our study was based on a regionally constrained dataset, we could not solve all syntaxonomic issues conclusively. This underscores the need for more comprehensive studies of the vegetation in the entire Alborz Mts as well as other Iranian mountain ranges in the future.

Taxonomic reference: Catalogue of Life (Bánki et al. 2024).

Abbreviations: DCA = detrended correspondence analysis, ICPN = International Code of Phytosociological Nomenclature (Theurillat et al. 2021), TWINSPAN = two-way indicator species analysis.

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[*] Jürgen Dengler and Alireza Naqinezhad shall be considered as joint last authors.

Keywords

Alborz Mts, alpine, *Astragalo-Brometea*, grassland, Iran, montane steppe, phytosociology, rock vegetation, scree vegetation, snowbed vegetation, syntaxonomy, vegetation classification

Introduction

Iran is one of the richest countries in terms of floristic diversity in SW Asia. Plant diversity, geographic complexity, climatic diversity and a history of anthropogenic activities have led to diverse vegetation types across the country. Most of the country is covered with various mountain ranges, of which the Alborz range is the second longest. Having a wide elevational range of over 5000 m, high heterogeneity and contrasting climatic conditions, it is considered a centre of endemism in Iran (Noroozi et al. 2019; Noroozi 2020) and part of the Irano-Anatolian biodiversity hotspot (Mittermeier et al. 2005). Mt. Damavand, at 5671 m a.s.l. and the highest summit in SW Asia, is located in the eastern parts of the Central Alborz Mts, representing one of the richest parts of the Alborz centre of endemism (Noroozi et al. 2019).

Due to the relatively easier accessibility for vegetation scientists, the Alborz Mts in general and the Central Alborz and Mt. Damavand in particular have been subject to various floristic and vegetation studies over the past few decades. The first high-rank syntaxonomic units in the study area were outlined by Zohary (1973), who distinguished in the Alborz Mts two vegetation classes: *Artemisietea herbae-albae iranica* Zohary 1973 nom. inval. (Art. 2b ICPN), *Artemisia* wormwood steppe grasslands, and *Astragaletea iranica* Zohary 1973 nom. inval. (Art. 2b ICPN), subalpine tragacanthic vegetation. The alpine and subalpine vegetation of Central Alborz was intensively studied by Klein (1982, 1987, 2001), who classified the vegetation into three invalidly published classes, *Prangetea ulopterae* Klein 1987 nom. inval. (Art. 2b ICPN), *Onobrychidetea cornutae* Klein 1987 nom. inval. (Art. 2b ICPN), and *Oxytropidetea persicae* Klein 1982 nom. inval. (Art. 2b ICPN). Furthermore, the vegetation of alpine to nival scree habitats of Central Alborz was assigned to the *Didymophysetea aucheri* Klein et Lacoste 1999 nom. inval. (Art. 3b ICPN) (Klein and Lacoste 1999). Noroozi et al. (2010, 2014, 2017) studied specifically the alpine and nival habitats of Alborz and NW Iran and revised/validated some previously described vegetation units, leading to a new syntaxonomic scheme, including a new class of nival scree communities *Didymophyso aucheri-Dracocephaletea aucheri* Noroozi et al. 2013 with two new orders. Additionally, juniper woodlands of the Alborz Mts, which are not in the scope of our study, were phytosociologically classified (Ravanbakhsh et al. 2015). Moreover, a general overview of plant communities existing on a 3000-m elevational transect of Mt. Tuchal, Central Alborz was presented by Akhani et al. (2013), classifying the vegetation into five "elevational zones", without assigning them to syntaxa. Despite these efforts, and considering the vast area, high heterogeneity and diverse flora of the Alborz Mts, the formal phytosociological classification of the area is still far from complete, particularly for the lower elevations and semi-natural stands. Moreover, many of the higher syntaxa currently carry only invalid or provisional names, and the geographic range of many associations is largely unknown.

Mt. Damavand harbours high vascular plant species richness both at the regional scale (more than 700 species in the south-facing parts alone (unpubl.)) and locally, with the highest known richness (61 species) values at the plot scale (25 m^2) known from Iran (Talebi et al. 2021). Klein (2001) and Klein and Lacoste (1999) each published only one plot from grasslands and scree habitats of Mt. Damavand. In a study of the subnival-nival vegetation of the Alborz range and other mountain ranges of NW Iran, Noroozi et al. (2017) published two associations from scree habitats of Mt. Damavand. Moreover, a modern pollen rain-vegetation study was conducted on a transect of vegetation from the alpine belt of Damavand down to lowlands (Dehghani et al. 2017). Apart from these minimal efforts, a comprehensive phytosociological study of this region is still lacking.

Therefore, in our paper we aim to provide a comprehensive documentation of the vegetation patterns of the southern slopes of Mt. Damavand, covering a 3000-m elevational gradient. Our four main aims were (1) to characterise and differentiate the occurring plant communities; (2) to place them into a formal hierarchical syntaxonomic classification system; (3) to describe the main environmental drivers affecting community assemblages, and (4) to compare the vegetation of the study area with other areas in the Irano-Turanian region.

Study area

The study was conducted on the southern slopes of Mt. Damavand (Figure 1), in the Central Alborz Mts, N Iran. The study area comprises around 100 km and extends from 35.83°–35.93° N, 51.99°–52.25° E and 1500–4800 m a.s.l. The closest cities to the region are Polur to the Southwest and Reneh-Larigan to the Southeast. This mountain is the highest summit of Iran and the entire SW Asia, and includes the most elevated stands of vascular plants in Iran (Noroozi et al. 2011).

Mt. Damavand is a large inter-plate composite cone representing an accumulation of more than 400 km^3 of trachyandesite lavas and pyroclastic material overlying the active fold and thrust belt of the Alborz Mts. The immediate basement to the Damavand volcano is a sedimentary sequence of carbonate, siliciclastic and volcanic rocks (Davidson et al. 2004). The most important soil types in

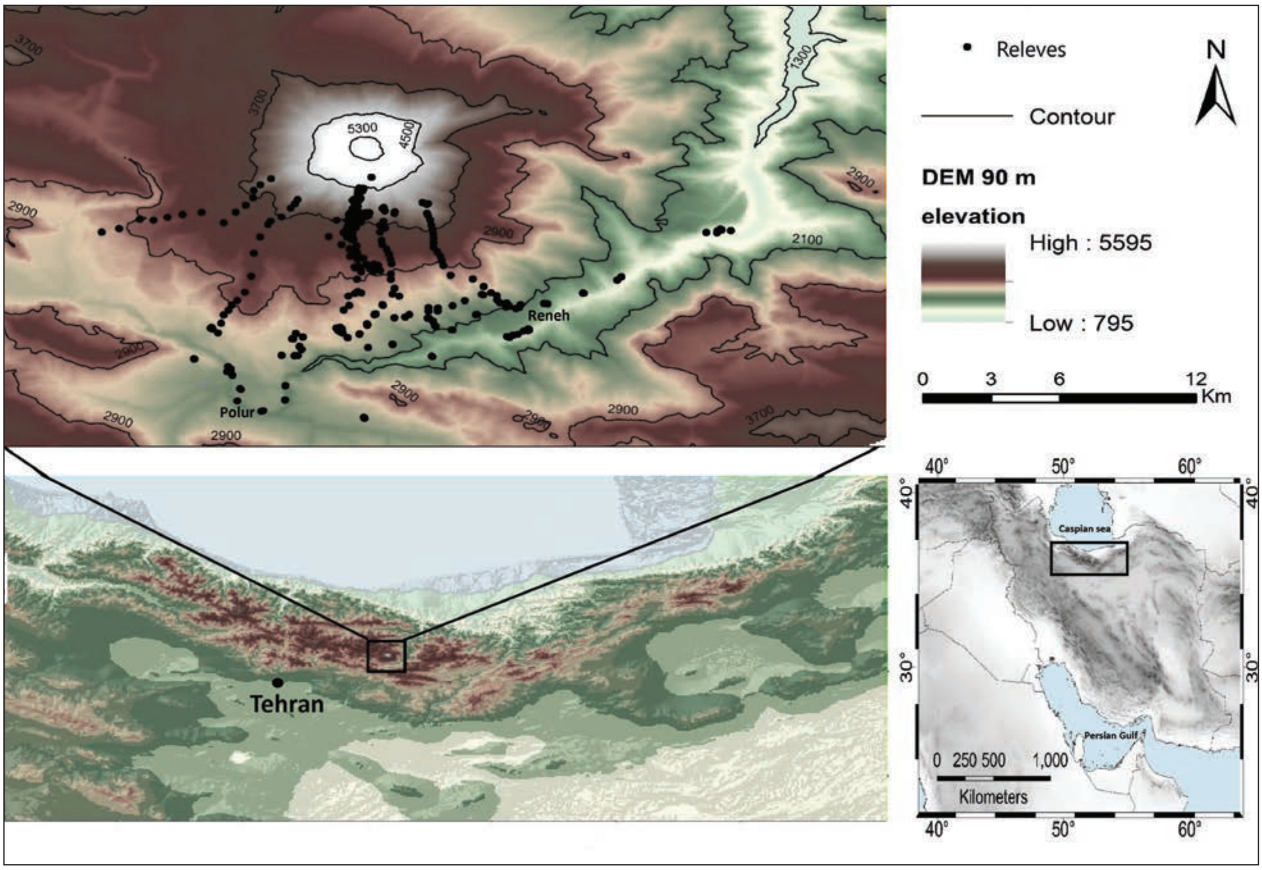

Figure 1. Map of the study region and distribution of the plots.

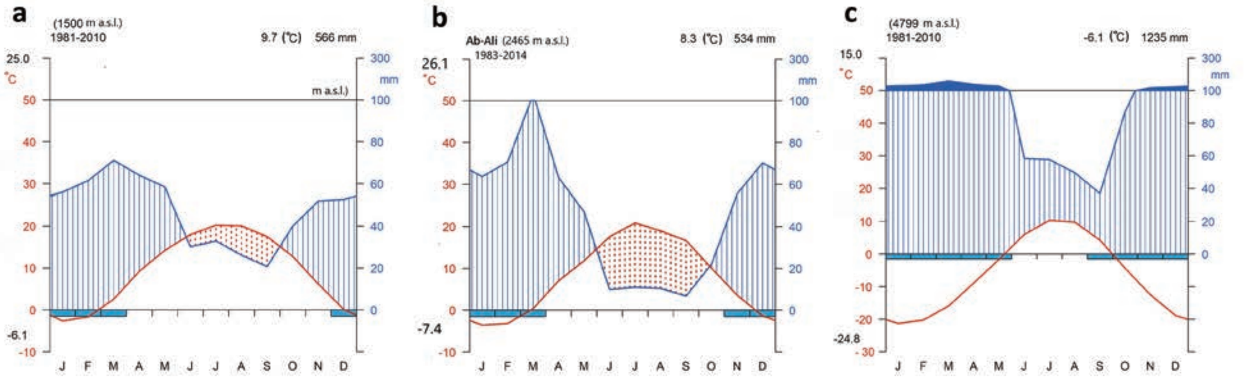

Figure 2. Climatic diagrams of the different elevations: a and c extracted from the CHELSA database (Karger et al. 2017, 2018), b: based on data of the Ab-Ali weather station. The diagrams were produced with the 'climatol' package (Guijarro 2019).

the Damavand area are Lithosols (from igneous rocks) and Brown soils (Dewan and Famouri 1964).

The higher elevations of the Alborz Mts are affected by north-westerly flows of polar air masses (Khalili 1973), comprising relatively dry summers and extremely cold snowy winters. Based on the global bioclimatic classification system, the study area belongs to the pluviseasonal-continental bioclimate regime (Djamali et al. 2011), which is characterised by the concentration of precipitation in winter and early spring. Climatic data of the Ab-Ali station (2450 m a.s.l.) show a mean annual precipitation of 548 mm, most of which occurs in April, with a mean of 85 mm. (Figure 2).

Based on paleopalynological studies, the region has been totally dominated by semi-arid steppes since the Quaternary period, with some less arid phases that resulted in moderate expansion of woodlands (Sharma et al. 2014). Except for valleys and some rocky slopes (up to 2500 m a.s.l.) which are partly covered with shrubs, and the highest limit of vegetation above 4000 m a.s.l. which is covered with scree communities (Noroozi et al. 2014), the region is mostly dominated by different types of grasslands. Grazing is the dominant land use in the region that mostly starts from mid-spring and lasts until early autumn. Other human activities include mowing of herbs, mining and tourism (ecotourism and mountaineering).

Methods

Sampling

A total of 330 relevés of 25 m^2 (including 7 relevés taken from Noroozi et al. 2014) were collected in all major vegetation types of the study region between 2010 and 2017. This included different xeric *Stipa-Artemisia* grassland, tall herb grassland (secondary pseudo-steppes), subalpine-alpine thorn-cushion grasslands, rocky and scree vegetation. Our sampling covered the complete southern slopes of Mt. Damavand from 1500 m a.s.l. to 4800 m a.s.l. (the highest limit of plant growth in the region).

Relevés were sampled in homogenous stands. In each plot, all vascular plants were recorded and total cover and cover values of each species estimated as percentage (Dengler and Dembicz 2023). All vascular plants were identified using Flora Iranica (Rechinger 1968–2015) and Flora of Iran (Assadi et al. 1989–2018). Environmental variables including elevation, slope inclination, aspect, percentage of stone and rocks, gravel and fine soil at the soil surface (estimated visually to sum up to 100%; see Dengler et al. 2016) were recorded for each plot.

Plant nomenclature was standardised to the Catalogue of Life (Bánki et al. 2024). For data storage we used the TURBOVEG program (Hennekens and Schaminée 2001). The vegetation-plot data are provided in Suppl. materials 1, 2 and are also stored in and available from the IranVeg database (Ramzi et al. 2024).

Vegetation classification

We used the TWINSPAN algorithm (Hill 1979), embedded in the JUICE program (Tichý 2002), with four cut-level values of 0, 5, 25, 50 and with a minimum group size of 32 for initial unsupervised classification. To achieve floristically well-characterised syntaxonomic units, we manually modified the delimitation and hierarchy of the TWINSPAN clusters in a few places, as documented in Suppl. material 1.

Diagnostic species (here and further used also for diagnostic subspecies) for all syntaxonomic ranks were based on phi values (Chytrý et al. 2002), standardised to equal plot number per association (Tichý and Chytrý 2006). We determined phi values hierarchically at all four syntaxonomic levels (class, order, alliance, association), adopting the approach used by García-Mijangos et al. (2021), Vassilev et al. (2024) and Vynokurov et al. (2024). We used thresholds of phi > 0.5 for highly diagnostic and phi > 0.25 for diagnostic species. Moreover, we required that the phi value in the target syntaxon must be at least 0.25 higher than in the syntaxon of the same rank with the next higher frequency of this species to support clear differentiation between similar syntaxa (see Tsiripidis et al. 2009; Vassilev et al. 2024). Since this approach of phi values (i.e. hierarchical phi values and comparison of phi values to the next similar syntaxon) is not yet implemented in JUICE, we completed these calculations in MS Excel, which did not allow testing for statistical significance (see Vassilev et al. 2024). To exclude spurious results, we used relatively high phi value thresholds and excluded species that had only one occurrence in the target vegetation.

Species were primarily considered diagnostic at the hierarchical level where they reached the highest phi value. If this was a lower rank, but they additionally met all criteria at a higher rank and they on average also had positive phi values in the other included lower-rank syntaxa, the species was considered as diagnostic also at the higher rank (named as transgressive diagnostic species and marked in pale grey) (see Table 2). Species that did not meet the criteria for being diagnostic in the entire dataset but only within the next higher syntaxon were considered differential species (see Dengler et al. 2005) and marked with a frame (Table 2). In the description of the syntaxa, highly diagnostic species are highlighted in bold and differential species with “(D)”.

Phytosociological nomenclature

We carefully searched the phytosociological literature of Iran and neighbouring regions for syntaxa matching our concepts (Klein 1982, 1987, 2001; Klein and Lacoste 1999; Parolly 2004; Noroozi et al. 2010, 2014, 2017; Mucina et al. 2016; Nowak et al. 2016, 2018, 2020; Świerszcz 2020; Vynokurov et al. 2024). If there were matching concepts of validly published names, we used the names validly published. Syntaxa not validly published before were formally described according to the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021), providing our data were comprehensive enough to allow such a step. For association-level units with less than 10 plots in our study, we refrained from a formal description (see ICPN Recommendation 7A) and kept them as informal “communities”.

Statistical analyses

All statistical analyses and visualisations were carried out in R, version 4.3.3 (R Core Team 2024). We used boxplots to visualise the differences in biodiversity, structural and ecological parameters among communities. To test for differences of these variables between syntaxa, we used one-way ANOVA. Where ANOVA revealed a significant pattern, Tukey’s post-hoc test at $p < 0.05$ was used to identify homogeneous groups of syntaxa. Results are presented as box-whisker plots. The floristic relationships among the plots and syntaxa and the underlying environmental variables were assessed using detrended correspondence analysis (DCA), computed in the ‘vegan’ package (Oksanen et al. 2017).

Results

General floristic features

A total of 416 vascular plant taxa were recorded in the 330 plots. The most constant taxa were *Festuca valesiaca* (49%), *Bromus paulsenii* (34%), *Thymus kotschyanus* (31%), *Bromus tectorum* (30%), *Erysimum caespitosum*

Table 1. Syntaxonomic scheme of the plant communities of Mt. Damavand. The full descriptions of the new syntaxa are given in the text and Appendix 1.

- **1. Rocky communities – Unclear class**
  - **Order 1.1 *Tanacetalia kotschyi* Klein 1982**
    - Allliance 1.1.1 *Campanulion lauricae* Klein 1982
      - 1.1.1.1 *Veronica aucheri-Corydalis rupestris* community
      - 1.1.1.2 *Iranecio oligolepis* community
    - Alliance 1.1.2 Undescribed
      - 1.1.2.1 *Salvia xanthocheila* community
      - 1.1.2.2. *Rosa iberica* community
- **2. Scree communities – *Didymophyso aucheri-Dracocephaletea aucheri* Noroozi et al. 2013**
  - **Order 2.1 *Didymophysetalia aucheri* Noroozi et al. 2013**
    - Alliance 2.1.1 *Didymophysion aucheri* Noroozi et al. 2013
      - 2.1.1.1 *Dracocephaletum aucheri* Noroozi et al. 2013
      - 2.1.1.2 *Myosotido olympicae-Lamietum tomentosi* Talebi et al. 2024 (see Appendix 1)
- **3. Snow-bed communities – *Salicetea herbaceae* Br.-Bl. 1948**
  - **Order 3.1** Undescribed
    - Alliance 3.1.1 *Taraxaco brevirostris-Polygonion serpyllacei* Noroozi et al. 2010
      - 3.1.1.1 *Ranunculo crymophili-Oxyrietum digynae* Noroozi et al. 2017
- **4. Irano-Turanian grassland communities – *Astragalo-Brometea* Quézel 1973**
  - **Order 4.1 *Drabetalia pulchellae* Noroozi et al. ex Noroozi in Talebi et al. 2024 (see** Appendix 1**)**
    - Alliance 4.1.1 *Acantholimion demavendici* Noroozi et al. 2010
      - 4.1.1.1 *Senecioni iranici-Astragaletum macrosemii* Noroozi et al. ex Noroozi in Talebi et al. 2024 (see Appendix 1)
      - 4.1.1.2 *Cousinietum harazensis* Talebi et al. 2024 (see Appendix 1)
    - Alliance 4.1.2 *Astragalion iodotropidis* Noroozi et al. 2010
      - 4.1.2.1 *Astragalus iodotropis-Bromus paulsenii* community
      - 4.1.2.2 *Astragaletum iodotropidis* Noroozi et al. 2010
      - 4.1.2.3 *Astragaletum ochrochlori* Talebi et al. 2024 (see Appendix 1)
  - **Order 4.2 *Astragalo-Brometalia* Quézel 1973**
    - Alliance 4.2.1 Undescribed
      - 4.2.1.1 *Astragalo lilacini-Astragaletum microcephali* Talebi et al. 2024 (see Appendix 1)
    - Alliance 4.2.2 *Artemision aucheri* Talebi et al. 2024 (see below)
      - 4.2.2.1 *Astragalo compacti-Feruletum persicae* Talebi et al. 2024 (see Appendix 1)
      - 4.2.2.2 *Artemisietum aucheri* Talebi et al. 2024 (see Appendix 1)
      - 4.2.2.3 *Caccinio strigosae-Oreosalsoletum montanae* Talebi et al. 2024 (see Appendix 1)
  - **Order 4.3** Undescribed
    - Alliance 4.3.1 *Cousinion petrocauli* Talebi et al. 2024 (see Appendix 1)
      - 4.3.1.1 *Astragaletum retamocarpi* Talebi et al. 2024 (see Appendix 1)
      - 4.3.1.2 *Heracleo anisactidis-Prangetum ferulaceae* Talebi et al. 2024 (see Appendix 1)

(29%), *Poa araratica* (29%), *Artemisia chamaemelifolia* (28%), *Draba pulchella* (27%), *Achillea aucheri* (27%) and *Alopecurus textilis* (26%). Species richness in 25 m^2 varied from 4 to 61 taxa (average 21) depending on the vegetation type. The lowest values were found in alpine scree vegetation and the highest values in subalpine grasslands.

TWINSPAN classification and its interpretation

The TWINSPAN classification showed a separation of the studied plots into two major groups of alpine-nival (above ca. 3000 m a.s.l.) and montane-subalpine (up to ca. 3000 m a.s.l.) plots (see Suppl. material 1 and relevant raw data). In the alpine-nival group, the subsequent division was into screes, snowbeds and alpine thorn-cushion grasslands. The montane-subalpine group was split by TWINSPAN into natural grasslands vs. semi-natural pseudo-steppes. The communities of rocky habitats occur in both subgroups of alpine-nival and montane-subalpine.

Syntaxonomic overview

We distinguished 18 associations and association-rank communities, grouped into nine alliances, seven orders and four classes (Table 1). The classification is supported by the synoptic table showing the diagnostic species at all levels (abbreviated version in Table 2, full version in Suppl. material 2).

Vegetation-environment relationships

DCA showed a considerable floristic variation between the 18 plant communities, which were mostly well separated on the first ordination plain (Figure 3). The first ordination axis was mainly governed by elevation, whereas the second reflected variation in inclination and soil features. Vegetation units of the alpine-nival zones were located on the right side of the diagram, those of the montane-subalpine zones on the left. The communities of the alpine zone were well separated, but some in the nival zone scree, rocky and thorn-cushion associations were not that clearly separated because they share some common species. Aspect particularly differentiated three associations (4.1.2.1, 4.1.2.2 and 4.1.2.3) belonging to wind-protected and depression areas that occurred in the upper part of the diagram.

Except for the associations developing on mown sites (4.3.1.1 and 4.3.1.2), which prefer soils with fine structure, all other associations showed high content of rocks in these habitats (Figure 4). The highest vegetation cover was recorded in the mown associations while the lowest values were found in the rocks, scree and snowbed associations (Figure 4).

Table 2. Abridged synoptic table of the plant communities of the southern slopes of Mt. Damavand. All syntaxa from association to class rank are shown. For the meaning of the syntaxon codes, see Table 1. The table was shortened by only showing the 10 most diagnostic species per syntaxon plus all species with at least 5% frequency in the overall dataset. "[...]" indicates places where species lists have been shortened. The full table together with the individual relevés and the precise phi values is available in Suppl. material 2. Diagnostic species are listed by decreasing fidelity in the respective syntaxon; companion species are sorted by decreasing overall frequency. Diagnostic species are highlighted in dark grey, transgressive diagnostic species in light grey and differential species with a frame. This symbology is always copied to all subordinate syntaxa.

Rank	All	Cl.	Cl.	Cl.	Cl.	Ord.	Ord.	Ord.	Ord.	Ord.	Ord.	All.	All.	All.	All.	All.	All.	All.	All.	All.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.
Class		1	2	3	4	1	2	3	4	4	4	1	1	2	3	4	4	4	4	4	1	1	1	1	2	2	3	4	4	4	4	4	4	4	4	4	4	4
Order						1	1	1	1	2	3	1	1	1	1	1	1	2	2	3	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	3	3
Alliance												1	2	1	1	1	2	1	2	1	1	1	2	2	1	1	1	1	1	2	2	2	1	2	2	2	1	1
Association																					1	2	1	2	1	2	1	1	2	1	2	3	1	1	2	3	1	2
Number of plots included	330	25	37	4	264	25	37	4	118	125	21	8	17	37	4	72	46	76	49	21	4	4	10	7	16	21	4	31	41	10	12	24	76	21	19	9	11	10
Mean species richness	21.0	14.5	8.2	10.5	22.5	14.5	8.2	10.5	16.2	29.7	24.0	9.3	19.8	8.2	10.5	15.3	16.8	29.5	49.0	24.0	8.8	9.8	20.2	19.4	5.1	11.4	10.5	13.0	17.6	14.0	14.3	22.2	29.5	41.6	27.8	20.0	24.3	23.8
Cl. 1 (2 diagnostic species)																																						
Valeriana sisymbriifolia	0.9	8	.	.	0	8	.	.	1	.	.	13	6	.	.	.	2	.	.	.	.	25	.	14	.	.	.	.	.	.	.	4	.	.	.	.	.	.
All. 1.1.1 (1 diagnostic species)																																						
Galium delicatulum	5.8	16	3	.	5	16	3	.	11	0	.	38	6	3	.	13	9	1	.	.	50	25	10	.	.	5	.	.	22	10	.	13	1	.	.	.	.	.
Assoc. 1.1.1.1 (2 diagnostic species)																																						
Corydalis rupestris	0.9	12	.	.	.	12	.	.	.	.	.	38	.	.	.	.	.	.	.	.	75	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asperula glomerata subsp. *bracteata*	2.7	12	5	.	2	12	5	.	3	.	.	38	.	5	.	6	.	.	.	.	75	.	.	.	.	10	.	6	5	.	.	.	.	.	.	.	.	.
Assoc. 1.1.1.2 (2 diagnostic species)																																						
Iranecio oligolepis	1.2	16	.	.	.	16	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nepeta racemosa	16.4	28	27	.	14	28	27	.	20	4	10	50	18	27	.	14	30	13	2	10	.	100	10	29	.	48	.	3	22	20	42	29	13	5	.	.	9	10
All. 1.1.2 (10 diagnostic species)																																						
Parietaria judaica	3.3	44	.	.	.	44	.	.	.	.	.	.	65	.	.	.	.	.	.	.	.	.	50	86	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scrophularia variegata	6.1	52	.	.	3	52	.	.	3	1	.	.	76	.	.	3	4	4	.	.	.	.	80	71	.	.	.	.	5	.	.	8	4	.	.	.	.	.
Tanacetum polycephalum	30.9	68	.	.	32	68	.	.	15	32	14	.	100	.	.	18	11	67	27	14	.	.	100	100	.	.	.	.	32	10	.	17	67	62	.	.	9	20
Cervaria cervariifolia	2.1	28	.	.	.	28	.	.	.	.	.	.	41	.	.	.	.	.	.	.	.	.	30	57	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunus pseudoprostrata	11.5	48	.	.	10	48	.	.	.	22	5	.	71	.	.	.	.	14	29	5	.	.	60	86	.	.	.	.	.	.	.	.	14	62	.	11	9	.
Gypsophila aretioides	2.7	28	.	.	1	28	.	.	.	0	5	.	41	.	.	.	.	1	.	5	.	.	40	43	.	.	.	.	.	.	.	.	1	.	.	.	9	.
Dianthus orientalis	8.5	36	.	.	7	36	.	.	1	14	5	.	53	.	.	1	.	14	12	5	.	.	60	43	.	.	.	.	2	.	.	.	14	19	.	22	9	.
Pimpinella tragium	8.2	44	.	.	6	44	.	.	12	1	.	25	53	.	.	14	9	3	.	.	50	.	40	71	.	.	.	.	24	.	.	17	3	.	.	.	.	.
Eremogone polycnemifolia	1.2	16	.	.	.	16	.	.	.	.	.	.	24	.	.	.	.	.	.	.	.	.	30	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dracocephalum kotschyi	0.9	8	.	.	0	8	.	.	.	0	.	.	12	.	.	.	.	1	.	.	.	.	10	14	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Assoc. 1.1.2.1 (10 diagnostic species)																																						
Salvia xanthocheila	2.7	32	.	.	0	32	.	.	.	1	.	.	47	.	.	.	.	.	2	.	.	.	70	14	.	.	.	.	.	.	.	.	.	5	.	.	.	.
Dielsiocharis kotschyi	1.5	20	.	.	.	20	.	.	.	.	.	.	29	.	.	.	.	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pseudosedum multicaulis	0.9	12	.	.	.	12	.	.	.	.	.	.	18	.	.	.	.	.	.	.	.	.	30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sisymbrium gaubae	0.9	12	.	.	.	12	.	.	.	.	.	.	18	.	.	.	.	.	.	.	.	.	30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fibigia suffruticosa	0.6	8	.	.	.	8	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosa canina	0.6	8	.	.	.	8	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex scutatus	0.6	8	.	.	.	8	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene commelinifolia	0.6	8	.	.	.	8	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ephedra major	0.9	8	.	.	0	8	.	.	.	0	.	.	12	.	.	.	.	1	.	.	.	.	20	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Galium hyrcanicum	0.9	8	.	.	0	8	.	.	.	0	.	.	12	.	.	.	.	1	.	.	.	.	20	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Assoc. 1.1.2.2 (8 diagnotic species)																																						
Rosa iberica	1.5	20	.	.	.	20	.	.	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.	71	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sempervivum iranicum	0.9	12	.	.	.	12	.	.	.	.	.	.	18	.	.	.	.	.	.	.	.	.	.	43	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ziziphora clinopodioides subsp. *rigida*	3.0	20	.	.	2	20	.	.	1	1	.	.	29	.	.	.	2	5	.	.	.	.	10	57	.	.	.	.	.	.	.	4	5	.	.	.	.	.
Tanacetum parthenium	1.2	16	.	.	.	16	.	.	.	.	.	.	24	.	.	.	.	.	.	.	.	.	10	43	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhamnus pallasii	2.4	16	.	.	2	16	.	.	.	3	.	.	24	.	.	.	.	3	4	.	.	.	10	43	.	.	.	.	.	.	.	.	3	10	.	.	.	.

Rank	All	Cl.	Cl.	Cl.	Cl.	Ord.	Ord.	Ord.	Ord.	Ord.	Ord.	All.	All.	All.	All.	All.	All.	All.	All.	All.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.
Class		1	2	3	4	1	2	3	4	4	4	1	1	2	3	4	4	4	4	4	1	1	1	1	2	2	3	4	4	4	4	4	4	4	4	4	4	4
Order						1	1	1	1	2	3	1	1	1	1	1	1	2	2	3	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	3	3
Alliance												1	2	1	1	1	2	1	2	1	1	1	2	2	1	1	1	1	1	2	2	2	1	2	2	2	1	1
Association																					1	2	1	2	1	2	1	1	2	1	2	3	1	1	2	3	1	2
Number of plots included	330	25	37	4	264	25	37	4	118	125	21	8	17	37	4	72	46	76	49	21	4	4	10	7	16	21	4	31	41	10	12	24	76	21	19	9	11	10
Mean species richness	21.0	14.5	8.2	10.5	22.5	14.5	8.2	10.5	16.2	29.7	24.0	9.3	19.8	8.2	10.5	15.3	16.8	29.5	49.0	24.0	8.8	9.8	20.2	19.4	5.1	11.4	10.5	13.0	17.6	14.0	14.3	22.2	29.5	41.6	27.8	20.0	24.3	23.8
Silene aucheriana	4.8	12	.	.	5	12	.	.	1	5	5	.	18	.	.	1	.	12	4	5	.	.	.	43	.	.	.	.	2	.	.	.	12	10	.	.	9	.
Allium capitellatum	1.2	8	.	.	1	8	.	.	1	0	.	.	12	.	.	1	.	1	.	.	.	.	.	29	.	.	.	.	2	.	.	.	1	.	.	.	.	.
Poa sterilis	2.4	8	.	.	2	8	.	.	1	2	.	.	12	.	.	.	2	7	.	.	.	.	.	29	.	.	.	.	.	.	.	4	7	.	.	.	.	.
Cl. 2 (2 diagnostic species)																																						
Achillea aucheri	13.9	8	89	.	4	8	89	.	9	.	.	25	.	89	.	15	.	.	.	.	50	.	.	.	94	86	.	35	.	.	.	.	.	.	.	.	.	.
Assoc. 2.1.1.1 (1 diagnostic species, central association)																																						
Didymophysa aucheri	7.0	.	59	.	0	.	59	.	1	.	.	.	.	59	.	1	.	.	.	.	.	.	.	.	94	33	.	3	.	.	.	.	.	.	.	.	.	.
Assoc. 2.1.1.2 (4 diagnostic species)																																						
Myosotis olympica	4.8	.	41	.	0	.	41	.	1	.	.	.	.	41	.	1	.	.	.	.	.	.	.	.	.	71	.	3	.	.	.	.	.	.	.	.	.	.
Lamium tomentosum	5.5	8	41	.	0	8	41	.	1	.	.	25	.	41	.	1	.	.	.	.	25	25	.	.	.	71	.	3	.	.	.	.	.	.	.	.	.	.
Elymus longearistatus	4.8	4	35	.	1	4	35	.	2	.	.	13	.	35	.	.	4	.	.	.	.	25	.	.	.	62	.	.	.	.	17	.	.	.	.	.	.	.
Crepis multicaulis	9.7	.	41	25	6	.	41	25	14	.	.	.	.	41	25	17	9	.	.	.	.	.	.	.	.	71	25	19	15	10	8	8	.	.	.	.	.	.
Cl. 3 (6 diagnostic species)																																						
Ranunculus crymophilus	1.2	.	.	100	.	.	.	100	.	.	.	.	.	.	100	.	.	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.	.	.	.	.	.	.
Dichodon cerastoides	1.5	.	.	100	0	.	.	100	1	.	.	.	.	.	100	.	2	.	.	.	.	.	.	.	.	.	100	.	.	.	8	.	.	.	.	.	.	.
Erigeron uniflorus	3.9	.	11	75	2	.	11	75	5	.	.	.	.	11	75	7	2	.	.	.	.	.	.	.	6	14	75	16	.	.	8	.	.	.	.	.	.	.
Artemisia melanolepis	12.7	.	14	100	13	.	14	100	28	.	.	.	.	14	100	43	4	.	.	.	.	.	.	.	6	19	100	97	2	10	.	4	.	.	.	.	.	.
Catabrosella parviflora	6.4	.	5	75	6	.	5	75	14	.	.	.	.	5	75	21	2	.	.	.	.	.	.	.	.	10	75	48	.	10	.	.	.	.	.	.	.	.
Cerastium purpurascens	10.6	.	27	75	8	.	27	75	19	.	.	.	.	27	75	29	2	.	.	.	.	.	.	.	19	33	75	65	2	10	.	.	.	.	.	.	.	.
Cl. 4 (8 diagnostic species)																																						
Polygonum alpestre	13.9	.	.	.	17	.	.	.	31	.	48	.	.	.	.	10	63	.	.	48	.	.	.	.	.	.	.	10	10	70	83	50	.	.	.	.	55	40
Thymus kotschyanus	35.8	8	3	.	44	8	3	.	47	45	14	13	6	3	.	26	78	74	2	14	.	25	.	14	.	5	.	.	46	50	67	96	74	5	.	.	18	10
Veronica biloba	30.0	12	.	.	36	12	.	.	48	23	14	.	18	.	.	40	61	38	14	14	.	.	20	14	.	.	.	23	54	30	50	79	38	24	11	.	9	20
Polygonum rottboellioides	21.8	.	.	.	27	.	.	.	39	16	5	.	.	.	.	35	46	26	10	5	.	.	.	.	.	.	.	6	56	10	25	71	26	.	26	.	9	.
Papaver bracteatum	16.4	.	.	.	20	.	.	.	17	22	33	.	.	.	.	4	37	36	.	33	.	.	.	.	.	.	.	.	7	10	8	63	36	.	.	.	27	40
Silene bupleuroides	11.2	4	.	.	14	4	.	.	17	4	52	.	6	.	.	.	43	7	.	52	.	.	.	14	.	.	.	.	.	20	42	54	7	.	.	.	36	70
Ord. 4.1 (9 diagnostic species)																																						
Onobrychis cornuta	24.8	4	.	.	31	4	.	.	52	15	5	.	6	.	.	58	41	25	.	5	.	.	.	14	.	.	.	6	98	50	.	58	25	.	.	.	9	.
Veronica kurdica	10.9	.	.	.	14	.	.	.	31	.	.	.	.	.	.	31	30	.	.	.	.	.	.	.	.	.	.	13	44	40	17	33	.	.	.	.	.	.
Draba pulchella	24.8	8	24	50	26	8	24	50	58	.	.	25	.	24	50	71	39	.	.	.	.	50	.	.	.	43	50	58	80	40	33	42	.	.	.	.	.	.
Alopecurus textilis	24.8	16	24	25	26	16	24	25	58	.	.	50	.	24	25	71	37	.	.	.	25	75	.	.	.	43	25	52	85	80	17	29	.	.	.	.	.	.
Chenopodium foliosum	12.7	4	3	.	15	4	3	.	32	2	.	13	.	3	.	35	28	3	.	.	.	25	.	.	.	5	.	26	41	10	33	33	3	.	.	.	.	.
Artemisia chamaemelifolia	28.5	28	22	.	30	28	22	.	53	12	5	38	24	22	.	60	43	20	.	5	75	.	.	57	.	38	.	32	80	70	50	29	20	.	.	.	.	10
Carex pseudo-foetida	5.2	.	.	.	6	.	.	.	14	.	.	.	.	.	.	17	11	.	.	.	.	.	.	.	.	.	.	39	.	.	17	13	.	.	.	.	.	.
All. 4.1.1 (central alliance)																																						
Assoc. 4.1.1.1 (4 diagnostic species)																																						
Astragalus macrosemius	12.1	4	11	.	13	4	11	.	30	.	.	13	.	11	.	49	.	.	.	.	.	25	.	.	.	19	.	94	15	.	.	.	.	.	.	.	.	.
Senecio iranicus	4.2	.	.	.	5	.	.	.	12	.	.	.	.	.	.	19	.	.	.	.	.	.	.	.	.	.	.	42	2	.	.	.	.	.	.	.	.	.
Draba siliquosa	6.4	.	14	.	6	.	14	.	14	.	.	.	.	14	.	22	.	.	.	.	.	.	.	.	13	14	.	52	.	.	.	.	.	.	.	.	.	.
Potentilla polyschista	5.5	.	11	.	5	.	11	.	12	.	.	.	.	11	.	19	.	.	.	.	.	.	.	.	6	14	.	45	.	.	.	.	.	.	.	.	.	.
Assoc. 4.1.1.2 (5 diagnostic species)																																						
Acantholimon demawendicum	7.0	.	.	.	9	.	.	.	19	.	.	.	.	.	.	32	.	.	.	.	.	.	.	.	.	.	.	6	51	.	.	.	.	.	.	.	.	.
Cousinia harazensis	11.2	4	.	.	14	4	.	.	29	2	.	.	6	.	.	43	7	3	.	.	.	.	.	14	.	.	.	.	76	30	.	.	3	.	.	.	.	.
Campanula stevenii	10.3	4	.	.	13	4	.	.	26	2	.	.	6	.	.	40	4	3	.	.	.	.	.	14	.	.	.	6	66	20	.	.	3	.	.	.	.	.
Acantholimon erinaceum	6.4	4	.	.	8	4	.	.	16	1	.	.	6	.	.	25	2	1	.	.	.	.	10	.	.	.	.	.	44	.	.	4	1	.	.	.	.	.
Silene palinotricha	3.3	.	.	.	4	.	.	.	9	.	.	.	.	.	.	15	.	.	.	.	.	.	.	.	.	.	.	.	27	.	.	.	.	.	.	.	.	.

Rank	All	Cl.	Cl.	Cl.	Cl.	Ord.	Ord.	Ord.	Ord.	Ord.	Ord.	All.	All.	All.	All.	All.	All.	All.	All.	All.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.
Class		1	2	3	4	1	2	3	4	4	4	1	1	2	3	4	4	4	4	4	1	1	1	1	2	2	3	4	4	4	4	4	4	4	4	4	4	4
Order						1	1	1	1	2	3	1	1	1	1	1	1	2	2	3	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	3	3
Alliance												1	2	1	1	1	2	1	2	1	1	1	2	2	1	1	1	1	1	2	2	2	1	2	2	2	1	1
Association																					1	2	1	2	1	2	1	1	2	1	2	3	1	1	2	3	1	2
Number of plots included	330	25	37	4	264	25	37	4	118	125	21	8	17	37	4	72	46	76	49	21	4	4	10	7	16	21	4	31	41	10	12	24	76	21	19	9	11	10
Mean species richness	21.0	14.5	8.2	10.5	22.5	14.5	8.2	10.5	16.2	29.7	24.0	9.3	19.8	8.2	10.5	15.3	16.8	29.5	49.0	24.0	8.8	9.8	20.2	19.4	5.1	11.4	10.5	13.0	17.6	14.0	14.3	22.2	29.5	41.6	27.8	20.0	24.3	23.8
All. 4.1.2 (9 diagnostic species)																																						
Astragalus iodotropis	11.2	.	.	.	14	.	.	.	31	.	.	.	.	.	.	10	65	.	.	.	.	.	.	.	.	.	.	.	17	100	100	33	.	.	.	.	.	.
Piptatherum laterale	12.1	4	.	.	15	4	.	.	32	1	.	13	.	.	.	8	70	1	.	.	.	25	.	.	.	.	.	.	15	60	92	63	1	.	.	.	.	.
Taraxacum brevirostris	6.7	.	.	.	8	.	.	.	19	.	.	.	.	.	.	3	43	.	.	.	.	.	.	.	.	.	.	6	.	40	83	25	.	.	.	.	.	.
Cirsium lappaceum	14.2	4	11	25	16	4	11	25	29	6	.	13	.	11	25	3	70	9	.	.	.	25	.	.	.	19	25	.	5	60	83	67	9	.	.	.	.	.
Potentilla argyroloma	7.9	8	.	.	9	8	.	.	19	1	.	25	.	.	.	6	41	1	.	.	.	50	.	.	.	.	.	3	7	50	83	17	1	.	.	.	.	.
Herniaria glabra	6.7	.	.	.	8	.	.	.	16	2	.	.	.	.	.	4	35	4	.	.	.	.	.	.	.	.	.	.	7	30	25	42	4	.	.	.	.	.
Polygonum patulum	5.8	.	.	.	7	.	.	.	13	2	5	.	.	.	.	3	28	4	.	5	.	.	.	.	.	.	.	.	5	.	25	42	4	.	.	.	9	.
Leonorus cardiaca	2.7	.	.	.	3	.	.	.	8	.	.	.	.	.	.	3	15	.	.	.	.	.	.	.	.	.	.	.	5	10	8	21	.	.	.	.	.	.
Assoc. 4.1.2.1 (central association)																																						
Assoc. 4.1.2.2 (2 diagnostic species)																																						
Tragopogon kotschyi	6.7	.	.	.	8	.	.	.	15	2	10	.	.	.	.	1	37	3	.	10	.	.	.	.	.	.	.	.	2	20	75	25	3	.	.	.	.	20
Hordeum violaceum	1.8	.	.	.	2	.	.	.	5	.	.	.	.	.	.	1	11	.	.	.	.	.	.	.	.	.	.	.	2	.	33	4	.	.	.	.	.	.
Assoc. 4.1.2.3 (3 diagnostic species)																																						
Astragalus ochrochlorus	16.4	4	.	.	20	4	.	.	29	14	5	.	6	.	.	14	52	22	2	5	.	.	.	14	.	.	.	.	24	.	.	100	22	5	.	.	9	.
Cousinia multiloba	2.7	.	.	.	3	.	.	.	8	.	.	.	.	.	.	3	15	.	.	.	.	.	.	.	.	.	.	.	5	.	.	29	.	.	.	.	.	.
Plantago atrata	2.4	.	.	.	3	.	.	.	6	.	5	.	.	.	.	.	15	.	.	5	.	.	.	.	.	.	.	.	.	.	8	25	.	.	.	.	9	.
Ord. 4.2 (39 diagnostic species)																																						
Artemisia aucheri	22.4	24	.	.	26	24	.	.	2	14	.	.	35	.	.	.	4	24	98	.	.	.	50	14	.	.	.	.	.	.	.	8	24	95	100	100	.	.
Bromus tectorum	30.6	32	.	.	35	32	.	.	5	34	14	.	47	.	.	4	7	57	84	14	.	.	70	14	.	.	.	.	7	.	.	13	57	90	84	67	18	10
Kochia prostrata	11.2	4	.	.	14	4	.	.	.	3	.	.	6	.	.	.	.	5	65	.	.	.	10	.	.	.	.	.	.	.	.	.	5	76	63	44	.	.
Bromus danthoniae	14.5	.	.	.	18	.	.	.	.	14	10	.	.	.	.	.	.	24	57	10	.	.	.	.	.	.	.	.	.	.	.	.	24	81	32	56	18	.
Alyssum minus	21.5	8	.	.	26	8	.	.	3	30	10	.	12	.	.	4	.	50	53	10	.	.	20	.	.	.	.	.	7	.	.	.	50	71	26	67	.	20
Ferula persica	7.0	.	.	.	9	.	.	.	.	2	.	.	.	.	.	.	.	4	41	.	.	.	.	.	.	.	.	.	.	.	.	.	4	43	21	78	.	.
Taeniatherum caput-medusae	8.8	4	.	.	11	4	.	.	.	.	.	.	6	.	.	.	.	.	57	.	.	.	10	.	.	.	.	.	.	.	.	.	.	71	58	22	.	.
Galium spurium	14.2	4	.	.	17	4	.	.	.	17	5	.	6	.	.	.	.	28	49	5	.	.	10	.	.	.	.	.	.	.	.	.	28	52	58	22	9	.
Senecio glaucus	7.6	.	.	.	9	.	.	.	.	2	.	.	.	.	.	.	.	3	47	.	.	.	.	.	.	.	.	.	.	.	.	.	3	52	53	22	.	.
Ziziphora tenuior	8.5	.	.	.	11	.	.	.	.	5	.	.	.	.	.	.	.	8	45	.	.	.	.	.	.	.	.	.	.	.	.	.	8	52	58	.	.	.
[…]																																						
Stipa arabica	22.4	44	.	.	24	44	.	.	3	18	.	.	65	.	.	.	7	30	76	.	.	.	70	57	.	.	.	.	.	10	.	8	30	71	100	33	.	.
Alyssum marginatum	20.6	4	.	.	25	4	.	.	3	33	10	.	6	.	.	.	9	54	41	10	.	.	10	.	.	.	.	.	.	.	.	17	54	71	21	11	18	.
Teucrium polium	7.6	.	.	.	9	.	.	.	.	3	.	.	.	.	.	.	.	5	43	.	.	.	.	.	.	.	.	.	.	.	.	.	5	71	32	.	.	.
Lamium amplexicaulis	7.6	.	.	.	9	.	.	.	.	7	.	.	.	.	.	.	.	12	33	.	.	.	.	.	.	.	.	.	.	.	.	.	12	38	32	22	.	.
Viola occulta	11.5	.	.	.	14	.	.	.	2	14	.	.	.	.	.	.	4	24	37	.	.	.	.	.	.	.	.	.	.	.	.	8	24	52	37	.	.	.
Linaria simplex	7.0	.	.	.	9	.	.	.	2	1	.	.	.	.	.	3	.	1	41	.	.	.	.	.	.	.	.	.	5	.	.	.	1	38	63	.	.	.
Herniaria incana	16.4	.	.	.	20	.	.	.	3	28	5	.	.	.	.	4	2	46	29	5	.	.	.	.	.	.	.	.	7	.	.	4	46	67	.	.	9	.
Callipeltis cucullaris	7.3	4	.	.	9	4	.	.	.	3	.	.	6	.	.	.	.	5	39	.	.	.	10	.	.	.	.	.	.	.	.	.	5	52	42	.	.	.
Eryngium billardieri	6.7	4	.	.	8	4	.	.	.	6	5	.	6	.	.	.	.	9	27	5	.	.	10	.	.	.	.	.	.	.	.	.	9	33	5	56	9	.
Alyssum dessertorum	21.5	8	.	.	26	8	.	.	6	28	24	.	12	.	.	6	7	46	45	24	.	.	20	.	.	.	.	.	10	.	.	13	46	71	37	.	18	30
Sophora alopecuroides	7.9	.	.	.	10	.	.	.	1	7	10	.	.	.	.	.	2	12	29	10	.	.	.	.	.	.	.	.	.	.	.	4	12	33	21	33	9	10
Lappula barbata	9.7	16	.	.	11	16	.	.	.	7	.	.	24	.	.	.	.	12	39	.	.	.	40	.	.	.	.	.	.	.	.	.	12	43	47	11	.	.
Alyssum linifoluum	6.1	.	.	.	8	.	.	.	.	6	.	.	.	.	.	.	.	11	24	.	.	.	.	.	.	.	.	.	.	.	.	.	11	38	21	.	.	.
Camelina rumelica	5.2	.	.	.	6	.	.	.	.	5	.	.	.	.	.	.	.	8	22	.	.	.	.	.	.	.	.	.	.	.	.	.	8	33	21	.	.	.
Asperula arvens	12.1	4	.	.	15	4	.	.	3	17	5	.	6	.	.	1	7	28	27	5	.	.	10	.	.	.	.	.	2	.	.	13	28	48	11	11	9	.
Galium verticillatum	5.8	4	.	.	7	4	.	.	.	1	5	.	6	.	.	.	.	1	33	5	.	.	10	.	.	.	.	.	.	.	.	.	1	43	37	.	9	.

Rank	All	Cl.	Cl.	Cl.	Cl.	Ord.	Ord.	Ord.	Ord.	Ord.	Ord.	All.	All.	All.	All.	All.	All.	All.	All.	All.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.
Class		1	2	3	4	1	2	3	4	4	4	1	1	2	3	4	4	4	4	4	1	1	1	1	2	2	3	4	4	4	4	4	4	4	4	4	4	4
Order						1	1	1	1	2	3	1	1	1	1	1	1	2	2	3	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	3	3
Alliance												1	2	1	1	1	2	1	2	1	1	1	2	2	1	1	1	1	1	2	2	2	1	2	2	2	1	1
Association																					1	2	1	2	1	2	1	1	2	1	2	3	1	1	2	3	1	2
Number of plots included	330	25	37	4	264	25	37	4	118	125	21	8	17	37	4	72	46	76	49	21	4	4	10	7	16	21	4	31	41	10	12	24	76	21	19	9	11	10
Mean species richness	21.0	14.5	8.2	10.5	22.5	14.5	8.2	10.5	16.2	29.7	24.0	9.3	19.8	8.2	10.5	15.3	16.8	29.5	49.0	24.0	8.8	9.8	20.2	19.4	5.1	11.4	10.5	13.0	17.6	14.0	14.3	22.2	29.5	41.6	27.8	20.0	24.3	23.8
Verbascum cheiranthifolium	19.4	16	.	.	23	16	.	.	2	32	14	.	24	.	.	1	2	53	31	14	.	.	20	29	.	.	.	.	2	.	.	4	53	52	21	.	27	.
Psatyrostachys fragilis	12.7	12	.	.	15	12	.	.	8	14	.	.	18	.	.	8	7	22	27	.	.	.	20	14	.	.	.	.	15	.	.	13	22	29	26	22	.	.
All. 4.2.1 (11 diagnostic species)																																						
Astragalus microcephalus	22.7	8	.	.	28	8	.	.	.	50	.	.	12	.	.	.	.	82	22	.	.	.	20	.	.	.	.	.	.	.	.	.	82	48	5	.	.	.
Ceratocephala testiculata	18.2	.	.	.	23	.	.	.	7	36	5	.	.	.	.	7	7	59	12	5	.	.	.	.	.	.	.	.	12	.	.	13	59	29	.	.	.	10
Draba nemorosa	16.1	.	.	.	20	.	.	.	5	34	19	.	.	.	.	1	11	55	2	19	.	.	.	.	.	.	.	.	2	.	.	21	55	5	.	.	18	20
Agropyron cristatum	19.7	4	.	.	24	4	.	.	7	38	19	.	6	.	.	10	2	62	10	19	.	.	10	.	.	.	.	.	17	.	.	4	62	24	.	.	36	.
Bromus tomentellus	15.5	.	.	.	19	.	.	.	14	27	.	.	.	.	.	11	20	45	.	.	.	.	.	.	.	.	.	.	20	.	8	33	45	.	.	.	.	.
Drabopsis verna	12.1	.	.	.	15	.	.	.	2	25	5	.	.	.	.	.	4	41	12	5	.	.	.	.	.	.	.	.	.	.	.	8	41	24	5	.	.	10
Astragalus laricus	3.3	.	.	.	4	.	.	.	.	9	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.	.
Astragalus lilacinus	12.1	.	.	.	15	.	.	.	7	22	10	.	.	.	.	11	.	37	4	10	.	.	.	.	.	.	.	.	20	.	.	.	37	10	.	.	9	10
Delphinium aquilegifolium	3.0	.	.	.	4	.	.	.	.	8	.	.	.	.	.	.	.	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13	.	.	.	.	.
Euphorbia cheiradenia	7.0	4	.	.	8	4	.	.	3	14	.	.	6	.	.	.	9	24	.	.	.	.	10	.	.	.	.	.	.	.	8	13	24	.	.	.	.	.
[…]																																						
All. 4.2.2 (21 diagnostic species)																																						
Cousinia eryngioides	4.8	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	42	67	.	.
Atriplex aucheri	4.5	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	37	67	.	.
Stachys inflata	7.3	.	.	.	9	.	.	.	.	1	.	.	.	.	.	.	.	1	47	.	.	.	.	.	.	.	.	.	.	.	.	.	1	33	53	67	.	.
Eremopyrum bonaepartis	3.9	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	42	44	.	.
Caroxylon dendroides	3.0	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	32	44	.	.
Noaea mucronata	7.9	.	.	.	10	.	.	.	.	2	.	.	.	.	.	.	.	3	49	.	.	.	.	.	.	.	.	.	.	.	.	.	3	33	79	22	.	.
Crepis sancta	7.9	4	.	.	9	4	.	.	.	3	.	.	6	.	.	.	.	5	43	.	.	.	10	.	.	.	.	.	.	.	.	.	5	29	58	44	.	.
Malcolmia africana	3.0	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	26	44	.	.
Lappula spinocarpa	2.4	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	32	22	.	.
Allium rubellum	3.3	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14	37	11	.	.
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Assoc. 4.2.2.1 (26 diagnostic species)																																						
Pimpinella aurea	2.4	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	38	.	.	.	.
Minuartia meyeri	7.6	4	.	.	9	4	.	.	1	5	.	.	6	.	.	1	.	8	35	.	.	.	10	.	.	.	.	.	2	.	.	.	8	62	21	.	.	.
Acinus graveolens	6.4	4	.	.	8	4	.	.	.	6	.	.	6	.	.	.	.	11	24	.	.	.	10	.	.	.	.	.	.	.	.	.	11	52	5	.	.	.
Astragalus caragana	2.7	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	38	5	.	.	.
Arenaria serpyllifolia	7.3	4	.	.	9	4	.	.	.	7	5	.	6	.	.	.	.	12	27	5	.	.	10	.	.	.	.	.	.	.	.	.	12	52	11	.	9	.
Valerianella plagiostephana	5.2	4	.	.	6	4	.	.	.	6	.	.	6	.	.	.	.	9	18	.	.	.	10	.	.	.	.	.	.	.	.	.	9	43	.	.	.	.
Astragalus compactus	1.8	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	29	.	.	.	.
Scariola orientalis	8.8	4	.	.	11	4	.	.	.	7	.	.	6	.	.	.	.	12	39	.	.	.	10	.	.	.	.	.	.	.	.	.	12	62	21	22	.	.
Bufonia oliveriana	2.7	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	1	16	.	.	.	.	.	.	.	.	.	.	.	.	.	1	33	5	.	.	.
Salvia chloroleuca	4.8	.	.	.	6	.	.	.	.	6	5	.	.	.	.	.	.	9	16	5	.	.	.	.	.	.	.	.	.	.	.	.	9	38	.	.	9	.
[…]																																						
Centaurea virgata	8.5	.	.	.	11	.	.	.	1	10	14	.	.	.	.	1	.	17	22	14	.	.	.	.	.	.	.	.	2	.	.	.	17	48	5	.	27	.
Assoc. 4.2.2.2 (18 diagnostic species)																																						
Euphorbia szovitsii	4.2	.	.	.	5	.	.	.	1	1	.	.	.	.	.	.	2	1	24	.	.	.	.	.	.	.	.	.	.	.	.	4	1	5	58	.	.	.
Koelpinia linearis	2.1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37	.	.	.
Nonnea caspica	2.7	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	1	16	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5	37	.	.	.
Glaucium elegans	1.5	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26	.	.	.
Trigonella monspeliaca	3.0	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	37	11	.	.

Rank	All	Cl.	Cl.	Cl.	Cl.	Ord.	Ord.	Ord.	Ord.	Ord.	Ord.	All.	All.	All.	All.	All.	All.	All.	All.	All.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.
Class		1	2	3	4	1	2	3	4	4	4	1	1	2	3	4	4	4	4	4	1	1	1	1	2	2	3	4	4	4	4	4	4	4	4	4	4	4
Order						1	1	1	1	2	3	1	1	1	1	1	1	2	2	3	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	3	3
Alliance												1	2	1	1	1	2	1	2	1	1	1	2	2	1	1	1	1	1	2	2	2	1	2	2	2	1	1
Association																					1	2	1	2	1	2	1	1	2	1	2	3	1	1	2	3	1	2
Number of plots included	330	25	37	4	264	25	37	4	118	125	21	8	17	37	4	72	46	76	49	21	4	4	10	7	16	21	4	31	41	10	12	24	76	21	19	9	11	10
Mean species richness	21.0	14.5	8.2	10.5	22.5	14.5	8.2	10.5	16.2	29.7	24.0	9.3	19.8	8.2	10.5	15.3	16.8	29.5	49.0	24.0	8.8	9.8	20.2	19.4	5.1	11.4	10.5	13.0	17.6	14.0	14.3	22.2	29.5	41.6	27.8	20.0	24.3	23.8
Astragalus oxyglotis	1.2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21	.	.	.
Euphorbia bungei	1.2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21	.	.	.
Papaver dubium	4.2	4	.	.	5	4	.	.	.	2	.	.	6	.	.	.	.	4	20	.	.	.	10	.	.	.	.	.	.	.	.	.	4	14	37	.	.	.
Conringia persica	3.6	4	.	.	4	4	.	.	.	2	.	.	6	.	.	.	.	3	18	.	.	.	.	14	.	.	.	.	.	.	.	.	3	5	37	11	.	.
Hyoscyamus pusillus	1.8	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26	11	.	.
[…]																																						
Assoc. 4.2.2.3 (9 diagnostic species)																																						
Oreosalsola montana	2.7	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.	.
Caccinia strigosa	3.3	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	11	78	.	.
Atraphaxis spinosa	3.9	4	.	.	5	4	.	.	.	.	.	.	6	.	.	.	.	.	24	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.	26	78	.	.
Capparis spinosa	1.2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	44	.	.
Malabaila secacule	4.2	.	.	.	5	.	.	.	.	3	.	.	.	.	.	.	.	5	20	.	.	.	.	.	.	.	.	.	.	.	.	.	5	19	5	56	.	.
Tragopogon longirostris	0.9	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.
Acanthophyllum microcephalum	2.4	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	1	14	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5	11	44	.	.
Hordeum glaucum	2.1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	16	33	.	.
Krascheninnikovia ceratoides	2.4	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	1	14	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5	16	33	.	.
Ord. 4.3 (16 diagnostic species)																																						
Vicia canescens	4.5	.	.	.	6	.	.	.	.	.	71	.	.	.	.	.	.	.	.	71	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	55	90
Potentilla canescens	7.6	16	.	.	8	16	.	.	1	1	90	.	24	.	.	.	2	1	.	90	.	.	10	43	.	.	.	.	.	.	.	4	1	.	.	.	91	90
Tragopogon buphthalmoides	5.2	.	.	.	6	.	.	.	.	2	67	.	.	.	.	.	.	4	.	67	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	91	40
Galium verum	10.0	.	.	.	13	.	.	.	3	10	76	.	.	.	.	.	9	16	2	76	.	.	.	.	.	.	.	.	.	.	.	17	16	5	.	.	55	100
Cousinia pterocaulos	4.8	.	.	.	6	.	.	.	.	2	62	.	.	.	.	.	.	4	.	62	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	36	90
Eremogone gypsophiloides	13.3	.	.	.	17	.	.	.	4	17	76	.	.	.	.	.	11	28	4	76	.	.	.	.	.	.	.	.	.	.	.	21	28	10	.	.	73	80
Thinopyrum intermedium	24.5	4	.	.	30	4	.	.	8	37	90	.	6	.	.	.	20	61	12	90	.	.	10	.	.	.	.	.	.	.	.	38	61	29	.	.	82	100
Dactylis glomerata	12.7	8	.	.	15	8	.	.	6	12	76	.	12	.	.	.	15	20	4	76	.	.	.	29	.	.	.	.	.	.	.	29	20	10	.	.	73	80
Verbascum oreophilum	2.7	.	.	.	3	.	.	.	.	.	43	.	.	.	.	.	.	.	.	43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	45	40
Taraxacum syriacum	31.2	.	.	.	39	.	.	.	21	41	90	.	.	.	.	7	43	67	16	90	.	.	.	.	.	.	.	.	12	20	8	71	67	38	.	.	91	90
[…]																																						
Achillea arabica	16.1	.	.	.	20	.	.	.	8	21	67	.	.	.	.	.	22	34	6	67	.	.	.	.	.	.	.	.	.	20	.	33	34	14	.	.	73	60
Poa bulbosa	33.3	48	.	.	37	48	.	.	10	50	86	.	71	.	.	4	20	82	12	86	.	.	80	57	.	.	.	.	7	10	8	29	82	29	.	.	91	80
Assoc. 4.3.1.1 (11 diagnostic species)																																						
Astragalus retamocarpus	4.2	.	.	.	5	.	.	.	.	2	52	.	.	.	.	.	.	4	.	52	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	100	.
Chaerophyllum macrospermum	3.9	4	.	.	5	4	.	.	.	.	57	.	6	.	.	.	.	.	.	57	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	82	30
Convolvulus arvensis	3.6	.	.	.	5	.	.	.	.	5	24	.	.	.	.	.	.	8	2	24	.	.	.	.	.	.	.	.	.	.	.	.	8	5	.	.	45	.
Medicago sativa	9.1	.	.	.	11	.	.	.	1	12	48	.	.	.	.	.	2	20	8	48	.	.	.	.	.	.	.	.	.	.	.	4	20	14	5	.	64	30
Orobanche alba	0.9	.	.	.	1	.	.	.	.	.	14	.	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	27	.
Salvia nemorosa	0.9	.	.	.	1	.	.	.	.	.	14	.	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	27	.
Cephalaria microcephala	0.6	.	.	.	1	.	.	.	.	.	10	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18	.
Coronilla varia	0.6	.	.	.	1	.	.	.	.	.	10	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18	.
Lalemanthia peltata	1.5	.	.	.	2	.	.	.	.	2	10	.	.	.	.	.	.	4	.	10	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	18	.
Chondrilla juncea	2.7	.	.	.	3	.	.	.	.	2	19	.	.	.	.	.	.	4	4	19	.	.	.	.	.	.	.	.	.	.	.	.	4	10	.	.	27	10
[…]																																						

Rank	All	Cl.	Cl.	Cl.	Cl.	Ord.	Ord.	Ord.	Ord.	Ord.	Ord.	All.	All.	All.	All.	All.	All.	All.	All.	All.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.	Ass.
Class		1	2	3	4	1	2	3	4	4	4	1	1	2	3	4	4	4	4	4	1	1	1	1	2	2	3	4	4	4	4	4	4	4	4	4	4	4
Order						1	1	1	1	2	3	1	1	1	1	1	1	2	2	3	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	3	3
Alliance												1	2	1	1	1	2	1	2	1	1	1	2	2	1	1	1	1	1	2	2	2	1	2	2	2	1	1
Association																					1	2	1	2	1	2	1	1	2	1	2	3	1	1	2	3	1	2
Number of plots included	330	25	37	4	264	25	37	4	118	125	21	8	17	37	4	72	46	76	49	21	4	4	10	7	16	21	4	31	41	10	12	24	76	21	19	9	11	10
Mean species richness	21.0	14.5	8.2	10.5	22.5	14.5	8.2	10.5	16.2	29.7	24.0	9.3	19.8	8.2	10.5	15.3	16.8	29.5	49.0	24.0	8.8	9.8	20.2	19.4	5.1	11.4	10.5	13.0	17.6	14.0	14.3	22.2	29.5	41.6	27.8	20.0	24.3	23.8
Assoc. 4.3.1.2 (10 diagnostic species)																																						
Prangos ferulacea	2.7	.	.	.	3	.	.	.	.	2	33	.	.	.	.	.	.	3	.	33	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	70
Trifolium repens	1.8	.	.	.	2	.	.	.	.	.	29	.	.	.	.	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	60
Isatis cappadocica	3.9	4	.	.	5	4	.	.	.	3	33	.	6	.	.	.	.	5	2	33	.	.	10	.	.	.	.	.	.	.	.	.	5	5	.	.	9	60
Achillea millefolium	3.3	.	.	.	4	.	.	.	1	1	43	.	.	.	.	.	2	1	.	43	.	.	.	.	.	.	.	.	.	.	.	4	1	.	.	.	27	60
Muscari caucasica	13.0	4	.	.	16	4	.	.	2	23	52	.	6	.	.	.	4	38	.	52	.	.	10	.	.	.	.	.	.	.	.	8	38	.	.	.	27	80
Salvia atropatana	2.1	.	.	.	3	.	.	.	.	2	24	.	.	.	.	.	.	3	.	24	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	9	40
Heracleum anisactis	0.9	.	.	.	1	.	.	.	.	.	14	.	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30
Astragalus modestus	13.0	.	.	.	16	.	.	.	17	11	43	.	.	.	.	11	26	18	.	43	.	.	.	.	.	.	.	3	17	20	.	42	18	.	.	.	18	70
Campeiostachys elongatiformis	10.0	20	.	.	11	20	.	.	3	10	52	.	29	.	.	.	7	17	2	52	.	.	20	43	.	.	.	.	.	.	.	13	17	5	.	.	36	70
Ranunculus elbursensis	0.9	.	.	.	1	.	.	.	.	1	10	.	.	.	.	.	.	1	.	10	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	20
Differential species for two classes																																						
Veronica aucheri	7.3	24	38	.	2	24	38	.	3	1	.	63	6	38	.	4	.	1	.	.	100	25	.	14	88	.	.	6	2	.	.	.	1	.	.	.	.	.
Differential species for two alliances																																						
Poa pratensis	5.5	28	.	.	4	28	.	.	.	2	38	.	41	.	.	.	.	4	.	38	.	.	40	43	.	.	.	.	.	.	.	.	4	.	.	.	9	70
Minuartia lineata	12.7	28	.	.	13	28	.	.	23	6	.	.	41	.	.	11	41	11	.	.	.	.	.	100	.	.	.	3	17	30	25	54	11	.	.	.	.	.
Helichrysum psychrophilum	5.2	8	5	.	5	8	5	.	11	.	.	25	.	5	.	.	28	.	.	.	.	50	.	.	.	10	.	.	.	10	67	17	.	.	.	.	.	.
Companion species																																						
Festuca valesiaca	46.1	4	49	75	49	4	49	75	60	42	5	.	6	49	75	81	28	68	12	5	.	.	.	14	19	71	75	58	98	60	8	25	68	29	.	.	.	10
Bromus paulsenii	31.2	32	59	75	27	32	59	75	59	.	.	100	.	59	75	71	41	.	.	.	100	100	.	.	6	100	75	90	56	100	42	17	.	.	.	.	.	.
Poa araratica	28.5	32	16	50	30	32	16	50	61	5	.	75	12	16	50	74	41	8	.	.	100	50	.	29	13	19	50	81	68	60	50	29	8	.	.	.	.	.
Erysimum caespitosum	26.4	12	54	50	23	12	54	50	51	2	.	38	.	54	50	67	26	3	.	.	25	50	.	.	56	52	50	84	54	40	.	33	3	.	.	.	.	.
Dracocephalum aucheri	17.3	12	51	50	13	12	51	50	28	.	.	38	.	51	50	46	.	.	.	.	75	.	.	.	81	29	50	87	15	.	.	.	.	.	.	.	.	.
Rochelia persica	14.2	8	.	.	17	8	.	.	6	23	14	.	12	.	.	1	13	38	12	14	.	.	20	.	.	.	.	.	2	10	.	21	38	29	.	.	9	20
Cerastium dichotomum	10.6	12	.	.	12	12	.	.	2	19	.	.	18	.	.	1	2	32	12	.	.	.	30	.	.	.	.	.	2	.	.	4	32	29	.	.	.	.
Filago arvensis	10.6	4	.	.	13	4	.	.	10	12	.	.	6	.	.	6	17	20	14	.	.	.	.	14	.	.	.	.	10	10	8	25	20	24	11	.	.	.
Geranium persicum	10.3	.	.	.	13	.	.	.	3	22	14	.	.	.	.	.	7	36	2	14	.	.	.	.	.	.	.	.	.	.	.	13	36	5	.	.	9	20
Silene marshalii	8.8	.	.	.	11	.	.	.	.	17	14	.	.	.	.	.	.	28	10	14	.	.	.	.	.	.	.	.	.	.	.	.	28	24	.	.	9	20
Melica jacquemonti	8.5	8	.	.	10	8	.	.	10	8	.	.	12	.	.	3	22	13	8	.	.	.	20	.	.	.	.	.	5	.	8	38	13	19	.	.	.	.
Gagea confusa	7.9	.	.	.	10	.	.	.	8	12	.	.	.	.	.	6	11	20	4	.	.	.	.	.	.	.	.	3	7	.	.	21	20	10	.	.	.	.
Descurainia sophia	7.0	16	.	.	7	16	.	.	4	7	10	.	24	.	.	7	.	12	6	10	.	.	40	.	.	.	.	.	12	.	.	.	12	5	11	.	18	.
Tulipa montana	7.0	12	.	.	8	12	.	.	1	10	.	.	18	.	.	1	.	17	12	.	.	.	30	.	.	.	.	.	2	.	.	.	17	29	.	.	.	.
Stachys lavandulifolia	6.7	8	.	.	8	8	.	.	.	12	.	.	12	.	.	.	.	20	10	.	.	.	20	.	.	.	.	.	.	.	.	.	20	24	.	.	.	.
Bupleurum exaltatum	6.4	16	.	.	6	16	.	.	1	6	.	.	24	.	.	1	.	9	18	.	.	.	30	14	.	.	.	.	2	.	.	.	9	29	.	33	.	.
Ferula ovina	5.8	12	.	.	6	12	.	.	.	9	19	.	18	.	.	.	.	14	2	19	.	.	30	.	.	.	.	.	.	.	.	.	14	.	5	.	36	.
Ziziphora clinopodioides subsp. *elbursensis*	5.8	8	11	.	5	8	11	.	11	.	.	25	.	11	.	18	.	.	.	.	50	.	.	.	.	19	.	29	10	.	.	.	.	.	.	.	.	.
Polygonum serpyllaceum	5.5	8	22	50	2	8	22	50	5	.	.	25	.	22	50	6	4	.	.	.	.	50	.	.	.	38	50	10	2	10	8	.	.	.	.	.	.	.
[…]																																						

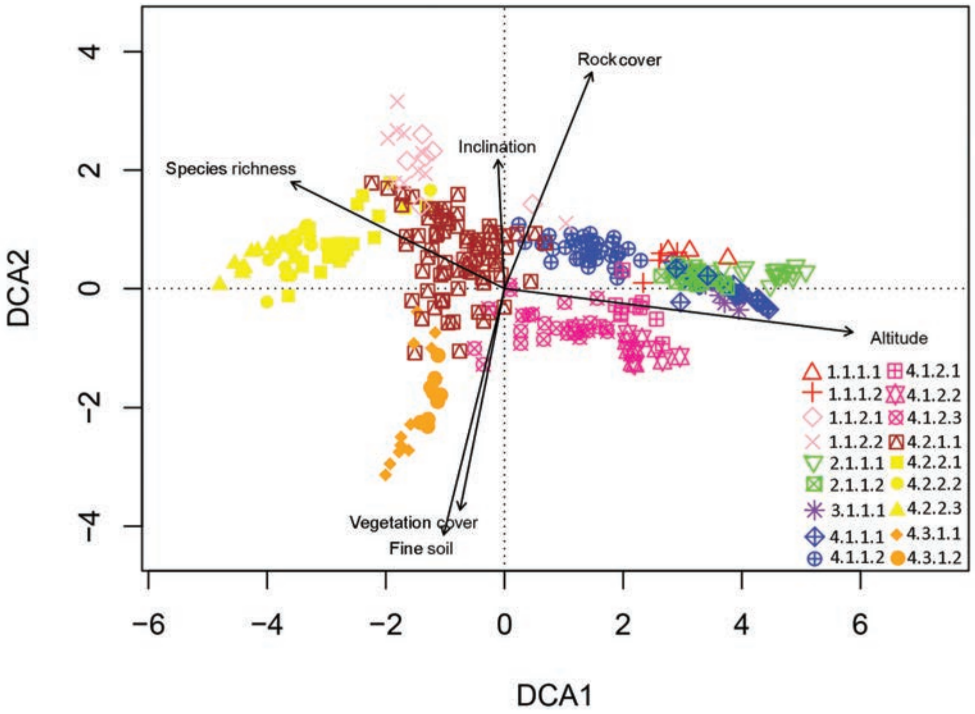

Figure 3. DCA ordination of the relevés and underlying environmental and vegetation features (eigenvalues and gradient lengths of axis 1: 0.86/9.87, axis 2: 0.58/6.26). The colors correspond to the nine alliances. 1.1.1.1. *Veronica aucheri-Corydalis rupestris* community; 1.1.1.2. *Iranecio oligolepis* community; 1.1.2.1. *Salvia xanthocheila* community; 1.1.2.2. *Rosa iberica community*; 2.1.1.1. *Dracocephaletum aucheri*; 2.1.1.2. *Myosotido olympicae-Lamietum tomentosi*; 3.1.1.1. *Ranunculo crymophili-Oxyrietum digynae*; 4.1.1.1. *Senecio iranici-Astragaletum macrosemius*; 4.1.1.2. *Cousinietum harazensis*; 4.1.2.1. *Astragalus iodotropis-Bromus paulsenii*; 4.1.2.2. *Astragaletum iodotropidis*; *Astragaletum ochrochlori*; 4.2.1.1. *Astragalo lilacini-Astragaletum microcephali*; 4.2.1.2 *Astragalo compacti-Feruletum persicae*; 4.2.2.2. *Artemisietum aucheri*; 4.2.2.3. *Caccinio strigosae-Oreosalsoletum montanae*; 4.3.1.1. *Astragaletum retamocarpi*; 4.3.1.2. *Heracleo anisactidi-Prangetum ferulaceae.*

The individual syntaxa in the regional context

1. Class: unknown – Chasmophytic communities

Diagnostic species: *Pimpinella tragium*, *Valeriana sisymbrifolia*, *Veronica aucheri* (D)

1.1. *Tanacetalia kotschyi*

Diagnostic species: *Pimpinella tragium*, *Valeriana sisymbrifolia*

This order comprises vegetation of subalpine and alpine rocky habitats of Iran, east of Anatoli, Transcaucasus and north of Iraq (Klein 1982).

1.1.1. *Campanulion lauricae*

Diagnostic species: *Galium delicatulum*, *Helichrysum psychrophilum* (D), *Lamium tomentosum* (D) (central alliance)

The alliance was introduced for subalpine-alpine rocky habitats of the central Alborz Mts. *Campanula laurica* is an endemic species of Alborz Mts and mostly recorded in montane and subalpine elevations. It was observed sparsely in rocky outcrops of our study region, up to 3000 m a.s.l., but was not recorded in our relevé.

1.1.1.1. *Veronica aucheri-Corydalis rupestris* community (Figure 5a)

Diagnostic species: *Artemisia chamaemelifolia* (D), ***Asperula glomerata* subsp. *bracteosa***, ***Corydalis rupestris***

This association predominated west-ward exposed steep rocks (mean of 75°) in the high alpine zone and elevationally ranged between 3700–4100 m a.s.l. The average species richness of the plots was 4 (Figure 4). Except for *Corydalis rupestris* which is an obligatory chasmophyte species, other character species can also be observed in scree and grassland habitats. *Veronica aucheri*, a restricted endemic of central Alborz Mts (Fischer 1981) is characterised as the main species of the community, and a frequent species in rocky habitats above 3000 m elevation. *Corydalis rupestris* is an obligate rocky species distributed in subalpine-alpine rocky habitats of Iran and Afghanistan (Wendelbo 1974) and mostly observed between 2250 and 4000 m a.s.l. in the study area.

1.1.1.2. *Iranecio oligolepis* community (Figure 5b)

Diagnostic species: *Alopecurus textilis* (D), ***Iranecio oligolepis***, ***Nepeta racemosa***

This association occupied gentle leeward-exposed rocky slopes in the high alpine zone of the study area, ranging elevationally between 3700 and 3900 m a.s.l. Contrary to the *Veronica aucheri-Corydalis rupestris* community, soil is deeper and mean species richness is higher (ca. 10 species per relevé) (Figure 4). *Iranecio oligolepis* is a strictly local endemic in the alpine zone of Mt. Damavand (Dittrich et al. 1989).

1.1.2. Alliance unknown

Diagnostic species: ***Cervaria cervariifolia***, ***Dianthus orientalis***, *Dracocephalum kotschyi*, *Eremogone polycnemifolia*, ***Gypsophila aretioides***, *Minuartia lineata* (D), ***Parietaria judaica***, ***Pimpinella tragium***, *Poa pratensis* (D), ***Prunus pseudoprostrata***, ***Scrophularia variegata***, *Stipa arabica* (D), ***Tanacetum polycephalum***

This group comprised rocky habitats of the subalpine elevational zone of the region.

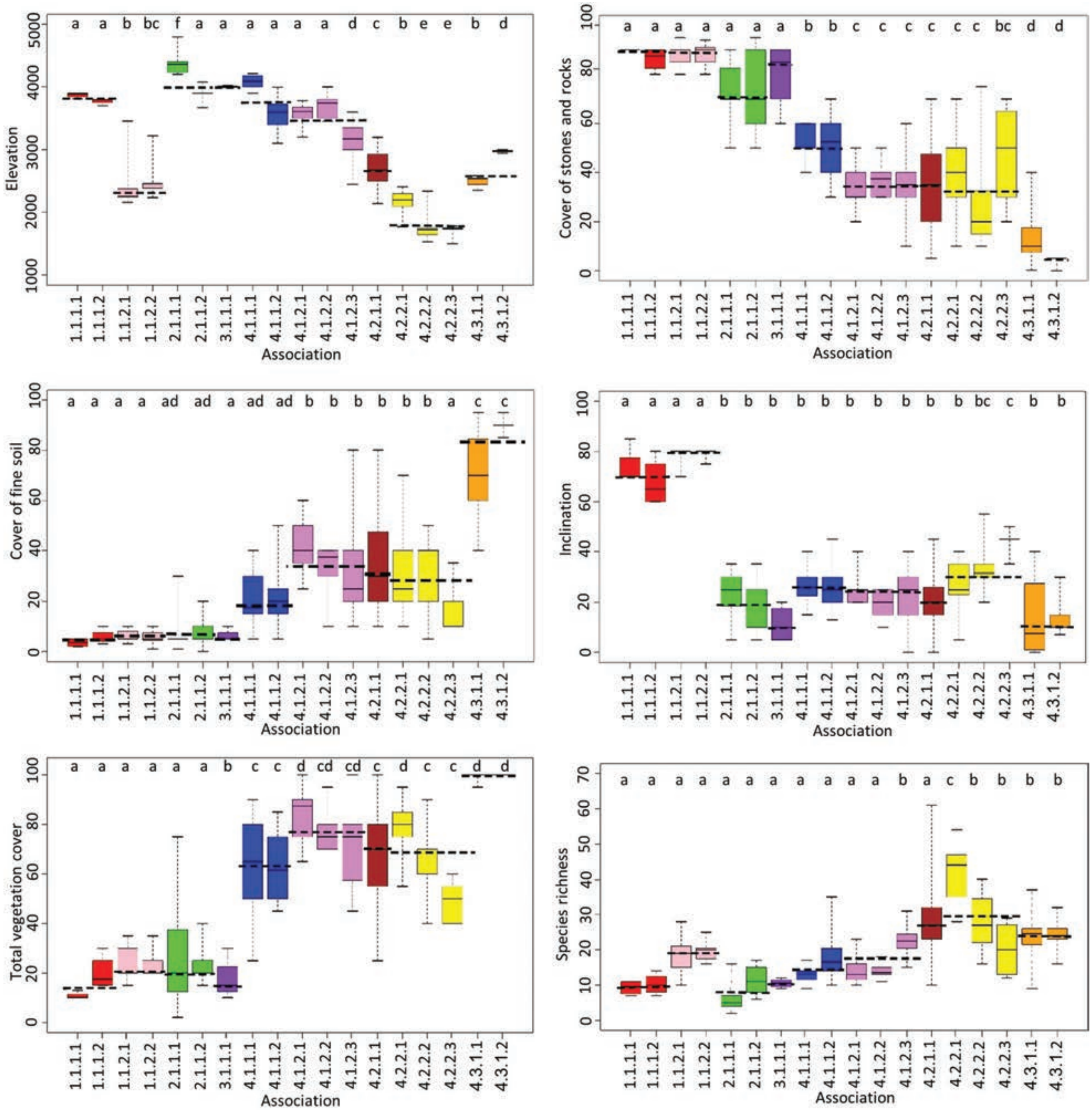

Figure 4. Boxplots showing the range of elevation, stone and rocks, fine soil, inclination, total vegetation cover, richness of syntaxonomic units. Dashed line shows the mean value for each alliance. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test.

1.1.2.1. *Salvia xanthocheila* community (Figure 5c)

Diagnostic species: *Bromus tectorum* (D), ***Dielsiocharis kotschyi***, *Ephedra major*, *Fibigia suffruticosa*, *Galium hyrcanicum*, *Lappula barbata* (D), ***Pseudosedum multicaule***, *Rosa canina*, *Rumex scutatus*, ***Salvia xanthocheila***, *Silene commelinifolia*, ***Sisymbrium gaubae***

This community was observed on exposed rocky outcrops of subalpine zone, ranging elevationally between 2000 and 2300 m a.s.l. The community occupies slopes with an average inclination of 80° and mean species richness is 20 species per relevé (Figure 4). *Salvia xanthocheila* is a sub-endemic element of the Iranian highlands and mostly growing on rocky habitats (Rechinger 1989).

1.1.2.2. *Rosa iberica* community (Figure 5d)

Diagnostic species: *Allium capitellatum*, *Arabis caucasica*, ***Rosa iberica***, ***Rhamnus pallasii***, *Poa sterilis*, ***Sempervivum iranicum***, *Silene aucheriana*, ***Tanacetum parthenium***, ***Ziziphora clinopodioides* subsp. *rigida***

This community mostly occupied shaded and leeward rocky slopes with available soil that predominantly occurred in valleys where conditions are more suitable for growth of shrubs and nano-phanerophytes. It was observed in the elevational range of 2100 to 2500 m a.s.l. Mean species richness is almost 19 species per relevé (Figure 4) and includes the shrub species of *Rosa iberica*, *Rhamnus pallasii*, and *Lonicera iberica*.

2. *Didymophyso aucheri-Dracocephaletea aucheri* - Scree communities

Diagnostic species: ***Achillea aucheri***, ***Didymophysa aucheri***, *Veronica aucheri* (D)

This class comprises open plant communities on unstable or stable screes in the alpine and subnival–nival zones of Alborz and North-West mountains of Iran. The communities of this class are distinguished from alpine snowbed and thorn cushion grasslands by low vegetation cover, high proportion of open scree cover and distinctive species composition (Noroozi et al. 2014).

2.1. *Didymophysetalia aucheri*

Diagnostic species: ***Achillea aucheri***, ***Didymophysa aucheri***

2.1.1. *Didymophysion aucheri*

Diagnostic species: ***Achillea aucheri***, ***Didymophysa aucheri***

This alliance included open communities at the upper limit of vascular plant species in the subnival–nival zone of Central Alborz. Very low cover–abundance of grasses, absence of thorn- cushions, low species richness, sparse plant cover and a high percentage of open scree are the main features of this alliance (Noroozi et al. 2014).

2.1.1.1. *Dracocephaletum aucheri* (Figure 5e)

Diagnostic species: ***Didymophysa aucheri*** (central association)

This association was located on the highest elevation in the study area and has also been recorded as the highest association in the Iranian mountains (Noroozi et al. 2014). The elevational range for the association was between 4200 and 4800 with the optimum range of 4300–4600 m a.s.l. The association was mainly covered by scree (60–90%) with a mean vegetation cover of 20%, and located on slopes of 20–40 percent inclination. Mean species richness is 5 species per relevé (Figure 4). The diagnostic species of the association are sub-endemic of the alpine region of Iran.

2.1.1.2. *Myosotido olympicae-Lamietum tomentosi* (Figure 5f)

Diagnostic species: *Crepis multicaulis*, *Elymus longearistatus*, *Lamium tomentosum*, ***Myosotis olympica* subsp. *demawendica***

This association was mainly recorded on scree habitats in lower elevations ranging from 3700 to 4070 m a.s.l. and occupied the moraines with gentle leeward slopes (5–35°) on the bottom of the valleys, where the average extent of stone and rocks is 70% and the mean vegetation cover is 20%. There is a high snow accumulation particularly in winter. Mean species richness is 10 species per relevé (Figure 4). *Myosotis olympica* subsp. *demawendica* is an endemic species for the alpine zone of central Alborz Mts (Riedl 1967), *Lamium tomentosum* is distributed from Alborz Mts to the Caucasus region (Rechinger et al. 1989) and *Elymus longearistatus* and *Crepis multicaulis* are widespread Irano-Turanian elements (Bor 1970).

3. *Salicetea herbaceae* - Snowbed communities

Diagnostic species: ***Artemisia melanolepis***, ***Catabrosella parviflora***, *Cerastium purpurascens*, ***Dichodon cerastoides***, ***Erigeron uniflorus***, ***Ranunculus crymophilus***

3.1. Order unknown

Diagnostic species: ***Artemisia melanolepis***, ***Catabrosella parviflora***, *Cerastium purpurascens*, ***Dichodon cerastoides***, ***Erigeron uniflorus***, ***Ranunculus crymophilus***

3.1.1. *Taraxaco brevirostris-Polygonion serpyllacei*

Diagnostic species: ***Catabrosella parviflora***, *Cerastium purpurascens*, ***Dichodon cerastoides***, ***Erigeron uniflorus***, ***Ranunculus crymophilus***

This alliance included snow-bed and meltwater communities, where snow accumulates in depressions and runnels during winter and persists until mid-summer and is mostly dominated by small herbs. The growth period is too short to allow the occurrence of chamaephytes and large hemicryptophytes (Noroozi et al. 2010, 2017).

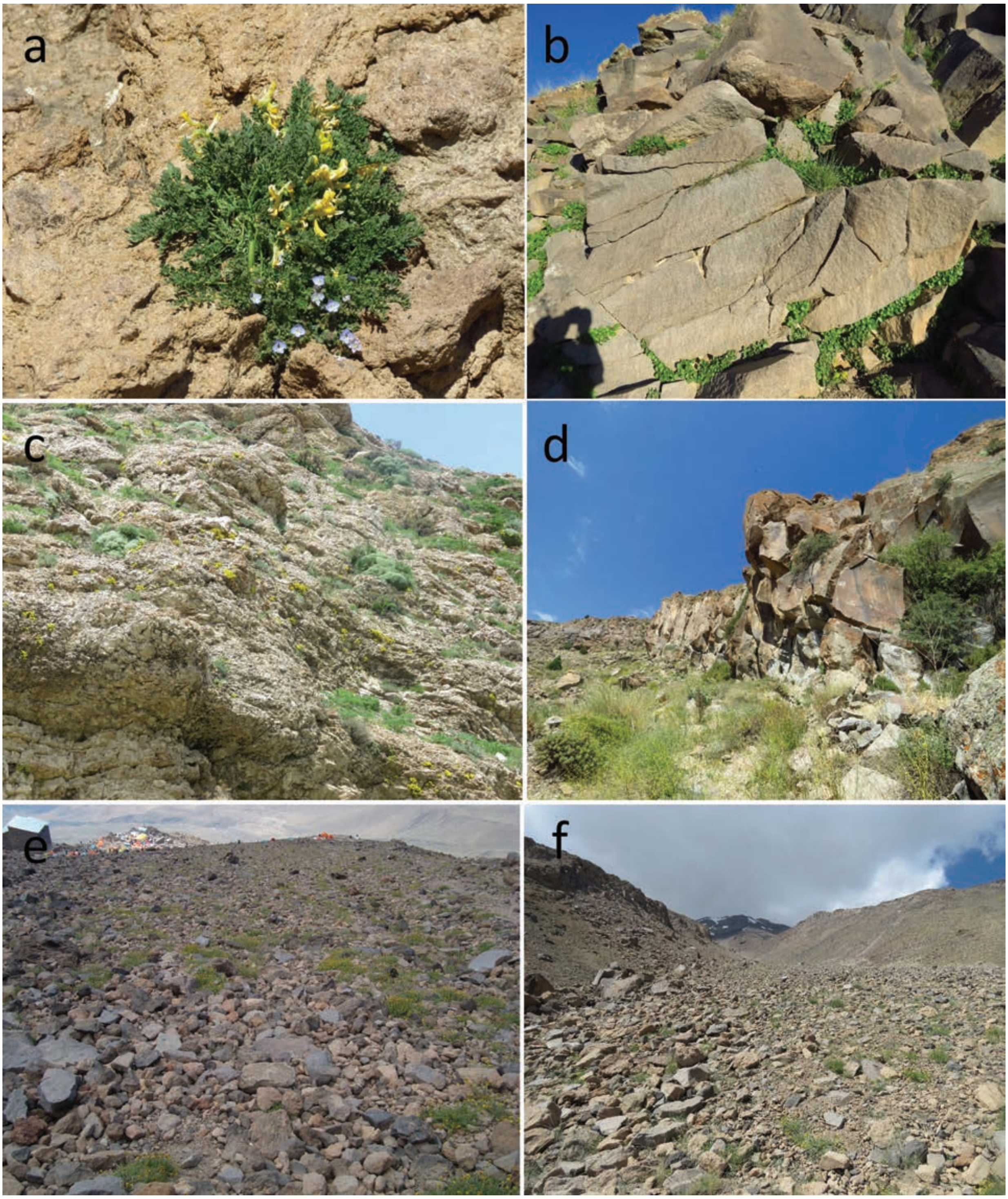

Figure 5. Photos of vegetation units belonging to the *Tanacetalia kotschyi* (a-d) and *Didymophyso aucheri-Dracocephaletea aucheri* (e and f): a. *Veronica aucheri-Corydalis rupestris* community (1.1.1.1); b. *Iranecio oligolepis* community (1.1.1.2); c. *Salvia xanthocheila* community (1.1.2.1); d. *Rosa iberica* community (1.1.2.2); e. *Dracocephaletum aucheri* (2.1.1.1); f. *Myosotido olympicae-Lamietum tomentosi* (2.1.1.2) (Photos: Amir Talebi).

3.1.1.1. *Ranunculo crymophili-Oxyrietum digynae* (Figure 6a)

Diagnostic species: ***Dichodon cerastoides***, ***Erigeron uniflorus***, ***Ranunculus crymophilus***

This association occurred in only one restricted location in high elevations, between 3950 and 4100 m a.s.l., in the south-eastern parts of the study area. It is a snow-bed, formed on a gentle depression with a low degree of inclination (5–15°), where snow accumulates and persists until mid-summer. Mean species richness is almost 10 species per relevé (Figure 4). This association was firstly reported from NW of Iran, Sahand mountain (Noroozi et al. 2017) within the same habitat type and supporting the same floristic composition suggesting a wide geographic range.

4. *Astragalo-Brometea* – Irano-Turanian grasslands

Diagnostic species: *Astragalus modestus*, *Papaver bracteatum*, *Polygonum alpestre*, *Polygonum rottboellioides*, *Silene bupleuroides*, *Taraxacum syriacum*, *Thymus kotschyanus*, *Veronica biloba*

This class includes high mountain grasslands, xerophytic dwarf-shrub and thorn-cushion communities of Anatolia, the Levant and NW Iran (Parolly 2004).

4.1. *Drabetalia pulchellae*

Diagnostic species: ***Alopecurus textilis***, *Artemisia chamaemelifoliamifolia*, ***Blitum virgatum***, *Campanula stevenii*, ***Carex pseudo-foetida***, *Cousinia harazensis*, *Draba pulchella*, ***Onobrychis cornuta***, *Veronica kurdica*

This order comprises all thorn-cushion associations in the alpine zone of the study region. The order was firstly proposed as provisional based on insufficient vegetation data from a local study site (Noroozi et al. 2010). Due to high similarity in ecological attributes and species composition in the alpine zone, we validated this order in this study. The association of this order was classified in two alliances, based on a gradient of humidity, and five associations/communities.

4.1.1. *Acantholimion demavendici*

Diagnostic species: *Acantholimon demawendicum*, *Astragalus macrosemius* (central alliance)

The physiognomy of this alliance is dominated by thorn-cushion species. It occupies dry and wind exposed habitats in the alpine region (Noroozi et al. 2010).

4.1.1.1. *Senecio iranici-Astragaletum macrosemii* (Figure 6b)

Diagnostic species: *Artemisia melanolepis* (D), ***Astragalus macrosemius***, *Catabrosella parviflora* (D), *Cerastium purpurascens* (D), *Draba siliquosa*, *Potentilla polyschista*, *Senecio iranicus*

This association is typical for the nival zone vegetation, ranging elevationally between 4000 to 4200 m a.s.l. Vegetation cover ranges from 40 to 80% and mean stone cover reaches to 55%. Mean species richness is 12 species per relevé (Figure 4). *Astragalus macrosemius*, *Bromus paulsenii* and *Alopecurus textilis* predominated the association. This association was originally classified within scree vegetation units of *Didymophysetea aucheri* and *Physoptychio gnaphalodis-Brometalia tomentosi* (Noroozi et al. 2014). However, due to high plant coverage and physiognomy which mostly is dominated by thorn-cushion and grasses, we believe it should be classified in a grassland class.

4.1.1.2. *Cousinietum harazensis* (Figures 6c, 8)

Diagnostic species: ***Acantholimon demawendicum***, *Acantholimon erinaceum*, ***Campanula stevenii***, ***Cousinia harazensis***, *Silene palinotricha*

This association featured the main vegetation formation of the alpine belt and was mainly confined to southern and south-eastern slopes of Mt. Damavand. The association covers southward and exposed habitat of the study area, at elevations ranging from 3000 to 4000 m a.s.l. The average vegetation cover is 60% and mean species richness is 25 species in 25 m^2 (Figure 4). *Cousinia harazensis* is an alpine species, and geographically distributed in Central Alborz particularly in Mt. Damavand and surrounding highlands (Rechinger 1972). *Acantholimon demawendicum* is an endemic of the Alborz range, and *Acantholimon erinaceum*, a central and SW Asian element, are among other important diagnostic species of this association (Rechinger and Schimann-Czeika 1974).

4.1.2. *Astragalion iodotropidis*

Diagnostic species: ***Astragalus iodotropis***, ***Cirsium lappaceum***, *Helichrysum psychrophilum* (D), *Herniaria glabra*, *Leonuurus cardiaca*, *Minuartia lineata* (D), ***Piptatherum laterale***, *Polygonum patulum*, ***Potentilla argyroloma***, ***Taraxacum brevirostre***, ***Tragopogon kotschyi***

This alliance comprises alpine grasslands with good soil and water supply. These communities provide excellent habitats for summer grazing and are probably endemic in Central Alborz (Noroozi et al. 2010).

4.1.2.1. *Bromus paulsenii-Astragalus iodotropis* community (Figures 6d, 8)

Diagnostic species: none of its own

This association showed an intermediate status in composition and ecological condition between *Cousinietum harazensis* and *Astragaletum iodotropidis.* This community was clearly separated on the DCA ordination (Figure 3). It forms on mid slopes between depressions and exposed lands and usually surrounds *Astragaletum iodotropidis*. This community occurs between 3450 and 3900 m a.s.l. Mean species richness is almost 14 species per relevés (Figure 4). *Bromus paulsenii* and *Astragalus iodotropidis* are dominant and constant species of this community. This community shows the same structure (ecologically and to some extent floristically) as *Galio decumbentis-Thymetum pubescentis* in Tuchal Mt. (Noroozi et al. 2010) but with different *Galium* and *Thymus* species (*Gallium delicatulum* and *Thymus kotschyanus* in our study). Due to its intermediate state and lack of an appropriate number of strictly characteristic species we proposed it as a community.

4.1.2.2. *Astragaletum iodotropidis* (Figures 6e, 8)

Diagnostic species: *Hordeum violaceum*, ***Tragopogon kotschyi*** (central association)

Astragaletum iodotropidis occurred on leeward slopes, depressions and margins of snow-beds where snow cover and soil humidity remain for a longer time. This association was distributed between 3450 and 4000 m a.s.l. on steep to moderate slopes (average 25°). The community is characterized by a low percentage of rock cover (average

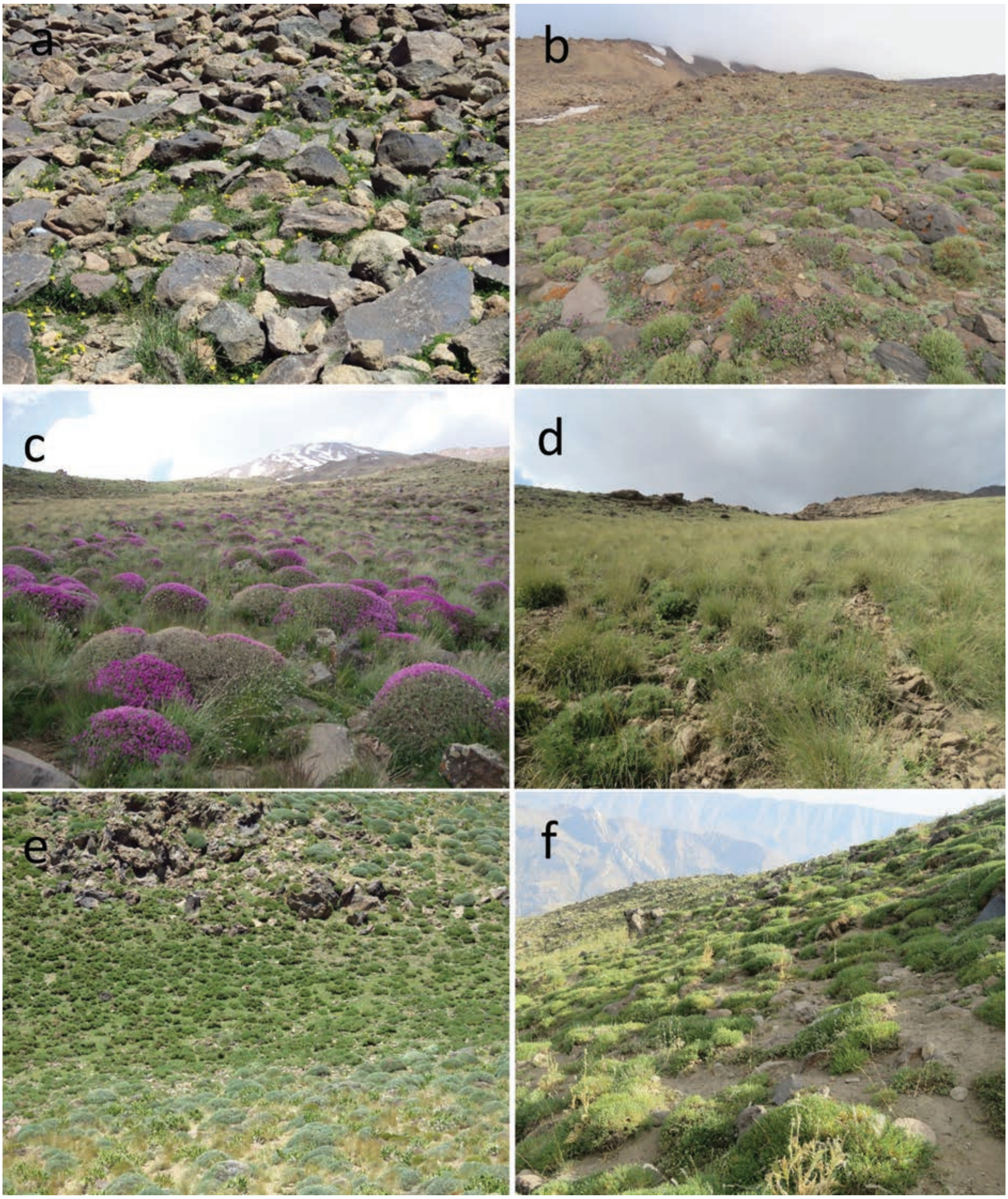

Figure 6. Photos of vegetation units belonging to *Salicetea herbaceae* (a) and *Astragalo-Brometea* (b-f): a. *Ranunculo crymophili-Oxyrietum digynae* (3.1.1.1); b. *Senecio iranici-Astragaletum macrosemii* (4.1.1.1); c. *Cousinietum harazensis* (4.1.1.2); d. *Astragalus iodotropis-Bromus paulsenii* community (4.1.2.1); e. *Astragaletum iodotropidis* (4.1.2.2); f. *Astragaletum ochrochlori* (4.1.2.3) (Photos: Amir Talebi).

3%) and high plant cover percentage (average 85%) of predominantly short and creeping hemicryptophytes. Mean species richness is almost 13 species per relevé (Figure 4). Other important characteristic species of the association include *Helichrysum psychrophilum*, with its main distribution from Iran to Turkey (Georgiadou et al. 1980). *Hordeum violaceum* is widely distributed in SW Asia (Bor 1970) and *Tragopogon kotschyi* distributed from Alborz to eastern Anatolia (Rechinger 1977).

4.1.2.3. *Astragaletum ochrochlori* (Figure 6f)

Diagnostic species: *Astragalus ochrochlorus*, *Bromus tomentellus* (D), *Cousinia multiloba*, *Plantago atrata*, *Taraxacum syriacum* (D)

The *Astragaletum ochrochlori* association is ecologically and physiognomically close to the *Astragaletum iodotropidis* association, but is located mainly at lower elevation (2500 to 3500 m a.s.l., with optimum range between

2900 and 3400 m a. s. l.). This association occurred on leeward gentle slopes and depressions with relatively low stone cover (average 35%). Mean of total vegetation cover was between 70% and average species richness was 21 per relevés (Figure 4). Grazing is an important management regime in this vegetation type, leading to a higher presence of *Papaver bracteatum* as an opportunistic species. The most important characteristic species is *Astragalus ochrochlorus* which is an endemic thorn-cushion species in Alborz Mts (Zarre et al. 2008) and elevationally ranges between 2300 to 3700 m a.s.l.

4.2. *Astragalo-Brometalia*

Diagnostic species: *Acinos graveolens*, *Adonis aestivalis*, *Alyssum dessertorum*, *Alyssum marginatum*, *Arenaria serpyllifolia*, ***Artemisia aucheri***, *Asperula arvensis*, ***Bassia prostrata***, *Bilacunaria microcarpa*, ***Bromus tectorum***, ***Bromus danthoniae***, ***Alyssum minus***, *Callipeltis cucullaris*, *Camelina rumelica*, *Eryngium billardieri*, *Consolida teheranica*, *Callicephalus nitens*, ***Ferula persica***, ***Galium spurium***, *Galium verticillatum*, *Haplophyllum acutifolium*, *Herniaria incana*, *Lamium amplexicaule*, *Lappula barbata*, *Linaria simplex*, *Meniocus linifolius*, *Minuartia meyeri*, *Orobanche mutelii*, *Psathyrostachys fragilis*, *Scariola orientalis*, ***Senecio glaucus***, *Sisymbrium altissimum*, *Sophora alopecuroides*, *Stipa arabica*, *Teucrium polium*, ***Taeniatherum caput-medusae***, *Trigonella monantha*, *Verbascum cheiranthifolium*, *Tragopogon collinum*, *Viola occulta*, *Ziziphora tenuior*

This order represents xerophytic mountain vegetation dominated with thorn-cushion communities and dwarf shrublands of the subalpine zone (Parolly 2004).

4.2.1. Alliance unknown

Diagnostic species: *Agropyron cristatum*, *Astragalus laricus*, *Astragalus lilacinus*, ***Astragalus microcephalus***, *Bromus tomentellus*, ***Ceratocephala testiculata***, *Delphinium aquilegifolium*, *Draba nemorosa*, *Draba nuda*, *Euphorbia cheiradenia*, *Geranium persicum*, *Iris barnumiae*, *Rochelia persica*

4.2.1.1 *Astragalo lilacini-Astragaletum microcephali* (Figure 7a)

Diagnostic species: *Agropyron cristatum*, *Astragalus laricus*, *Astragalus lilacinus*, ***Ceratocephala testiculata***, *Delphinium aquilegifolium*, *Draba nemorosa*, *Draba nuda*, *Euphorbia cheiradenia*, *Geranium persicum*, *Iris barnumiae*, *Poa bulbosa* (D), *Rochelia persica*, *Tanacetum polycephalum* (D), *Taraxacum syriacum* (D), *Thinopyrum intermedium* (D)

This group covers the subalpine zones of the region with a wide range of habitat and vegetation features. It is distributed across an elevational range of 2300 to 3000 m a.s.l., on grounds with an average inclination of 20°. The mean total vegetation cover is 70% and the mean species richness of almost 25 in 25 m^2 (Figure 4). *Astragalus lilacinus* is a herbaceous species, endemic to Iran and mostly distributed in steppes of the Alborz range and NW Iran (Zarre et al. 2008). Dominant species in this community include *Thinopyrum intermedium*, *Agropyron cristatum*, *Campeiostachys elongatiformis*, *Thymus kotschyanus*, *Tanacetum polycephalum* and *Festuca valesiaca*.

4.2.2. *Artemision aucheri*

Diagnostic species: *Aegilops triuncialis*, *Allium rubellum*, *Asparagus persicus*, ***Atriplex aucheri***, *Caccinia strigosa*, *Conringia persica*, ***Cousinia eryngioides***, ***Crepis sancta***, ***Eremopyrum bonaepartis***, *Erodium cicutarium*, *Hordeum glaucum*, *Krascheninnikovia ceratoides*, *Lappula spinocarpa*, *Malabaila secacul*, ***Malcolmia africana***, *Medicago monspeliaca*, ***Nitrosalsola dendroides***, ***Noaea mucronata***, *Onosma microcarpa*, ***Stachys inflate***, *Turgenia latifolia*

This new alliance comprises communities of xeric habitats under drier condition of the lower elevations (montane zone) of the study area. An extensive presence of annual life form and xerophytic taxa are features of this vegetation unit. Most of the main taxa are also widespread across the Irano-Turanian phytogeographical region. This alliance is also called "*Stipa-Artemisia* steppes" (Akhani 1998) and widely distributed in the most montane zones of Iran. However, various *Artemisia* species predominate in various mountains. *Artemisia aucheri*, an important sub-montane and montane steppe element in Iran and Afghanistan (Podelch 1986), reached up to 2800 m a.s.l. in Mt. Damavand. Most of the diagnostic species of this community are widespread elements of the montane zone of the Iranian plateau and are expected to occur over a large territory of Iran.

4.2.2.1. *Astragalo compacti-Feruletum persicae* (Figure 7b)

Diagnostic species: ***Acinus graveolens***, *Allium stamineum*, ***Arenaria serpyllifolia***, *Arrhenatherum kotschyi*, ***Astragalus caragana***, ***Astragalus compactus***, *Astragalus demavendicola*, *Astragalus microcephalus* (D), ***Bufonia oliveriana***, *Carduus transcaspicus*, *Centaurea virgata*, *Cousinia behboudiana*, *Crupina crupinastrum*, *Heteropappus altaicus*, *Henrardia persica*, ***Minuartia meyeri***, *Papaver argemone*, *Phlomis olivieri*, *Phalaris minor*, ***Pimpinella aurea***, *Prunus pseudoprostrata* (D), *Salvia chloroleuca*, *Salvia hypoleuca*, *Sanguisorba minor*, ***Scariola orientalis***, *Sedum rubens*, *Trigonella coerulescens*, ***Valerianella plagiostephana***

This community, ranging elevationally from 1900 to 2400 m a.s.l., is located in transition from montane to subalpine zones. The habitat is relatively steep (approximate mean of 25°) and stone cover is high (average 45%). This community is characterised by the richest number of species, with the mean species richness of 42 species per relevé (Figure 4). Compared to other associations in the alliance, this community is located in a higher elevational range, receiving more precipitation and showing higher vegetation cover (average 80%) particularly dominant hemicryptophytes. *Ferula persica* is an endemic species of Iran and mostly recorded from the Alborz Mts, and *Astragalus compactus* is an Irano-Anatolian species (Zarre et

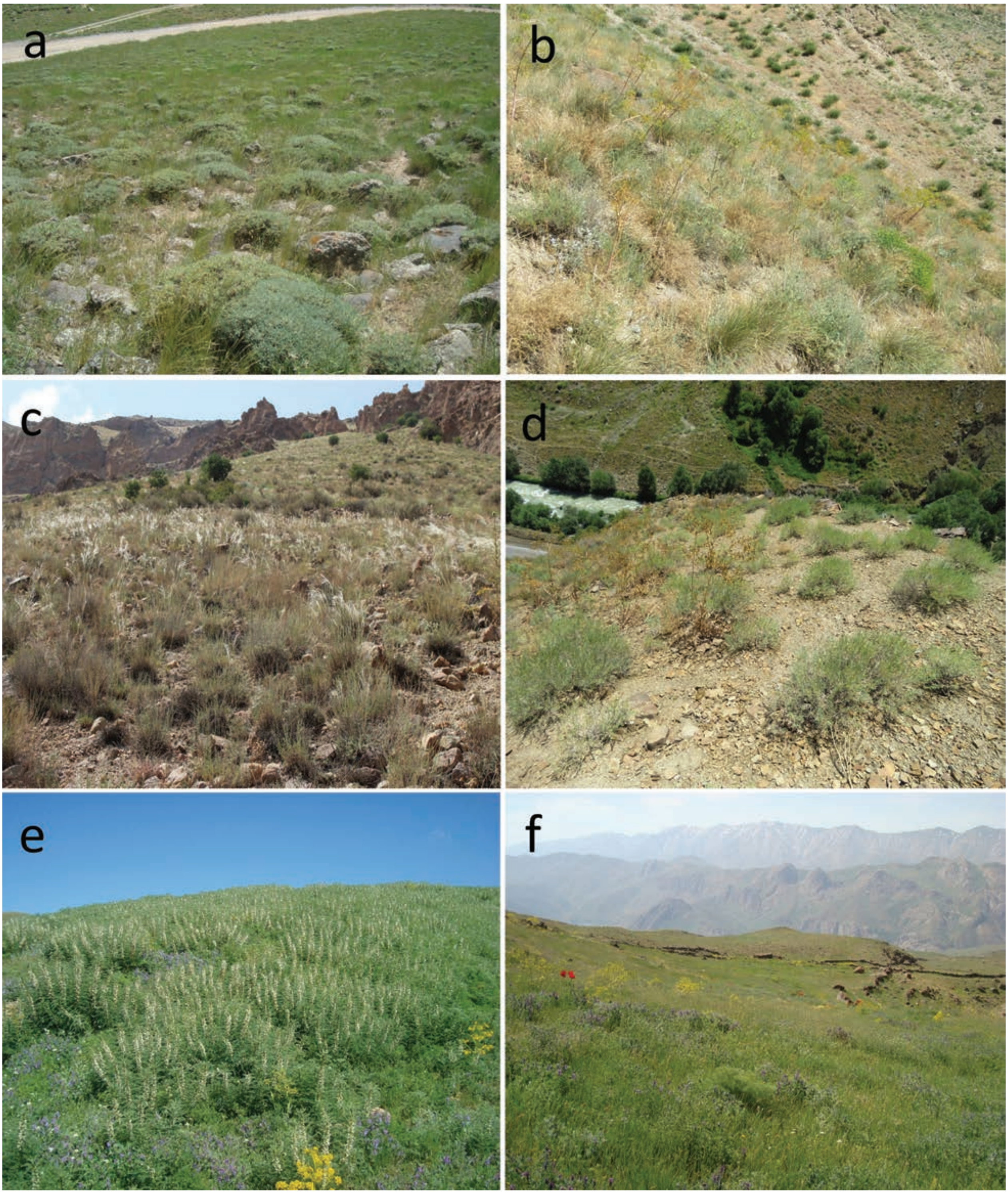

Figure 7. Photos of vegetation units belonging to *Astragalo-Brometea*: a. *Astragalo lilacini-Astragaletum microcephali* (4.2.1.1); b. *Astragalo compacti-Feruletum persicae* (4.2.2.1); c. *Artemisietum aucheri* (4.2.2.2); d. *Caccinio strigosae-Oreosalsoletum montanae* (4.2.2.3); e. *Astragaletum retamocarpi* (4.3.1.1); f. *Heracleo anisactidis-Prangetum ferulaceae* (4.3.1.2) (Photos: Amir Talebi).

al. 2008). High cover values were recorded for some tall herbs such as *Ferula persica* and *Bilacunaria microcarpa*, and some annual taxa, especially *Taeniatherum caput-medusae*. There are scattered shrubs of *Berberis integerrima*, *Rhamnus pallasii*, *Prunus divaricata* and *Cotoneaster nummularioides* in many parts of this community. It should be mentioned that the community is in the potential zone of *Juniperus excelsa* steppe woodlands with some transitional species with *Junipero exelsae-Rhamnetum pallasii* (Ravanbakhsh et al. 2015). In our study region, *Juniperus excelsa* stands are mostly restricted to rocky outcrops or cliffs, likely due to long-term anthropogenic activities.

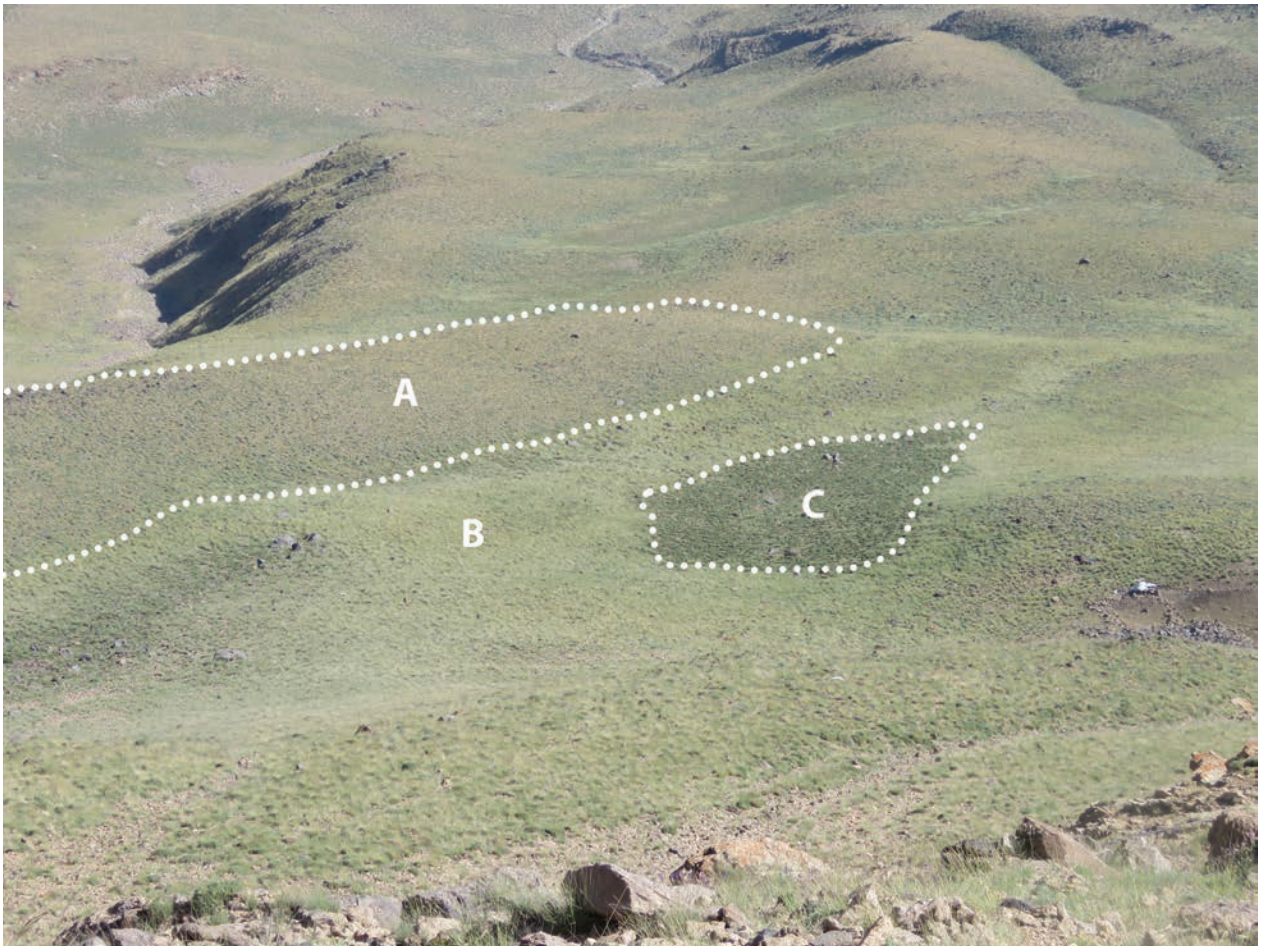

Figure 8. Spatial distribution of three associations in alpine zone. A. *Cousinietum harazensis*; B. *Bromus paulsenii-Astragalus iodotropis* community; C. *Astragaletum iodotropidis*. (Photo: Amir Talebi).

Moreover, the *Astragalo compacti-Feruletum persicae* shows some similarity to the *Astragalus compactus-Stipa arabica* community proposed in the same elevational zone of Tuchal Mt. (Akhani et al. 2013).

4.2.2.2. *Artemisietum aucheri* (Figure 7c)

Diagnostic species: *Aegilops tauschii*, *Anchusa arvensis*, ***Artemisia aucheri***, *Astragalus oxyglotis*, *Dysphania botrys*, *Clypeola jonthlaspi*, *Conringia persica*, *Euphorbia bungei*, ***Euphorbia szovitsii***, ***Glaucium elegans***, *Heliotropium europaeum*, *Hyoscyamus pusillus*, ***Koelpinia linearis***, *Marrubium cuneatum*, ***Nonea caspica***, *Papaver dubium*, *Salsola tragus*, *Saponaria orientalis*, ***Stipa arabica***, *Trigonella monspeliaca*

This association comprises steppe vegetation in the lowermost limit of elevational range of the study region, from 1530 to 1800 m a.s.l. It probably also occurs even lower, where we did not sample. The average species richness is almost 25 taxa in 25 m^2 (Figure 4). Due to the high elevation barrier of Damavand peak, lower elevations including this association receive less precipitation and humidity, leading to drier climatic conditions. Such xeric climatic conditions result in the presence of a high number of annuals, xerophytic and spinose taxa. Scattered stands of *Celtis caucasica* is one of the physiognomic features of this vegetation type. In many places the ground is covered with gravel and sandy soil. All of the characteristic species are widespread elements over the Irano-Turanian region, indicating the wide geographic range of the association.

4.2.2.3. *Caccinio strigosae-Oreosalsoletum montana* (Figure 7d)

Diagnostic species: ***Acanthophyllum microcephalum***, ***Atraphaxis spinosa***, ***Caccinia strigosa***, ***Capparis spinosa***, *Hordeum glaucum*, *Krascheninnikovia ceratoides*, ***Malabaila secacul***, ***Oreosalsola montana***, ***Tragopogon coelesyriacus***

This species-poor association was recorded within the elevation range of 1500 to 1700 m a.s.l. It is mainly well developed on steep slopes (average 45°) with high cover of rock and stone (up to 70% and average of 50%) and calcareous substrates. Vegetation cover is low (between 45 and 60% and an average of 50%) and the dominance of dwarf shrubs taxa is remarkable, with the existence of bare ground creating a suitable habitat for some ruderal species. Average species richness is 20 taxa in 25 m^2 (Figure 4). The main characteristic species of the association, *Oreosalsola montana*, is a dwarf shrub distributed from North-west of Iran to Tien-shan and Pamir. This species is recorded from mountainous regions of Azerbaijan, Alborz, Kopet-Dagh and Kerman Mts of Iran, and in habitats characterised by rocky and steep inclination (Hedge et al. 1997). *Caccinia strigosa* is an endemic species, known from the montane zone of the Alborz Mts and mostly observed in waste soils or steep and bare soils (Riedl 1967).

4.3. Order: unknown

Diagnostic species: ***Achillea arabica***, ***Achillea millefolium***, *Campeiostachys elongatiformis*, ***Chaerophyllum macrospermum***, *Chondrilla juncea*, ***Cousinia pterocaulos***, ***Dactylis glomerata***, *Echinops pungens*, ***Eremogone gypsophiloides***, ***Galium verum***, ***Medicago sativa***, *Orobanche crenua*, *Poa bulbosa*, ***Potentilla canescens***, ***Rumex elbursensis***, *Salvia atropatana*, ***Taraxacum syriacum***, ***Thinopyrum intermedium***, ***Tragopogon buphthalamoides***, *Veronica orientalis*, ***Verbascum oreophilum***, ***Vicia canescens***

4.3.1. Alliance: *Cousinion pterocauli*

Diagnostic species: ***Achillea arabica***, ***Achillea millefolium***, *Campeiostachys elongatiformis*, ***Chaerophyllum macrospermum***, *Chondrilla juncea*, ***Cousinia pterocaulos***, ***Dactylis glomerata***, *Echinops pungens*, ***Eremogone gypsophiloides***, ***Galium verum***, ***Medicago sativa***, *Orobanche crenua*, *Poa pratensis* (D), ***Potentilla canescens***, ***Rumex elbursensis***, *Salvia atropatana*, ***Tragopogon buphthalamoides***, *Veronica orientalis*, ***Verbascum oreophilum***, ***Vicia canescens***

Plant communities belonging to this alliance covered the grasslands in the subalpine elevational zone that are under a mowing management regime, situated between 2300 and 3000 m a.s.l. Fine-textured soil, and protection against early grazing and mowing activity, has resulted in a dense and tall plant cover dominated by hemicryptophytes. Due to the high productivity and palatability of the forbs, mowing is a common practice in this vegetation type, and its formation may be the result of long-term management. *Cousinia pterocaulos* is distributed from central Alborz to the Talish region of Azerbaijan Republic.

4.3.1.1. *Astragaletum retamocarpi* (Figure 7e)

Diagnostic species: ***Astragalus retamocarpus***, ***Chaerophyllum macrospermum***, ***Convolvulus arvensis***, ***Cephalaria microcephala***, *Chondrilla juncea*, *Coronilla varia*, *Lalemanthia peltata*, *Medicago sativa*, ***Orobanche alba***, ***Salvia nemorosa***, *Scabiosa argentea*

This association is a natural or semi-natural vegetation unit and its expansion is probably a result of long term management activities including protection against early grazing and mowing in the middle of the growing season. The elevational range for this association was between 2300 and 2700 m a.s.l., inclination was between 0 and 30°, often formed on leeward or flat slopes. Soil was deep and well developed and with a low cover of stone and rock (average 10%) and mostly on moderate slopes (average 10°). Total vegetation cover was mostly 100% and plant canopy reached more than 2 m. Average species richness is 24 taxa in 25 m^2 (Figure 4). Tall hemicryptophytes, particularly *Astragalus retamocarpus* and *Chaerophyllum macrospermum*, were the main species forming the physiognomy of the association in spring and summer, respectively. *Astragalus retamocarpus* distributes from central Alborz of Iran to central Asia whereas *Chaerophyllum macrospermum* is distributed from Anatoli to central Asia. Physiognomy of the association is dominated by *Astragalus retamocarpus* in spring but replaced with late flowering species, especially *Chaerophyllum macrospermum* in summer.

4.3.1.2. *Heracleo anisactidis-Prangetum ferulacea* (Figure 7f)

Diagnostic species: ***Achillea millefolium***, ***Astragalus modestus***, ***Heracleum anisactis***, ***Isatis cappadocica***, ***Muscari caucasica***, ***Prangos ferulacea***, *Ranunculus elbursensis*, ***Trifolium repens***, ***Salvia atropatana***

This community was observed on mown sites at the higher elevations, in the range of 2900–3000 m a.s.l., where the grasslands are protected by stony borders against grazing. Habitat features are the same as the previous association. Average species richness is almost 22 species in 25 m^2 (Figure 4). The main characteristic species, *Heracleum anisactis* and *Astragalus modestus*, are endemic elements of Iran. *Prangos ferulacea* and *Trifolium repens* are widely distributed over Europe and SW Asia, and *Salvia atropatana* is sub-endemic of Iran (SE Turkey, N Iraq, Iran and Turkmenistan) (Rechinger et al. 1989).

Discussion

Syntaxonomy of the studied communities in the supraregional context

Our study represents the first detailed syntaxonomic analysis of the vegetation along the 3000-m elevational gradient of Mt. Damavand. Four major vegetation types (rocky, scree, snow-beds and grasslands) reflecting four phytosociological classes were identified in this elevational gradient. However, a few uncertainties remain, particularly in the classification of some montane-subalpine grasslands. Certain vegetation units have been provisionally assigned as communities due to the need for further sampling to confirm their status. Specifically, we call for more extensive sampling in other parts of the Alborz Mountains and adjacent ranges to validate and more precisely define higher syntaxa. Notably, the high endemism in these mountains leads to significant differences from nearby regions such as the Caucasus, Anatolia and Central Asia (Noroozi et al. 2010; Nowak et al. 2020, 2021), emphasizing the uniqueness of the flora in this area.

Rocky or chasmophytic habitat features a dominant physiognomy of most mountain and alpine belts of the Irano-Turanian region (Noroozi 2020; Nowak et al. 2021), yet they have been poorly studied in Iran. The exception is the alpine rock habitats of the central Alborz, classified under the order *Tanacetalia kotschyi* Klein 1982, which are a vicariant of the *Silenetalia odontopetalae* Quézel 1973 from the Taurus Mountains (Southern Turkey) (Quézel 1973; Klein 1982). This habitat serves as a refuge for a large number of neo- and paleo-endemics as well as monotypic genera (Akhani and Ziegler 2002; Naqinezhad and Esmailpoor 2017; Nowak et al. 2021). The rocky communities in Damavand can be divided into two groups: alpine, and montane-subalpine. We have assigned the alpine group to the *Campanulion louricae*, although many diagnostic species of this alliance also occur at lower elevations. However, we believe that the communities at lower elevations should be classified under a separate alliance, which requires further plot data.

The scree vegetation of the Alborz range is differentiated from two other alpine vegetation types, snowbed and thorn cushion grasslands, by their low vegetation cover and distinctive species composition, with a high rate of local endemism (Noroozi et al. 2014). This led to comparatively easier syntaxonomic assignment in this alpine habitat compared to syntaxonomincal complexity in other alpine or montane vegetation. Due to local endemism in this unique habitat, we assume that relevant association and higher ranks can be described in every local mountain area of Iran and Irano-Turanian region (see Nowak et al. 2015, 2021; Vynokurov et al. 2024).

The snowbed vegetation, characterised by low species diversity and limited spatial extent, has posed challenges for classification. Klein (1982) proposed two orders uniting high-mountain chionophilous communities of the Central Alborz, *Catabroselletalia parviflorae* Klein 1982 nom. inval. (Art. 2b ICPN) and *Trachydietalia depressae* Klein 1982 nom. inval. (Art. 2b ICPN), belonging to the class *Oxytropidetea persicae* Klein 1982 nom. inval. (Art. 2b ICPN), and highlighted their ecological and physiognomic affinities with the class *Salicetea herbaceae*. However, proposed high-rank units represented features of the snowbed vegetation and high-mountain thorn-cushion communities (Noroozi et al. 2010). Noroozi et al. (2010) suggested modifying this concept and to classify the real snow-bed communities into a new order *Taraxaco brevirostris-Polygonetalia serpyllacei* nom. inval. (Art. 3b ICPN). The class-level unit was undefined until now. Based on the presence of widespread Holarctic species in both our dataset and other studies (Noroozi et al. 2017), such as *Dichodon cerastioides*, *Oxyria digyna*, *Gnaphalium supinum*, and *Erigeron uniflorus*, we assign the syntaxa of these snowbed communities to the class *Salicetea herbaceae*. This placement is provisional, pending more extensive sampling across different regions of the Alborz range and other high-elevation environments in Iran.

The majority parts of the studied mountains are covered by steppes and grasslands ranging from lowland to alpine areas. These major vegetation types represent a diversity of physiognomy and floristic composition, including lowland *Stipa-Artemisia* semi-deserts, montane-subalpine to alpine thorn-cushion communities, and semi-natural grasslands. Classification of the alpine thorn-cushion communities, which dominate much of the alpine areas of the Alborz, has been challenging. Klein (1982) considered the alpine thorn-cushion communities as part of the chionophilous class *Oxytropidetea persicae*, mostly within the order *Trachydetalia depressae*, and partly the *Catabrosselletalia parviflorae*. Noroozi et al. (2010) suggested splitting the alpine snow-bed communities and alpine thorn-cushion communities into two distinct orders, and proposed an order *Drabetalia pulchellae* Noroozi et al. nom. inval. (Art. 3b ICPN) to unite the latter ones. Using a larger number of collected plots, we validated this order in this study and placed therein the *Senecioni iranici-Astragaletum macrosemii* community, previously classified within the scree class *Didymophyso aucheri-Dracocephaletea* aucheri (Noroozi et al. 2014). While no class has been established for this order, we tentatively place the alpine grasslands of the Damavand in the class *Astragalo-Brometea*, given their ecological, floristic (at generic level), and physiognomic similarities.

The classification of the montane-subalpine vegetation remains particularly challenging. Zohary (1973) proposed for the first time a class-level unit for the tragacanthic vegetation of the subalpine belt in this region, *Astragaletea iranica* Zohary 1973 nom. inval. (Art. 2b ICPN). Later, Klein (1987) suggested two new classes for the lower alpine and subalpine belts of Alborz: *Onobrychidetea cornutae* Klein 1987 nom. inval. (Art. 2b ICPN) uniting tragacanthic communities, and *Prangetea ulopterae* Klein 1987 nom. inval. (Art. 2b ICPN), comprising tall-herb communities dominated by large *Apiaceae* species. Parolly (2004) suggested to synonimize them and to consider within the class *Astragalo-Brometea* Quézel 1973, which was originally described from the Taurus Mountains, Southern Turkey (Quézel 1973), due to a high number of shared taxa, such as *Astragalus microcephalus*, *Bromus tomentellus*, *Festuca valesiaca*, *Teucrium polium*, *Stipa holosericea*, etc.

In Middle Asia, feather-grass steppes have been classified under the provisional order *Carici stenophylloidis-Stipetalia arabicae* within the *Astragalo-Brometea* (Nowak et al. 2016, 2018). Recently these units have been assigned to *Carici stenophylloidis-Stipetalia drobovii* within the class *Artemisio persicae-Stipetea drobovii* (Nowak et al. 2024). Despite the significant distance from Middle Asia, there are notable similarities in species composition (at both the species and generic levels) as well as habitat conditions between these units and those in our study. Many characteristic species of the proposed order, including *Carex stenophylla*, are also found in the montane steppes of Iran. Furthermore, the *Bromus tectorum-Stipa arabica* community proposed from western Pamir (Nowak et al. 2016), shows considerable overlap in floristic composition and habitat features with the Damavand vegetation. Recently, it has been shown that Irano-Turanian vegetation of Armenia, Transcaucasia, is significantly distinct from the original concept of *Astragalo-Brometea*, and it was classified within an order *Cousinio brachypterae-Stipetalia arabicae* Vynokurov et al. 2024, and within a potential new class, preliminarily called "*Ziziphora tenuior-Stipa arabica* grasslands" (Vynokurov et al. 2024). As the question of the proper class for this vegetation type cannot be solved without a broad-scale comparison involving all available data from the South-Western Asia, we decided to keep the name *Astragalo-Brometea* so far in the current study. At the order level, the classification also has some uncertainties.

The Damavand vegetation has some close similarities with the newly described *Cousinio brachypterae-Stipetalia arabicae*, which unites Armenian dry grasslands and xeric thorn-cushion communities (Vynokurov et al. 2024). In particular, numerous species of Irano-Turanian distribution are in common, such as *Achillea arabica*, *Bromus danthoniae*, *Onobrychis cornuta*, *Stipa arabica*, *S. holosericea*, *Thymus kotschyanus*, *Ziziphora tenuior*, as well as more widely distributed annual species like *Asperula arvensis*, *Meniocus linifolius*, *Taeniatherum caput-medusae*, etc. However, the *Cousinio brachypterae-Stipetalia arabicae* united Irano-Turanian vegetation exclusively from the lower elevations of Armenia, whereas subalpine communities belonged to Euro-Siberian class *Festuco-Brometea*. In the Central Alborz, the presence of Euro-Siberian species in the subalpine zone was much lower, and the similarities between montane and subalpine grasslands and thorn-cushion communities were significantly increased. This prompted us to merge them into a single order-level unit, preliminary classified as *Astragalo-Brometalia*, pending broader-scale comparisons. It should be noted that features such as high rock cover and steep inclination as well as presence of large *Apiaceae* species (e.g. *Ferula persica*, *Bilacunaria microcarpa* and *Pimpinella aurea*) might suggest to assign some communities of this group, particularly the *Astragalo compacti-Feruletum persicae*, to the invalidly-published class *Prangetea ulopterae* (Klein 1982). More systematic sampling is needed to achieve a more definitive classification of these grasslands.

A notable contribution of our study is the classification of semi-natural, mown tall-forb grasslands, which had not been previously examined in Iran. These grasslands, shaped by long-term grazing and mowing practices, are dominated by tall hemicryptophytes, leading to the decline of annuals and thorn-cushion species. The mown communities were assigned to the new alliance *Cousinion petrocauli*, probably belonging to an undescribed order within the *Astragalo-Brometea*. Despite their wide geographic range, we did not find closely related communities described elsewhere. Floristic similarities with Middle Asian communities (Nowak et al. 2020; Świerszcz et al. 2020) were weak, although *Astragalus retamocarpus* appears as a shared species. Our findings emphasize the uniqueness of these mown communities and call for more research to establish their broader regional significance.

Biodiversity and ecological patterns of the communities

Elevation emerged as the primary environmental gradient shaping vegetation patterns along the study transect, as expected given its influence on temperature, humidity, and other ecological factors (Körner 2007; Odland 2009). The percentage of rock and fine soil were other influential factors shaping plant communities on a gradient from tall herb grasslands of mown sites on one side to cliff and scree communities on the other side (Figure 3). The species richness of tall herb communities is partly lower than other communities in the same elevational belt. This pattern might be attributed to the negative impact of mowing on all growth forms except for hemicryptophytes (Talebi et al. 2021). On the contrary, the transition zone between montane and subalpine grasslands, exemplified by the *Astragalo compacti-Feruletum persicae*, displayed the highest plot-scale species richness. This elevational zone is the richest in Mt. Damavand (Talebi et al. 2021) and the whole of Iran (Noroozi et al. 2019). The elevational zone around 2400 m, with its steep slopes and high rock cover, had the highest species richness recorded in our study (61 taxa in a 25 m^2 plot) (see also Ramzi et al. 2024), although this is lower than species richness observed in other regions of the Palaearctic (Biurrun et al. 2021; Vynokurov et al. 2024). The comparatively lower richness in Iran, despite the high gamma diversity, warrants further macroecological investigation, which could benefit from the use of databases like GrassPlot (Dengler et al. 2018).

Conclusions and outlook

Large-scale phytosociological studies in Iran have often relied on sparse sampling across different regions or vegetation units. This highlights the need for detailed studies to address existing gaps and introduce new units to build a comprehensive vegetation databases (see Ramzi et al. 2024). We studied vegetation patterns in a unique mountain setting along one of the longest elevational gradients found in Iran and entire Southwest Asia. We have identified vegetation units primarily at the levels of alliance and association, aligning them with existing syntaxa at higher classification levels. Given the length of the gradient, elevation emerged as the most influential factor shaping species composition across the vegetation units. However, the current database is insufficient for fully clarifying the syntaxonomic complexity, particularly concerning *Stipa* grasslands at lower elevations, which cover vast areas of the Iranian Plateau. To achieve a consistent and comprehensive classification system for the wider region, extensive and systematic sampling across the Alborz Mountains and other mountain systems in Iran is essential.

Data availability

The original data from Mt. Damavand (species composition and header data of the plots) are provided in the Supplementary materials of this article.

Author contributions

AT, AN and FA conceived the idea, AT conducted field sampling, AT, AN and JD performed the statistical analyses and syntaxonomic classification, while DV led the interpretation of the syntaxa in the international context. The manuscript was mainly written by AT and AN and smaller parts by JD, while all authors critically revised and approved it.

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Appendix 1: Formal descriptions of new syntaxa

The new syntaxa are sorted by their number in the text, irrespective of their rank.

2.1.1.2 *Myosotido olympicae-Lamietum tomentosi* ass. nov. hoc loco

Holotypus hoc loco: relevé 309, 27 July 2018, 35.9247° N, 52.1085° E, elevation: 3900 m a.s.l., aspect: 180°, slope: 35°, plot size: 25 m^2, vascular plant species richness: 19, vegetation cover: 30%, author of the relevé: Amir Talebi.

Vascular plant composition: *Achillea aucheri* 6%, *Elymus longearistatus* 4%, *Artemisia chamaemelifolia* 5%, *Astragalus macrosemius* 0.5%, *Bromus paulsenii* 10%, *Cerastium purpurascens* 0.8%, *Cirsium lappaceum* 3%, *Crepis multicaulis* 0.6%, *Dracocephalum aucheri* 0.8%, *Erysimum caespitosum* 2%, *Festuca valesiaca* 1%, *Helichrysum psychrophilum* 1%, *Lamium tomentosum* 3%, *Myosotis olympica* 1%, *Nepeta racemosa* 5%, *Polygonum serpyllaceum* 0.5%

4.1 *Drabetalia pulchellae* Noroozi et al. ex Noroozi in Talebi et al. 2024 ord. nov. hoc loco

Holotypus hoc loco: *Acantholimion demavendici* Noroozi et al. 2010, p. 310

Diagnostic species: ***Alopecurus textilis***, *Artemisia chamaemelifoliamifolia*, ***Blitum virgatum***, *Campanula stevenii*, ***Carex pseudo-foetida***, *Cousinia harazensis*, *Draba pulchella*, ***Onobrychis cornuta***, *Veronica kurdica*

Note: The order has been provisionally published by Noroozi et al. (2010). Since our current study supported this concept, J. Noroozi agreed to validate his concept in the paper at hand.

4.1.1.1 *Senecio iranici-Astragaletum macrosemii* Noroozi et al. ex Noroozi ass. nov. hoc loco

Holotypus hoc loco: relevé 271, 20 July 2016, 35.9309°N 52.1084°E, elevation: 4216 m a.s.l., aspect: 180°, slope: 15°, plot size: 25 m^2, vascular plant species richness: 16, vegetation cover: 75%, author of the relevé: Amir Talebi

Vascular plant composition: *Achillea aucheri* 3%, *Artemisia melanolepis* 10%, *Astragalus macrosemius* 55%, *Carex pseudo-foetida* 4%, *Cerastium purpurascens* 3%, *Chenopodium foliosum* 2%, *Colpodium parviflorum* 3%, *Draba siliquosa* 1%, *Dracocephalum aucheri* 3%, *Erysimum caespitosum* 3%, *Poa araratica* 1%, *Senecio iranicus* 3%, *Potentilla polyschista* 3%, *Veronica aucheri* 0.5%, *Veronica biloba* 0.2%, *Veronica kurdica* 0.5%

Note: Due to the low number of collected plots (3), Noroozi et al. (2014) had described the association only provisionally. We now could confirm the concept with a larger dataset.

4.1.1.2 *Cousinietum harazensis* ass. nov. hoc loco

Holotypus hoc loco: relevé 224, 30 June 2016, 35.9165°N 52.1053°E, elevation: 3495 m a.s.l., aspect: 240°, slope: 35°, plot size: 25 m^2, vascular plant species richness: 14, vegetation cover: 80%, author of the relevé: Amir Talebi

Vascular plant composition: *Acantholimon demawendicum* 6%, *Acantholimon erinaceum* 13%, *Alopecurus textilis* 5%, *Astragalus modestus* 0.5%, *Bromus paulsenii* 5%, *Campanula stevenii* 1%, *Cousinia harazensis* 8%, *Draba pulchella* 0.7%, *Erysimum caespitosum* 0.5%, *Festuca valesiaca* 20%, *Onobrychis cornuta* 10%, *Poa araratica* 3%, *Silene palinotricha* 0.2%, *Veronica kurdica* 0.8%

4.1.2.3 *Astragaletum ochrochlori* ass. nov. hoc loco

Holotypus hoc loco: relevé 73, 27 July 2018, 35.9233°N 52.0326°E, elevation: 3100 m a.s.l., aspect: 220°, slope: 12°, plot size: 25 m^2, vascular plant species richness: 27, vegetation cover: 85%, author of the relevé: Amir Talebi

Vascular plant composition: *Alopecurus textilis* 3%, *Eremogone gypsophiloides* 3%, *Astragalus iodotropis* 3%, *Astragalus modestus* 3%, *Astragalus ochrochlorus* 12%, *Bro-*

mus tomentellus 3%, *Cirsium lappaceum* 12%, *Cousinia multiloba* 3%, *Draba pulchella* 3%, *Eremopoa persica* 0.6%, *Erysimum caespitosum* 3%, *Filago arvensis* 0.6%, *Herniaria glabra* 3%, *Noccaea stenocarpa* 3%, *Onobrychis cornuta* 12%, *Papaver bracteatum* 3%, *Plantago atrata* 3%, *Piptatherum laterale* 3%, *Poa bulbosa* 3%, *Polygonum alpestre* 0.6%, *Polygonum patulum* 0.6%, *Polygonum rottboellioides* 0.6%, *Silene bupleuroides* 3%, *Taraxacum syriacum* 3%, *Thymus kotschyanus* 3%, *Veronica biloba* 0.6%, *Veronica kurdica* 3%

4.2.1.1 ***Astragalo lilacini-Astragaletum microcephali*** **ass. nov. hoc loco**

Holotypus hoc loco: relevé 113, 10 June 2017, 35.89°N 52.10917°E, elevation: 2798 m a.s.l., aspect: 170°, slope: 15°, plot size: 25 m^2, vascular plant species richness: 27, vegetation cover: 75%, author of the relevé: Amir Talebi

Vascular plant composition: *Achillea arabica* 5%, *Alyssum desertorum* 0.5%, *Alyssum marginatum* 0.1%, *Astragalus bounophilus* 0.5%, *Astragalus lilacinus* 0.2%, *Astragalus microcephalus* 35%, *Bromus tomentellus* 7%, *Carex divisa* 2%, *Ceratocephala testiculata* 0.2%, *Dianthus orientalis* 0.2%, *Draba nemorosa* 0.2%, *Draba nuda* 1%, *Thinopyrum intermedium* 7%, *Elymus repens* 8%, *Festuca valesiaca 25%*, *Filago arvensis* 0.1%, *Galium spurium* 0.1%, *Geranium persicum* 0.2%, *Herniaria incana* 0.5%, *Ixiolirion tataricum* 0.1%, *Muscari caucasica* 0.2%, *Poa bulbosa* 8%, *Rochelia persica* 0.2%, *Stipa arabica* 2%, *Taraxacum syriacum* 1%, *Thymus kotschyanus* 5%, *Tragopogon reticulatus* 0.1%

4.2.2 ***Artemision aucheri*** **all. nov. hoc loco**

Holotypus hoc loco: *Artemisietum aucheri* Talebi et al. 2024 (this paper)

Diagnostic species: *Aegilops triuncialis*, *Allium rubellum*, *Asparagus persicus*, ***Atriplex aucheri***, *Caccinia strigosa*, *Conringia persica*, ***Cousinia eryngioides***, ***Crepis sancta***, ***Eremopyrum bonaepartis***, *Erodium cicutarium*, *Hordeum glaucum*, *Krascheninnikovia ceratoides*, *Lappula spinocarpa*, *Malabaila secacul*, ***Malcolmia africana***, *Medicago monspeliaca*, ***Nitrosalsola dendroides***, ***Noaea mucronata***, *Onosma microcarpa*, ***Stachys inflate***, *Turgenia latifolia*

4.2.2.1 ***Astragalo compacti-Feruletum persicae*** **ass. nov. hoc loco**

Holotypus hoc loco: relevé 90, 10 May 2017, 35.87556°N 52.13833°E, elevation: 2210 m a.s.l., aspect: 160°, slope: 25°, plot size: 25 m^2, vascular plant species richness: 51, vegetation cover: 85%, author of the relevé: Amir Talebi

Floristic composition: *Acanthophyllum microcephalum* 1%, *Acinus graveolens* 0.05%, *Alyssum desertorum* 0.01%, *Alyssum marginatum* 0.01%, *Alyssum minus* 0.2%, *Arenaria serpyllifolia* 0.1%, *Arrhenatherum kotschyi* 0.1%, *Artemisia aucheri* 0.5%, *Artemisia scoparia* 0.5%, *Astragalus caragana* 1%, *Astragalus compactus* 6%, *Astragalus microcephalus* 5%, *Bromus danthoniae* 2%, *Bromus tectorum* 10%, *Bupleurum exaltatum* 0.1%, *Callipeltis cucullaris* 0.01%, *Carduus transcaspicus* 4%, *Cerastium dichotomum* 0.05%, *Cerasus pseudoprostrata* 1%, *Crupina crupinastrum* 0.1%, *Dianthus orientalis* 5%, *Erodium cicutarium* 0.5%, *Ferula persica* 5%, *Filago arvensis* 0.01%, *Galium spurium* 0.01%, *Galium verticillatum* 0.05%, *Helichrysum plicatum* 0.2%, *Heteropappus altaicus* 0.1%, *Hypericum scabrum* 0.2%, *Bassia prostrata* 6%, *Linaria simplex* 0.1%, *Melica jacquemontii* 0.1%, *Minuartia meyeri 0.01%*, *Noaea mucronata* 0.01%, *Nonea caspica* 0.05%, *Orobanche mutelii* 0.01%, *Phlomis olivieri* 0.2%, *Psathyrostachys fragilis* 5%, *Salvia chloroleuca* 1%, *Scariola orientalis* 2%, *Senecio glaucus* 0.1%, *Silene conoidea* 0.01%, *Silene swertiaefolia* 0.5%, *Sisymbrium altissimum* 0.1%, *Stipa arabica* 1%, *Sophora alopecuroides* 0.5%, *Taeniatherum caput-medusae* 17%, *Tanacetum polycephalum* 0.5%, *Trigonella monantha* 1%, *Valerianella plagiostephana* 0.1%, *Verbascum cheiranthifolium* 0.2%, *Viola occulta* 0.01%

4.2.2.2 ***Artemisietum aucheri*** **ass. nov. hoc loco**

Holotypus hoc loco: relevé 207, 35.8713°N 52.1695°E, elevation: 1761 m a.s.l., aspect: 120°, slope: 30°, plot size: 25 m^2, vascular plant species richness: 36, vegetation cover: 65%, author of the relevé: Amir Talebi

Vascular plant composition: *Aegilops tauschii* 2%, *Alyssum desertorum* 0.2%, *Meniocus linifolius* 0.1%, *Alyssum marginatum* 0.1%, *Alyssum meniocoides* 0.1%, *Alyssum minus* 1%, *Artemisia aucheri* 12%, *Artemisia scoparia* 0.5%, *Bromus danthoniae* 0.1%, *Bromus tectorum* 0.2%, *Centaurea benedicta 0.5%*, *Caccinia strigosa* 1%, *Camelina rumelica* 0.2%, *Consolida teheranica* 0.2%, *Cousinia eryngioides* 0.1%, *Crepis sancta* 1%, *Eremopyrum bonaepartis* 0.2%, *Euphorbia szovitsii* 0.01%, *Koelpinia linearis* 0.2%, *Galium spurium* 0.3%, *Krascheninnikovia ceratoides* 5%, *Lappula barbata* 0.1%, *Lappula spinocarpa* 0.2%, *Linaria simplex* 0.1%, *Malabaila secacul* 0.5%, *Medicago sativa* 2%, *Noaea mucronata* 0.5%, *Nonea caspica* 0.1%, *Senecio glaucus* 0.1%, *Sisymbrium altissimum* 0.2%, *Sophora alopecuroides* 0.3%, *Stipa arabica* 5%, *Taeniatherum caput-medusae* 20%, *Turgenia latifolia* 0.5%, *Viola occulta* 0.1%, *Ziziphora tenuior* 0.1%

4.2.2.3 ***Caccinio strigosae-Oreosalsoletum montanae*** **ass. nov. hoc loco**

Holotypus hoc loco: relevé 286, 35.8739°N 52.1752°E, elevation: 1735 m a.s.l., aspect: 150°, slope: 45°, plot size: 25 m^2, vascular plant species richness: 24, vegetation cover: 50%, author of the relevé: Amir Talebi

Vascular plant composition: *Alyssum minus* 0.2%, *Artemisia aucheri* 8%, *Atraphaxis spinosa* 10%, *Atriplex aucheri* 1%, *Bromus brachystachys* 2%, *Bromus danthoniae 0.2%*, *Bromus tectorum* 4%, *Bupleurum exaltatum* 3%, *Caccinia strigosa* 1%, *Cousinia eryngioides* 2%, *Eryngium billardieri* 5%, *Ferula persica* 7%, *Galium spurium* 0.3%, *Bilacunaria microcarpa* 1%, *Malabaila secacul* 2%, *Onosma microcarpa* 2%, *Oreosalsola montana* 15%, *Psathyrostachys fragilis* 3%, *Scariola orientalis* 0.2%, *Sophora alopecuroides* 1%, *Stachys inflata* 3%, *Tragopogon coelesyriacus* 0.5%

4.3.1 ***Cousinion petrocauli*** **all. nov. hoc loco**

Holotypus hoc loco: *Astragaletum retamocarpi* Talebi et al. 2024 (this paper)

Diagnostic species: ***Achillea arabica***, ***Achillea millefolium***, *Campeiostachys elongatiformis*, ***Chaerophyllum macrospermum***, *Chondrilla juncea*, ***Cousinia pterocaulos***, ***Dactylis glomerata***, *Echinops pungens*, ***Eremogone gypsophiloides***, ***Galium verum***, ***Medicago sativa***, *Orobanche crenua*, *Poa pratensis* (D), ***Potentilla canescens***, ***Rumex elbursensis***, *Salvia atropatana*, ***Tragopogon buphthalamoides***, *Veronica orientalis*, ***Verbascum oreophilum***, ***Vicia canescens***

4.3.1.1. *Astragaletum retamocarpi* ass. nov. hoc loco

Holotypus hoc loco: relevé 265, 35.8727°N 52.1008°E, elevation: 2548 m a.s.l., aspect: 120°, slope: 10°, plot size: 25 m^2, vascular plant species richness: 17, vegetation cover: 100%, author of the relevé: Amir Talebi

Floristic composition: *Achillea arabica* 4%, *Astragalus retamocarpus* 55%, *Chaerophyllum macrospermum* 50%, *Cousinia pterocaulos* 3%, *Dactylis glomerata* 5%, *Echinops pungens* 3%, *Eremogone gypsophiloides* 5%, *Ferula ovina* 5%, *Galium verum* 3%, *Papaver bracteatum* 3%, *Poa bulbosa* 5%, *Polygonum alpestre* 2%, *Potentilla canescens* 5%, *Taraxacum syriacum* 2%, *Thinopyrum intermedium* 10%, *Tragopogon buphthalamoides* 2%, *Vicia canescens* 7%

4.3.1.2. *Heracleo anisactidis-Prangetum ferulaceae* ass. nov. hoc loco

Holotypus hoc loco: relevé 179, 35.9017° N 52.1122° E, elevation: 2977 m a.s.l., aspect: 150°, slope: 7°, plot size: 25 m^2, vascular plant species richness: 21, vegetation cover: 100%, author of the relevé: Amir Talebi

Vascular plant composition: *Achillea millefolium* 30%, *Astragalus modestus* 5%, *Chaerophyllum macrospermum* 5%, *Cousinia pterocaulos* 3%, *Dactylis glomerata* 4%, *Elymus repens* 20%, *Eremogone gypsophiloides* 6%, *Galium verum* 5%, *Heracleum anisactis* 7%, *Isatis cappadocica* 7%, *Muscari caucasica* 2%, *Poa pratensis* 10%, *Prangos ferulacea* 3%, *Potentilla canescens* 20%, *Rumex elbursensis* 10%, *Silene bupleuroides* 4%, *Solenanthus stamineus* 3%, *Taraxacum syriacum* 4%, *Thinopyrum intermedium* 20%, *Verbascum oreophilum* 3%, *Vicia canescens* 30%

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Supplementary material

Supplementary material 1
Header and raw percentage data of all 330 vegetation plots (*.xlsx)
Link: https://doi.org/10.3897/VCS.136825.suppl1

Supplementary material 2
Complete relevé and synoptic table (*.xlsx)
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RESEARCH PAPER GRASSLANDS OF ASIA

Vascular plant diversity of the high mountains of Fereydunshahr, Central Zagros, Iran

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Abstract

Questions: The mountains of Fereydunshahr County are one of the centers of plant endemism within the Zagros, however, its flora and vegetation remain relatively understudied. In this study we undertook research on the plant species diversity of the subalpine and alpine zones of this area, their life forms, chorology, and vegetation types. **Study area:** Mountains of Fereydunshahr County, Central Zagros, West Iran. **Methods:** Plant specimens were collected during the growing seasons of 2018 to 2020. A complete species list was prepared including their life forms, chorotypes, elevation range, and major vegetation types. **Results:** A total of 308 vascular plant species have been identified belonging to 185 genera and 47 families. The largest plant families recorded during the study are *Asteraceae* with 44 species, *Fabaceae* 32, *Brassicaceae* 29, and *Lamiaceae* 27. At genus level *Astragalus* with 23 species is the richest. Hemicryptophyte with 162 (53%) species is the major life form. Most of the species are Irano-Turanian elements (52%). A total of 57 species (19%) are endemic to Iran and 23 species (7%) are endemic to Zagros. Most species belong to the montane-subalpine zone (33%), followed by subalpine (20%), montane (15%), lowland-montane (10%), alpine (9%), and lowland-subalpine (5%). In the alpine zone a high proportion of the species are endemic, while the montane zone has a very low proportion of endemics. From the identified species, 24% belong to subalpine and alpine thorn-cushion grasslands, 19% to montane steppe shrublands, 5% to subalpine tall-umbelliferous vegetation types, 5% to wetlands, and 5% to chasmophyte vegetation. **Conclusions:** The area has a rich flora, but at the same time is under high pressure from anthropogenic activities, especially a very high level of overgrazing. The region is not a protected area, therefore, establishment of a protected area and efficient conservation planning for the region is highly recommended.

Taxonomic reference: Flora of Iran (Assadi et al. 1989–2021) and, for families not yet covered in the previous source, Flora Iranica (Rechinger 1963–2015).

Abbreviations: ES = Euro-Siberian; IT = Irano-Turanian; M = Mediterranean; SS = Saharo-Sindian.

Keywords

alpine habitats, endemic species, mountains, plant diversity, Southwest Asia, vegetation types, Zagros

Introduction

Mountains are storehouses of global biodiversity and embrace half of the world's biodiversity hotspots (Mittermeier et al. 2011). Alpine ecosystems are found above the treeline, covering 3% of the Earth's land area and harbouring approximately 10,000 plant species (Nagy and Grabherr 2009; Körner 2021). These species are severely impacted by ongoing climate change (Dullinger et al. 2012; Pauli et al. 2012). Iran, with a total surface area of about 1.6 million km^2, is a high plateau in Southwest Asia, and almost half of the country is composed of high mountains, surrounding the interior lowlands. The alpine zone of the Iranian Mountains covers only about 1% of the surface of the country but harbours 4% of non-endemic and 7% of the endemic flora of Iran (Noroozi et al. 2019b). In spite of the high endemic diversity of these habitats, there are many mountains that are not well explored yet and their subalpine and alpine plant diversity is not well known.

The Zagros is the largest mountain range in Iran, stretching from the northwest to the south of the country, with many peaks over 3,500 m a.s.l., harbouring wide scattered alpine ecosystems over a large area. The Zagros lies within the Irano-Turanian (IT) phytogeographic region (Zohary 1973; Manafzadeh et al. 2017) and has been identified as an area of endemism inside of the Irano-Anatolian global biodiversity hotspot (Mittermeier et al. 2011; Noroozi et al. 2019b, 2021). A global biodiversity hotspot is a region with a high number of endemic species and heavy impacts from human activities, resulting in a high priority for conservation (Mittermeier et al. 2011). The Zagros is home to a large number of endemic taxa, many of them limited to subalpine and alpine zones (Noroozi et al. 2020). Due to the large area and inaccessibility of certain areas, the Zagros is one of the less-known mountain ranges of the Iranian Plateau in terms of biodiversity. There are many centers of endemism in the Zagros, most of which are located in areas with high elevational amplitudes (Noroozi et al. 2019a). These areas were likely refugia, where many montane species of this mountain range survived during the last glacial periods (see Ahmadzadeh et al. 2013; Rajaei et al. 2013).

One of these centers of endemism is the mountains of Fereydunshahr County in Central Zagros, which covers only a small part of this mountain range (Figure 1). There have been several floristic and vegetation studies in the region and adjacent areas, including the flora and vegetation survey of Fereydunshahr (Nekookho 2008), the floristic study of Pashandegan forest reserve of Fereydunshahr (Hamidi Rad 2012), the study of the flora of Afus region (Shirvani Shahenayati et al. 2020) and the floristic study of Golestankooh area (Akhavan Roofigar and Bagheri 2021). However, the flora and vegetation at high elevations within this area have not been well documented. Therefore, the main goals of the current study are to conduct a floristic survey of the subalpine and alpine zones of the mountains of Fereydunshahr, their life forms, chorology, elevation zones and also the major vegetation types they are linked to. This study will contribute to the existing information on the plant diversity of the region and help to fill the gaps in the knowledge of biodiversity and conservation for the area.

Study area

The Fereydunshahr County (32° 56' N, 50° 07' E) is located about 180 km west of the city of Isfahan with an elevation of about 2,500 m a.s.l., surrounded by high mountains belonging to the Zagros range (Figure 1). The size of the study area is around 150 km^2, which covers less than 0.05% of the Zagros surface area. The most significant mountains of the study area are Mount Didtseri (3,620 m a.s.l.) in the north, Mount Zardigari (no-hunting area of the peak Setbleh) (3,700 m a.s.l.) in the northwest, Mount Kalabis kobi (3,000 m a.s.l.) in the northeast, Mount Tsikhe (3,320 m a.s.l.) in the west, and Mount Tatara (3,520 m a.s.l.) in the south. The region's geomorphology is shaped significantly by the Zagros Fault, which divides the area into the Elevated Zagros to the west and the Sanandaj-Sirjan zone to the east (Motaghi et al. 2017). The diverse limestone formations and soil composition, consisting mainly of Inceptisols and Entisols, reflect the area's rich geological history (Motaghi et al. 2017). The diverse landscape creates a variety of microclimates that support different vegetation types and ecological zones. The region is characterized by a Mediterranean climate regime with cold and wet winters and dry and warm summers (Djamali et al. 2011; Rivas-Martínez et al. 2011). The mean annual temperature is 11.65°C and the annual precipitation is 540 mm (Fereydunshahr meteorological station; Figure 2).

The main vegetation types of the region are defined based on previous studies which were reviewed in Noroozi et al. (2020). They are described briefly here for a better understanding of the study area:

Montane steppe shrublands is the main vegetation type in the montane zone, but reaching to the subalpine zone in some parts too. The species of the genera *Amygdalus*, *Cotoneaster* and *Cerasus* are the most characteristic shrubs in this vegetation type, and *Astragalus microcephalus* is usually the most common species. This vegetation type covers an elevation from ca. 1,200 to 2,700 m a.s.l.

Subalpine tall-umbelliferous vegetation types (Figure 3) are dominated by tall plants of the *Apiaceae* family such as *Ferula haussknechtii*, *Ferulago angulata* (Figure 3A), *Prangos ferulacea*, and *P. uloptera* (Figure 3B). These are typically found at elevations ranging from 2,500 to 3,500 m a.s.l., mostly on steep slopes with a high proportion of scree and stones, and poor soil content. This vegetation type was described as a provisional class named *Prangetea ulopterae* from Central Alborz (Klein 1988, 2001). Other dominant species are *Dorema aucheri*, *Ferula microcolea*, *Ferulago contracta*, *Pimpinella tragium*, *Rheum ribes*, *Rhabdosciadium aucheri*, and *R. straussii*.

Subalpine and alpine thorn-cushion grasslands are commonly found on the windswept slopes of subalpine and alpine zones (Figure 4). Three prominent species dominating these plant communities in the subalpine zone of Central Zagros (up to 3,500 m a.s.l.) are *Acantholimon hohenackeri*, *Astragalus brachycalyx*, and *Bromus tomentellus* (Figure 4A). Alongside these taxa, other frequently observed species include *Acantholimon aspadanum*, *A. senganense*, *Astragalus alyssoides*, *A. andalanicus*, *A. cephalanthus*, *A. rhodosemius*, and *A. susianus*. In the alpine zone (above ca. 3,500 m a.s.l.), *Astragalus murinus*, *A. raswendicus*, and *Cousinia multiloba* (Figure 4B) are the most dominant thorn-cushions. *Onobrychis cornuta* is another thorn-cushion species usually dominating in both subalpine and alpine windswept slopes (Figure 4C).

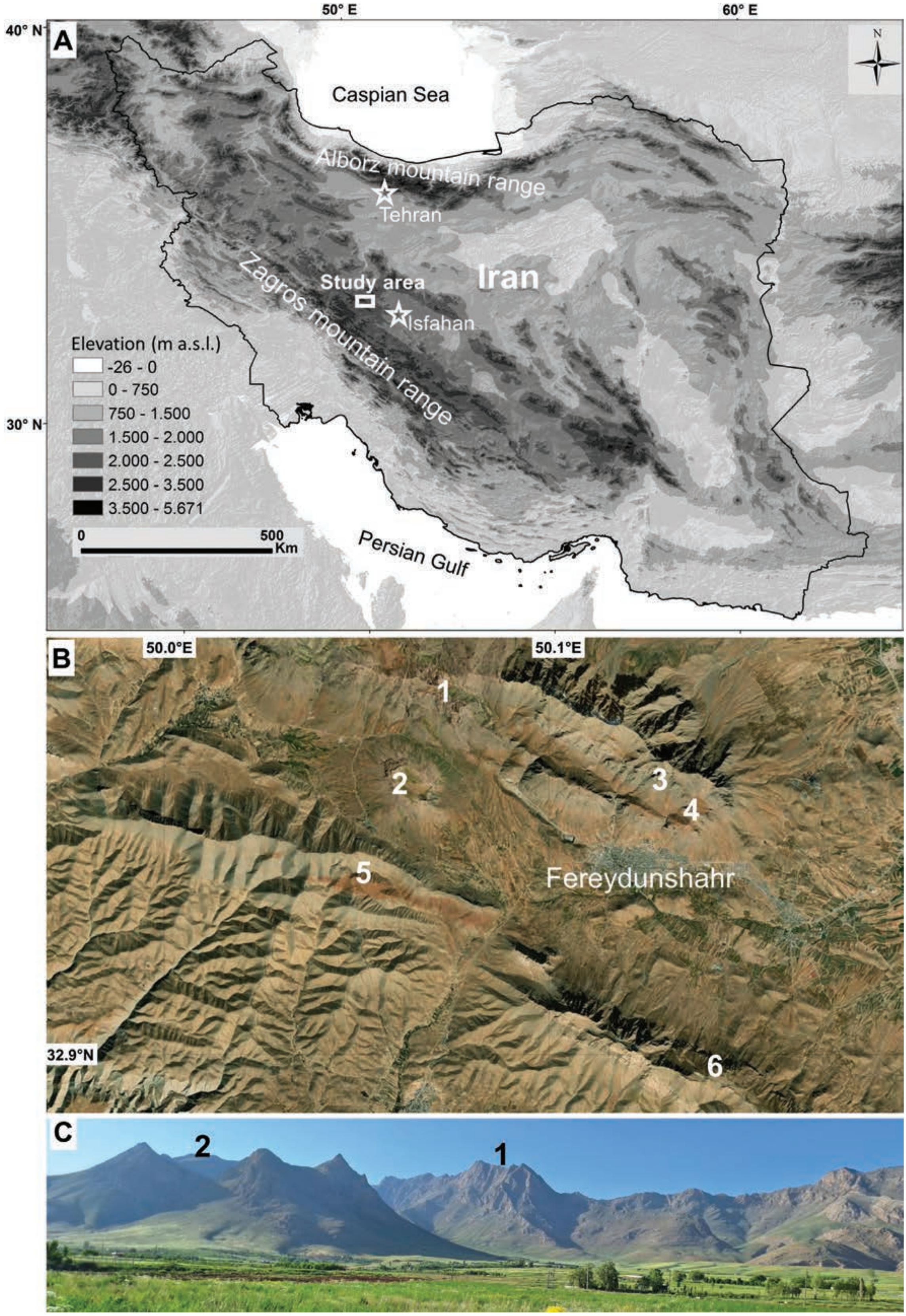

Figure 1. A. Topographic map of Iran and the location of the study area (made by Arc GIS). **B.** Satellite map of Fereydunshahr (map taken from Google Earth) showing the mountains within the study area. Mountain peaks are marked with white numbers: 1. Mount Zardigari (3,700 m a.s.l.) in the northwest, 2. Mount Tsikhe (3,320 m a.s.l.) in the west, 3. Mount Didtseri (3,620 m a.s.l.) in the north, 4. Mount Kalabis kobi (3,000 m a.s.l.) in the northeast, 5. Mount Ski Resort (3,091 m a.s.l.) in the west and 6. Mount Tatara (3,520 m a.s.l.) in the south. **C.** A view of the mountains around the city of Fereydounshahr. **A** was produced using ArcGIS; **B** is taken from Google Earth; **C** by MY.

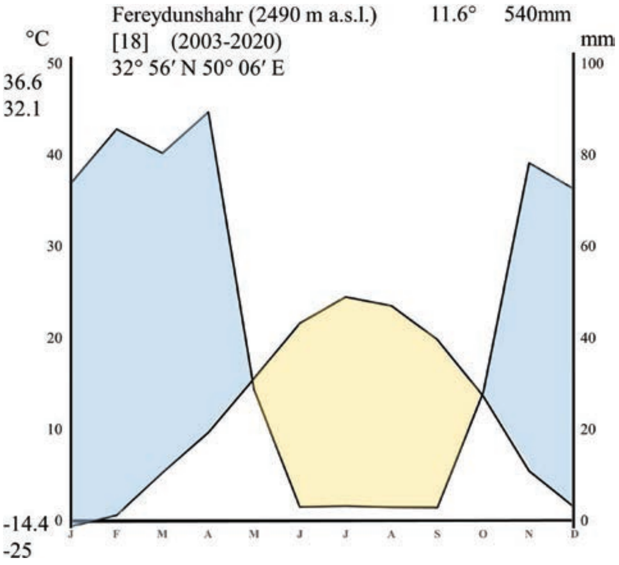

Figure 2. Climatic diagram of Fereydunshahr derived from the meteorological data collected by the Fereydunshahr meteorological station (https://www.irimo.ir/).

Chasmophytic vegetation (Figure 5) is distributed from the montane up to the nival zone. The substrate for this habitat is composed of volcanic rocks and limestone. Several characteristic species for this habitat in the subalpine and alpine zones are *Arabis caucasica* (Figure 5B), *Aubrieta parviflora*, *Corydalis rupestris*, *Dionysia bazoftica* (Figure 5C), *Graellsia saxifragifolia* (Figure 5D), *Pentanema pulicariiforme*, *Rosularia elymaitica*, and *Silene chlorifolia*.

Wetlands are found in areas with high moisture levels, such as near streams and wet meadows, at various elevations. They include species such as *Carex microglochin*, *Juncus articulatus*, *J. bufonius*, *J. inflexus*, *J. turkestanicus*, and *Mentha longifolia*.

Methods

Initially, several areas were delimited by closely examining the topographic map of Fereydunshahr County and its surrounding mountains. These areas were chosen to represent the diverse ecological and floristic characteristics

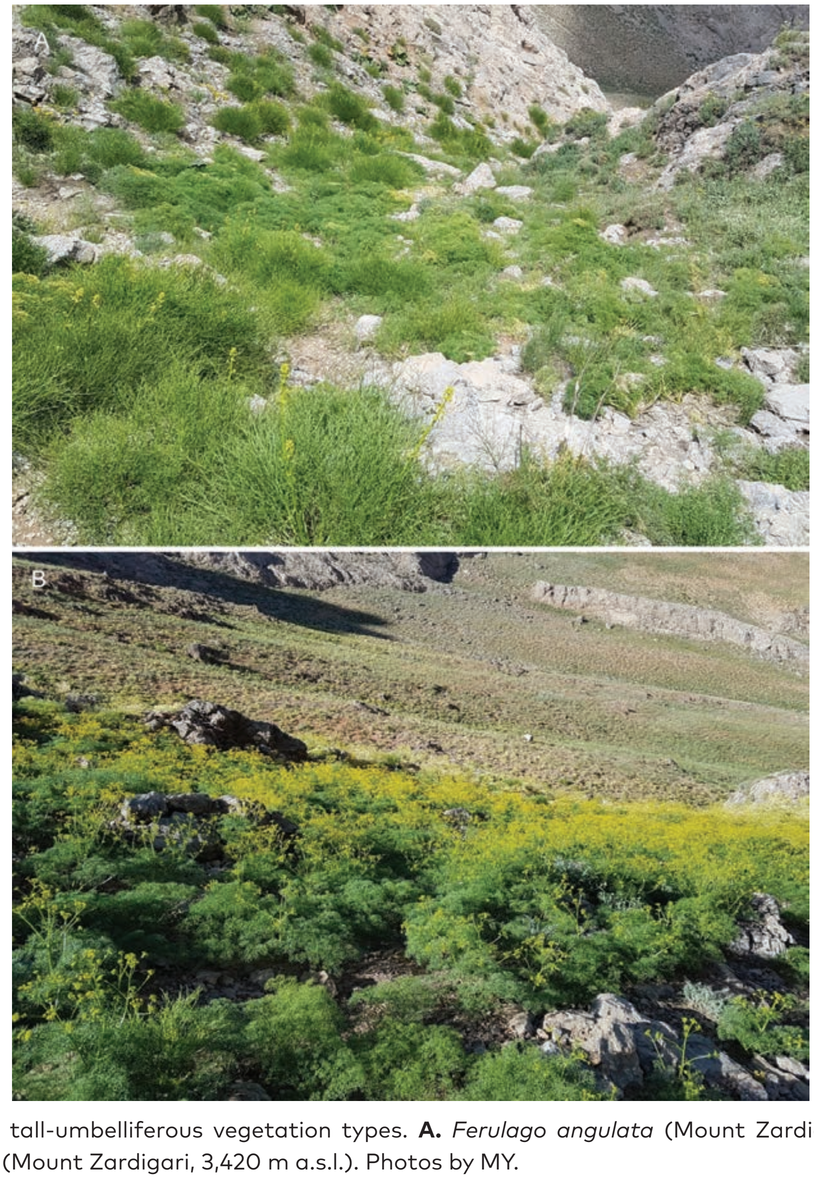

Figure 3. Subalpine tall-umbelliferous vegetation types. **A.** *Ferulago angulata* (Mount Zardigari, 3,450 m a.s.l.). **B.** *Prangos uloptera* (Mount Zardigari, 3,420 m a.s.l.). Photos by MY.

of the region. The multiple sites were selected to capture a wide range of environmental conditions, which can significantly influence plant species composition, such as different elevations, slopes, and aspects. This study was limited to an elevation range of between 2,500 to 3,700 m a.s.l.

The fieldwork was carried out during the growing season from April to September across three years (2018–2020) in the selected subalpine and alpine areas of Fereydunshahr. Sampling was done completely randomly from the slope to the top of the mountain, allowing us to cover a broad range of elevations and microhabitats. Over 1000 vascular plant specimens were collected, each tagged with detailed location, elevation, and habitat information. The collected specimens were identified using

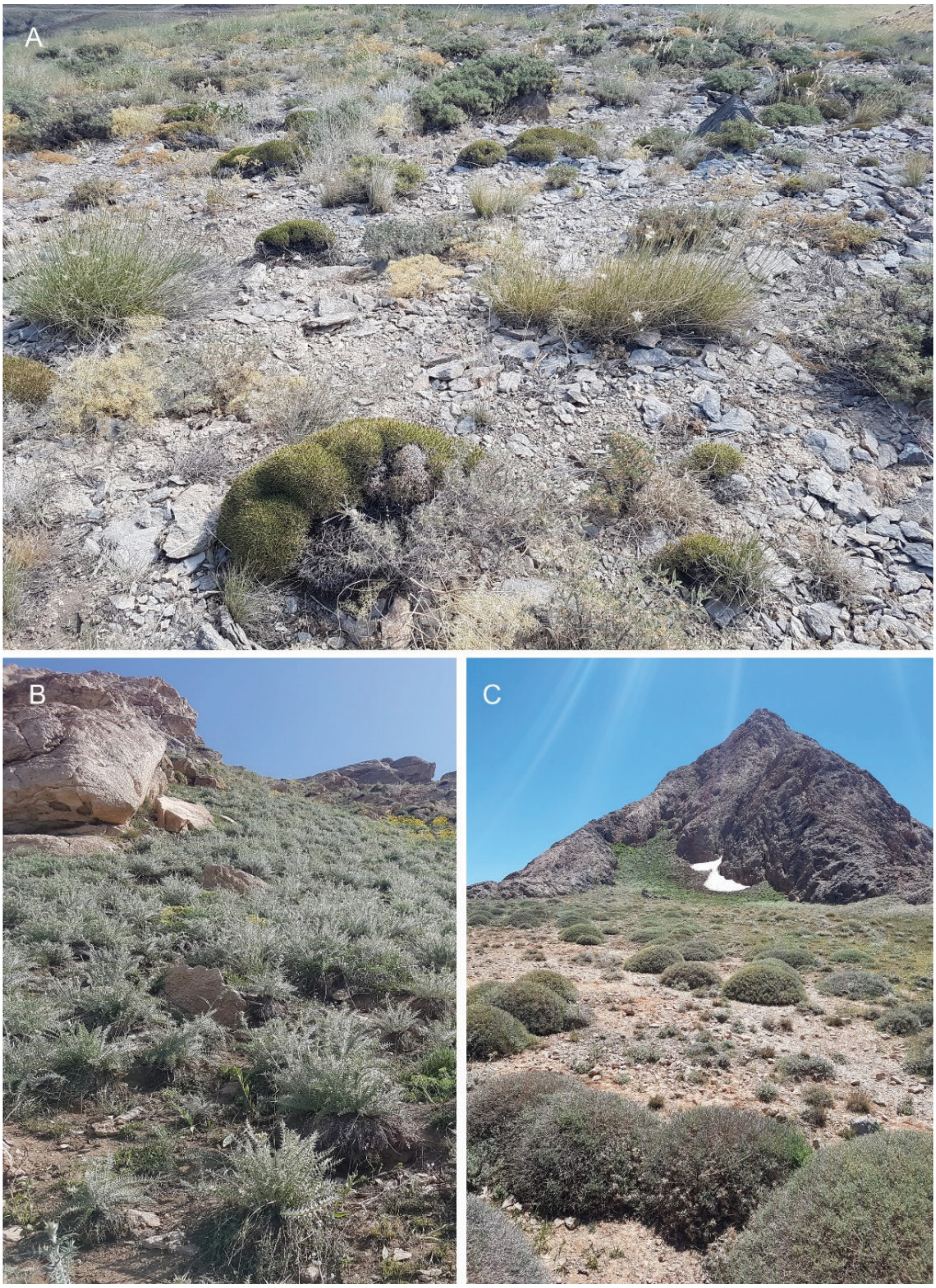

Figure 4. Subalpine and alpine thorn-cushion grasslands. **A.** *Acantholimon hohenackeri*, *Astragalus brachycalyx*, *Bromus tomentellus*, *Dianthus macranthus* (Mount Ski Resort, 3,000 m a.s.l). **B.** *Cousinia multiloba* (Mount Tatara, 3,500 m a.s.l). **C.** *Onobrychis cornuta* (Mount Zardigari, 3,535 m a.s.l. Photos by MY.

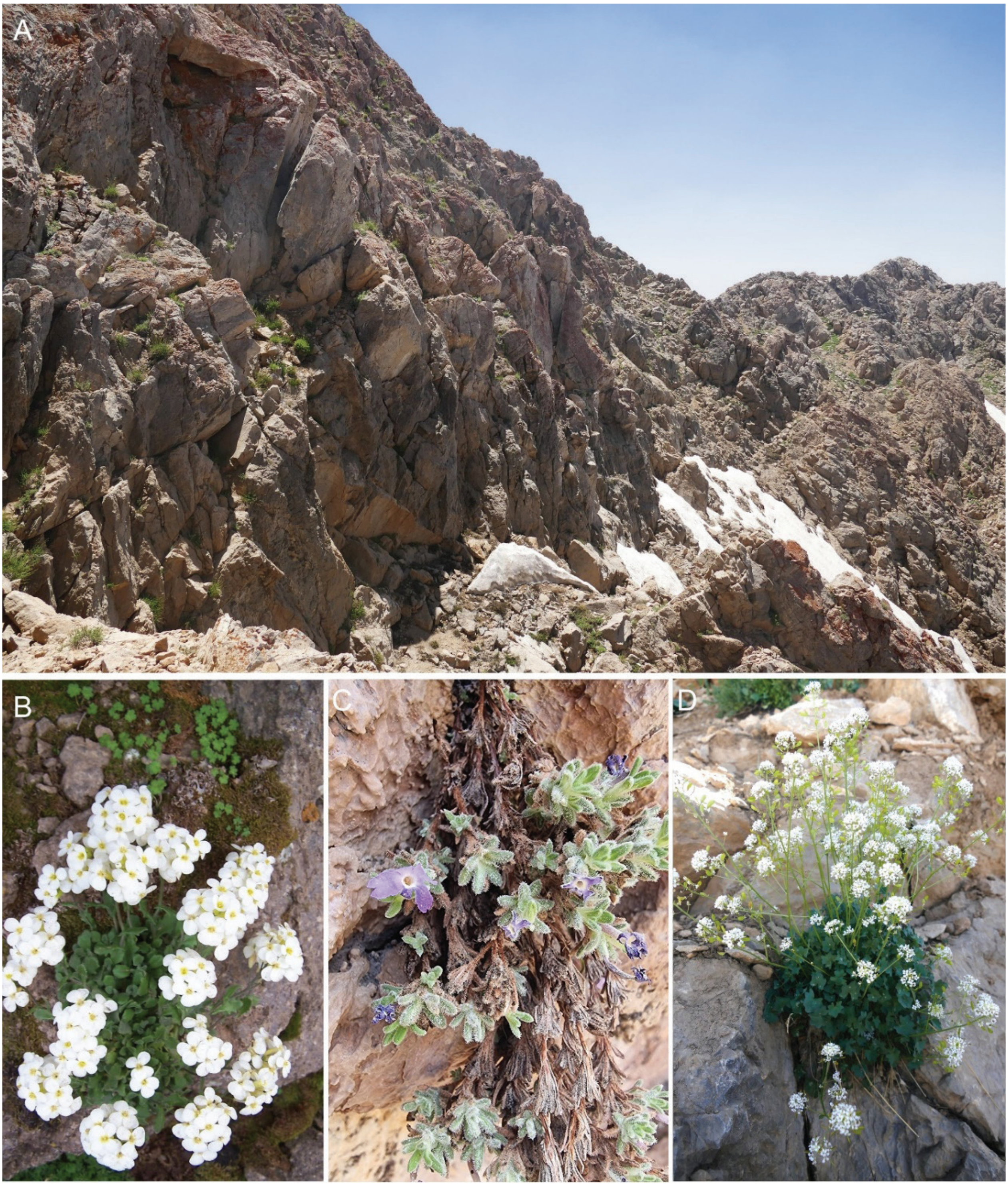

Figure 5. A. View of the rock habitat with chasmophytic vegetation (Mount Zardigari, 3,700 m a.s.l.). Examples of chasmophytic species: **B.** *Arabis caucasica* (Mount Zardigari, 3,400 m a.s.l). **C.** *Dionysia bazoftica* (Mount Tatara, 3,050 m a.s.l). **D.** *Graellsia saxifragifolia* (Mount Zardigari, 3,400 m a.s.l. Photos by MY.

relevant floras including Flora Iranica (Rechinger 1963–2015) and Flora of Iran (Assadi et al. 1989–2021). All specimens were deposited in the Herbarium of the University of Isfahan (HUI) for future reference and study. We assigned the species to the major vegetation types (to one or to a combination of types), the elevation zones, and chorotypes, based on our field observations during this study, our observations in other mountain ranges, literature studies, and using Flora Iranica (Rechinger 1963–2015), and Flora of Iran (Assadi et al. 1989–2021). Raunkiaer's classification system (Raunkiaer 1934) was used to determine the life forms of plants, classified into five groups: chamaephytes, geophytes, hemicryptophytes, phanerophytes, and therophytes.

Results and discussion

Flora

A total of 308 vascular plant species belonging to 185 genera and 47 families were identified in this study (Appendix 1). From those, 306 species are angiosperms, while there is only one pteridophyte (*Equisetum arvense*) and one gymnosperm (*Juniperus excelsa*) species. Eudicots accounted for 261 species (85%), while Monocots accounted for 45 species (15%). The largest plant families identified in the area were *Asteraceae* with 44 species, *Fabaceae* with 32 species, *Brassicaceae* with 29 species, *Lamiaceae* with 27 species, *Apiaceae* with 20 species, and *Poaceae* with 18 species (Figure 6A). The order of big families in this region is similar to the entire flora of the Zagros mountain range (Noroozi et al. 2020). Furthermore, the highest number of species among the genera was found in the genus *Astragalus* (23 species), followed by *Allium* (7 species), *Scorzonera* (6 species), *Nepeta* and *Stachys* (both with 5 species; Figure 6B). *Astragalus*, the biggest genus in Iran in terms of number of species (ca. 885 species) and also number of endemics (ca. 589 species; Maassoumi and Khajoei Nasab 2023), is the richest genus in the study area too with high number of endemics to Iran (14 species) and Zagros (6 species). *Allium*, the third biggest genus of Iran with ca. 140 species and ca. 60% endemics (Noroozi et al. 2019b), is the second richest genus in the study area with seven species and only one endemic to Iran. Interestingly, *Cousinia*, which is the second biggest genus of Iran with ca. 300 species and ca. 80% endemics, only has four species in the study area, two of them endemic to Iran. The low species richness of this genus in the study area is probably linked to the fact that *Cousinia* is represented by a low number of species in the alpine zone of Iran (Noroozi et al. 2008).

Life forms

Species adaptations towards climatic variables are reflected in a plant's life forms (Raunkiaer 1934; Cornelissen et al. 2003). Our results show that hemicryptophytes are the most common life form in the study area with 53%, followed by therophytes, geophytes, chamaephytes, and phanerophytes (Figure 7A). Hemicryptophytes are a dominant life form in alpine habitats worldwide (Körner 2021), and the most common one with 76% in the alpine flora of Iran (Noroozi et al. 2008). They are successful in alpine habitats due to having buds located at or just below ground, which protects from frost and desiccation, and also their low-growing structures reduce exposure to wind and retain heat (Körner 2021). Of the 49 therophyte species identified, only three are specifically subalpine and alpine and the rest belong to lower elevation zones reaching the subalpine zone. The strategy of therophytes creates an adaptation to the water limit of the Mediterranean climate, and they are the most dominant life form in Mediterranean open lands, in terms of number of species (e.g. Pignatti 2003; Lazarina et al. 2019). However, this life form has a low proportion in alpine habitats compared to lower elevations, due to the short growing season in alpine habitats (Körner 2021). In the alpine flora of Iran, this life form is only 2.5% of the total, which is very low compared to the flora of lower elevations of the region (Noroozi et al. 2008). The proportion of geophytes significantly increases along the elevation gradient in the Mediterranean regions (Lazarina et al. 2019), but in our study, geophytes are more common in the montane zone and less present in alpine habitats. Only 7% of the subalpine and alpine species of this study are geophytes. This result is in line with the proportions of geophytes in the alpine flora of Iran (6%; Noroozi et al. 2008). Phanerophytes, mainly shrubs, are distributed predominantly in the montane zone (montane steppe shrublands) but also extend into the lower elevations of the subalpine zone. Species of *Amygdalus*, *Cerasus*, *Cotoneaster*, *Rosa*, and *Daphne* are among them. *Juniperus excelsa* is another species which in some areas of Alborz and Zagros is dominant in the treeline zone creating *Juniperus* woodlands, but it has become very scarce in most parts of these mountains, including the study area, more likely due to anthropogenic activities (Akhani et al. 2013; Ravanbakhsh et al. 2016).

Chorotypes

In terms of chorotypes, the majority of the identified species belong to the IT region (52%). Other significant chorotypes include combinations of the IT, Euro-Siberian (ES), and Mediterranean (M) regions (Figure 7B). Interestingly, the floristic affinity with the ES region is stronger than with the M region (Figure 7B), while for the entire Zagros flora, the floristic affinity with the M region is stronger (Noroozi et al. 2020). This can be due to the elevation zone of the study area, as with increasing elevation, the floristic affinity to the ES region increases and to the M and Saharo-Sindian (SS) regions decreases. This may be due to climatic factors such as higher precipitation and lower temperatures at higher elevations. In addition, the Alborz and Zagros have always acted as migration corridors between Central Asia and the European mountains (Manafzadeh et al. 2014) which can be another reason for the high floristic similarity between these mountains and the ES high mountains. The floristic affinity with the SS region is very poor in the study area (Figure 7B), which could be expected due to the very dry climate (Djamali et al. 2011) and poor mountain ecosystems of the SS region.

Approximately 19% of the identified species are endemic to Iran, and 7% are endemic to the Zagros mountain range. Comparative studies, such as those by Noroozi et al. (2019a, 2019b), have documented endemic species distribution across Iran, showing different rates of endemism in different parts, including the Zagros mountain range. Based on Noroozi et al. (2019a), mountains of Fereydunshahr are centers of endemism and among the top 10% richest endemic hotspots in the Iranian Plateau.

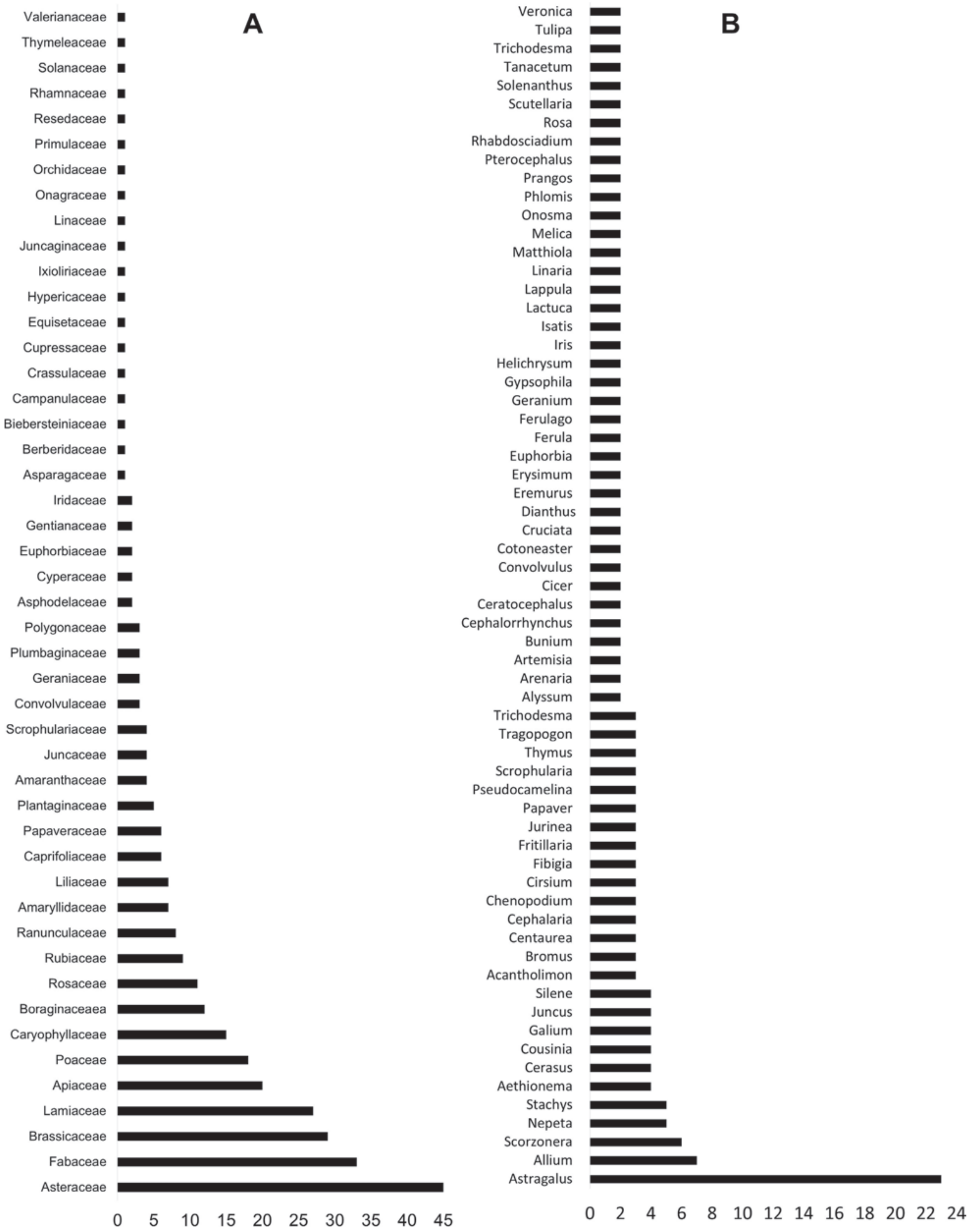

Figure 6. The number of plant species in each family **(A)** and each genus **(B)** within the study area. Only genera having more than two species are shown.

Species within elevation zone

A considerable number of species are distributed in both montane and subalpine zones (33%; Table 1), 20% of the species are subalpine and only 9% are alpine species, while 8% of species are distributed across both the subalpine and alpine zones. Montane species (15%) are particularly prevalent in the study area. Many species recorded in this study have their optimal elevation distribution in the montane zone, but their upper elevation

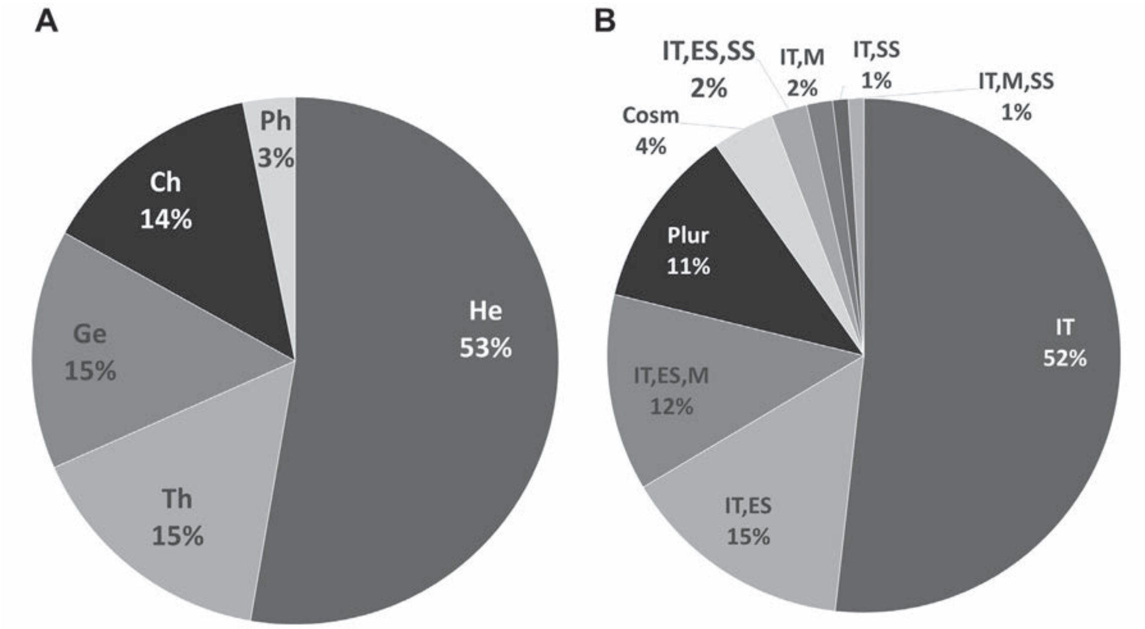

Figure 7. A) The percentage of life forms in the study area (Ch: chamaephytes, Ge: geophytes, He: hemicryptophytes, Ph: phanerophytes, and Th: therophytes). **B)** Chorotypes of species in the region (IT: Iranian-Turanian, ES: Euro-Siberian, M: Mediterranean, SS: Saharo-Sindian, Cosm: Cosmopolitan, Plur: Pluriregional).

range extends to the subalpine zone (above 2,500 m a.s.l) and thus are frequent within the study area. The highest summit within the study area is 3,700 m a.s.l. and only a small area of true alpine habitat exists within the study area. Therefore, the size of the alpine zone in this region is small, and only ca. 9% of the species are real alpine species. The decreasing species richness along elevation gradients that is observed during this study, follows the general trend observed in mountains worldwide, driven by reductions in both surface area and temperature (Peters et al. 2016; Körner 2021).

Although the number of alpine species is low, most of them are endemics to Iran (57%). In the lower elevation zones, the rate of endemics is lower, with 38% and 20% for subalpine and montane zones, respectively (Table 1). This is in line with previous studies that show that the rate of endemism increases along elevation gradients in different parts of the world (Irl et al. 2015; Steinbauer et al. 2016), and our specific region (Noroozi et al. 2019b, 2024). High endemism at higher elevations is caused by increasing isolation which increases allopatric speciation rates (Hughes and Atchison 2015; Steinbauer et al. 2016).

Species within major vegetation types

As presented in Table 2, most of the species belong to the subalpine and alpine thorn-cushion grasslands (24%), which cover a major part of the study area and have the biggest gamma diversity. Moreover, this vegetation type has an optimal length of growing season at this elevation due to its short snow cover duration. The length of snow cover determines the length of growing season in alpine habitats, one of the most important factors determining the species composition in general (Körner 2021), and in the high mountains of Iran in particular (Noroozi et al. 2010; Noroozi and Körner 2018). Additionally, the tightly packed apical meristems of cushions, along with a dense layer of stems and dead leaves, can effectively buffer against environmental extremes (Cavieres et al. 2007). This makes cushion plants important foundation species that facilitate and support many other species that struggle to survive or cannot exist at all in the surrounding open areas, they function as micro-refugia by facilitating less stress-tolerant species in severe environments (Cavieres and Badano 2009; Butterfield et al. 2013). This facilitation has an im-

Table 1. Occurrence of plant species in different elevation zones of Fereydunshahr. The number of species in each zone, their proportion of the entire flora, number of endemics to Iran in each zone and proportion of the endemics in each zone are presented.

Category	Elevation range (m a.s.l.)	No. species	% species	No. endemics	% endemics
Montane-Subalpine (ms)	1200–3400	102	33	26	25
Subalpine (s)	2700–3400	62	20	23	37
Montane (m)	1200–2700	46	15	9	20
Lowland-Montane (lm)	<1200–2700	30	10	0	0
Alpine (a)	3400–4000	28	9	16	57
Subalpine-Alpine (sa)	2700–4000	24	8	5	22
Lowland-Subalpine (ls)	<1200–3400	16	5	0	0

Table 2. Number and percentage of species and endemic species in different vegetation types of Fereydunshahr.

Vegetation types	No. Species	% Species	No. Endemics	% Endemics
Subalpine and alpine thorn-cushion grasslands	75	24	28	38
Montane steppe shrublands & Subalpine and alpine thorn-cushion grasslands	69	23	21	30
Montane steppe shrublands	57	19	8	14
Montane steppe shrublands & Subalpine tall-umbelliferous vegetation types & Subalpine and alpine thorn-cushion grasslands	24	8	2	8
Ruderal	28	9	1	4
Subalpine tall-umbelliferous vegetation types	16	5	9	56
Wetlands	14	5	1	7
Chasmophytes	14	5	6	43
Subalpine tall-umbelliferous vegetation types & Subalpine and alpine thorn-cushion grasslands	11	4	3	27

portant role in increasing the alpha, gamma and phylogenetic diversity of the communities with a dominant cushion life form (Butterfield et al. 2013; Cavieres et al. 2014).

Moreover, 19% of species belong to montane steppe shrublands, 5% to subalpine tall-umbelliferous vegetation types, 5% to wetlands, and 5% to chasmophytic vegetation. A high proportion of species are distributed in both montane steppe shrublands and subalpine and alpine thorn-cushion grasslands (23%). The rest of the species belong to multiple vegetation types which are uncommon within the study area. The rate of endemicity in different vegetation types is very variable. A high proportion of species in the subalpine tall-umbelliferous vegetation types are endemic to Iran (56%), followed by chasmophytic vegetation (43%), subalpine and alpine thorn-cushion grasslands (38%), montane steppe shrublands (14%), wetlands (7%) and ruderals (4%). In general, across diverse regions, the proportion of endemics is high in scree and chasmophytic habitats (Hobohm 2014) and low in wetlands and ruderal habitats which usually are widely distributed (Naqinezhad et al. 2010; Hobohm 2014). We do not have an entire species list for the subalpine tall-umbelliferous vegetation types of Zagros, or entire high mountains of Iran, or Southwest Asia, to be able to compare with other vegetation types to confirm if high endemicity is a general character for this vegetation type or just a local character. However, we know that scree habitats in high mountains have rich endemic diversity (Hobohm 2014) and subalpine tall-umbelliferous vegetation types are typical of steep slopes with screes in Southwest Asian Mountains (Noroozi 2020).

Conclusion

In general, this study provides valuable insights into the flora of the subalpine and alpine zones of Fereydunshahr County with their life forms, chorotypes, elevation zones, and vegetation types occurring in the area. This study also highlights the species richness of certain areas. However, there were several limitations to the study that need to be considered. Despite extensive fieldwork and efforts to identify all species, the species list presented in this study may not be comprehensive, due to seasonal variations, inaccessibility of certain areas, and the problem of overlooking small species. Further research, including detailed vegetation data collection and analysis is required, to fully understand these ecosystems, the dynamics within plant communities, and the effects of environmental variables on species composition and vegetation dynamics, to ensure an accurate representation of the region's flora. Such in-depth investigations are essential for developing effective conservation strategies and ensuring the sustainable management of these valuable ecological areas.

Although the region is identified as a center of endemism, there is no protected area to conserve the natural habitats of the region (Noroozi et al. 2019a). The area faces several significant threats that put the rich biodiversity and endemic species of the area at risk. Habitat destruction driven by anthropogenic activities such as overgrazing, agricultural expansion, and infrastructure projects such as roads, dams and mines, fragment and reduce natural habitats. Based on paleobotanical studies, the vegetation types of Zagros have been clearly impacted by anthropogenic activities over the last five millennia (Djamali et al. 2009). According to genetic studies, goats were domesticated in the Zagros (Zeder and Hesse 2000) and the history of goat herding in the Central Zagros goes back to ca. 10,000 years ago (Gallego-Llorente et al. 2016). Currently, overgrazing by livestock is very significant in these mountains and leads to soil erosion and degradation of the plant communities (Hashemi et al. 2019; Bagheri et al. 2022). The abundance of poisonous and/or thorny species, such as *Euphorbia*, *Cirsium*, and *Cousinia* (overgrazing indicators) in the highlands of Fereydunshahr indicates that there is a high pressure from overgrazing. Illegal harvesting and the collection of rare plants for trade also threaten the existence of many species. Climate change and global warming, altering precipitation patterns and temperature regimes, which can shift vegetation zones and disturb the ecological balance of the high mountain biodiversity, are a threat to all alpine habitats (Dullinger et al. 2012; Pauli et al. 2012). Addressing these threats is fundamental for comprehensive protection and conservation strategies, including habitat preservation, strict regulation of land use, and community engagement in conservation efforts to preserve the unique ecological value and biodiversity of the mountains of Fereydunshahr.

Data availability

All data are presented in the paper.

Author contributions

AB and JN got the idea and planned the research. MY conducted the field sampling, identified the species, analyzed the data, and drafted the manuscript. AB and JN contributed to species identification, and manuscript writing and editing. All authors read and agreed to the published version of the manuscript.

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Appendix 1

Table A1. Complete list of vascular plants in the subalpine and alpine zones of the mountains in Fereydunshahr along with their characteristics. Abbreviations: **Life form:** Ch = chamaephyte, He = hemicryptophyte, Ph = phanerophyte, Th = therophyte, Ge = geophyte; **Chorotypes:** Cosm = Cosmopolitan, ES = Euro-Siberian, IT = Irano-Turanian, M = Mediterranean, Plur = Pluriregional, SS = Sahara-Sindian; **Endemic:** Ir = endemic to Iran, Za = endemic to Zagros; **Elevation zones:** a = alpine, s = subalpine, m = montane, lm = lowland-montane, ls = lowland-subalpine, ms = montane-subalpine, sa = subalpine-alpine; **Vegetation types:** 1 = Ruderal, 2 = Wetlands, 3 = Chasmophytic vegetation, 4 = Montane steppe shrublands, 5 = Subalpine tall-umbelliferous vegetation, 6 = Subalpine and alpine thorn-cushion grasslands.

Species	Endemic	Vegetation types	Elevation zones	Life form	Chorotype
Amaranthaceae					
Chenopodium album L.	-	1	ls	Th	Cosm
Chenopodium botrys L.	-	1	ms	Th	Plur
Chenopodium foliosum Asch.	-	1	sa	Th	Plur
Noaea mucronata (Forssk.) Asch. & Schweinf.	-	1	m	Ch	IT, M, SS
Amaryllidaceae					
Allium ampeloprasum L.	-	4	lm	Ge	IT, M, SS
Allium austroiranicum R.M.Fritsch	Ir	5	s	Ge	IT
Allium fibrosum Regel	-	4, 6	ms	Ge	IT
Allium stipitatum Regel	-	6	sa	Ge	IT, ES
Allium pseudoampeloprasum Miscz. ex Grossh.	-	4	m	Ge	IT, ES
Allium scabriscapum Boiss.	-	4	m	Ge	IT
Allium xiphopetalum Aitch. & Baker	-	4, 6	ms	Ge	IT
Apiaceae					
Apium nodiflorum (L.) Lag.	-	5	ms	Ge	Plur
Astrodaucus orientalis (L.) Drude	-	1	m	Th	IT
Bunium caroides (Boiss.) Hausskn. ex Bornm.	-	1	ms	Ge	IT
Bunium luristanicum Rech.f.	Ir	1	m	Ge	IT
Dorema aucheri Boiss.	Ir	5	s	He	IT
Elaeosticta nodosa (Boiss.) Boiss.	Za	4	m	Ge	IT
Eryngium billardieri Delile	-	5	ms	He	IT, ES
Ferula haussknechtii H.Wolff ex Rech.f.	-	5	s	He	IT
Ferula microcolea (Boiss.) Boiss.	Ir	5	s	He	IT
Ferulago angulata (Schltdl.) Boiss.	-	5	s	He	IT
Ferulago contracta Boiss. & Hausskn.	Ir	5	s	He	IT
Pimpinella tragium Vill.	-	5, 6	sa	He	IT, M, ES
Prangos ferulacea (L.) Lindl.	-	5	s	He	IT, M
Prangos uloptera DC.	-	5	s	He	IT
Rhabdosciadium aucheri Boiss.	Za	5	s	He	IT
Rhabdosciadium straussii Hausskn. ex Bornm.	Ir	5	s	He	IT
Scandix iberica M.Bieb.	-	1	ls	Th	IT, ES
Thecocarpus meifolius Boiss.	Ir	5	ms	He	IT
Turgenia latifolia (L.) Hoffm.	-	1	ls	Th	IT, M, ES
Zeravschania aucheri (Boiss.) Pimenov	Ir	5	ms	He	IT
Asparagaceae					
Muscari neglectum Guss. ex Ten.	-	4	ms	Ge	IT, M, ES
Asphodelaceae					
Eremurus persicus (Jaub. & Spach) Boiss.	-	6	sa	Ge	IT
Eremurus spectabilis M.Bieb.	-	6	s	Ge	IT, ES
Asteraceae					
Achillea wilhelmsii K.Koch	-	1	lm	He	IT, M, ES
Arctium lappa L.	-	1	m	He	Plur
Artemisia haussknechtii Boiss.	-	3	sa	He	IT
Artemisia persica Boiss.	-	6	a	Ch	IT, ES
Centaurea aucheri (DC.) Wagenitz	-	4, 6	ms	He	IT
Centaurea depressa M.Bieb.	-	1	m	Th	IT, ES
Centaurea virgata Lam.	-	1	m	He	IT, ES
Cephalorrhynchus microcephalus (DC.) Schchian	-	1	lm	Ge	IT
Cephalorrhynchus rechingerianus Tuisl	-	1	Ls	Ge	IT
Cichorium intybus L.	-	1	Ls	He	Plur
Cirsium bracteosum DC.	-	4, 6	ms	He	IT
Cirsium congestum Fisch. & C.A.Mey. ex DC.	-	4	m	He	IT, ES
Cousinia bachtiarica Boiss. & Hausskn.	Za	6	s	He	IT

Species	Endemic	Vegetation types	Elevation zones	Life form	Chorotype
Cousinia cylindracea Boiss.	Ir	6	s	He	IT
Cousinia lasiolepis Boiss.	-	6	a	He	IT
Cousinia multiloba DC.	-	6	a	He	IT
Crepis micrantha Czerep.	-	4	lm	Th	Plur
Echinops ritrodes Bunge	-	4, 6	ms	He	IT
Gundelia tournefortii L.	-	4	m	He	IT, M, ES
Helichrysum globiferum Boiss.	Ir	4, 6	ms	Ch	IT
Helichrysum oligocephalum DC.	Ir	6	s	Ch	IT
Iranecio paucilobus (DC.) B.Nord.	-	6	s	He	IT
Inula britannica L.	-	4, 6	ms	He	IT, M, ES
Jurinea eriobasis DC.	Ir	4	m	He	IT
Jurinea meda Bornm.	Za	6	a	He	IT
Jurinea prasinophylla Rech.f.	Za	4	m	He	IT
Lactuca orientalis (Boiss.) Boiss.	-	4, 6	ms	He	Plur
Lactuca serriola L.	-	4	m	He	Plur
Pentanema pulicariiforme (DC.) Rech.f.	Ir	3	s	He	IT
Phagnalon persicum Boiss.	Ir	3	a	He	IT
Psychrogeton alexeenkoi Krasch.	-	3	a	He	IT, ES, SS
Scorzonera calyculata Boiss.	Ir	6	a	He	IT
Scorzonera ispahanica Boiss.	Ir	4	m	He	IT
Scorzonera laciniata L.	-	4	lm	Th	IT, M, ES
Scorzonera pseudolanata Grossh.	-	4	m	He	IT, Es
Scorzonera ramosissima DC.	-	6	s	Ch	IT
Scorzonera mucida Rech.f., Aellen & Esfand	-	4	m	Ge	IT
Senecio vernalis Waldst. & Kit	-	4, 6	ms	Th	IT, M, ES
Tanacetum polycephalum Sch.Bip.	-	6	a	He	IT
Tanacetum uniflorum (Fisch. & C.A.Mey. ex DC.) Sch.Bip.	-	4, 6	ms	Ch	IT, ES
Tragopogon bakhtiaricus Rech.f.	Za	6	a	He	IT
Tragopogon jesdianus Boiss. & Buhse.	Ir	4, 6	ms	He	IT
Tragopogon longirostris Sch.Bip	-	4, 6	ms	He	IT, M, ES
Xeranthemum longepapposum Fisch. & C.A.Mey.	-	4, 6	ms	Th	IT, ES
Berberidaceae					
Leontice leontopetalum L.	-	4	m	He	IT, ES, SS
Biebersteiniaceae					
Biebersteinia multifida DC.	-	6	s	Ge	IT, ES
Boraginaceae					
Anchusa italica Retz.	-	1	m	He	IT, M, ES
Lappula barbata (M.Bieb.) Gürke	-	4, 6	ms	Th	IT, M, ES
Lappula microcarpa (Ledeb.) Gürke	-	6	s	Th	IT, M, ES
Nonea persica Boiss.	Ir	4, 6	ms	He	IT
Onosma demavendica Riedl.	Ir	4, 6	ms	Ge	IT
Onosma kotschyi Boiss.	Ir	4, 6	ms	He	IT
Rindera lanata Bunge	-	4, 6	ms	He	IT, ES
Solenanthus circinnatus Ledeb.	-	6	s	He	IT, ES
Solenanthus stamineus J.F.Macbr.	-	6	a	He	IT, M, ES
Trachelanthus cerinthoides Kunze	-	4, 6	ms	He	IT
Trichodesma aucheri DC.	Ir	4, 6	ms	He	IT
Trichodesma incanum (Bunge) A. DC.	-	4, 6	ls	He	IT, ES
Brassicaceae					
Aethionema arabicum (L.) Andrz. ex DC.	-	4	lm	Th	IT, ES
Aethionema elongatum Boiss.	-	4, 6	ms	He	IT
Aethionema stenopterum Boiss.	Ir	3	ms	He	IT
Aethionema trinervium (DC.) Boiss.	-	6	sa	He	IT
Alyssum bracteatum Boiss. & Bushe	Ir	4, 6	ms	He	IT
Alyssum heterotrichum Boiss.	-	4, 6	ms	He	IT
Arabis caucasica Willd.	-	3	sa	He	IT, M, ES
Aubrieta parviflora Boiss.	-	3	ms	He	IT
Brossardia papyracea Boiss.	-	4	m	He	IT
Cardaria draba (L.) Desv.	-	1	m	Th	Cosm
Clypeola lappacea Boiss.	-	4, 6	ms	Th	IT
Conringia persica Boiss.	-	4, 6	ms	Th	IT
Descurainia sophia (L.) Webb ex Prantl	-	1	ms	Th	IT, M, ES
Drabopsis verna K.Koch	-	4, 6	ms	Th	IT, M, SS
Erysimum badghisi (Korsh.) Lipsky ex N.Busch	-	6	s	He	IT
Erysimum griffithianum Boiss.	-	4, 6	ms	He	IT

Species	Endemic	Vegetation types	Elevation zones	Life form	Chorotype
Fibigia macrocarpa (Boiss.) Boiss.	-	4, 6	ms	He	IT
Fibigia suffruticosa (Vent.) Sweet	-	4, 6	ms	He	IT
Fibigia umbellata (Boiss.) Boiss.	-	6	a	He	IT
Graellsia saxifragifolia (DC.) Boiss.	-	3	a	He	IT
Isatis cappadocica Desv.	-	6	s	He	IT
Isatis kotschyana Boiss. & Hohen. ex Boiss.	-	4, 6	ms	He	IT
Lepidium latifolium L.	-	1	ms	Ge	IT, M, ES
Matthiola alyssifolia Bornm.	-	4, 6	ms	He	IT
Matthiola ovatifolia Boiss.	Ir	4, 6	ms	He	IT, M
Peltaria angustifolia DC.	-	4	m	Th	IT
Pseudocamelina aphragmodes (Boiss.) N. Busch	Za	6	a	He	IT
Pseudocamelina campylocarpa (Boiss.) N. Busch	Za	6	s	He	IT
Pseudocamelina glaucophylla N. Busch	Ir	4, 6	ms	He	IT
Campanulaceae					
Asyneuma cichoriiforme (Boiss.) Bornm.	-	4, 6	ms	He	IT, M
Caprifoliaceae					
Cephalaria juncea Boiss.	Ir	4, 6	ms	He	IT
Cephalaria microcephala Boiss.	-	6	s	He	IT
Cephalaria syriaca (L.) Schrad. ex Roem. & Schult.	-	4, 6	ms	Th	IT, M, ES
Pterocephalus canus Coult. ex DC.	-	4, 6	ms	He	IT
Pterocephalus ghahremanii Jamzad	Za	6	s	He	IT
Valeriana sisymbriifolia Kabath	-	5, 6	s	He	IT
Caryophyllaceae					
Acanthophyllum crassifolium Boiss.	-	4, 6	ms	Ch	IT
Arenaria persica Boiss.	Za	6	a	Ch	IT
Arenaria serpyllifolia L.	-	4, 6	ms	Th	Plur
Cerastium dichotomum L.	-	4, 6	ms	Th	Plur
Dianthus libanotis Labill.	-	4, 6	ms	Ch	IT, ES
Dianthus macranthus Boiss.	Ir	6	s	He	IT
Gypsophila persica Barkoudak	Ir	4, 6	ms	He	IT
Gypsophila virgata Boiss.	-	4, 6	ms	Ch	IT
Mesostemma kotschyanum (Fenzl ex Boiss.) Vved.	-	5	s	He	IT
Minuartia lineata Bornm.	-	6	sa	He	IT
Silene aucheriana Boiss.	-	6	sa	He	IT, ES
Silene chlorifolia Sm.	-	6	sa	He	IT, ES
Silene morganae Freyn	-	4, 6	ms	He	IT, M, ES
Silene meyeri Fenzl ex Boiss. & Buhse	-	3	sa	Ch	IT, ES
Vaccaria grandiflora Jaub. & Spach	-	1	lm	Th	Plur
Convolvulaceae					
Convolvulus arvensis L.	-	1	lm	He	Cosm
Convolvulus urosepalus Pau.	Za	6	s	Ch	IT
Cuscuta campestris Yunck.	-	1	lm	Th	Plur
Crassulaceae					
Rosularia elymaitica (Boiss. & Hausskn. ex Boiss.) A. Berger	Ir	3	s	He	IT, ES
Cupressaceae					
Juniperus excelsa M.Bieb.	-	3	s	Ph	IT, ES
Cyperaceae					
Carex microglochin Wahlenb.	-	2	a	Ge	Plur
Eleocharis uniglumis (Link) Schult.	-	4	m	He	Cosm
Equisetaceae					
Equisetum arvense L.	-	2	lm	He	Plur
Euphorbiaceae					
Euphorbia decipiens Boiss. & Buhse	Ir	6	s	He	IT
Euphorbia heteradena Jaub. & Spach	-	4, 5, 6	ms	He	IT, ES
Fabaceae					
Astragalus alyssoides Lam.	-	6	sa	He	IT
Astragalus andalanicus Boiss. & Hausskn.	-	6	sa	Ch	IT
Astragalus apricus Bunge	-	6	sa	He	IT
Astragalus brachycalyx Phil.	-	6	s	Ch	IT
Astragalus brachyodontus Boiss.	Ir	4, 6	ms	He	IT
Astragalus callistachys Buhse	Ir	4	m	Ch	IT
Astragalus cephalanthus DC.	Ir	4, 6	ms	Ch	IT
Astragalus chrysotrichus Boiss.	Za	4, 6	ms	He	IT
Astragalus compactus Reiche	-	6	s	Ch	IT, ES
Astragalus curvirostris Boiss.	-	4, 6	ms	He	IT, ES, SS

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Astragalus cyclophyllon Beck	Ir	4, 6	ms	He	IT
Astragalus eriosphaerus Boiss. & Hausskn.	Ir	4, 6	ms	Ch	IT
Astragalus fragiferus Bunge	Ir	6	a	Ch	IT
Astragalus holopsilus Bunge	Za	4, 6	ms	He	IT
Astragalus megalotropis Bunge	-	4, 6	ms	He	IT, ES
Astragalus microphysa Boiss.	Ir	6	a	Ch	IT
Astragalus murinus Boiss.	Za	6	a	Ch	IT
Astragalus ovinus Boiss.	-	5, 6	sa	He	IT
Astragalus patrius Maassoumi	Ir	6	a	He	IT, ES
Astragalus ptychophyllus Boiss.	Za	4, 6	ms	Ch	IT
Astragalus raswendicus Hausskn. & Bornm.	Za	6	s	Ch	IT
Astragalus rhodosemius Boiss. & Hausskn.	Ir	6	sa	Ch	IT
Astragalus susianus Boiss.	Za	6	Sa	Ch	IT
Cicer oxyodon Boiss. & Hohen.	-	4, 5, 6	ms	He	IT
Cicer spiroceras Jaub. & Spach	Ir	4, 5, 6	ms	He	IT
Coronilla varia L.	-	4	lm	He	IT, M, ES
Lotus corniculatus L.	-	4, 5, 6	ms	He	IT, M, ES
Onobrychis cornuta (L.) Desv.	-	6	sa	Ch	IT, Es
Ononis spinosa L.	-	2	lm	Ch	IT, M, ES
Oxytropis chrysocarpa Boiss.	-	6	a	He	IT
Trigonella aphanoneura Rech.f.	Za	5	s	He	IT
Vicia variabilis Freyn & Sint. ex Freyn	-	4, 5, 6	ls	He	IT
Gentianaceae					
Centaurium erythraea Rafn	-	6	s	He	IT, M, ES
Gentiana olivieri Griseb.	-	4, 5, 6	ms	He	IT, ES
Geraniaceae					
Erodium cicutarium (L.) L'Hér.	-	4	m	Th	IT, M, ES
Geranium persicum Schönb.-Tem.	-	4, 5, 6	ms	Ge	IT
Geranium tuberosum L.	-	4, 5, 6	ms	Ge	IT, M, ES
Hypericaceae					
Hypericum scabrum L.	-	4, 5, 6	ms	He	IT, ES
Iridaceae					
Iris iberica Steven.	-	4, 6	ms	Ge	IT
Iris hymenospatha B.Mathew & Wendelbo	Ir	4	m	Ge	IT
Ixioliriaceae					
Ixiolirion tataricum (Pall.) Schult. & Schult.f.	-	4	m	Ge	Plur
Juncaceae					
Juncus articulatus L.	-	2	m	Ge	Plur
Juncus bufonius L.	-	2	ms	Th	Cosm
Juncus turkestanicus V.I.Krecz. & Gontsch.	-	2	ls	Th	IT, ES
Juncus inflexus L.	-	2	ls	He	Cosm
Juncaginaceae					
Triglochin palustris L.	-	2	ls	Ge	Plur
Lamiaceae					
Dracocephalum kotschyi Boiss.	Ir	6	s	Ch	IT
Eremostachys macrophylla Montbret & Aucher ex Benth.	-	4, 5, 6	ms	He	IT, ES
Lamium amplexicaule L.	-	1	lm	Th	IT, M, ES
Mentha longifolia (L.) L.	-	2	ms	He	Plur
Nepeta laxiflora Benth.	Za	5, 6	s	He	IT
Nepeta lasiocephala Benth.	Ir	6	a	He	IT
Nepeta persica Boiss.	-	4, 5, 6	ms	Ch	IT
Nepeta sessilifolia Bunge	Ir	3	a	He	IT
Nepeta sintenisii Bornm.	-	4, 5, 6	ms	He	IT
Phlomis anisodonta Boiss.	Ir	6	sa	He	IT
Phlomis olivieri Benth.	-	4	lm	Ch	IT
Salvia aristata Aucher ex Benth.	Ir	4	m	He	IT
Salvia atropatana Bunge	-	4, 6	ms	He	IT
Salvia hydrangea DC. ex Benth.	-	4, 5, 6	ms	He	IT, M
Salvia sclarea L.	-	4, 6	ms	He	IT, M, ES
Scutellaria multicaulis Boiss.	Ir	6	sa	He	IT
Scutellaria pinnatifida A.Ham.	-	5, 6	s	He	IT
Stachys acerosa Boiss.	Ir	5, 6	sa	Ch	IT
Stachys benthamiana Boiss.	Ir	4, 6	ms	He	IT
Stachys inflata Benth.	-	4, 6	ms	He	IT, ES, SS
Stachys lavandulifolia Vahl	-	4, 6	ms	He	IT, ES

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Stachys pilifera Benth.	Za	6	a	He	IT
Teucrium orientale L.	-	4, 5, 6	ls	He	IT, ES
Thymus carmanicus Jalas	-	6	a	Ch	IT
Thymus daenensis Celak.	Ir	6	s	He	IT
Thymus kotschyanus Boiss. & Hohen.	-	4, 6	ms	Ch	IT
Ziziphora clinopodioides Lam.	-	4, 6	ms	Ch	IT, ES
Liliaceae					
Fritillaria imperialis L.	-	5, 6	s	Ge	IT
Fritillaria persica L.	-	5, 6	s	Ge	IT
Fritillaria reuteri Boiss.	Ir	2	s	Ge	IT
Gagea gageoides (Zucc.) Vved.	-	2	ms	Ge	IT, ES
Ornithogalum orthophyllum Ten.	-	4	ms	Ge	Plur
Tulipa biflora Pall.	-	4, 5, 6	ms	Ge	IT, ES
Tulipa stylosa Fisch.	-	4, 5, 6	ms	Ge	IT
Linaceae					
Linum album Kotschy ex Boiss.	Ir	4	m	He	IT
Onagraceae					
Epilobium hirsutum L.	-	2	lm	He	Plur
Orchidaceae					
Dactylorhiza umbrosa (Kar. & Kir.) Nevski	-	2	ms	Ge	IT, ES
Papaveraceae					
Corydalis rupestris Kotschy	-	3	s	Ge	IT, ES
Glaucium corniculatum (L.) Curtis	-	4	m	Th	Cosm
Papaver armeniacum (L.) DC	-	6	sa	He	IT
Papaver cylindricum Cullen	-	4	m	Th	IT, M, ES
Papaver decaisnei Hochst. & Steud. ex Elkan	-	4	m	Th	IT, SS
Roemeria refracta DC.	-	1	lm	Th	IT, ES, SS
Plantaginaceae					
Linaria lineolata Boiss.	-	5, 6	s	He	IT, ES
Linaria pyramidalis F.Dietr.	-	5, 6	s	He	IT, ES
Plantago lanceolata L.	-	4	m	He	Plur
Veronica farinosa Hausskn.	Za	5, 6	s	He	IT
Veronica orientalis Mill.	-	4, 5, 6	ms	He	IT, M, ES
Plumbaginaceae					
Acantholimon aspadanum Bunge	Za	6	sa	Ch	IT
Acantholimon hohenackeri (Jaub. & Spach) Boiss.	-	6	s	Ch	IT
Acantholimon senganense Bunge	-	6	sa	Ch	IT
Poaceae					
Arrhenatherum kotschyi Boiss.	-	4	m	Ge	IT
Boissiera squarrosa (Sol.) Nevski	-	4	m	Th	Plur
Bromus danthoniae Trin.	-	4	lm	Th	IT, ES, SS
Bromus tectorum L.	-	4	lm	Th	Cosm
Bromus tomentellus Boiss.	-	6	s	He	IT, M, ES
Cynodon dactylon (L.) Pers.	-	4	m	Ge	Cosm
Dactylis glomerata L.	-	4, 6	ls	He	Cosm
Eremopoa persica (Trin.) Roshev.	-	4, 5, 6	ms	Th	Plur
Heteranthelium piliferum (Sol.) Hochst. ex Jaub. & Spach	-	4	lm	Th	IT, M, ES
Hordeum violaceum Boiss. & Hohen.	-	2	s	He	IT, M, ES
Melica jacquemontii Decne.	-	6	s	Ge	Plur
Melica persica Kunth.	-	6	s	Ge	IT
Poa bulbosa L.	-	4, 6	ls	Ge	Plur
Setaria viridis (L.) P.Beauv.	-	4	lm	Th	Plur
Sorghum halepense (L.) Pers.	-	1	lm	Ge	Cosm
Stipa lagascae Roem. & Schult.	-	4	lm	He	IT, SS
Taeniatherum crinitum (Schreb.) Nevski	-	4	lm	Th	Plur
Zingeria trichopoda (Boiss.) P.A.Smirn.	-	4	m	Th	IT, M
Polygonaceae					
Atraphaxis spinosa L.	-	4	m	Ch	Plur
Polygonum arenastrum Boreau	-	4, 5, 6	ls	Th	Plur
Rheum ribes L.	-	6	s	He	IT, M, ES
Primulaceae					
Dionysia bazoftica Jamzad	Za	3	a	Ch	IT
Ranunculaceae					
Adonis aestivalis L.	-	1	lm	Th	IT, M, ES
Anemone biflora DC.	-	4, 5, 6	ms	Ge	IT, ES

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Ceratocephala falcata (L.) Pers.	-	4	lm	Th	IT, M, ES
Consolida barbata (Bunge) Schrödinger	-	4	lm	Th	IT, ES
Ficaria kochii (Ledeb.) Iranshahr & Rech.f.	-	4, 5, 6	ms	Ge	IT
Ranunculus arvensis L.	-	1	m	Th	IT, M, ES
Thalictrum isopyroides C.A. Mey	-	4, 6	ls	He	IT, ES
Resedaceae					
Reseda lutea L.	-	4	m	He	Plur
Rhamnaceae					
Rhamnus cornifolia Boiss. & Hohen.	-	6	s	Ch	IT
Rosaceae					
Amygdalus haussknechtii (C.K.Schneid.) Bornm.	Ir	4, 6	ms	Ph	IT
Cerasus brachypetala Boiss.	-	6	s	Ph	IT
Cerasus mahaleb (L.) Mill.	-	6	s	Ph	Plur
Cerasus microcarpa (C.A.Mey.) K.Koch	-	6	s	Ph	IT
Cerasus pseudoprostrata Pojark.	-	6	s	Ch	IT
Cotoneaster nummularius Fisch. & C.A.Mey.	-	4	m	Ph	Plur
Cotoneaster luristanicus G.Klotz	-	4	m	Ph	IT
Potentilla recta L.	-	4	m	He	Plur
Rosa canina L.	-	4	lm	Ph	IT, M, ES
Rosa orientalis A.Dupont ex Ser.	-	4, 6	ms	Ph	IT
Sanguisorba minor Scop.	-	4	m	He	Plur
Rubiaceae					
Asperula rechingeri Ehrend. & Schönb.-Tem.	Ir	6	a	He	IT
Callipeltis cucullaris (L.) DC.	-	4, 5, 6	ms	Th	IT, ES, SS
Cruciata laevipes Opiz	-	4, 5, 6	ls	He	Plur
Cruciata taurica (Pall. ex Willd.) Ehrend.	-	4	ms	He	IT, M, ES
Galium megalanthum Boiss.	-	6	s	He	IT
Galium pseudokurdicum (Ehrend.) Schönb.-Tem.	-	6	a	Ch	IT
Galium subvelutinum (DC.) K.Koch	-	6	s	He	IT
Galium verum L.	-	4	m	He	Cosm
Rubia rigidifolia Pojark.	Ir	4, 5, 6	ms	Ch	IT
Scrophulariaceae					
Scrophularia frigida Boiss.	Ir	6	a	He	IT
Scrophularia nervosa Benth.	Ir	4, 6	ms	He	IT
Scrophularia striata Boiss.	-	4	lm	He	IT
Verbascum speciosum Schrad.	-	4	lm	He	IT, ES
Solanaceae					
Hyoscyamus kurdicus Bornm.	-	6	s	He	IT
Thymeleaceae					
Daphne mucronata Royle	-	4, 6	ms	Ph	IT, SS
Valerianaceae					
Valerianella dactylophylla Boiss. & Hohen.	-	4	lm	Th	IT, M, ES

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