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VEGETATION CLASSIFICATION AND SURVEY

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EDITORIAL

Vegetation Classification and Survey: the first year

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Abstract

We report on the completed first volume of Vegetation Classification and Survey (VCS), which included ten Research Papers, six Short Database Reports, two Long Database Reports, two Forum Papers and one Report. We highlight three outstanding papers as examples of contributions of which we would like to see more in the future. Finally, we announce a new article type “VCS Methods” and report about the status of two upcoming Special Collections. Lists of colleagues who served as reviewers or linguistic editors in 2020 are included in appendices.

Abbreviations: IAVS = International Association for Vegetation Science; VCS = Vegetation Classification and Survey.

Keywords

article processing charge, ecoinformatics, editorial, gold open access, International Association for Vegetation Science (IAVS), scientific journal, vegetation classification, vegetation survey, vegetation-plot database

Introduction

With this Editorial, we open the second volume of Vegetation Classification and Survey (VCS), a gold open access journal of the International Association for Vegetation Science (IAVS). Establishing a new high-quality journal is a big challenge in these days (some would even say, it is a crazy task), but we think that we are off to a good start.

Our first volume included 22 articles: ten Research Papers, six Short Database Reports, two Long Database Reports, two Forum Papers, one Report and one Editorial. The first authors of these papers came from 15 countries and six continents (i.e., all continents except Antarctica). Altogether, the papers had 145 authors from 26 countries (persons who authored more than one paper are only counted once). Of the research papers, three used the Braun-Blanquet system (Guarino et al. 2018) and three the EcoVeg system (Faber-Langendoen et al. 2014) for naming the vegetation units. Three additional papers did not apply a particular classification system, but used informal units instead, while one paper presented a new classification algorithm.

As Chief Editors of VCS, we emphasise that this successful inaugural volume would not have been possible without the huge support provided by IAVS. Most importantly, IAVS members have been exempted from article processing charges. This exemption will continue in 2021, i.e., papers submitted until 31 December 2021 will be published free of charge after acceptance if the first author is an IAVS member. Besides these financial aspects, the success of the journal relies on the dedication and trust of the authors, reviewers and on the editorial team, who shared our enthusiasm (see also Appendix 1 and 2). Last but not least, we gratefully acknowledge Pensoft, our publisher, whose team has been working tirelessly to make this journal happen.

We expected challenges regarding open access when we wrote our inaugural Editorial one year ago (Jansen et al 2020), especially from the need to require article processing charges and the need to guarantee a high quality of the publications. While we can already assert that the quality of the published papers is pleasingly high, the challenges of asking for money is thankfully still another year away from us given the generous support by IAVS.

Journal management

Papers submitted to VCS are managed and published in the software framework and manuscript management system ARPHA, which was developed by Pensoft. Whereas not everything runs as smoothly and intuitively as one would wish, we are quite taken by the many thoughtful details unique to ARPHA. For hickups and hurdles we can be sure of a never-tired publishing team, eager to fulfil our wishes. If you encounter any glitches or detect a gap in the detailed Author Guidelines, please contact the current Managing Editor.

If you want to have a look at all the articles published in VCS so far, please visit https://vcs.pensoft.net/browse_journal_articles. If you are interested in the number of citations, and who is citing them, you can visit https://scholar.google.de/citations?hl=de&user=X-sKKBm0AAAAJ.

VCS is also partnering with the Vegetation Science Blog (https://vegsciblog.org/), the official blog of the IAVS journals. All five IAVS periodicals (Journal of Vegetation Science, Applied Vegetation Science, Vegetation Classification and Survey, Palaearctic Grasslands, IAVS Bulletin) use the blog as a joint platform to highlight new papers and inform readers about journal developments, new issues and forthcoming special issues. Of the VCS authors of 2020, four used this opportunity to increase the visibility of their publication. Moreover, there have been seven contributions from us editors.

Outstanding papers in 2020

It was difficult to choose outstanding papers from Volume 1 as all contributions had a similarly high level. Nevertheless we want to highlight three papers that, in our opinion, are exemplary for the kind of contributions we would like to see more of in the future.

Abutaha et al. (2020) provided the first classification of the vegetation units on Gebel Elba, an arid mountain range in southeastern Egypt, and identified the environmental factors controlling their distribution. Gebel Elba has vegetation similar to the highlands of East Africa and the southwestern Arabian Peninsula. On the basis of 169 relevés, and using TWINSPAN, the authors identified seven communities along the elevational gradient. They found that each community was restricted to a confined habitat depending on its drought resistance ability. A canonical ordination revealed the importance of elevation and soil quality in determining the vegetation structure of Gebel Elba. The species richness increased with elevation as a result of reduced stress and increased water availability at the upper wadis, showing the importance of orographic precipitation, soil quality and the complex topography in determining the vegetation pattern in this arid region.

Central Asia is another region where vegetation classification in general and the Braun-Blanquet approach in particular do not have a strong tradition. Therefore, it is really impressive how the team of Arkadiusz Nowak has been systematically sampling and analysing one vegetation type of Tajikistan and neighbouring regions after the other. A long series of publications in various international journals has emerged from these studies (e.g. Nowak et al. 2015, Świerszcz et al. 2020). In VCS, Nowak et al. (2020) addressed the diversity of tall-forb vegetation. They used a rich dataset of 244 relevés from throughout Tajikistan and southern Kyrgysztan, classified them with TWINSPAN, and characterised the resulting units comprehensively in terms of diagnostic species, distribution (i.e., maps), environmental and biodiversity variables. Further they translated their results into a formal syntaxonomy, concluding that most of the stands belong to the class *Prangetea ulopterae*, comprising the Irano-Turanian tall-forb communities. The authors also nicely used the opportunity of an online journal to include colour figures at no cost, visualising the structure (and beauty) of their study communities with two photo plates. We hope that other author teams will follow this example in the future.

Vegetation classification is an essential tool for nature conservation. Around the world natural forests have been replaced by agricultural land along human history, but this loss is still in progress in many regions. Tropical and subtropical forests have dramatically declined over the last decades. An example is the tropical seasonally dry forests in South America. Zeballos et al. (2020) conducted a vegetation survey on the southernmost representation of these forests, the subtropical espinal forests in Central Argentina. They sampled 122 plots of forest stands in the Córdoba region, and classified them into four vegetation types of seasonally dry subtropical forest. The main environmental factors affecting species composition were temperature and precipitation seasonality as well as soil-texture and sodium content. The authors emphasise that the remaining forest patches represent only 3% of the potential extent of that vegetation type in Córdoba, with only a small fraction included in protected areas. Therefore, they call for urgent conservation measures to preserve the last remaining forest patches.

News and prospects for 2021

Starting with Volume 2, we introduce a new article type called "VCS Methods". As the label suggests, it will be reserved for methodological papers on vegetation classification and survey, i.e. the description of new methods or the evaluation of existing methods using test data sets and case studies. Methods can be from all fields covered by VCS, including field sampling, databasing, classification methodology or any tool and method used in vegetation ecoinformatics. A paper of 2020 that would have fitted in this category is Attorre et al. (2020).

We also introduce a new article type "Short Communication" for the Permanent Collection *Phytosociological Nomenclature*. It is intended for short papers presenting validations, typifications etc. of previously published syntaxa, provided that these nomenclatural novelties are relevant for a wider international audience. Please note that nomenclatural proposals (e.g., for *nomina conservanda*) should be directly sent to the responsible editor (wolfgang.willner@univie.ac.at). Once a year, the new proposals will be published in conjunction with the Report of the Committee for Changes and Conservation of Names (CCCN), with all authors of proposals being co-authors (additionally, the authors of individual proposals will be indicated in the Report). Publication of nomenclatural proposals will be permanently free of charge. For guidelines on proposals, see Appendix 2 in Theurillat et al. (2021).

In summer 2020, we announced two Special Collections: *Classification of grasslands and other open vegetation types in the Palaearctic* (edited by Idoia Biurrun, Jürgen Dengler, Monika Janišová and Arkadiusz Nowak) and *The 'International Vegetation Classification' initiative: case studies, syntheses, and perspectives on ecosystem diversity around the globe* (edited by Don Faber-Langendoen, Wolfgang Willner, Changcheng Liu, John Hunter and Gonzalo Navarro). Both teams have finished their evaluation of submitted abstracts, and the invited papers are expected to be submitted during the next few months. Since VCS has a continuous publishing model, contributions will be published as soon as they are accepted. In fact, the first paper of the Palaearctic grasslands collection has already been published in Volume 1 (Nowak et al. 2020). Besides being labelled as part of a collection on the title page, all papers belonging to a collection can be accessed via the "Collections" menu under "Articles" or "Issues" on the VCS website or by going directly to https://vcs.pensoft.net/collections (click on the title of the collection to see the list of papers).

If the flow of submissions remains at the current high level, every three months we plan to select an Editors' Choice paper of the previous quarter and highlight it in a vegsciblog entry with a photo (or other illustration), while mentioning also all the other published articles of that period. At the end of the year we intend to compose the cover of the annual volume (online and print-on-demand) from these four photos or illustrations. Therefore, we would like to encourage all authors to submit suitable photos when their article is accepted.

A major goal, given the science evaluation systems in many countries, is the inclusion of VCS in Scopus and the Web of Science at the earliest possible date. Authors can help to achieve this goal in various ways: by submitting high-quality papers to VCS, by serving as reviewers, and, not to forget, by citing VCS papers in other journals!

Author contributions

W.W. planned and drafted this editorial while all other authors made significant contributions.

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Appendix 1

Reviewers for VCS in 2020

We thank the following colleagues who served during the last year as reviewers for VCS (number of reviews in brackets):

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- Christian Berg (1)
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Appendix 2

Linguistic Editors for VCS in 2020

We thank the following colleagues who served during the last year as Linguistic Editors for VCS (number of edited papers in brackets):

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- Megan McNellie (2)
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VEGETATION CLASSIFICATION AND SURVEY

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RESEARCH PAPER

Floristic patterns of the neotropical forests, savannas and scrublands with *Trithrinax campestris* (Arecaceae) in central Argentina

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Abstract

Aims: *Trithrinax campestris* is one of the palm species with the southernmost distribution in the Neotropics. Despite that the vegetation types in which *T. campestris* occurs are nowadays heavily threatened by land use and land cover changes, their floristic composition and structure are still to be documented. In order to characterize *T. campestris* habitats, the aim of this study was to describe the floristic composition of the vegetation types in which this palm occurs and their relationships with different environmental factors.

Study area: The survey was conducted in central Argentina in an area comprising the southern extreme of the distribution of *T. campestris* in the following phytogeographic areas: Espinal, Lowland and Mountain Chaco.

Methods: Following the Braun-Blanquet approach we collected 92 floristic relevés recording a total of 601 vascular plant species. Vegetation was classified through the ISOPAM hierarchical analysis. Bioclimatic and elevation data were related to the floristic data through the ISOMAP ordination. Remote-sensed images (Landsat TM, ETM+ and OLI) were used to characterize the fire frequency in the 92 stands.

Results: Four vegetation types that differed in floristic composition and in diagnostic species were discriminated: 1.1 *Celtis tala*/*Sida rhombifolia* closed forest; 1.2 *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest; 2.1 *Jarava pseudoichu*/*Vachellia caven* open savanna; and 2.2 *Acalypha variabilis*/*Nassella cordobensis* scrubland. The ISOMAP ordination showed that differences in floristic composition were related to elevation, topography and climatic variables. Out of the 92 stands, only 21 showed the occurrence of fires during the period 1999–2018.

Conclusions: Our results evidenced that vegetation types (forests, savannas and scrublands) comprising *T. campestris* developed in a wide range of environmental conditions. This is the first study that focuses on all vegetation types in which *T. campestris* occurs in central Argentina and it is relevant for conservation and sustainable management of the only native palm species in the flora of this part of the country.

Taxonomic reference: Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga et al. 2008) and its online update (http://www.darwin.edu.ar).

Abbreviations: ISOMAP = isometric feature mapping; ISOPAM = isometric partitioning around medoids.

Keywords

Chaco, chorotype, endemism, environmental variable, Espinal, floristic composition, palm, species richness, vegetation type

Introduction

Trithrinax Martius is a neotropical genus of palms (Arecaceae) distributed in the subtropical and warm temperate region of South America, from almost sea level up to an elevation of 1,500 m (Cano et al. 2013). It belongs to the subfamily Coryphoideae and to the tribe Cryosophileae (Dransfield et al. 2005, 2008), and occurs in Brazil, Argentina, Bolivia, Paraguay, and Uruguay (Henderson et al. 1995; Dransfield et al. 2008; Pintaud et al. 2008; Zuloaga et al. 2008; Gaiero et al. 2012). *Trithrinax* comprises three species (*T. brasiliensis*, *T. schizophylla* and *T. campestris*), widely distributed in different habitats and vegetation types. The northern limit of its distribution lies in Santa Cruz Department, Bolivia, where *T. schizophylla* occurs, while in the southern extreme of its range, in central Argentina and Uruguay, *T. campestris* is found (Cano et al. 2013). *Trithrinax* species are more tolerant to drought and lower temperatures than other species of palms (Boyer 1992; Riffle and Craft 2003; Meerow 2005). Particularly, it has been documented that *T. campestris* may resist even less than -10°C (Meerow 2005), which may explain its distribution at higher latitudes.

The distribution area of *T. campestris* is mainly restricted to central Argentina (Cano et al. 2013) where the vegetation types in which the palm occurs, belong to the Espinal and Chaco phytogeographical provinces (Cabrera 1976). Previous studies report the presence of this species in various vegetation types with different soil and climatic conditions and different disturbance histories (Sayago 1969; Luti et al. 1979). In each habitat the importance of *T. campestris* ranges from some scattered, isolated individuals, to locally dense populations where the species becomes dominant in the community (Sayago 1969). From the phytogeographic point of view, Kurtz (1904), Sayago (1969) and Cabido et al. (2018) reported the occurrence of *T. campestris* in forests, grasslands or in savannas of the Lowland Chaco area, while Giorgis et al. (2017) recognized the presence of the palm as a co-dominant and subordinate species across different vegetation types in the Mountain Chaco. Within the Espinal phytogeographic province, Lewis and Collantes (1973) identified a floristic district based in part on the occurrence of this species. More recently, Lewis et al. (2009) also reported the occurrence of some isolated patches of Espinal forests comprising *T. campestris* in the eastern area of Córdoba province, central Argentina. However, none of these studies performed on Chaco or Espinal reported the complete floristic composition of the patches in which this palm occurs. Moreover, the effect of those factors that have been previously reported as major drivers influencing the distribution of palm vegetation types worldwide (Eiserhardt et al. 2011) such as climatic (e.g., water and temperature seasonality related variables), edaphic and anthropic (e.g., agriculture, fire and herbivory) have not been explored comprehensively for this palm species (Sayago 1969; Luti et al. 1979). Therefore, the vegetation types in which *T. campestris* occurs, their composition and structure, as well as the relationship with the main environmental variables are still to be documented.

As many palms worldwide, *T. campestris* is a keystone species for local people that traditionally use the leaves and spines to make handicrafts such as baskets and a variety of objects (Moraes 2001; Cano 2014). Moreover, this palm is being evaluated for the production of biofuels. At the same time, vegetation types with *T. campestris* are threatened because many habitats previously occupied by communities with palms are currently replaced by soybean and corn crops and also by pastures (Cano 2014; Mendoza et al. 2016; and personal observation by the authors). Knowledge of the effects of human activities (i.e., fire and grazing) on the population dynamics of *T. campestris*, as well as its germination ecology, is still preliminary. Cano (2014) reported an evident lack of seedlings and saplings due to anthropogenic fires and cattle grazing, while Mendoza et al. (2016) highlighted the lack of new palm seedlings related to extremely low seed germination observed in field and laboratory experiments. The persistent leaf-sheaths protect the stems of adult individuals what may be an adaptation to anthropogenic originated fires (Cano et al. 2013). Individuals of *T. campestris* seen in the field frequently show fire marks in the naked stems which lose their sheath layers (Cano et al. 2013 and personal observations by the authors). However, seedlings are not resistant to fire episodes, showing that fire may represent an important threat for the long-term survival for *Trithrinax* wild populations (Cano et al. 2013). In the last decades mature specimens have been exported to European countries for use in gardening (in 2003 the exportation of *T. campestris* generated an income of 600,000 USD; SENASA, Argentina, http://www.senasa.gob.ar/senasa-comunica/noticias/). Furthermore, the invasion by exotic species represents an additional potential threat for the vegetation types in which *T. campestris* occurs (Giorgis et al. 2017; Cabido et al. 2018; Zeballos et al. 2020). Cano et al. (2013) defined the conservation status of *T. campestris* as vulnerable, mainly due to habitat destruction and conversion to agriculture, and further insights on vegetation types with *T. campestris* are urgently needed to develop proper conservation and management strategies.

This study aimed to describe for the first time the whole floristic composition of vegetation types of the main habitats in which *T. campestris* occurs in central Argentina. Since disturbance may have introduced dramatic changes in the physiognomy of vegetation, we also explored the patterns of life forms distribution. In addition, and taking into account that the habitats in which *T. campestris* occurs involve different phytogeographic units, we also establish the proportion of chorotypes and endemic species present, as well as the origin of all the taxa recorded in each vegetation type. Finally, the association between the floristic composition and the main environmental variables (i.e., bio-climatic, topographic and edaphic) and fire frequency, were assessed.

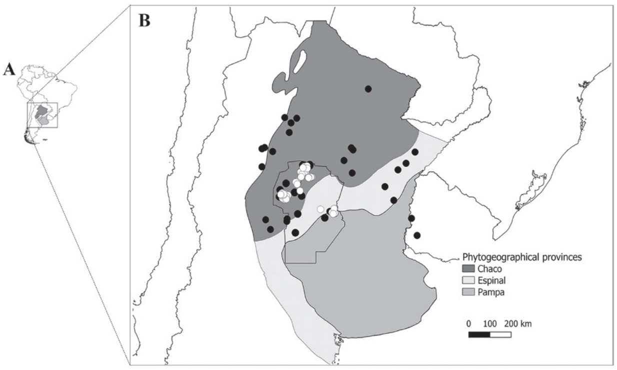

Figure 1. A Location of the study area (Córdoba province) in South-America; **B** Location of Córdoba province in central Argentina and overall distribution of *Trithrinax campestris* (black dots) in Argentina and Uruguay (according to Cano et al. (2013) and Flora australis database) and sample plots (relevés; white dots) collected in this study in Córdoba province. The location of Chaco (dark grey), Espinal (light grey), and Pampa (intermediate grey) phytogeographic provinces in central and northern Argentina are depicted based on Cabrera (1976).

Methods

Study area and vegetation survey

The survey was conducted in central Argentina, Córdoba province, covering *ca*. 161,000 km² (Figure 1). Sampling sites were distributed in habitats where the presence of *T. campestris* had been reported in previous works by Kurtz (1904), Sayago (1969), Lewis and Collantes (1973) and Luti et al. (1979), as well as in sites where specimens deposited in the Herbarium of the National University of Córdoba (CORD) had been collected. The study area is partially included in the Espinal phytogeographic province and the Western (Lowland) and Mountain Chaco districts according to the phytogeographic scheme of Argentina (Cabrera 1976). Following the Biogeographic Map of South America by Rivas-Martínez et al. (2011), our vegetation types are mainly included in the South Chacoan Province within the Chacoan Region (Chaqueña), and in the Xerophytic Pampean Region. The eastern extreme of the study area belongs to the Espinal (Lewis and Collantes 1973; Cabrera 1976; Zeballos et al. 2020), and is characterized by seasonally dry subtropical forests and woodlands distributed on lowlands with deep and well to imperfectly drained soils, in the proximity of the Pampean phytogeographic province. The northern extreme occupies part of the Lowland Chaco ecosystem (Western Chaco District sensu Cabrera, 1976) with xerophytic forests on well to excessively drained soils and part of the Mountain Chaco District (Cabrera 1976) occupying low hillsides and slopes with shallow and rocky substrates and small valley bottoms with deeper soils. Finally, the western extreme of the study area also belongs to the Mountain Chaco District; the landscape is dominated by open woodlands and scrublands on dry gentle and steep slopes alternating with flat areas ("pampas") with deeper soils and narrow valley bottoms likely to suffer occasional flooding. At the beginning of the 20th century, the study area was covered by xerophytic forests dominated by *Aspidosperma quebracho-blanco*, *Schinopsis lorentzii* and species of *Prosopis* in the lowlands. In the mountains, the landscape was dominated by a mosaic of woodlands, shrublands and grasslands and the main tree species were *Lithraea molleoides*, *Schinopsis marginata* and *Ruprechtia apetala* (Kurtz 1904; Sayago 1969; Luti et al. 1979). Decades of exploitation of Chaco and Espinal forests driven by timber and firewood extraction (Schofield and Bucher 1986) and the advances of the agricultural frontier (Arturi 2005; Guida-Johnson and Zuleta 2013; Fehlenberg et al. 2017) have altered the original distribution patterns of vegetation types (Zak et al. 2008; Hoyos et al. 2013; Agost 2015; Giorgis et al. 2017; Cabido et al. 2018; Garachana et al. 2018; Kowaljow et al. 2018; Zeballos et al. 2020).

The study area is characterized by two main geomorphologic units: an old Cambric mountain system comprising three main ranges and lowlands filled with Pleistocene and Holocene sediments, distributed both to the east and west of the mountains (Carignano et al. 2014). The study area comprises a climatic gradient from subtropical in the lowland Espinal and Chaco areas (200 to 400 m), to warm temperate in the northern and western mountain localities (500 to 1200 m). Average annual temperature ranges from 17 to 20°C in the flat areas to 13 to 14°C in the northern and western hills (Cabido et al. 1998). Average annual rainfall is highest in the north-east, ranging from 700 to 900 mm, decreasing to less than 600 mm to the west of the study area. Over the whole area, more than 80% of the rainfall is concentrated from October to March (warm season in Southern Hemisphere).

The vegetation survey was designed to cover the geographic, topographic and ecological variability of vegetation types in which *T. campestris* is present regardless of its abundance (Figure 2). Sampling followed the Zürich-Montpellier School of phytosociology (Braun-Blanquet 1932), and comprised 92 georeferenced 20 × 20 m² plots. In each plot, all vascular plants were recorded and species cover was estimated using the cover-abundance scale of Braun-Blanquet (1932) (+= <1% cover; 1 = 1–5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–100%). The height and cover of the tree, shrub and herb layers were visually estimated. Species nomenclature,

Figure 2. Examples of vegetation types comprising *Trithrinax campestris* in the study area in central Argentina. **A** Palm savanna with *T. campestris* in a matrix of grasslands on gentle hillside slopes; **B** Scrubland dominated by *Vachellia caven* and *T. campestris* on rocky soils; **C** Mountain Chaco forest dominated by *Schinopsis marginata* with scattered individuals of *T. campestris* on steep mountain slopes; and **D** Espinal forest with *Celtis tala*, *Prosopis nigra* and *T. campestris* on deep soils in lowland areas.

their distributional range and species origin (i.e., native or exotic) followed the catalogue of vascular plants of the Southern Cone (Zuloaga et al. 2008) and its online update (http://www.darwin.edu.ar/). Endemic taxa at the national and local levels followed Giorgis et al. (under review). Endemic at the local levels means endemic species restricted to the study area and surrounding provinces (mainly Córdoba and San Luis). Fourteen out of the 92 vegetation plots are registered in the Global Index of Vegetation-Plot Database (Dengler et al. 2011; http://www.givd.info) under ID SA-AR-002.

To assess the main trends of species distribution patterns and their representation in the study area, species chorotypes (groups of species with a similar distribution), were assigned following the criteria proposed by Cabido et al. (1998) and Zeballos et al. (2020): Southern-Brazilian (1), Chaquenian (2), Low Mountain Chaco (3), Arid Chaco and Monte (4) and Exotic (5). Additionally, the mean percentage of each chorotype per plot as well as the mean species richness and number of exotics per relevé were calculated. Life forms followed Zeballos et al. (2020) thus sorted as: cactus (c), climber (cl), epiphyte (e), fern (f), grass (g), graminoid (gr), herb (h), parasite (p), palm (pl), shrub (s) and tree (t).

Environmental variables

Bioclimatic variables and elevation were interpolated from the WorldClim database (http://www.worldclim.org; Fick and Hijmans 2017), at a spatial resolution of 30 seconds (*ca.* 1 km^2) for continental South America. As the main bioclimatic variables that constrain the distribution of palm species and communities worldwide are related to water availability and temperature (Eiserhardt et al. 2011) the following variables were selected: Precipitation of the Wettest Quarter(PWeQ), Minimum Temperature of the Coldest Month (MTCM), Precipitation Seasonality (PS), Precipitation of the Wettest Month (PWeM), Annual Precipitation (AP), and Precipitation of the Driest Quarter (PDQ) (see O'Donnell and Ignizio 2012 for details concerning all the bioclimatic variables). To obtain data on topographic and edaphic variables for each plot (slope and organic matter content of the surface soil layer), all the 92 relevés were plotted on digitalized maps of the soils of Córdoba province provided at two different scales (i.e., 1:500,000 and 1:50,000) (Gorgas and Tassile 2006; http://visor.geointa.inta.gob.ar/?p=857). The 1:50,000 scale was preferentially used, but some information gaps at this scale were completed with data provided by the map at 1:500,000. Both maps depict soil cartographic units and describe the internal heterogeneity of each unit through representative soil profiles providing an analysis of their chemical and physical properties.

Following Argañaraz et al. (2015a) and Argañaraz et al. (2020) the fire history frequency was characterized for the 92 sampling sites.Time series of Landsat TM, ETM+, and OLI images (30 m of spatial resolution), covering the study area, acquired between 1999 and 2018 were used. This fire database was derived automatically using ABAMS (Automatic Burned Area Mapping Software), a tool based on the algorithm proposed by Bastarrika et al. (2011) and updated versions implemented in Google Earth Engine. We considered any continuous burned patch as a single fire event except when the intensity of the burned signal was markedly different. Specifically, fire frequency is the number of times that a plot was burned for the period of time considered. The minimum mapping unit of the fire database is of 5 ha (Argañaraz et al. 2015a). We converted vector layers of burned areas to raster format as binary layers (burned or unburned) and determined the fire frequency for the 92 sites.

Data analyses

The ISOmetric feature mapping and Partition Around Medoids (ISOPAM) ordination and classification method were employed to analyze the 92 relevés. This analysis was used to detect the major vegetation types and their corresponding diagnostic species groups (Schmidtlein et al. 2010; Černý et al. 2015; Cabido et al. 2018). Hierarchical ISOPAM was run on the Bray-Curtis dissimilarity matrix. This matrix was constructed with the floristic table after Braun-Blanquet scores were transformed to the central class values (Kent 2012). The maximum number of clusters on each hierarchical level was arbitrarily set to ten and standardized G statistics to five. For each vegetation type, diagnostic species were selected using the phi coefficient of fidelity (Chytrý et al. 2002). Those species with phi ≥ 0.1 and a statistically significant association ($p < 0.001$) with a particular vegetation type according to Fisher's exact test, were considered as diagnostic. These analyses were performed in the JUICE 7.0 program (Tichý 2002). Each vegetation type was named after the first two species that showed: 1) phi ≥ 0.2 and a statistically significant ($p < 0.001$) association with a given vegetation type; and 2) constancy >30%. The vegetation matrix was ordinated through isometric feature mapping (ISOMAP; Tenembaum et al. 2000; Černý et al. 2015), using the number of neighbors to the optimal value from the first hierarchical level of the ISOPAM classification.

Incidence-based rarefaction and extrapolation (R/E) curves using sample size-based and coverage-based methods were performed to evaluate whether plant species from the different vegetation types classified by the ISOPAM method were well represented (Budka et al. 2018; Zeballos et al. 2020). Chao2, Jackknife 1 and Jackknife 2 non-parametric estimators for incidence data were used to estimate the total number of species that would be present in each vegetation type. Further, the coverage estimate for each plant community is given because it represents the estimated fraction of the entire population of individuals in the community that belong to the species represented in the sample. Non-parametric estimators for incidence data, and incidence-based rarefaction and extrapolation (R/E) curves were performed using the *SpadeR* and *iNEXT* R-packages (Chao and Chiu 2016), respectively. Analyses of variance were performed in order to evaluate the differences in mean species richness, mean percentage of each chorotype per relevé as well as the differences in the mean species richness and number of exotics per relevé among vegetation types. In all cases, the normality of the data and the homoscedasticity of variances were checked and when these requirements were not met, the data were natural log transformed. The relationship between the floristic composition and fire frequency as well as bioclimatic and edaphic variables was assessed through the *envift* function from the vegan R-package (http://CRAN.R-project.org/package=vegan). Bioclimatic and elevation data extractions were conducted using the *extract* function. Those variables with the highest squared correlation coefficient were related to the ISOMAP ordination. Furthermore, to evaluate how the vegetation structure of stands, as well as *T. campestris* cover, were affected by fire frequency, ANOVAs were performed. All analyses and graphs were performed in R *version* 3.5.1 (R Core Team 2018).

Results

Floristic composition

A total of 601 vascular plant species and infraspecific taxa (555 natives, including 68 endemics and 46 exotics), distributed among 77 families and 333 genera, were recorded in the 92 relevés (Table 1 and see also Suppl. material 1: Table S1.1). The most common families were Poaceae (108 species), Asteraceae (104), and Fabaceae (43), which together accounted for 42.4% of all species. Other common families were Euphorbiaceae (27 species), Solanaceae (26), Malvaceae (24), Cactaceae and Verbenaceae (22 species each). The most common genera were *Baccharis*, (13 species), *Euphorbia* (12), *Solanum* (11), *Tillandsia* (10), *Nassella* and *Croton* (8 species each). The predominant life forms were herbs (264 species), followed by grasses (108), shrubs (88), climbers (46), trees (27) and cacti (22). The most prominent chorotype was the Southern-Brazilian (56.08 ± 11.73% of all species, mean plus standard deviation), followed by the Chaquenian (29.67 ± 13.15%), the Low Mountain Chaco (11.08 ± 5.65%), and the Arid Chaco and Monte (0.12 ± 0.43%) chorotypes. Exotics were represented by 3.05 ± 3.19% of all species. The overall cover of *T. campestris* in the 92 relevés ranged from less than 1% to almost 40%.

Table 1. Synoptic table of the vegetation types classified by ISOPAM analysis showing the percentage constancy, mean Braun-Blanquet cover (as superscript) and phi values based on 92 relevés collected in Córdoba province, central Argentina. Species are sorted by decreasing fidelity within each vegetation type. Dark, medium and light grey indicates phi ≥ 0.3, phi ≥ 0.2 and phi ≥ 0.1, respectively. Vegetation type codes: 1.1 *Celtis tala*/*Sida rhombifolia* closed forest; 1.2 *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest; 2.1 *Jarava pseudoichu*/*Vachellia caven* open savanna; 2.2 *Acalypha variabilis*/*Nassella cordobensis* scrubland. Life forms (LF): c: cactus; cl: climber; e: epiphyte; f: fern; g: grass; gr: graminoid; h: herb; p: parasite; pl: palm; s: shrub; t: tree. Chorotypes (CT): (1) Southern-Brazilian, (2) Chaquenian, (3) Low Mountain Chaco, (4) Arid Chaco and Monte, (5) Exotic. Symbols: °: endemics at local level; *: endemics at the national level.

	LF	CT	Cluster 1		Cluster 2	
Vegetation type			**1.1**	**1.2**	**2.1**	**2.2**
Number of relevés			15	9	40	28
Trithrinax campestris	pl	2	100^2	100^1	100^2	100^1
Diagnostic species						
Sida rhombifolia	h	1	66.7^1	11.1^+	7.5^+	3.6^+
Celtis tala	t	1	100^2	77.8^2	55^1	46.4^1
Nassella hyalina	g	1	40^2		5^1	
Rivina humilis	h	1	66.7^1	11.1^+	5^+	3.6^+
Dicliptera squarrosa	h	1	53.3^2		12.5^+	10.7^+
Malvastrum coromandelianum	h	1	73.3^1	22.2^+	20^+	10.7^+
Holmbergia tweedii	s	2	33.3^1			
Schinus longifolius	s	2	46.7^1	11.1^+	10^+	3.6^+
Capsicum chacoënse	s	2	40^+		7.5^+	
Cyperus hermaphroditus	gr	1	26.7^+			
Araujia odorata	cl	1	53.3^+	22.2^+	5^+	3.6^+
Prosopis kuntzei	t	2		88.9^2		
Sarcomphalus mistol	t	2	6.7^+	88.9^2		
Jarava ichu var. *ichu*	g	3		55.6^2	10^2	
Aspidosperma quebracho-blanco	t	2	13.3^1	100^1	10^+	
Vachellia aroma	s	2		66.7^1	7.5^1	3.6^+
Senegalia praecox	t	2	13.3^2	88.9^1	2.5^+	3.6^1
Mimosa detinens	s	2		55.6^+		
Deinacanthon urbanianum	e	2	6.7^1	88.9^+		
Monteverdia spinosa	s	2	6.7^+	77.8^+	5^+	
Nicotiana glauca	s	1		44.4^+		
Gouinia paraguayensis	g	2		44.4^+		3.6^+
Croton lachnostachyus	s	3	33.3^1	77.8^1	17.5^+	10.7^+
*Tillandsia aizoides**	e	2	13.3^+	55.6^+	10^+	
Castela coccinea	t	2		55.6^+		
Opuntia quimilo	c	2		66.7^+		3.6^+
Cleistocactus baumannii	c	2		44.4^+		
Atamisquea emarginata	s	2		44.4^+		
Pseudabutilon pedunculatum	h	2	13.3^+	66.7^+	2.5^+	
Leptochloa crinita	g	2	6.7^+	44.4^+		
Harrisia pomanensis	c	2		44.4^+		3.6^+
Synedrellopsis grisebachii	h	2		66.7^+	5^+	7.1^+
Melica argyrea	g	1		33.3^+		
Jarava pseudoichu	g	3	46.7^1		85^3	71.4^2
Prosopis campestris°	t	2			32.5^2	3.6^+
*Condalia microphylla**	s	2	33.3^1	100^+	77.5^1	25^1
Lippia turbinata f. *turbinata*	s	2	20^+	11.1^1	70^1	50^1
Vachellia caven	s	1	53.3^1	11.1^1	97.5^2	100^2
Acalypha variabilis	h	1	26.7^1		45^1	96.4^2
*Nassella cordobensis**	g	3			15^1	64.3^1
Krapovickasia flavescens	h	1	6.7^+	11.1^+	45^+	89.3^1
Aristida circinalis	g	1			2.5^+	28.6^1
Sporobolus indicus	g	1	6.7^1		17.5^+	60.7^1
Aristida adscensionis	g	2		11.1^+	40^1	67.9^1
*Condalia montana**	t	3	20^2	11.1^+	20^1	64.3^1
Tripogonella spicata	g	1		11.1^+	5^+	39.3^1
Baccharis linearifolia	s	1			15^+	53.6^+
Microchloa indica var. *indica*	g	1		11.1^+	10^+	46.4^1
Schizachyrium salzmannii	g	1			2.5^+	25^1
Andropogon ternatus	g	1			2.5^1	25^1
Eustachys retusa	g	1		11.1^+	60^1	78.6^1
Gomphrena perennis var. *perennis*	h	1	6.7^1		10^1	42.9^1
Glandularia peruviana	h	1		11.1^+	45^+	71.4^+
Margyricarpus pinnatus	s	1			15^+	57.1^+
Glandularia venturii	h	2			15^+	57.1^+

Vegetation classification

The vegetation matrix was classified by the ISOPAM analysis into two main clusters (C1 and C2) and each cluster was further partitioned into two vegetation types (Table 1). Species constancy and average cover data are reported in synoptic Table 1 and also in the extended Suppl. material 1: Table S1.1. Cluster 1 comprised relevés collected mainly in the plains located to the east and north of the study area (Espinal and the Lowland Chaco, respectively), while Cluster 2 included relevés distributed predominantly, but not exclusively, in low mountain ranges and valley bottoms located to the north and west of the area (Lowland Chaco and the Mountain Chaco, respectively). Although the sample-size-based rarefaction showed that the curves of the four vegetation types had not yet reached the asymptote (Figure 3A), the observed species richness reached a high percentage of the species estimated using the non-parametric estimators (Table 2). The coverage-based rarefaction curves suggested that the four vegetation types identified were well represented since the sample coverage percentage showed values equal or higher than 0.85 in all types (Figure 3B, C; Table 2).

Table 2. Species observed (S_{obs}) and non-parametric estimators of species richness plus standard error for incidence data for each vegetation type. Vegetation type codes: 1.1 *Celtis tala*/*Sida rhombifolia* closed forest; 1.2 *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest; 2.1 *Jarava pseudoichu*/*Vachellia caven* open savanna; 2.2 *Acalypha variabilis*/*Nassella cordobensis* scrubland. Estimators: Chao2-bc: a bias-corrected form for the Chao2 estimator; Jackknife 1: Estimator that use the frequency of uniques; Jackknife 2: Estimators that use the frequencies of uniques and duplicates; and C. hat: Sample coverage index.

Non-parametric estimators	**1.1**	**1.2**	**2.1**	**2.2**
S_{obs}	250	163	444	399
Chao2-bc	344.72±24.06	220.80±19.35	553±25.17	568.29±39.99
Jackknife 1	351.73±14.02	219.89±10.37	570.75±15.82	527.25±15.87
Jackknife 2	400.33±23.25	249.25±16.67	625.75±26.96	606.93±26.90
C. hat	0.86	0.88	0.95	0.94

Descriptions of the vegetation types are given below:

***Cluster 1*:** Comprises two vegetation types distributed mainly in the lowlands of the Espinal phytogeographical

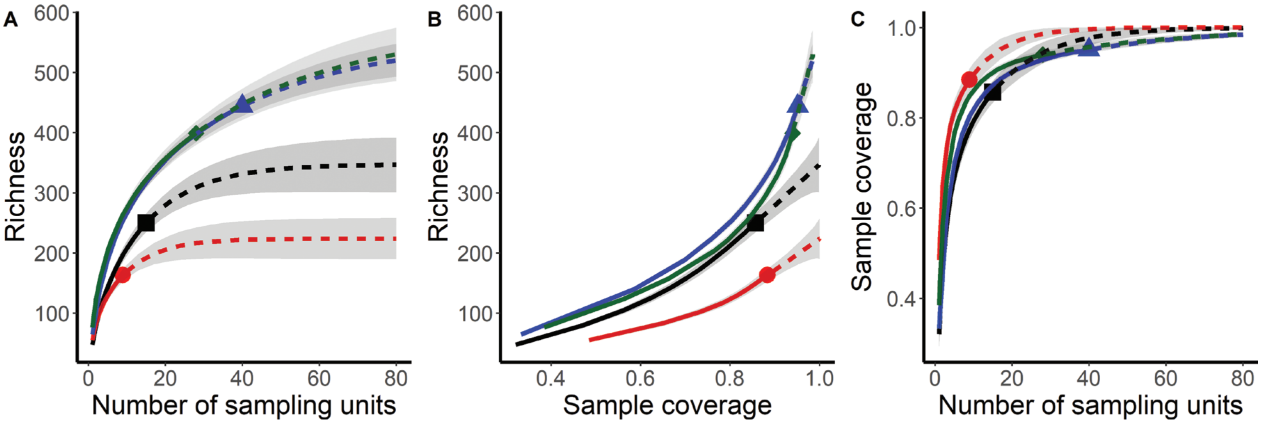

Figure 3. A Sample-size-based; **B** Coverage-based rarefaction and extrapolation sampling curves for species richness; **C** Sample completeness curves for each vegetation type. Solid line segments indicate rarefaction and dotted line segments indicate extrapolation (up to a maximum sample size of 40), while shaded areas indicate 95% confidence intervals (based on a bootstrap method with 100 replications). Colours and symbols: black square, 1.1 *Celtis tala/Sida rhombifolia* closed forest; red circle, 1.2 *Aspidosperma quebracho-blanco/Prosopis kuntzei* open forest; blue triangle, 2.1 *Jarava pseudoichu/Vachellia caven* open savanna; green diamond, 2.2 *Acalypha variabilis/Nassella cordobensis* scrubland.

province (and marginally in the adjacent Pampean territory) (Vegetation type 1.1) and the Western Chaco District (Vegetation type 1.2) in the north-east and north of the study area, respectively.

1.1 *Celtis tala/Sida rhombifolia* closed forest. Forests with a canopy height of 7.21 ± 0.39 m, dominated by a group of tree species typical of the Espinal forests such as *Celtis tala*, *Geoffroea decorticans* and *Prosopis nigra*. The tree layer showed the highest average percent cover value among the four vegetation types described (60.2 ± 7.65%; mean plus standard error), followed by the herb layer with an average cover of 59.3 ± 8.34% and a height of 0.59 ± 0.07 m, while the shrub layer exhibited a height of 2.64 ± 0.25 m and the lowest average cover (33 ± 5.97%). *Trithrinax campestris* reached its highest average cover in this vegetation type (17.48 ± 4.12%) and co-dominated the tree and/or the shrub layer in some of the relevés (e.g., in some of them *T. campestris* showed a cover of 38%). The tree *Celtis tala* together with some shrubs such as *Schinus longifolius* and *Capsicum chacoense*, the herb *Rivina humilis*, the grass *Nassella hyalina* and the climber *Araujia odorata* were diagnostic for this vegetation type (Table 1).

This vegetation type occurred mainly in the northeastern plains of the study area on deep soils but some stands were also found on the northern and western mountains occupying valley bottoms and gentle slopes, always on deep soils. In mountain valley bottoms with poor drainage or even very occasional flooding, *T. campestris* may also form pure stands. A total of 231 (213 natives and 18 exotics) species were recorded in this vegetation type, of which 19 are endemic (17 at the national and two at the local levels). The mean species richness per relevé was 47.3 ± 3.31. Among life forms, herbs (93 species, 37.2%) jointly with shrubs and grasses (46 species each, 18.4% each), were the most abundant, followed by climbers (24 species, 9.6%) and trees (22 species, 8.8%).

1.2 *Aspidosperma quebracho-blanco/Prosopis kuntzei* open forest. Open forest with a tree layer cover of 30.67 ± 9.94% and a height of 6.06 ± 0.95 m. A dense shrub layer (59.44 ± 4.29%) with a height of 3.31 ± 0.3 m and a cover of the herb layer of 55.56 ± 6.48% and a height of 0.56 ± 0.02 m were recorded. *Trithrinax campestris* was a subordinated to other species and generally with low mean cover values (5.34± 1.85%). Several tree species like *Aspidosperma quebracho-blanco*, *Prosopis kuntzei*, *Sarcomphalus mistol*, *Senegalia praecox* and shrubs such as *Vachellia aroma*, *Mimosa detinens*, *Castella coccinea*, *Atamisquea emarginata*, *Monteverdia spinosa*, were local dominants and the diagnostic species for this type (Table 1). Also, diagnostics were the succulent cacti *Opuntia quimilo*, *Cleistocactus baumannii* and *Harrisia pomanensis*, as well as the C_3 tussock grass *Jarava ichu* var. *ichu*.

This vegetation type usually forms isolated patches surrounded by soybean and corn crops in the lowlands of the northern part of the study area. A total of 153 (146 natives and seven exotics) species were recorded in this vegetation type of which 10 are endemic (eight at the national and two at the local levels). The mean species richness per relevé was 54.8 ± 3.24. The most abundant life forms were herbs (57 species, 34.9%), shrubs (28 species, 17.2%), grasses (32 species, 19.6%), trees (14 species, 8.6%) and climbers (13 species, 7.9%).

Cluster 2: This Cluster includes two vegetation types distributed mainly in low mountain slopes and valley bottoms located in the Mountain Chaco District in the north and west of the study area.

2.1 *Jarava pseudoichu/Vachellia caven* open savanna. Open savannas with a high grass and herb cover (average cover and height of the herbaceous layer were 78.28 ± 3.59% and 0.74 ± 0.02 m, respectively). The average cover of the tree and shrub layers was low (14.15 ± 2.16% and 34.3 ± 2.69%, respectively) while their height also showed low values (4.64 ± 0.33 and 3.31 ± 0.1 m, for the tree and shrub layers, respectively). *Trithrinax campestris* density varied from only scattered individuals to denser patches in almost pure stands, reaching an average cover of 14.44 ± 2.11%. The C$_3$ grass *Jarava pseudoichu* and the shrubs *Prosopis campestris*, *Condalia microphylla*, *Lippia turbinata* fo. *turbinata* and *Vachellia caven* were diagnostic species for this vegetation type (Table 1).

This vegetation type was widely distributed across gentle slopes and valley bottoms mostly in the mountains of the northern part of the study area though some stands are located to the west, on both gentle relief and more steep topography. In some stands, the dominant vegetation was an open scrubland dominated by *Vachellia caven*, while on slopes of the mountains to the west of the area remnants of Low Mountain Chaco Forest, dominated by *Schinopsis marginata*, *Lithraea molleoides* and *Ruprechtia apetala*, with only sparse individuals of *T. campestris*, were found. A total of 406 (375 natives and 31 exotic species) species were recorded of which 39 are endemics (31 at the national and eight at the local levels). The mean species richness per relevé was 64.3 ± 2.28. Herbs (197 species, 44.3%), grasses (87 species, 19.5%) and shrubs (68 species, 15.3%) were the most common life forms.

2.2 *Acalypha variabilis*/*Nassella cordobensis* scrubland. Open scrubland with an almost continuous grass and herb cover (the average cover of the herbaceous layer was 70.68 ± 4.73% with a height of 0.71 ± 0.05 m). Despite that in some stands on rocky substrate the shrub cover may increase, the average cover and height of this layer were medium to low (35.18 ± 3.30% and 2.34 ± 0.14 m, respectively). Tree cover and height were the lowest among the four types described (5.54 ± 2.65% and 3.46 ± 0.5 m, respectively). *Trithrinax campestris* was present generally with sparse individuals and showed the lowest average cover reported in this study (3.78 ± 0.92%). Among the diagnostic species, the small shrub *Acalypha variabilis* showed the highest constancy and average cover (Table 1). The list of diagnostic species is completed with the C$_3$ grass *Nasella cordobensis*, the C$_4$ grasses *Aristida circinalis*, *Sporobolus indicus*, *Aristida adscensionis*, *Microchloa indica*, *Tripogonella spicata*, *Schizachyrium salzmannii*, *Andropogon ternatus*, *Eustachys retusa* and some shrubs and herbs.

This vegetation type was distributed on gentle to steep slopes in the mountains of the northern part of the study area, though a few stands were also recorded in the mountains to the west. Soils were shallow and the percentage of bare rock was generally considerable. A total of 400 (385 natives and 15 exotics) species were recorded in this community, of which 47 are endemic (35 at the national and 12 at the local levels). The mean species richness per relevé was 76.5 ± 3.06. Herbs (181 species, 45.2%), grasses (77 species, 19.25%) and shrubs (53 species, 13.2%) were the most abundant life forms.

Richness and chorotype patterns among vegetation types

The total number of vascular plant species per relevé ranged between 29 and 103, and the mean species richness per relevé differed significantly among vegetation types ($F_{3,88}$= 15.04; p = 0.001). The *Acalypha variabilis*/*Nassella cordobensis* scrubland showed the highest mean species richness per relevé (Table 3), while the *Celtis tala*/*Sida rhombifolia* closed forest had the lowest richness; the other two vegetation types showed intermediate values. We recorded 52 endemic species at national level and 16 at local level; only 5 endemic species (*Gymnocalycium mostii*; *Gymnocalycium capillense*; *Apurimacia dolichocarpa*; *Alternanthera pumila* and *Trichocline plicata*) were restricted to the study area and surroundings. Significant differences in the representativeness of the different chorotypes were observed among the vegetation types, with the exception of the Arid Chaco and Monte chorotype (Table 3). The vegetation types differed significantly in their Southern-Brazilian chorotype representativeness ($F_{3,88}$ = 23.34; p = 0.001) as well as in the Chaquenian chorotype ($F_{3,88}$ = 40.73; p < 0.001). The Southern-Brazilian chorotype was the best represented with the exception of the *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest in which the Chaquenian chorotype exhibited the highest percentage of species (Table 3). Species of the Southern-Brazilian chorotype showed the highest proportion in the two vegetation types of Cluster 2 and in *Celtis tala*/*Sida rhombifolia* closed forest. The Arid Chaco and Monte chorotype was less represented in the four vegetation types (i.e., less than 1% on each one), and without significant differences between them ($F_{3,88}$ = 1.46; p = 0.23). The Low Mountain Chaco chorotype also showed differences between vegetation types ($F_{3,88}$ = 9.34; p = <0.001) with the highest values in both vegetation types of Cluster 2 (Table 3). The number of exotic species, as well as the proportion of exotics per relevé, showed significant differences between vegetation

Table 3. Species richness, number of exotics per plot and mean percentage of each chorotype per plot (plus standard error) for each vegetation types classified by ISOPAM analysis. Different letters denote statistically significant differences as identified by ANOVA post-hoc LSD Fisher test. Vegetation type codes: 1.1 *Celtis tala*/*Sida rhombifolia* closed forest; 1.2 *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest; 2.1 *Jarava pseudoichu*/*Vachellia caven* open savanna; 2.2 *Acalypha variabilis*/*Nassella cordobensis* scrubland.

Vegetation type	1.1	1.2	2.1	2.2
Species richness	47.33±3.31a	54.89±3.24ab	64.3±2.28b	76.57±3.06c
Number of exotics per plot	2.2±0.55ab	1.11±0.39bc	2.4±0.3a	1.07±0.19c
Southern-Brazilian	55.51±3.43b	34.32±2.61c	56.82±1.38b	62.69±1.22a
Chaquenian	31.68±3.3b	58.21±2.92a	28.31±1.31b	21.95±1.2c
Low Mountain Chaco	7.77±1.58c	5.65±0.73c	11.38±0.75b	14.21±1.01a
Arid Chaco and Monte	0.23±0.16a	0.32±0.06a	0.08±0.06a	0.04±0.04a
Exotic	4.08±1.35a	1.49±0.47bc	3.4.±0.47ab	1.11±0.22c

types ($F_{3,88}$ = 6.52; p = 0.0005 and $F_{3,88}$ = 4.4; p = 0.006, respectively) with the highest values observed in the *Celtis tala*/*Sida rhombifolia* closed forest and the *Jarava pseudoichu*/*Vachellia caven* vegetation type (Table 3).

Vegetation types, environmental variables and fire frequency

The ISOMAP ordination (Figure 4) showed that differences in floristic composition were related to elevation (Elev; $r^2 = 0.44$, $p = 0.001$;), minimum temperature of the coldest month (MTCM; $r^2 = 0.40$, $p = 0.001$), precipitation of the driest quarter (PDQ; $r^2 = 0.37$, $p = 0.001$), precipitation of the wettest month (PWeM; $r^2 = 0.37$, $p = 0.001$), annual precipitation (AP; $r^2 = 0.37$, $p = 0.001$), precipitation seasonality (PS; $r^2 = 0.33$, $p = 0.001$), precipitation of the wettest quarter (PWeQ; $r^2 = 0.31$, $p = 0.001$), organic matter content of the topsoil (OM; $r^2 = 0.29$, $p = 0.001$) and slope ($r^2 = 0.28$, $p = 0.001$). Elevation was the most important factor in relation to composition, with both vegetation types included in Cluster 2 characterized by mean elevations higher than 900 m, while elevation ranged from 340 to 436 m in average in Cluster 1. This elevation gradient mirrored trends in temperature related variables (e.g., minimum temperature of coldest month). The vegetation types included in Cluster 1 occupied warmer areas with higher precipitations with *ca.* 100 mm difference respect to Cluster 2. Slope exhibited an appreciable range of variation between both Clusters and was steeper in low mountain areas (Cluster 2). Organic matter content of the surface soil layer showed higher average values in Cluster 1.

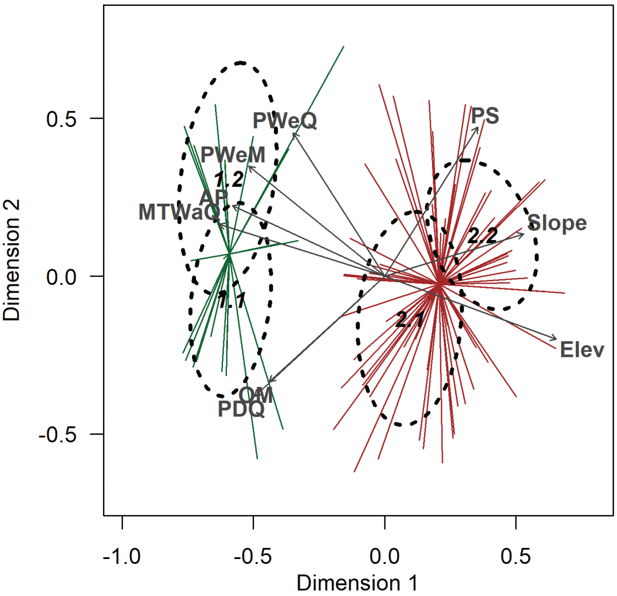

Figure 4. Isometric feature mapping plot (ISOMAP), based on Bray-Curtis dissimilarity of 92 relevés × 601 plant species matrix for those vegetation types that include *Trithrinax campestris* in central Argentina. Vegetation type codes: 1.1 *Celtis tala/Sida rhombifolia* closed forest; 1.2 *Aspidosperma quebracho-blanco/Prosopis kuntzei* open forest; 2.1 *Jarava pseudoichu/Vachellia caven* open savanna; 2.2 *Acalypha variabilis/Nassella cordobensis* scrubland. Environmental variables abbreviations: Elev: Elevation; MTCM: Minimum Temperature of Coldest Month; PWeQ: Precipitation of the Wettest Quarter; PS: Precipitation Seasonality, PWeM: Precipitation of the Wettest Month; AP: Annual Precipitation; PDQ: Precipitation of the Driest Quarter; OM: Organic matter. Colours: green, Cluster 1; red, Cluster 2.

Out of the 92 stands, only 21 showed the frequency of fires during the period 1999–2018. Overall, the fire frequency was not related to the floristic composition ($r^2 = 0.04$, $p = 0.12$). Eighteen sites were burned only once while three sites were burned three times during the period analyzed. Those stands that belong to the vegetation types of Clusters 2 showed a higher fire frequency since 13 out of 40 stands were burned in the *Jarava pseudoichu*/*Vachellia caven* open savanna while 4 out of 28 stands were burned in the *Acalypha variabilis*/*Nassella cordobensis* scrubland. The vegetation types of Cluster 1 showed just two stands burned each. However, the four vegetation types did not differ in their fire frequency ($F_{3,84}$ = 2.16; p = 0.09). Furthermore, the vegetation structure of stands (i.e., the percentage cover of each vegetation layer) of the different vegetation types did not show any significant differences between unburned and burned stands according to their tree ($F_{3,84}$ = 0.81; p = 0.49), shrub ($F_{3,84}$= 0.39; p = 0.76) and herb ($F_{3,84}$ = 0.18; p = 0.9) layers cover as well as in *T. campestris* cover ($F_{3,84}$ = 0.46; p = 0.71).

Discussion

In this study we describe for the first time the complete floristic composition of the main vegetation types in which *T. campestris* occurs in central Argentina. Our results evidenced that either as isolated individuals intermingled in forests (Cluster 1), in savannas and scrublands (Cluster 2), or as denser populations (likely in both Clusters) (Table 1 and Figure 4), this palm is able to occupy sites with different topography and soils along a wide gradient of environmental conditions. This wide gradient of environmental conditions was already observed by former botanists who studied the flora in central Argentina more than one hundred years ago (Lorentz 1876; Kurtz 1904), and several decades before our survey (Sayago 1969; Luti et al. 1979); however, none of them included complete floristic inventories.

Richness, endemism and chorological patterns among vegetation types

Relevés included in Cluster 2 revealed higher mean species number if compared with Cluster 1. The higher species richness recorded in vegetation types of Cluster 2 (*Jarava pseudoichu*/*Vachellia caven* open savanna and *Acalypha variabilis*/*Nassella cordobensis* scrubland)

(Table 3), might reflect the topographic and edaphic heterogeneity observed in the Low mountain Chaco habitats occupied by these vegetation types. In mountain environments, topography may influence the distribution of plant species and vegetation types by modifying soil properties, exposure, and temperature, as well as vegetation physiognomy and dynamics (Svenning 2001; Eiserhardt et al. 2011). In contrast, both vegetation types included in Cluster 1 (*Celtis tala/Sida rhombifolia* closed forest and *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest), are distributed in more homogeneous landscapes found in the plains and flatlands of the Espinal and Chaco domains. Vegetation types in Cluster 2 are also richer in species than other woody communities of plains and low mountain habitats in central Argentina (Giorgis et al. 2017; Cabido et al. 2018; Zeballos et al. 2020). Similar patterns of higher species diversity reflecting habitat heterogeneity have been reported elsewhere in the world for different types of vegetation (Whittaker 1960; Coblentz and Riiters 2004; Kreft and Jetz 2007) and specifically for communities rich in palm species (Guimarães et al. 2002; Resende et al. 2013). An additional factor influencing local species richness may be the physiognomy of vegetation which, is the results of complex feedback between climate, topography and disturbance (i.e., fire and grazing) (Giorgis et al. 2017; Argañaraz et al. 2020). Vegetation types comprised in Cluster 1 exhibited higher tree canopy cover and the differences in their canopy openness could determine gradients of light affecting the distribution of species. Cluster 2, instead, comprised open savannas and scrublands allowing for more light availability at the shrub and herb layers (Figure 2), which may enhance plant species richness. Strong influence of light gradients through competition for light and shade tolerance has been reported in other biomes, especially in tropical forests (Carson and Schnitzer 2008), but at the moment, our evidence is scarce and needs further research.

In addition to the variations in species richness among the vegetation types (Table 3), differences in the composition of endemic species were also observed. Vegetation types included in Cluster 2 showed the highest numbers of endemic species both at the national and local levels. *Jarava pseudoichu*/*Vachellia caven* open savanna and *Acalypha variabilis*/*Nassella cordobensis* scrubland comprised 8 and 12 endemism at local level, respectively, which evidenced the high natural value of these vegetation types and their importance for biodiversity conservation. The valuable pattern of endemism reflected in our data could be explained through the isolating effect of mountains with respect to lowlands; recent studies report a clear correlation between plant endemism and mountain isolation (Steinbauer et al. 2016; Camacho-Sanchez et al. 2019). Despite our findings, the distribution of many taxa is still scarcely known in Argentina and further floristic and chorological studies could change the status of many plant species.

The Southern-Brazilian and Chaquenian chorotypes were dominant in all the four vegetation types described (Table 3). The same pattern has also been reported by Cabido et al. (1998) and Zeballos et al. (2020) for woody vegetation types from central Argentina including mainly lowland vegetation types. The predominance of these chorotypes is not surprising since our study area includes sedimentary plains and low mountain habitats. Moreover, there are not significant barriers to the dispersal of taxa distributed in the eastern and northeastern area of the country (Southern-Brazilian chorotype) and from the northern flatlands of the Great Chaco in the northern region of Argentina, but also Bolivia and Paraguay (Chaquenian chorotype) (Fuentes and Navarro 2000; Steininger et al. 2001; Navarro et al. 2006). Many of the species reported in our survey with a Southern-Brazilian distribution have also been mentioned by Rodriguez et al. (2017) as components of *Butia yatay* palm groves and gallery forests in northeastern Argentina, where *T. campestris* is a subordinate element.

The overall number of exotics in our survey is lower with respect to those reported in previous floristic studies from central Argentina (Giorgis and Tecco 2014; Cabido et al. 2018; Zeballos et al. 2020). The number of exotic species ranged from 7 to 31 among the four vegetation types, with *Jarava pseudoichu*/*Vachellia caven* open savanna showing the highest record, while the mean number of exotics per plot was maximum in *Celtis tala/Sida rhombifolia* closed forest. Note that in this vegetation type even some exotics are considered diagnostic species (e.g., the grass *Chloris gayana* and the tree *Morus alba*). This higher exotic occurrence may be explained by the earlier expansion of agriculture in this area in comparison with that of the *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest, where the introduction of intensive agriculture is more recent (Zak et al. 2008; Cabido et al. 2018; Zeballos et al. 2020).

Vegetation types and environmental factors

Within Cluster 1, trends in floristic composition were mainly related to annual rainfall, other precipitation parameters associated to it, and the minimum temperature of the coldest month (Figure 4). On the other side, in Cluster 2 composition was mainly driven by elevation and topography but also by precipitation seasonality. *Celtis tala/Sida rhombifolia* closed forest and *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest occurred at the warmest part of the study area where annual rainfall is higher, whereas *Jarava pseudoichu*/*Vachellia caven* open savanna and *Acalypha variabilis*/*Nassella cordobensis* scrubland occupied the highest and coldest habitats in premontane hills to the north and west of the study area. Areas at higher elevations are characterized not only by lower temperatures, but also by different topographic conditions and rocky soils that which may avoid the establishment of species from the lowland Espinal and Chaco areas (Cabido et al. 2018; Zeballos et al. 2020).

Despite of the environmental differences between the vegetation types described, our results showed that

T. campestris can grow in a wide range of environmental conditions. In line with our results, previous studies dealing with palm communities in tropical and subtropical areas have emphasized the occurrence of palm species in different habitat types, such as floodplains, terraces, swamps, premontane hills, and even dry lands (Navarro 1997; Navarro et al. 2006; Balslev et al. 2010; Eiserhardt et al. 2011; Resende et al. 2013; Rodríguez et al. 2017). We should note that this species grows in warm temperate areas and sites not necessarily subjected to temporary or permanent flooding, as has been observed in many species of the family Arecaceae (Eiserhardt et al. 2011). Bjorholm et al. (2006) suggested that for species within the Coryphoideae subfamily, the present-day environmental regional factors have low explanatory power in its current distribution while non-environmental regional factors and/or long-term disturbance factors might have historically constrained their distribution. As Dalle et al. (2002) and Svenning et al. (2004) remarked, some palm species may be associated with disturbances that occurred more than 20 years ago. In this sense, a climatic reconstruction of central Argentina not only observed the presence of silicophytolith of the Arecaceae family but also registered a peak of higher aridity and warm climate experimented 1,600 years ago (Giorgis et al. 2015). These climatic conditions might have allowed that *T. campestris* reached the southernmost distribution in central Argentina.

Several authors have pointed to the effect of range management (e.g., fire and cattle grazing) on the physiognomy and composition of vegetation types comprising other Argentinian palm species (Morello and Adamoli 1974; Biani et al. 2007; Cabral and Castro 2007; Batista et al. 2014). Fire is a common and important disturbance driver in central Argentina and particularly in the study area (Argañaraz et al. 2015 a, b, 2020). Observations in the early works by Sayago (1969) and Luti et al. (1979), as well as more recent findings by Giorgis et al. (2013), Carbone et al. (2017) and Kowaljow et al. (2018), highlight the effect of fires on the structure and composition of Chaco vegetation in Córdoba. However, we registered a low fire frequency in the plots surveyed (i.e., 21 out of the 92 sampling sites were burned) at least for a period of twenty years. This result suggests that other drivers, such as land use change and grazing may be more important determining the structure and floristic patterns of those vegetation types in which *T. campestris* grows naturally. Nevertheless, our data concerning the effect of fires are only preliminary and longer time series of fire frequency are needed.

Conclusions and further perspectives

This study provides a detailed analysis of the vegetation types comprising *T. campestris*, the only native palm species in the flora from central Argentina. Moreover, our study highlights that *T. campestris* can grow in a variety of community types with different environmental conditions. These results are essential to develop adequate conservation strategies and useful for the sustainable management of this endangered species. It is accepted that the current distribution of palms is limited by climatic conditions prevailing during the cold season (Walther 2002), and that under warming scenarios some palm species may be extending their ranges into higher latitudes and altitudes (Walther et al. 2007; Giorgis et al. 2015). However, to our knowledge, there is no information about the behavior that *T. campestris* may show under changing scenarios of temperature and rainfall neither about its regeneration niche. Preliminary field observations suggest that a high number of seedlings could be associated with higher tree canopy cover while in more open sites the lack of regeneration could be related to more vulnerable populations. Future studies should extend the floristic survey to other areas in which the vegetation types comprising *T. campestris* have been reported (Cano et al. 2013; 2014), especially in San Luis and Santiago del Estero provinces, also located in central Argentina (see Figure 1). Similarly, future successional and demographic studies should complement our survey in order to give a more complete picture of the real conservation status of the species and of the vegetation types in which it occurs.

Data availability

A subset of the plots is included in the database SA-AR-002 – Vegetation of Central Argentina(Dengler et al. 2011; http://www.givd.info). The remaining subset will be included in the same database in 2021. The data are also available from the Corresponding author upon reasonable request.

Author contributions

SRZ, MRC, MAG, designed the survey; MAG, MRC, JJC, ATRA, PIM, did the field work; SRZ, MRC performed data analysis; SRZ, MAG, MRC, ATRA, JJC wrote the original manuscript; JA analyzed fire data; MVP, JA, PIM, PAT, AF, GF, MVV, GC contributed substantially to the final writing of the manuscript and in the interpretation of results.

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Supplementary material

Supplementary material 1
Extended synoptic table
Link: https://doi.org/10.3897/VCS/2021/59384.suppl1

VEGETATION CLASSIFICATION AND SURVEY

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VCS METHODS

Grassland with tradition: sampling across several scientific disciplines

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Abstract

The traditional, low-input use of grassland in Central and Eastern Europe has provided high-quality food, clothing and manure for millennia. As an outcome of sustainable low-intensity agriculture, some rural areas have globally significant species richness. Traditional farming is still well preserved in several regions of the Carpathian Mountains. This is a unique opportunity to use the wisdom of our ancestors to keep grassland biodiversity for our descendants. We present a sampling methodology to survey traditionally managed grassland ecosystems holistically, including abiotic, biological and cultural phenomena, and reflect thus the multidimensionality of traditional farming. Our main objective was to reveal the connection between particular management practices and precisely measured plot plant diversity. Our motivation was to identify traditional farming approaches that result in both high biodiversity and sustainable grassland utilization in particular region, and confirm their impact also using statistical tests. The multitaxon vegetation sampling at seven spatial scales combined with soil analyses, detailed land-use information derived from interviews with the land parcel owners, satellite pictures and historical materials provide potentially valuable data for several scientific disciplines including syntaxonomy, plant ecology, environmental anthropology and ethnology. Examples of grassland management practices based on traditional ecological knowledge can serve as an inspiration for developing modern biodiversity conservation strategies applicable for rural regions. The database Grassland with Tradition is registered in Global Index of Vegetation-Plot Databases (GIVD) with the identifier ID EU-00-032. To date it contains data from 31 study sites in 7 countries (Austria, Czech Republic, Slovakia, Hungary, Poland, Romania, Ukraine).

Syntaxonomic reference: Mucina et al. (2016).

Keywords

ecology, ethnology, grassland management, history, land use, low-input farming, local ecological knowledge, meadow, pasture, plant diversity, sampling approach, typology, vegetation-plot database

Introduction

A standard approach to vegetation survey is a single visit of the selected study site, particularly when the aim is classification of a certain vegetation type. Approaches based on re-sampling, permanent study plots or manipulative experiments allow for the study of ecological processes and temporal changes to vegetation. However, some goals of vegetation survey cannot be reached without cooperation with other scientific disciplines. This is particularly the case for studies of habitats that depend on human influence, such as traditionally managed grassland.

All semi-natural grassland habitats are partly or fully dependent on agricultural management (Halada et al. 2011) and their land-use history is usually crucial for conservation of their biodiversity (Diacon-Bolli et al. 2012; Bürgi et al. 2013). Traditional farming conditioned the emergence of all semi-natural grasslands in Europe, as it has contributed to forming their species composition and diversity over several centuries or even millennia (Bonn and Poschlod 1998; Poschlod and WallisDeVries 2002; Poschlod et al. 2009; Hejcman et al. 2013; Poschlod 2015). Grassland history is reflected in present grassland, but it is difficult to detect its traces clearly. Moreover, in traditional landscapes, each piece of land has different ownership structure, different management schemes and different histories (Babai and Molnár 2014; Kun et al. 2019), and it is not easy to make generalized management recommendations. The simple typology distinguishing between meadows (mown grasslands) and pastures (grazed grasslands) used nowadays in Western Europe does not cover the whole scale of applied management techniques and does not reflect the multidimensionality of traditional farming. It is often the case that each traditional land parcel represents a category of its own (cf. Janišová et al. 2020).

Traditional farming and local ecological knowledge

Traditional farming includes various types of low-input land utilization on private farms. This type of farming typically occurs within small parcels belonging usually to a single family, or, in some cases, to a commune or farmer associations. Different owners usually apply different farming practices according to the family customs and personal traditional knowledge, so that the landscape itself is very diverse (see also Johansen et al. 2019; Wehn et al. 2019). However, neither the size of land parcels nor the level of labour mechanization is decisive for our delimitation of traditional farming. The most important criterion is rural culture and traditions passed down from generation to generation, which underpin local farming approaches. In this aspect, traditional grassland management differs from modern high-input grassland management, as well as from low-intensity conservation grassland management. The main difference between traditional grassland management and a conservation approach is that local farmers prioritise temporal stability in fodder quantity and quality over biodiversity, which is the main assumption of a long-term ecological sustainability (Janišová et al. 2020). In most European countries, traditional farming is no longer practiced; it has been either substantially modified or replaced by modern farming approaches. However, in some remote mountain areas and in several regions of Eastern Europe, historic land use patterns and farming approaches have survived to the present day (Figure 1). Similarly, the local-ecological knowledge of the rural inhabitants has been preserved in these areas, which may become a tool for effective conservation of grassland biodiversity (Babai and Molnár 2014; Ivaşcu et al. 2016; Kun et al. 2019; Janišová et al. 2020).

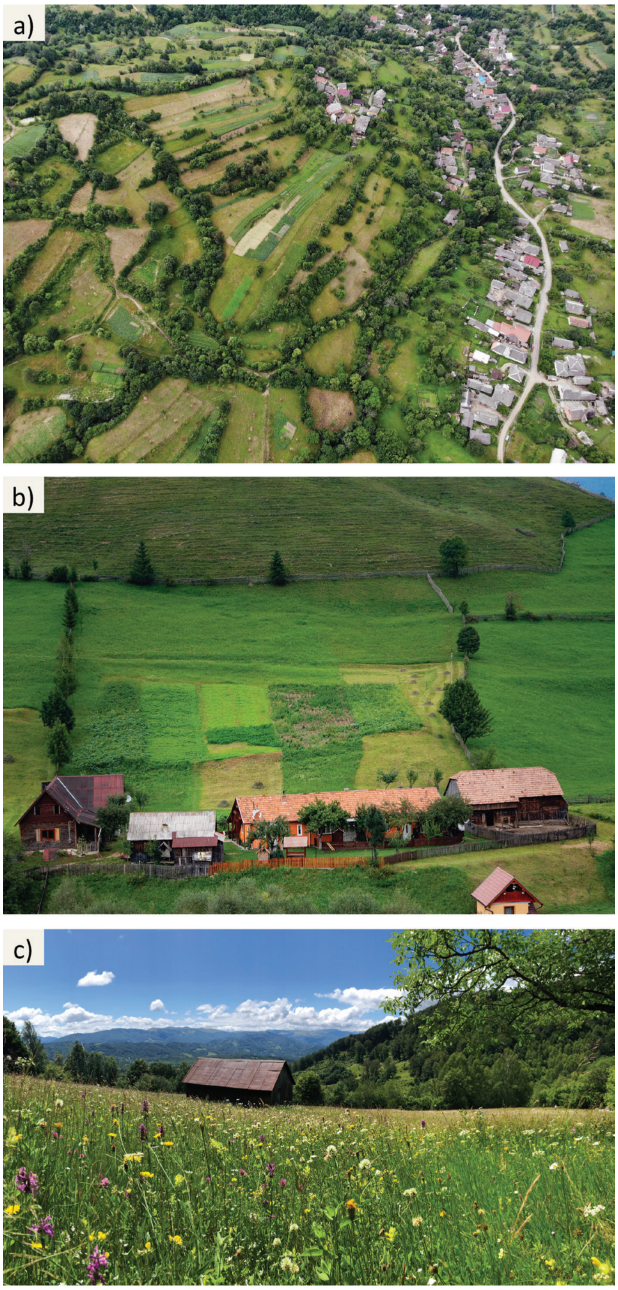


Figure 1. Traditional farming can maintain high levels of biodiversity and the Carpathian bio-cultural heritage is a well of wisdom for modern biodiversity conservation. Traditionally managed grasslands are often small-sized and very specific in their management. a) Domashyn, Ukraine, June 2018, M. Khytruk; b) Valea Rece, Romania, August 2019, M. Janišová; c) Bănița, Romania, June 2020, M. Janišová.

Anthropologic research status in the Carpathian countries

Studies of traditional farming systems are well represented in the fields of cultural and environmental anthropology and its branches of ethnography (the in-depth study of a particular cultural group) and ethnology (the comparative study of ethnographic data, society and culture). For example, Romania has a long history of ethnographic research of peasant households and beliefs concerning the natural environment. Since the mid-19th century, folk knowledge regarding plants was systematically studied, firstly by folklorists such as Simeon Mangiuca (1831–1890) and Simion Florea Marian (1847–1907). The latter compiled an impressive Encyclopaedia of traditional culture with information concerning plants used by the local Romanian population, in a massive manuscript (12.000 pages and a herbarium, see Marian 2008–2010). Later, with the development of ethnobotany, well-known Romanian botanists conducted studies (Borza 1935, 1968) and some ethnologists trained in botany (Butură 1979). Despite communist censorship, a considerable number of studies were published starting from the mid-19th century up until 1990, after which new studies were scarce and were carried out by only few researchers (e.g., Drăgulescu 2013, for Southern Transylvania). However, Romanian ethnobotanical research focuses mostly on the linguistic topics (vernacular names and its origin), empirical use, and spiritual importance of plants. Data on the traditional management of hay meadows and other grasslands, or the local economic importance of certain meadow-associated wild plant species, are absent. While the number of ethnographic and ethnological studies on the material culture of the peasant population in Romania increased in the 20th century, these studies provide limited information regarding traditional grassland management (hay meadows and pastures). Detailed information about tools and constructions can be found in Butură (1978), whilst in Vuia (1964) we find the first and the most important classification of pastoral practices for Romania.

In the aforementioned studies, the information on grassland use is scarce and can be partially conceived from the other agricultural practices described. For example, piecemeal information on traditional agricultural practices can be found in studies concerning beliefs and/or feasts of the Romanian villages that involve work regulations, such as interdictions and calendar of the labours (see Pamfile 1997, with the first edition in 1914; Marian 1994, with the first edition in 1898–1899). Important contributions can also be found from the interwar Rural Sociology School studies, that occurred between 1925–1948, under the guidance of Dimitrie Gusti (1880–1955). The main method used by sociologists was the monographic research (for example Conea 1940; Ionica 1944; Bernea 1985). The topic of hay meadow management was first addressed by the Rural Sociology School of Bucharest in their exhaustive monograph from Clopotiva (Conea 1944, which described the local mowing time and some other practices related to hay meadow management) and incidentally in the complex studies from Drăguș (Bărbat 1944).

The situation is fairly similar in the Ukrainian Carpathians. Despite active research by the ethnographers and geographers, studies on traditional farming practices are scarce. An exception is the widely studied Carpathian pastoralism (e.g. Kubijovyč 1936; Podolák 1966; Tyvodar 1994). Recently, some topics, such as various aspects of haymaking traditions and constructions, or glade farming, were studied by Igor Boiko and Janusz Łach (Boiko 2008, 2009a, b; Boiko and Łach 2020).

Within the Western Carpathians, most ethnographical studies were published during the 1960s and 1970s by Polish and Slovak authors. Bronisława Kopczyńska-Jaworska focussed mainly on mountain shepherding traditions and undertook studies in Poland, Slovakia and Romania (e.g., Kopczyńska-Jaworska 1959, 1961). In the 1960s, Ján Podolák developed a methodological manual for ethnographic research of livestock farming in Slovakia (Podolák 1962), which, besides the detailed description of grassland management practices, included a basic typology of traditional meadows and pastures. His detailed regional studies (e.g. Podolák 1961) as well as his national overviews (Podolák 1965, 2008) contributed significantly to recent knowledge on traditional grassland management practices.

Meanwhile, traditional rural cultures and local traditions became extinct in substantial areas of the Carpathian Mountains, limiting further ethnological research. Recently, traditional farming systems and local-ecological knowledge concerning meadows and pastures have been of interest for ethnologists (Boiko 2008, 2009a, b; Fruntelată et al. 2016; Iuga 2016 ; Boiko and Łach 2020), but also for botanical, agricultural, and landscape-focussed researchers. Numerous studies have taken place in the Carpathian regions with well-maintained traditional agriculture (Akeroyd and Page 2006, 2011; Dahlström et al. 2013; Babai and Molnár 2014, 2016; Biró et al. 2014; Molnár et al. 2015; Plieninger et al. 2015; Hartel et al. 2016; Ivașcu et al. 2016, 2018; Sõukand and Pieroni 2016; Špulerová et al. 2019; Kun et al. 2019). Some of these studies are the result of joint research: either a collaboration by biologists and ethnologists, or biologists who recognize the importance of integrating social aspects into landscape studies. This type of scientific approach was encouraged by some of the founding fathers of Romanian biology even at the beginning of the 20th century (like Antipa 1916), or by other biologists even later (Filipașcu 1981) but has been limited in its uptake. The findings of the aforementioned studies show how the collaboration between biology and ethnology is desirable and beneficial for both disciplines. We therefore see a need to develop an interdisciplinary approach to survey the still maintained traditionally managed grassland ecosystems holistically, including abiotic, biological and cultural phenomena, and reflect thus the multidimensionality of traditional farming.

Basic aims of our study approach

1. Survey of vegetation composition and diversity in traditionally managed grasslands. Recording species composition of vascular plants, bryophytes and lichens at seven spatial scales together with

environmental factors. Estimation of species richness, beta diversity and species pool in grasslands of each study site.
2. Record the local bio-cultural heritage and traditional ecological knowledge of the particular region.
3. Explanation of the impact of each single management practice used in traditional agriculture on plant species composition and diversity parameters at the plot level. Understanding the interaction of different management measures and their impacts on plant biodiversity and land productivity.
4. Clarification of the impacts of historical land use and landscape parameters on the structure, composition and diversity of current grassland vegetation. Examination of the relationship between phytosociological grassland classification and grassland typology based on factors other than floristic criteria, such as grassland location, its original purpose, historical land use and applied management practices.

Outline of our study approach

We developed a specific methodological approach to study traditionally managed grassland in the Carpathian Mountains which encompasses most of its context-specific characteristics. It includes the study of biological objects (plants, vegetation and their formative environment) as well as sociological objects (people, human communities and rural cultures). Therefore, it combines several scientific disciplines: botany and ecology with anthropology and history.

The described methodology has been developed and first tested in 2017. Since then, it was customized and applied to study bio-cultural heritage in 31 sites during two projects (NGS-288R-18, VEGA 02/0095/19). While the inspiration for botanical sampling of plant diversity using the nested-plot-series comes from the standard EDGG methodology (Dengler et al. 2016), our approach includes novel aspects such as broadening the scale to a site level, including the study of current grassland management practices by interviewing plot owners, gathering local ecological knowledge in particular region, and including historical information. In the following sections we describe the different elements of our methodology and provide recommendations for their successful implementation.

Site and plot selection

The study sites are to be selected in regions with long-term extensively managed grasslands (Figure 1). For the purpose of our study, the site is defined as a circle with an area of 25 km^2 with the proportion of managed rural landscape being at least 10% (Figure 2). In accordance with the study focus, the sites may represent different situations along the elevation gradient, different bedrock types or different political and agricultural histories within the investigated area (Table 1).

Instead of preferential plot selection within a site, a stratified random plot selection is applied in our approach. As land-use type is frequently determined by the terrain configuration and topography, the stratification is based exactly on these criteria. To maximise the variability in

Table 1. Country overview of site and plot numbers, elevation range, geology, typology and phytosociological affiliation of grasslands sampled as of 31 October 2020.

					Typology based on prevailing management schemes					**Phytosociological affiliation to classes**			
Country	**Number of sites**	**Number of plots**	**Elevation range (m)**	**Geological bedrock**	**permanent meadow**	**grazed meadow (spring or autumn grazing)**	**fallow meadow (crop-grassland rotation)**	**pastures (C–cow, SG-sheep and/or goat, H-horse, M – mixed)**	**abandoned**	***Festuco-Brometea***	***Molinio-Arrhenatheretea***	***Nardetea strictae***	***Mulgedio-Aconitetea***
Austria	1	6	235–473	limestone	0	0	1	3 SG, 1 H	1	5	1	0	0
Czech Republic	1	6	377–544	flysch	4	0	2		0	6	0	0	0
Hungary	2	12	147–556	limestone, loess, sediments	2	1	0	2 C, 1 SG, 2 H	4	11	0	1	0
Poland	1	6	904–1020	flysch	0	1	2	2 C	1	0	5	1	0
Romania	16	96	170–1330	flysch, limestone, volcanic, acidic plutonic, sediments	2	40	9	11 C, 20 SG, 13 M	1	16	43	37	0
Slovakia	6	36	190–1422	limestone, volcanic, acidic plutonic, flysch, sediments	3	3	6	5 C, 6 SG, 5 M	8	18	12	4	2
Ukraine	4	24	250–1053	flysch, loess, sediments	2	6	2	4 C, 1 SG, 4 M	5	2	18	4	0
All	31	186	147–1422		13	50	22	80	21	58	79	47	2

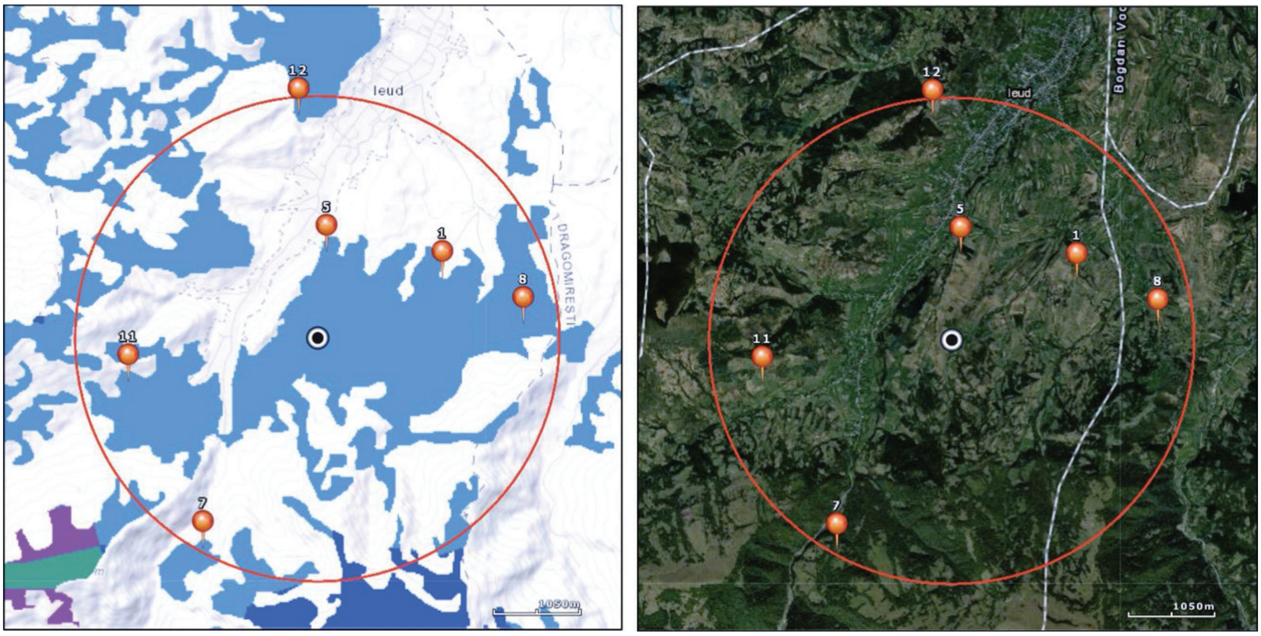


Figure 2. Sampling design within a site. Design consists of a circle of 25 km^2 with a minimum of 10% managed grassland area. Topographic map is used for stratified random selection of sampling plots (red pins with numbers): two in a flat area, one on a moderate W-N-E slope, one on a steep W-N-E slope, one on a moderate E-S-W slope and one on a steep E-S-W slope. Sampling plots are selected exclusively in the CORINE grassland habitats (blue-coloured patches) and a satellite map is used to check the active land-use and avoid abandoned land parcels.

vegetation composition on plots, each site is stratified by slope inclination (flat, moderate, steep) and slope exposition (W-N-E vs. E-S-W). In each combination of inclination and exposition, a series of 7 nested plots of increasing size (Figure 3) is randomly placed in a homogeneous vegetation patch. Six nested-plot series are thus placed within each site (Figure 2): two in a flat area, one on a moderate W-N-E slope, one on a steep W-N-E slope, one on a moderate E-S-W slope and one on a steep E-S-W slope. For our specific purpose, flat areas have inclination up to 5°, moderate slopes between 5 and 25°, and steep slopes above 25° (for flatter sites a threshold of 15° is used). As the plot selection is made *a priori*, two sets of coordinates are prepared for each site: 1) six sampling coordinates and 2) six reserve coordinates. If during the sampling the pre-selected location is found unsuitable for sampling due to various reasons (lack of access, land destruction, freshly ploughed, etc.) the reserve plot coordinates are used within the given stratification category.

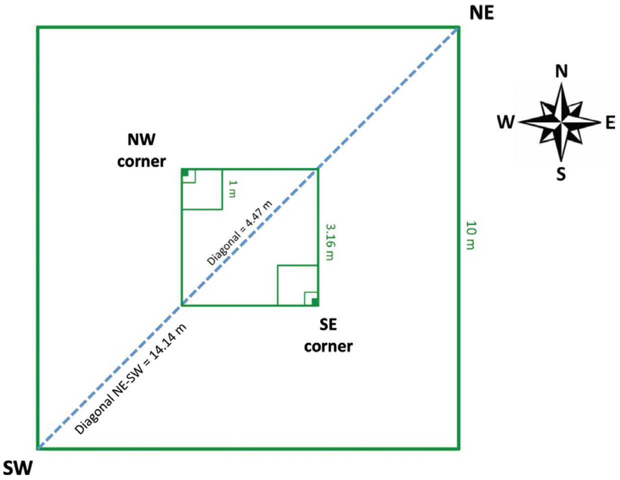
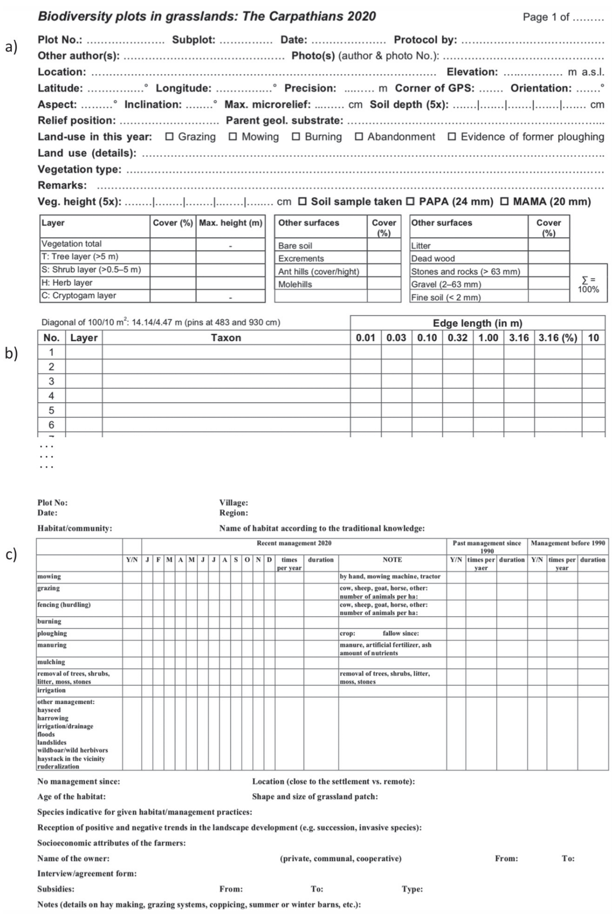


Figure 3. Arrangement of nested plots covering seven spatial scales. The sampling plots are established from the diagonal; after setting the location of the outer NE and SW corners, the inner NE and SW corners are set at 483 and 930 cm. Then the measuring tape is used to fix the 100-m^2 plot and a special rope with nodes is used to fix the 10-m^2 and the two 1-m^2 plots. The 1-m^2 sampling plots are placed in the NW and SE corners of the 10-m^2 plot and their outer corners are used for permanent marking by metal nuts of 20 mm (NW corner) and 24 mm (SE corner) buried to a depth of 5 cm.

Plot-scale plant diversity sampling

During the fieldwork, the location of the predetermined coordinates is identified and the actual vegetation is checked for homogeneity before a nested-plot-series is established. The nested plots cover seven spatial scales (0.0001 m^2, 0.001 m^2, 0.01 m^2, 0.1 m^2, 1 m^2, 10 m^2, 100 m^2) and their arrangement is shown in Figure 3. In each of the nested plots, the shoot presence of all species of vascular plants, bryophytes and lichens is recorded. Species relative abundance is estimated visually as a percentage cover in 10-m^2 plots. For this plot size, the detailed environmental data are obtained. Height of the herb layer is measured at five points – in the middle of the edges and in the plot centre. Percentage cover of herb layer, cryptogam layer and bare soil (plot surface not covered



Biodiversity plots in grasslands: The Carpathians 2020 Page 1 of ………

a)

Plot No.: ………………… **Subplot:** …………… **Date:** ………………… **Protocol by:** …………………………………
Other author(s): ……………………………………… **Photo(s)** (author & photo No.): ………………………………………
Location: ……………………………………………………………………………… **Elevation:** ……………… m a.s.l.
Latitude: ……………° **Longitude:** ……………° **Precision:** ……… m **Corner of GPS:** ……. **Orientation:** …….°
Aspect: ………° **Inclination:** ……..° **Max. microrelief:** ……… cm **Soil depth (5x):** ……|……|……|……|…… cm
Relief position: ……………………… **Parent geol. substrate:** ………………………………………………………
Land-use in this year: ☐ Grazing ☐ Mowing ☐ Burning ☐ Abandonment ☐ Evidence of former ploughing
Land use (details): ……………………………………………………………………………………………
Vegetation type: ……………………………………………………………………………………………
Remarks: ……………………………………………………………………………………………
Veg. height (5x): ……..|……..|……..|……..|…….. cm ☐ **Soil sample taken** ☐ **PAPA (24 mm)** ☐ **MAMA (20 mm)**

Layer	Cover (%)	Max. height (m)
Vegetation total		-
T: Tree layer (>5 m)		
S: Shrub layer (>0.5–5 m)		
H: Herb layer		
C: Cryptogam layer		-

Other surfaces	Cover (%)
Bare soil	
Excrements	
Ant hills (cover/hight)	
Molehills	

Other surfaces	Cover (%)	
Litter		
Dead wood		
Stones and rocks (> 63 mm)		∑ = 100%
Gravel (2–63 mm)		
Fine soil (< 2 mm)		

b)

Diagonal of 100/10 m^2: 14.14/4.47 m (pins at 483 and 930 cm)

			Edge length (in m)							
No.	**Layer**	**Taxon**	**0.01**	**0.03**	**0.10**	**0.32**	**1.00**	**3.16**	**3.16 (%)**	**10**
1										
2										
3										
4										
5										
6										

…
…
…

c)

Plot No: **Village:**
Date: **Region:**

Habitat/community: **Name of habitat according to the traditional knowledge:**

		Recent management 2020															Past management since 1990			Management before 1990		
	Y/N	J	F	M	A	M	J	J	A	S	O	N	D	times per year	duration	NOTE	Y/N	times per yaer	duration	Y/N	times per year	duration
mowing																by hand, mowing machine, tractor						
grazing																cow, sheep, goat, horse, other: number of animals per ha:						
fencing (hurdling)																cow, sheep, goat, horse, other: number of animals per ha:						
burning																						
ploughing																crop: fallow since:						
manuring																manure, artificial fertilizer, ash amount of nutrients						
mulching																						
removal of trees, shrubs, litter, moss, stones																removal of trees, shrubs, litter, moss, stones						
irrigation																						
other management: hayseed harrowing irrigation/drainage floods landslides wildboar/wild herbivors haystack in the vicinity ruderalization																						

No management since: **Location (close to the settlement vs. remote):**

Age of the habitat: **Shape and size of grassland patch:**

Species indicative for given habitat/management practices:

Reception of positive and negative trends in the landscape development (e.g. succession, invasive species):

Socioeconomic attributes of the farmers:

Name of the owner: **(private, communal, cooperative)** **From:** **To:**

Interview/agreement form:

Subsidies: **From:** **To:** **Type:**

Notes (details on hay making, grazing systems, coppicing, summer or winter barns, etc.):

Figure 4. Example of a form used during the fieldwork: a) header data, b) species data and c) land use data.

by vegetation) are estimated and other details on the particular vegetation and surrounding location are recorded in a purpose-designed form (Figure 4). Sampling equipment also includes a camera for documentation of the actual vegetation before the sampling start, GPS for precise measurement of SE and NW coordinates, and some other tools shown in Figure 5.

Data on topography, climate and soil

During the fieldwork, topography of each 10-m^2 plot is characterised by elevation (m), inclination (°), and microrelief (small-scale variability of microtopography expressed as a deviation from a smooth plane in cm). Further topographic and climatic data can be calculated *a posteriori* (e.g. calculation of solar radiation from the latitude, slope and aspect data is possible using the approach of McCune (2007)) or obtained from specialized databases (e.g. mean annual temperature, annual precipitation sum, precipitation of the driest quarter, and other climatic variables can be obtained from the WorldClim (Hijmans et al. 2005; http://www.worldclim.org/) or Chelsa (https://chelsa-climate.org) databases. Soil depth is measured on each plot at five random points with a steel rod of 1 cm diameter. Cover of stones and rocks (particle size diameter >63 mm) and cover of gravel (particle size diameter 2–63 mm) is estimated on the plot surface (%). A mixed soil sample of the uppermost 10 cm of the mineral soil is taken from five random locations. Air-dried soil samples are analysed in the lab for the following soil parameters: pH (measured in KCl), phosphorus (P), potassium (K) and magnesium (Mg) content in mg/kg, and calcium (Ca), organic carbon (C), and total nitrogen (N) content in g/kg. Humus soil content is calculated from the organic carbon content. The C/N ratio is calculated as a surrogate of soil accessible nutrients.

Data on management practices

Basic information on the management practices is obtained during the fieldwork using semi-structured outdoor or indoor interviews with the local farmers and landowners (Molnár et al. 2008). Our questions (see the section on question guidelines for the details) focus on agricultural practices used recently (since 2010) and during the two historical periods, 1950–1990 (the period of centrally planned economy in all investigated countries except Austria) and 1990–2010 (the period of market economy in all investigated countries). Based on the information from landowners and/or their neighbours we were able to derive several management variables with potential short- or long-term effects on grassland ecosystems, including the long-term effect of mowing, grazing, burning or ploughing, management stability, or the cumulative impact of recent traditional management practices which reflects both their heterogeneity and frequency. The cover of litter (cover of dead biomass on the plot surface) is estimated during the field sampling and can be used as a surrogate of grassland abandonment. Further important management variables include type of grazing animal(s) (e.g. horse, cow, sheep, goat, pig, goose), type of grazing system (e.g. spring grazing, autumn grazing, combination of spring and autumn grazing, whole-season grazing in enclosures, common pasture with whole-season free grazing, whole-season herding with a shepherd, folding/corralling), year of the last ploughing and the type of crop(s) grown at that time.

Data on landscape structure and heterogeneity

In addition to the management variables, we derived several variables that characterise the surrounding landscape and reflect the local historical grassland development. Along with the size of the actual land parcel around the sampling plot, we calculated the mean size of grassland parcels (in km^2) within 1-km^2 plot surroundings (a circle with a radius of 0.564 km centred at the plot) and the distance (in m) of the sampling plot to the nearest forest or hedge, using the satellite images (Google Earth). Proportion of non-forest habitats and habitat diversity in 4-km^2 plot surroundings (a circle with a radius of 1.128 km centred at the plot) were derived from the CORINE land cover maps with spatial resolution of 10–50 m (Bossard

Figure 5. a) Field equipment for biodiversity sampling includes 1: determination keys for local flora, 2: paper bags for soil and cryptogam samples, 3: plastic bags for plants to be determined later, 4: rope with nodes to allocate the small-sized plots, 5: 50-m long measuring tape for establishing the 100-m^2 plot, 6 and 7: 2-m long measuring tape or folding meter for defining the smallest plots and for measuring soil depth and plant height, 8: magnifying glass for plant identification, 9: metal nuts of different size for fixing the corners, 10: writing tools, 11: GPS device, 12: shovel for taking soil samples, 13: tent pegs for fastening the rope, 14: steel rod to measure soil depth. b) Recording of the above-ground vascular plants, bryophytes and lichens starts at 1 cm^2 of the SE and NW corners in the 10-m^2 plots. It takes about 3 hours to inspect the whole area, but the time can differ depending on the size of the team and type of vegetation. Rzepiska, Poland, August 2018, M. Chilinski. c) The biggest challenge during the vegetation sampling is to identify each single stem or leaf. Șurdești, Romania, June 2018, K. Nurowska. d) Ethnological part of the vegetation survey builds on traditional ecological knowledge of local people. Ieud, Romania, June 2018, M. Janišová; e) Outdoor interview with local inhabitants reveals valuable details on the sampled land parcel as well as on the farming system in the village. Mărișel, Romania, August 2019, M. Janišová.

et al. 2000). The 26 habitat classes distinguished in the plot neighbourhoods were combined into five habitat categories (water, non-forest, forest, agricultural, artificial) according to Janišová et al. (2014). The index of habitat diversity was calculated for each plot surroundings, based on the cover of 5 habitat categories in the plot neighbourhood as $H = -\Sigma p_i \ln p_i$ where p_i is the proportion of each habitat category.

Historical land-use information

Historical data on particular grassland parcels can be obtained from historical maps and, more recently, orthophotos (Figure 6). In our study, we used the georeferenced historical maps from the three military surveys of the Habsburg empire: Josephinische, Franziszeische and Franzisco-Josephinische Landesaufnahmen (https://mapire.eu/en/; Timár et al. 2010). These maps are available for the entire territory of the Carpathians, although the particular region might have changed its state affiliation several times during the last 250 years. For most of the map sheets, cropland and grassland area can be distinguished, the latter usually differentiated between meadows and pastures. Based on these data, we estimated the approximate grassland age of the studied grassland parcels. We considered grassland age to be the minimum age of the grassland patch at the plot location in years. Values usually ranged between 100 and 250 years.

The aerial and satellite photographs provide valuable plot-based management data, as they are usually available for several years or seasons. Radical interventions in the parcel vegetation by plowing and mowing can be usually dated and these data supplement information from landowners. Vegetation succession following abandonment or cessation of management activities can also be detected from aerial and satellite images.

Regional historical information is available from chronicle and archive materials. Chronical data mainly provides the demographic data and livestock numbers, while cadastral, konkretual (drawn up for the purpose of collecting taxes), or consolidation maps can be found in archives. The explanatory notes to these documents often contain valuable information on the historical management of individual land parcels. These data help to illustrate the context of the study region.

Along with the abovementioned sources, recent and historical literature is available on traditional agricultural practices, the latter mainly available in local languages only. Many pre-industrial agricultural textbooks are increasingly accessible online, as they fall out of copyright and become digitized by libraries (Burton and Riley 2018). Information on the inclusion of particular land parcels in subsidy schemes is usually available on the agricultural web portals of the respective country.

Ethnological field survey on local management practices and ecological knowledge

An anthropologist or ethnologist investigates contemporary social and cultural characteristics of a community, but also often looks into the community's history in order to understand the dynamics of the local culture. Qualitative methods are commonly used to carry out a social survey, because they are comprehensive (see Rotariu and Iluț 1997). These methods are i) observation; ii) interactive methods (such as interview, oral history, and narratives of life); and iii) ethnographic description (see Laplantine 2010, Geertz 1973). All these methods provide scientific knowledge created by means of the social interactions that happen between the researcher and the natives of a community.

The first strategic method to gather information during a field research is the observation. The goal is to understand the cultural phenomena by observing and recording as much information as possible about the social context in study locations. **Direct observation** implies recording (using a notebook, dictaphone, camera or video recorder) what the researcher is seeing, focusing on each detail. This means paying attention to everything that the persons who are being observed are doing. An easy example of direct observation we used during our research is the filming of the creation of a haystack, which will allow the researcher to access the information at any time afterwards. The second type of observation is **participant observation** (see also Spradley 1980 and Bernard 2006),

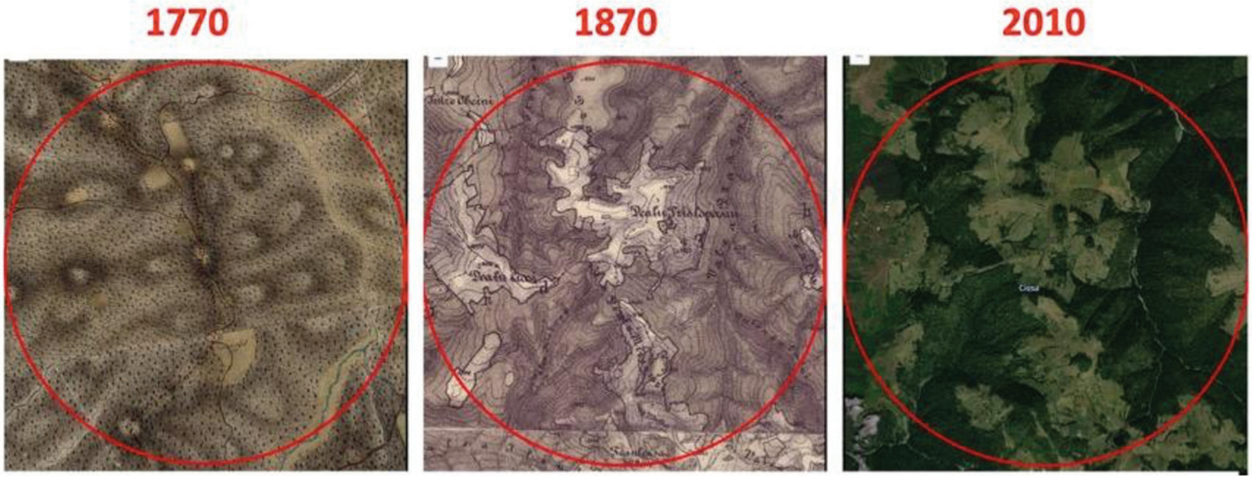


Figure 6. Historical maps and orthophotos are important sources of information about the historical and recent land use. In the picture we see the site of Ciosa (circled area) during the first (left) and second (middle) Habsburg military surveys, and in recent time (right picture). It is evident that the forest clearing occurred mostly during the last two centuries and the grassland area gradually increased.

a contextual observation where the researcher becomes immersed in the culture (s)he is studying. Participant observation allows researchers to better understand the techniques and the actions of the community.

In order to gather local traditional ecological knowledge, **interviews** are frequently used, which is an interactive method that takes the form of a dialogue between the researcher and the members of the communities (see Spradley 1979, Bernard 2006). When conducting an interview, the researcher should be aware of several points. First of all, it is important for the researcher to focus on the personal experience of the interlocutor, taking into account that traditional values are usually abstract or self-implied for a member of a community, but are present in the actions that the interlocutor is describing. His/her biography becomes the "embodiment" of tradition (Bot 2015). It is therefore recommended to avoid "general" questions, such as "What actions are done in spring to clean the meadows?" but ask, instead a more personal question, such as: "What actions do you and your family take for cleaning the meadows in spring?" In this manner, the respondent is giving an answer that (s)he knows is correct, otherwise (s)he may search in his memory for an answer that (s)he believes would please the researcher. By doing this, the interlocutor is personally involved in the interview and may find it easier to express their thoughts and experiences. Similarly, when a temporal dimension is in question, it is advisable to appeal to the respondent's own experience and memories. For example, to ascertain continuity of practices through a community, the following questions could be posed: "From whom did you learn …?" or "Have you seen somebody else in your family that has done this/that…? Whom?" Responses to these questions could reveal the way practices are handed down or introduced from one generation to the next.

There are several types of interviews that a researcher can choose from (see Bernard 2006: 210–250). First, there is the "**informal interview**", which does not have a clear structure and is mainly used to establish a first contact and a preliminary discussion with the interlocutors. Usually it is not recorded, but the researcher in his field notebook writes down the interesting ideas. It can lead to an appointment for a second interview. The second type of interview is the "**unstructured interview**", which is done according to a broad and very flexible plan. This type of interview consists of giving a topic to a person and letting her/him talk. This type of interview is very well adapted to the narratives of life. A third type of interview, the "**semi-structured interview**", is the most used in ethnological surveys. In this type, the structure and the guidelines are more understandable, there are clearer topics approached, sometimes in a special order, the questions are conceived in such a manner to cover all possible aspects of the theme discussed. Some of the questions are even repeated moments later, if the topic allows it, using different words, in order to verify the coherence of the dialogue, or to stir up the memory of the interlocutor. The fourth type of interview is the "**structured interview**", which is frequently used in sociological surveys, applied under the form of **questionnaires with questions formulated *a priori***, where the subject responds to questions with formulated answers.

After choosing the right type of interview that would fit the research, the next challenge is to find interviewees. It is recommended that the researcher is transparent about the reasons for the research and why (s)he would like to talk with people. In order to find out the best interlocutors when the community is unknown, it is advisable to make preliminary interviews with the local key stakeholders, such as the mayor, teachers, priests, or even veterinarians as we found out in the community of Șișești (Maramureș, Romania). These people could give valuable information about their own experiences concerning the topics of the interview, but they also can point to the people whom they think are suitable to participate in the research. This is similar to the **snowball sampling technique**, when research participants are asked to assist in identifying other potential local experts. This method is often applied in studies of traditional ecological knowledge, since it is known that local experts within a community are acknowledged by the community (Berkes 2018). Where the researcher does not speak the local language, it is recommended to have a translator familiar with local dialect. This step is particularly important given that traditional ecological knowledge is embedded in the local speech, certain local words have different meanings in different areas and can sometimes describe different practices or ecological concepts (e.g. vegetation succession, habitats, etc.).

When conducting an interview, the researcher should ideally talk in a simple language, without using obscure or complex scientific terms that the interviewee may not understand. After explaining the reason for the interview, the researcher should first gain verbal permission for the interview to be recorded. Written permission can often be granted following the interview, once trust has been built. In some cases it is necessary to encourage the interlocutor in speaking, e.g by demonstration of importance of the information obtained, or using the **probing techniques** (see Bernard 2006: 217–223) that stimulate the interview, such as: the silent probe (which implies we should not rush for the interlocutor to answer); the echo probe (repeating the last thing said by the interviewee and then asking her/him to continue; the "uh-huh" probe; the "tell-me-more" probe; and so on.

In parallel to recording the dialogue, ethnologists commonly use a notebook during interviews to write down fieldnotes (see Sanjek 1990), which may include interviewees' ideas, behaviour, emotions or other details. These notes can be a backup in case of failure to record the interview, but are also helpful as memory aids for recalling the interview content when analysing the data.

The ethnological field survey is followed by **transcription and translation** of the recorded interviews, and interpretation of the obtained information. It should be noted that this phase of ethnological research usually require more time than the field survey.

Question guidelines: thematic areas for investigation of traditional farming

Traditional farming can be studied at several hierarchical levels, such as the land parcel, the farm, the commune or the regional/national levels. Detailed knowledge about particular land parcels is often insufficient to understand the complexity of local traditions and requires additional historical information to set it in context. In order to guide researchers in this interdisciplinary approach, we have prepared a set of questions for interviewees with different foci.

1. Topics to be addressed in the questions asked to the parcel owner related to the sampled nested plot series.

   1.1. Topics related to regular grassland management: „How do you use this land parcel?“:
      a) *Cutting grass*: how many times per year is grass cut, when does cutting take place; how do you determine the right time to mow – what signs are to be found in the grass; manually or by mechanisation; mowing technique;
      b) *Spring grazing*: when does it start, and when does it end; does it depend on the weather; how many days in this specific plot; which animals; how many animals per specific area; why grazing is performed in the particular land parcel, what effects it has upon the vegetation; is it applied regularly or occasionally; is a rotation of grazing plots used within a year/between years; what kind of grazing is used – free, enclosure, with a shepherd, corralling (folding); is spring grazing used in combination with autumn grazing;
      c) *Autumn grazing*: when does it start, and when does it end; does it depend on the weather; how many days in this specific plot; which animals; how many animals per specific area; why grazing is performed in the particular land parcel, what effects it has upon the vegetation; is it applied regularly or occasionally; is a rotation of grazing plots used within a year/between years; what kind of grazing is used – free, enclosure, with a shepherd, corralling (folding); is autumn grazing used in combination with spring grazing;
      d) *Other types of grazing*: all-year; summer; occasional (including all details as in previous points);
      e) *Ploughing*: was the land parcel ever ploughed or harrowed; what is the date of the last ploughing; why is this land parcel suitable for crops; what crops were grown; how was the meadow/pasture restored; how long it was used for crops; was any kind of crop/grassland rotation applied, what sequence of crops was used and why;
      f) *Sowing*: have some seeds ever been added (artificial sowing) in the plot; which species; what seed mixture (local or commercial); has the local hayseed been used; have clover (*Trifolium* sp.), alfalfa (*Medicago* sp.), sainfoin (*Onobrychis* sp.), other legumes (*Lotus corniculatus*, *Anthyllis vulneraria*) ever been sown in the plot; if yes, why; how many seeds; how often; what are the sowing techniques; what are the effects upon the grassland quality and productivity;
      g) *Manuring*: is the parcel manured; why; how often; when during the year; what kind of manure, was a slurry-liquid manure applied; from which animals; how to prepare a high-quality dung; what are its effects on grass quality and quantity; which plants benefit from manuring and which are suppressed; what is the application technique used; how the bedding material impacts the dung quality;
      h) *Artificial fertilizers*: have artificial fertilizers (ammonium, nitrates, azot, marl, ash, some others) ever been applied; why; since which year; how often; when in the year; how was it applied; what are the effects on grass quality and quantity; what are the advantages and disadvantages; which plants benefit and which are suppressed;
      i) *Cleaning*: what techniques are used to clean the meadow/pasture from shrubs, trees, stones, mosses; have weeding and cleaning from unwanted plants been applied; which plants are unwanted and why (e.g. *Veratrum* sp., *Ononis* sp., *Pteridium aquilinum*, *Nardus stricta*, mosses); has the parcel been cleaned from litter, tree leaves, branches, stones, and rocks; has the parcel been burnt for cleaning;
      j) *Abandonment*: is the parcel managed continuously; are there periods with management interruption; when and for how many years; how abandonment affects grassland quality and productivity; what are the advantages and disadvantages of grassland abandonment;
      k) *Restoration*: what activities improve grassland quality and productivity, what kind of restoration has taken place in the parcel; how can an abandoned grassland/ overgrazed pasture/ degraded meadow be restored; how to restore a grassland digged on the surface by wild boars;
      l) *Other grassland management techniques*: irrigation, amelioration, anthill or molehill removal, others – details on their application.

   1.2. Topics related to quality and productivity of grasslands and grassland products:
      a) *Hay quality*: how many types of hay do you distinguish; what type of hay do you have

from this parcel; what other types of hay do you have on your land;

   b) *Land parcel quality*: what is the quality of this grassland, the owned land, the land in the region.

1.3. Topics related to organisation of the farm and farming activities:

   a) *Ownership*: is the farm private or collective; if private, how many animals do you own and how big is the grassland (pastures, meadows) and cropland area of your farm; do you use external source of fodder apart from your own hay;
   b) *Subsidies*: is the land parcel registered for subsidies; if yes, what kind of subsidy; what types of subsidies are received by the farm; what is the opinion about the subsidy system and possible improvements; what is the contribution of subsidies to the farm budget;
   c) *Farm organisation*: how is the farm organized; what kind of grasslands do you have; do you use rotation of crops, crop-grassland or meadow-pasture rotations; what are all types of subsidies in the farm (what is your opinion about the system and what are some possible improvements, what is the contribution of subsidies to the budget); what is the level of self-sufficiency in the farm; details on marketing; rentability of small farming; ideas for improvement;
   d) *Haymaking and grazing system*: details on spatio-temporal organization of mowing, grazing and manuring during the year; how is it related to the farm area, number of animals and distances between the parcels.

2. Questions to the parcel owners, local inhabitants and town hall officers related to farming and animal husbandry in the village/commune/region:
   a) *Animal husbandry in the village*: how many animals do people usually have in the household; what animals; which breeds do they prefer and why; what changes happened during the last decades (increasing/decreasing number of animals);
   b) *Job opportunities*: how many people work abroad, in the cities, how many are making a living from agriculture, how many receive subsidies for working the land or keeping animals;
   c) *Communal activities*: are there land-use organisations or associations helping farmers with agricultural topics; if yes, how do they help; is there communal activity planning and common land use organisation; describe if something like that exists;
   d) *Pastures in the village*: what types of pastures are present in the village, e.g. private (close or remote), common (close or remote); what is the grazing system, e.g. free grazing, fencing, herded pastures; are some parts of pastures cut for hay; where and according to which criteria were the pastures established; are they compact or dispersed; details on pasture cleaning and other private or communal activities; does the livestock in the village graze outside the stables during the year and how long (in weeks or months); how long the livestock stays in stables (details on different types of livestock);
   e) *Meadows in the village*: where and according to which criteria were the meadows established; are they compact or dispersed; what types of meadows can be distinguished according to grass quality, management practices, distance from the settlement, other criteria; are some activities prohibited on meadows before haymaking (animal or people access, collecting mushrooms, herbs, other); is haymaking an individual or a collective activity; how is it organised; which types of hay storage constructions are used; hay transport and haymaking details (if interesting); what is the main difference between the historical and recent meadow management;
   f) *Wintering of animals and winter fodder*: where the animals are housed in winter (in the village or in remote areas); how long (in weeks or months); which types of winter fodder are used in the village, e.g. hay, silage, pollarded trees and shrubs, compound feed; is additional fodder used from outside the village; what materials are used for bedding in the stables; details (and terminology) on summer or winter stables, field and meadow stables outside the village, if used;
   g) *Borders and boundaries*: distinguishing and marking borders between the properties (fences, hedges, allees, stones, others);
   h) *Introduced customs*: which farming customs are old and which are modern; which have local origin, and which were introduced; when were they introduced and why; have new grass or herb species been introduced to the village and when.

3. Questions to local inhabitants with experience of local farming traditions and willing to share personal ecological knowledge:
   a) *Haymaking details*: how the mowing time affects the hay and the meadow; do you practice rotation of mowing times on different meadows and why; what kind of weather is best for hay production; what adaptations are necessary in years with bad weather;

  b) *Mulching*: what happens if the cut grass is left on the parcel (is not removed, which is the principle of mulching); is the quality of mulched grassland sufficient/decreasing or increasing in time; which plants are sensitive to mulching; is mulching better for grassland quality and productivity than leaving the grass standing for one year, two years, burning, or other technique of cleaning; is the spring mulching better for grassland quality and productivity than the autumn mulching;
  c) *Burning*: are some meadows burned in the village; when (in spring, autumn, which month) and why; how does burning affect the grassland quality and productivity;
  d) *Transhumance*: does/did some transhumance grazing occur in the region; where in the village area; who is/was passing in transhumance (sheep owners from the village, from other regions);
  e) *Grazing in forest*: are/were the forests in the village grazed; which animals graze in the forest and at what time of year; what are the effects of forest grazing for the animals and for the forests;
  f) *Trees in grassland:* can you give details on usage of trees in grasslands, advantages and disadvantages; is/was pollarding used for getting winter-fodder; which trees; details on harvesting and application;
  g) *Cultivation of legumes*: when was legume (clover, alfalfa, sainfoin or other) cultivation introduced in the village; how are/were the legumes cultivated and harvested; where is/was the seed obtained from; what are the advantages of legume cultivation;
  h) *Influence of the political system*: was grassland management affected by communism (collectivisation, land consolidation, abandonment, change in crop priorities), if yes, when (years) and how; was grassland management affected by the political changes in post-communist era (end of collective farms and cooperatives, abandonment, change in crop priorities, migration of inhabitants abroad, other), if yes, when (years) and how;
  i) *Landscape change*: how has the region changed since the days of your grandparents; what is your reception of positive and negative trends in the landscape development (e.g. succession, invasive species);
  j) *Vegetation change*: which plant species became extinct or decreased in the village; which plant species are newly appearing or increasing in number/cover; which habitats are occupied by exotic, non-native species; are these species desired or unwanted; what means may be used to eradicate the particular unwanted species.

4. Questions related to age of the settlements and grassland parcels to be answered from historical documents:
  a) *Age of the village*: how old is the village/settlement;
  b) *Grassland age*: when was the forest cleared/burned and the grazing/mowing regime established; from which century do the oldest records on traditional grassland management come from;
  c) *Ethnic groups*: what are the main ethnic groups in the village/settlement; have other ethnic groups influenced grassland utilisation in the past or in recent times;
  d) *Demography*: is the number of inhabitants in the village the same/lower/ higher in comparison to 1900, 1950, 2000; is the proportion of inhabitants living from agriculture the same/lower/higher in comparison to 1900, 1950, 2000;
  e) *Animal numbers*: is the current number of livestock in the village the same/lower/higher in comparison to 1900, 1950, 1980, 1990, 2000, 2010, 2020 (what are the figures for cows, sheep and goats, horses, pigs separately);
  f) *Area of agricultural land*: is the current pasture/cropland/meadow area the same/decreasing/increasing in comparison to 1900/1950/2000.

Pros and Cons of our study approach

Pro 1: *Teamwork enriches each of the participants*

Participation of researchers from several disciplines allows for new insights and addresses the multifunctionality of traditional farming landscapes as a study object.

Pro 2: *Clear, detailed and unified methodology used for a huge area*

The value of the data increases with the size of the area on which the method is applied. Methods with a similar degree of detail have so far been applied only locally, often without the possibility of comparison with other areas.

Pro 3: *Simple but robust sampling design*

Thanks to the stratified random plot selection, the data are suitable for estimation of multiple diversity parameters. Species richness can be estimated at seven increasing spatial scales, while beta diversity and species pool can be estimated at the site level.

***Pro 4:** Question guidelines are provided for ethnobotanical studies focussing on traditional farming*

Our question guide was prepared by botanists and anthropologists in collaboration and both natural and social sciences qualifications were valued equally in its production. It is widely applicable in both disciplines.

***Pro 5:** Historical and landscape information opens new horizons*

Including historical and landscape information allows evaluation of vegetation change from new perspectives. History, landscape context, and management are increasingly seen by environmental scientists as key for understanding grassland biodiversity.

***Pro 6:** Keeping valuable local ecological knowledge*

Continuous abandonment of traditional agricultural practices across Europe raises concerns for the loss of traditional ecological knowledge (TEK; Burton and Riley 2018). TEK represents a cumulative body of knowledge practice and beliefs concerning environmental management, specifically agricultural management in Europe that supposedly developed through generations of interaction between local communities and their environment. Recording TEK is crucial to preserve the cultural heritage of each investigated region.

***Pro 7:** Estimating significance of management practices at the plot level*

Gathering both vegetation and management data for all the plots allows for proofing the importance of particular management methods for biodiversity values.

***Pro 8:** Capturing the grassland dynamics*

In contrast to phytosociological sampling based on a single visit of the sampled area, our approach tries to capture the vegetation development by asking about the past. This methodology proves the dynamic management of grasslands, since it records precise agricultural practices that were carried out by individual farmers on the grasslands they own. Moreover, it shows how the continuity or discontinuity in traditional grassland management may correlate with current biodiversity patterns.

***Con 1:** It is labourious and time consuming*

The interview protocol was developed during the three years of our project. It was clear from the beginning that it is not possible for a single team to perform both the vegetation sampling and the interviews in numerous study sites, as the period between flowering of the grasses and the first cut is too short and also because the interviews need special skills to obtain high quality information. We started with a collection of questions to determine the workflow associated with the management of local grasslands by consulting agricultural workbooks (Klapp 1965; Opitz von Boberfeld 1994). We began with more than 100 questions (including over 70 questions to the landowners) and reduced them during the following years to those questions that connected with the plot biodiversity.

Experience has shown that with good logistics, it is possible to carry out the vegetation survey part of our methodology on one study site in three days, concentrating on two land parcels (and nested plot series) per day. However, more than one visit to communities was necessary in order to carry out the anthropological part of our methodology (e.g. in certain situations where the local people do not have time to respond due to their daily activities, the researcher has to come back another time and try again). We found that the research team should ideally consist of two anthropologists to support each other in data collection particularly when the study site is new to the researchers. The best strategy is to make two teams, the anthropologists and the biologists, logistically independent, so that they can work together, but also in different places during a single day: either to go to the sampling parcel and to ask about the specific management practices for that very place, or to return to the village if there are no people nearby the parcel, or to stay in the settlement, visit the town hall and to take interviews that would provide more context concerning the local practices in general. Spending more time with the local communities would help the researchers to understand better the local practices and find suitably knowledgable interviewees.

***Con 2:** It is concise and thus not always covering all important aspects*

By focusing only on specific parcels in the landscape where the vegetation surveys are carried out, researchers may miss the wider picture of the agricultural practices and landscape management of the community. It is therefore recommended to integrate individual site-specific management with the wider agricultural and economic activities at the landscape level. Some of the activities at this level are organized by the community according to their own local rules. Consequently, it is usually necessary to obtain additional oral or historical information on the common use of resources in the recent past.

"Grassland with Tradition" database

The database "Grassland with Tradition" is registered in Global Index of Vegetation-Plot Databases (GIVD, https://www.givd.info/faces/database_details.xhtml) with the identifier ID EU-00-032. As to 31 October 2020

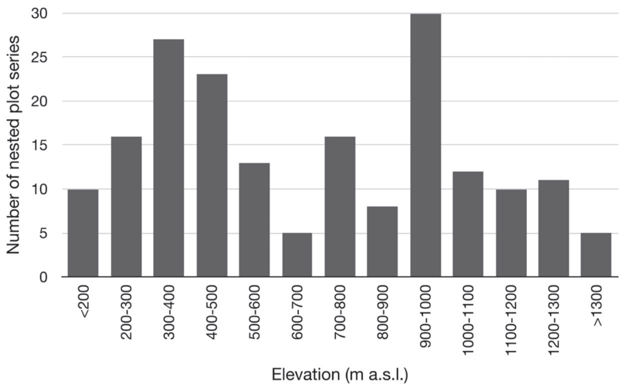


Figure 7. "Grassland with Tradition" database: Distribution of nested plot series along the elevation gradient (as to 31 October 2020).

it contains 186 nested plot series recorded in the Carpathian Mountains within seven different countries. The sampling was conducted during 2017–2020. The sampled plots are distributed at elevation between 147 and 1422 m (Figure 7) and over various geological bedrock types including plutonic and volcanic rocks, limestone, flysch, loess, and sediments (Table 1). The main land-use categories (meadows, pastures and abandoned land) are further divided according to the combination of applied management practices (Figure 8). The meadows include five basic categories regarding the additional application of ploughing and grazing, and its timing. Permanent meadows were never ploughed and are used exclusively by regular mowing. Meadows on former cropland include grassland in active crop-grassland rotation systems or older fallows which are now used exclusively as meadows. Three types of grazed meadows can be distinguished, either with exclusive spring or autumn grazing and those grazed during both these periods. In the regions with best-preserved farming traditions (Figure 9) grazed medows represent the absolute majority of local meadow types. Most of the sampled pastures are used for grazing cows or sheep as single grazing animal (Figure 8). Regarding the phytosociological affiliation (Table 1, Figure 8), mesic grasslands of the *Arrhenatherion elatioris* alliance (*Molinio-Arrhenatheretea* class) and *Violion caninae* (*Nardetea strictae* class) prevail, followed by semi-dry grasslands of the *Bromion erecti* and *Cirsio-Brachypodion* alliances (*Festuco-Brometea* class). According to the actual land-use consulted with the landowners we distinguished three categories of grassland management: i) management according to continuous living tradition, ii) management according to modified tradition, and iii) management not based on tradition. Although the classification criteria of traditional land-use are sometimes fuzzy and subjective, there is a clear decreasing trend of traditional farming along the Carpathian arch from the southeast to the northwest (Figure 9).

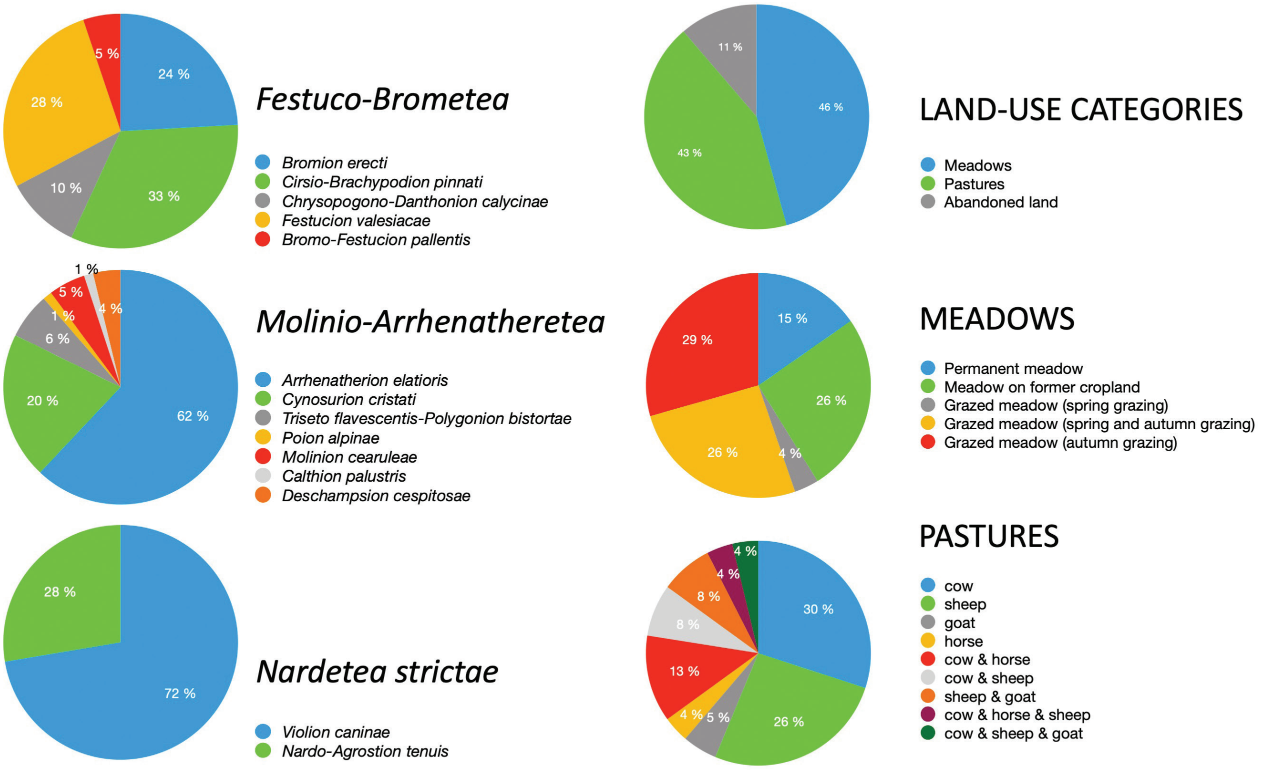


Figure 8. "Grassland with Tradition" database: Representation (as to 31 October 2020) of i) grassland syntaxa (phytosociological classes and alliances); ii) land-use categories; iii) types of meadows according to the presence/absence of additional management by ploughing and grazing; iv) types of pastures according to grazing animal(s).

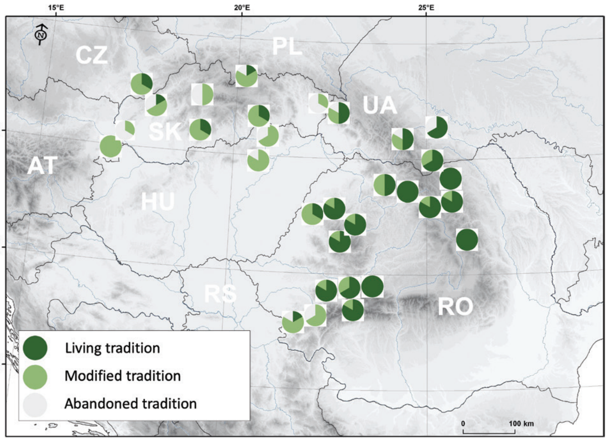


Figure 9. "Grassland with Tradition" database: Distribution of living, modified, and abandoned tradition in grassland management of the sites studied so far (as to 31 October 2020). In each study site, six parcels were selected by a stratified random selection considering the topographic situation (aspect and slope) and habitat type (managed grassland). According to the actual land-use type on those parcels (consulted with the landowners) we distinguished three categories of grassland management: i) management according to continuous living tradition, ii) management according to modified tradition, and iii) management not based on tradition. Although the classification criteria of traditional land-use are sometimes fuzzy and subjective, clear differences in farming approaches are obvious between the Western and Eastern Carpathians.

Author contributions

M.J. conceived the idea, edited and analysed the database, and outlined the first draft of the text; M.J. and M.M. developed and described the botanical and A.I. and C.M.I. the ethnological parts of the methodology; all authors participated in the fieldwork, contributed to the database, discussed and commented on the previous versions of the manuscripts.

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SHORT COMMUNICATION PHYTOSOCIOLOGICAL NOMENCLATURE

Validation of the names of some Cretan high mountain syntaxa, with considerations about Article 3i, ICPN

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Abstract

To comply with the International Code of Phytosociological Nomenclature (ICPN), we validate the names *Saturejo spinosae-Scutellarietalia hirtae*, *Arenarion creticae*, *Verbascion spinosi* and *Lomelosio sphacioticae-Centranthetum sieberi*. Two divergent interpretations of Article 3i about the point at issue in the validation of the first three names are discussed.

Syntaxonomic reference: Bergmeier (2002), unless indicated otherwise in the text.

Keywords

Crete, high mountains, phytosociology, syntaxon, validation

Introduction

In a monographic paper on the vegetation of the high mountains of Crete, Bergmeier (2002) described as new the associations *Arenario fragillimae-Silenetum antri-jovis*, *Berberido creticae-Astragaletum cretici*, *Cicero incisi-Silenetum variegatae*, *Fumano paphlagonicae-Helianthemetum hymettii*, *Gypsophilo nanae-Arenarietum creticae*, *Hyperico kelleri-Anchusetum cespitosae*, *Paronychio macrosepalae-Juniperetum oxycedri* and *Sideritido syriacae-Verbascetum spinosi*, as well as the alliances *Alysso sphaciotici-Valantion apricae*, *Astragalion cretici* and *Colchico cretensis-Cirsion morinifolii*.

While the names of these syntaxa had been validly published, the author further intended to validate the names of four other syntaxa, namely the alliance *Arenarion creticae* and the order *Saturejo-Scutellarietalia*, both invalidly (ICPN Art. 5) proposed "ad interim" by Dimopoulos et al. (1997: 334), as well as the *Verbascion spinosi* in Zaffran (1990: 470) and the *Lomelosio sphacioticae-Centranthetum sieberi* in Zaffran (1990: 529). As argued below, one can consider that the attempt to validate the first three names failed because the provisions of Article 3i of ICPN (Theurillat et al. 2021) were not fulfilled.

With this nomenclatural note we validate these names in following the syntaxonomic concept of Bergmeier (2002) that is also adopted in the EuroVegChecklist (Mucina et al. 2016). At the same time, having been made aware during the revision process that the underlying nomenclatural question is disputable, we discuss the critical point at issue.

Interpretation of Article 3i with regard to the validation of syntaxon names

Among the reasons causing the invalidity of a syntaxon name, Art. 3i states: "When it has been published on or after 1 January 2002 without being indicated explicitly as new". Despite the term 'explicit' appears to be clear, interpretations are nonetheless possible. Thus, it might be disputed whether the present validation of three of the names addressed (*Saturejo spinosae-Scutellarietalia hirtae*, *Verbascion spinosi* and *Arenarion creticae*) is necessary, arguing that the wording '*valid. hoc loco*' used by Bergmeier (2002: 242–244) in his attempt to validate the names is to be regarded as an 'explicit indication as new' in the sense of Art. 3i.

By stating *valid. hoc loco* (as against merely *valid.*, which might indeed refer to someone and somewhere else's validation) Bergmeier (2002) intended to designate, by validation, unambiguously referenced, the hitherto invalid names as new. In his attempt, Bergmeier (2002) did not want to claim the authorship of the syntaxa but to perform merely the formal act of validation, while appreciating the fact that the novel syntaxa were described, though invalidly, by the original authors. Although it is evident that the names of the syntaxa that Bergmeier (2002) attempted to validate were not accompanied by the literal expression of 'new', the aim of the author was nevertheless made clear in the abstract in specifying the "… nomenclaturally relevant new or validated names", and in using for each of the allegedly validated names the indication *valid. hoc loco* (Bergmeier 2002: 240–243). The question is whether the implicitly clear approach is sufficiently explicit regarding Art. 3i.

The indication *valid. hoc loco* used by Bergmeier (2002) may well imply that this expression is sufficiently unambiguous (arguably even less ambiguous, or more explicit, than some expressions used in vernacular languages accepted by Art. 3i until 31 December 2020). The then authoritative third edition of the ICPN (Weber et al. 2000), Art. 6, stated that "… a provisional name is validated only when the validation is indicated *expressis verbis*, and all other conditions are fulfilled (see Art. 3i)", which suggested that a particular *expressis verbis* indication was needed when validating, and that the expression *valid. hoc loco* (in full: *validatio hoc loco*) would be adequate in this respect. However, Art. 3i of the same edition established that names are invalid when published on or after 1 January 2002 "without being indicated *expressis verbis* as new (e.g. 'ass. nov.', 'all nov.', 'comb. nov.', 'stat. nov.', 'nom. nov.', etc.); this applies also to the validation of invalidly published names".

The expression *expressis verbis* (literally 'in express terms') used in the third edition of the ICPN means 'explicitly' (which is the term used in the 4th edition of the ICPN), that is directly, unambiguously stated, not left to implication. In writing *valid. hoc loco*, Bergmeier (2002) did not comply with an explicit indication. Since an explicit indication of 'new' was requested in 2002 (Art. 3i), this provision should have been effectively published as part of the publication of the missing provisions according to Art. 6 in order to validate the names *Saturejo spinosae-Scutellarietalia hirtae*, *Verbascion spinosi* and *Arenarion creticae*. Therefore, when Bergmeier (2002) wrote in the abstract: "A hierarchical conspectus of the syntaxa is provided which includes the following nomenclaturally relevant new or validated names of various ranks ...", he made a distinction between the names he described as new and those he attempted to validate, without explicitly indicating the validated names as new.

Since it is desirable for the sake of stability to keep the names in question in their syntaxonomic circumscription as provided by Bergmeier (2002) and as they are retained by Mucina et al. (2016), we provide below their formal validation in accordance with a strict, formal interpretation of Art. 3i. At the same time, we acknowledge that a more precise wording of Art. 3i or a binding decision by the Committee of Change and Conservation of Names (CCCN) on this case might be desirable.

Validations

(1) *Saturejo spinosae-Scutellarietalia hirtae* Dimopoulos et al. ex Bergmeier ord. nov. – Typus: *Verbascion spinosi* Zaffran ex Bergmeier hoc loco (see below). Diagnostic species: table 9 in Bergmeier (2002).

The *Saturejo spinosae-Scutellarietalia hirtae* was to be validated by selecting the alliance *Verbascion spinosi* published in Zaffran (1990: 470) as the nomenclatural type (Bergmeier 2002: 241). However, the attempt to validate the *Verbascion spinosi* chosen as the type failed (see below) and, consequently, that of the order's name (Art. 3o).

(2) *Verbascion spinosi* Zaffran ex Bergmeier all. nov. – Typus: *Sideritido syriacae-Verbascetum spinosi* Bergmeier 2002 (Bergmeier 2002: 242). Diagnostic species: table 9 in Bergmeier (2002: 241).

The name *Verbascion spinosi* was invalidly published in Zaffran (1990: 470) because of a missing type (Arts. 3o and 5). In his attempt to validate the name, Bergmeier (2002: 239, 242) designated a type. However, the name was not explicitly indicated as new. Consequently, the attempt to validate failed since on or after 1 January 2002 the 'explicit indication as new' is requested for the valid publication of a name (Arts. 3i and 6).

(3) *Arenarion creticae* Dimopoulos et al. ex Bergmeier all. nov. – Typus: *Gypsophilo nanae-Arenarietum creticae* Bergmeier 2002 (Bergmeier 2002: 240). Diagnostic species: table 10 in Bergmeier (2002: 243).

The *Arenarion creticae* was invalidly (Art. 5) published "ad interim" by Dimopoulos et al. (1997: 334). In his attempt to validate the name, Bergmeier (2002: 240) designated a type but did not explicitly indicate the name as new. Consequently, the attempt to validate failed since on or after 1 January 2002 the 'explicit indication as new' is requested for the valid publication of a name (Arts. 3i and 6).

(4) *Lomelosio sphacioticae-Centranthetum sieberi* Zaffran ex Bergmeier ass. nov. – Typus: relevé 48, separate table 29 in Zaffran (1990).

The name '*Lomelosio-Kentranthetum sieberi*' was not validly published in Zaffran (1990: 529) because no type was given for this new association (Art. 5). In his attempt to validate the name, Bergmeier (2002: 243) selected the relevé 35 of the separate table 29 in Zaffran (1990) as typus. However, one of the name-giving taxa, *Centranthus sieberi* Heldr., is missing in that relevé. Consequently, the attempt to validate failed (Arts. 3o, 5 and 16). The relevé 48 selected here is the only relevé in Zaffran (1990, table 29) that contains both name-giving species, and hence the only element suitable as the type relevé.

Author contributions

Both authors contributed in equal parts.

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REPORT

Global Vegetation Project: an interactive online map of open-access vegetation photos

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Abstract

The Global Vegetation Project (http://gveg.wyobiodiversity.org) is a new initiative to host an online database of open-access, georeferenced vegetation photos. The mission of the Global Vegetation Project is 'to inspire and empower people of all ages to learn about the diversity of vegetation on our planet and to provide educators with a resource for teaching ecology online'. The beta release includes two R-Shiny web applications that allow users to 1) submit photos of plant communities through a user-friendly online portal and 2) explore submissions made by others through an interactive global map. The spatial coordinates of each photo are used to extract information about the location including long-term and recent climate data to create Walter and Leith climate diagrams for each photo. User submitted photos can be filtered by biome, temperature, precipitation, and elevation on the map. The Global Vegetation Project will evolve to match the needs of vegetation scientists and ecology educators. We intend to enhance the educational value of the mapping application by incorporating additional search features, global data layers, and the publication of curricula geared towards primary, secondary, and post-secondary education. We encourage the global community of vegetation scientists to use this resource in their classrooms and to contribute photos of vegetation to grow this valuable resource for the world.

Keywords

community ecology, ecology, geodatabase, global database, gVeg, R-Shiny

Mission and scope

Understanding the structure and dynamics of vegetation on Earth requires international collaboration and data sharing at a global scale. Recently, several biological databases have been made available and are being used to study global biodiversity: sPlot provides a database of vegetation relevés (Bruelheide et al. 2019), the Global Index of Vegetation-Plot Databases (GIVD) provides a metadatabase of vegetation relevés (Dengler et al. 2011), the Global Biodiversity Information Facility provides a database of species occurrences and distributions (https://www.gbif.org) (GBIF 2020) and TRY provides a database of plant traits (Kattge et al. 2020). There are many others. However, despite the importance of digital media in research and education, there was no database of georeferenced global vegetation photos or a map to explore them, until now.

To fill these gaps, we have launched a new initiative called the Global Vegetation Project (http://gveg.wyobiodiversity.org) to host a database of globally-distributed vegetation photos. The Global Vegetation Project is, as far as we know, the first global online repository of open access, georeferenced photos of plant communities. Our mission is 'to inspire and empower people of all ages to learn about the diversity of vegetation on our planet and to provide educators with a resource for teaching online'. This project was inspired by the urgent need for online teaching resources in ecology classrooms and the lack of an open-access central repository of georeferenced photos which represent all of the major vegetation types across our diverse planet.

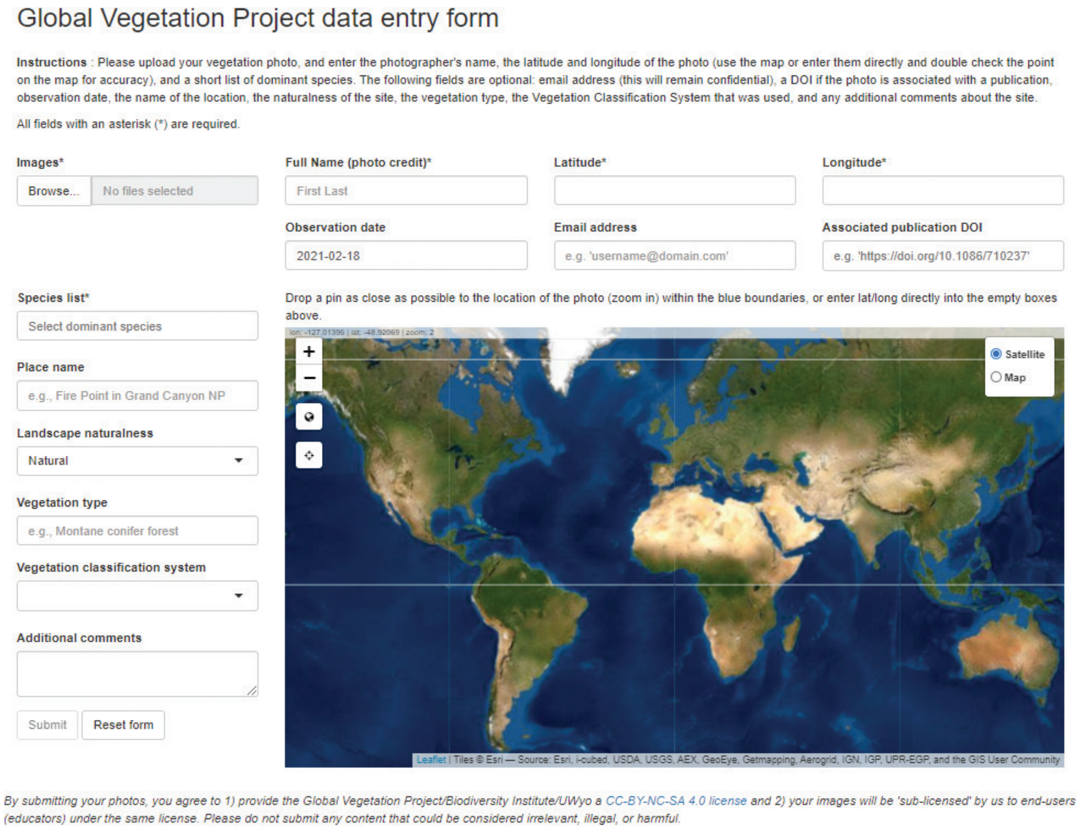
We aim to bring the field into the classroom in a previously impossible way, enabling visual and interactive experiences that link vegetation and climate at the global scale. The long-term vision is to curate a global database of vegetation photographs that can be explored interactively through an online map and search interface. Curricula will be developed for a range of educational levels to challenge students to tackle a variety of learning outcomes such as 1) understanding how annual and seasonal climate shapes vegetation composition and physiognomy, 2) identifying examples of functional convergence in different regions of the planet, and 3) hypothesizing how climate change might affect the distribution of vegetation types in the future. In some ways, the project has similarities to iNaturalist (https://www.inaturalist.org/), which has had a powerful impact on ecology education. The difference is that we focus on communities of plants (i.e., vegetation) rather than individual species and our project will directly provide curricular resources for online education.

Accomplishments in the beta release

To date, we have developed two R-Shiny web applications (Chang et al. 2019) hosted on a RStudio Shiny Server. These applications allow users to 1) submit photos of plant communities through a user-friendly online portal and 2) explore submissions made by others through an interactive global map.

We invite vegetation ecologists and community scientists to contribute through a photo submission portal where users upload an image and submit information about their photo (Figure 1). The required information includes the photographer's name, geographical coordinates in decimal degrees, and a short list of dominant plant species. We include optional fields for observation date, email address, place name, landscape naturalness, vegetation type, vegetation classification system, associated publication DOIs, and additional comments. We have imported the Leipzig Catalogue of Vascular Plants (LCVP) as a dropdown to standardize taxon names (Freiberg et al. 2020), but also allow users to provide any species names that they prefer. Rather than requiring users to use one approach to vegetation classification, such as EcoVeg (Faber-Langendoen et al. 2018), we include a dropdown menu with options for a variety of vegetation classification systems (e.g., International Vegetation Classification, International Code of Phytosociological Nomenclature, etc.). If a system is not on our list, users can simply enter the classification system they used to define their vegetation type. We encourage users with large batches of photos to contact us to facilitate batch uploads of photos and metadata. By submitting photos, users agree to provide the Global Vegetation Project a CC-BY-NC-SA 4.0 license and user images will be 'sub-licensed' by us to end-users (e.g., educators) under the same license.

Each submission is stored within a Microsoft SQL Server relational database and our associated cloud file storage



Global Vegetation Project data entry form

Instructions : Please upload your vegetation photo, and enter the photographer's name, the latitude and longitude of the photo (use the map or enter them directly and double check the point on the map for accuracy), and a short list of dominant species. The following fields are optional: email address (this will remain confidential), a DOI if the photo is associated with a publication, observation date, the name of the location, the naturalness of the site, the vegetation type, the Vegetation Classification System that was used, and any additional comments about the site.

All fields with an asterisk (*) are required.

Images* Browse... No files selected

Full Name (photo credit)* First Last

Latitude*

Longitude*

Observation date 2021-02-18

Email address e.g. 'username@domain.com'

Associated publication DOI e.g. 'https://doi.org/10.1086/710237'

Species list* Select dominant species

Place name e.g., Fire Point in Grand Canyon NP

Landscape naturalness Natural

Vegetation type e.g., Montane conifer forest

Vegetation classification system

Additional comments

Drop a pin as close as possible to the location of the photo (zoom in) within the blue boundaries, or enter lat/long directly into the empty boxes above.

lon: -127.01396 | lat: -48.92069 | zoom: 2

● Satellite
○ Map

Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

By submitting your photos, you agree to 1) provide the Global Vegetation Project/Biodiversity Institute/UWyo a CC-BY-NC-SA 4.0 license and 2) your images will be 'sub-licensed' by us to end-users (educators) under the same license. Please do not submit any content that could be considered irrelevant, illegal, or harmful.

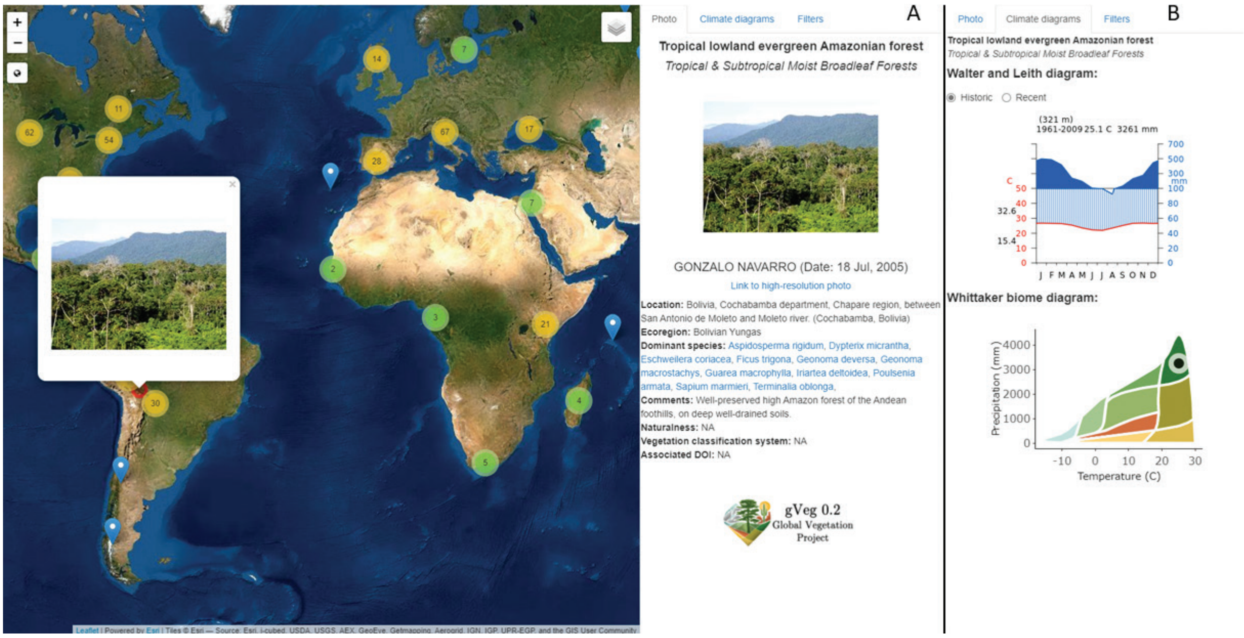
Figure 1. Screen shot of the photo submission application being hosted at http://gveg.wyobiodiversity.org.

server. Image attributes are written to relational tables within the database, with records having the image metadata as well as the cloud storage URL to the image file. These data are backed up nightly to an offsite location and maintained for at least 15 days. The web application programming interface (API) is built upon ASP.NET, and provides multiple end points for data retrieval (https://documenter.getpostman.com/view/11557311/SztD4mhW?version=latest). The API conducts validation of each user submission to ensure minimum data requirements are met. Valid submissions then undergo a second inspection by the maintainers of the Global Vegetation Project to ensure that images are appropriate and to correct identifiable errors. The Advanced Research Computing Center (ARCC) at the University of Wyoming provides robust cyber-infrastructure and security that the Global Vegetation Project uses for its data visualization and storage needs. This includes the open-source software Shiny-Server from RStudio running on a fault tolerant virtual machine, 100 gigabit networking, and S3 storage through the open-source Ceph project.

The location data of each photo is used as a spatial reference to extract a variety of additional information about the photo. We extract historic (1961–2009) and recent (2010–2018) climate data on annual and monthly timescales (Karger et al. 2017; Trabucco and Zomer 2018), elevation (Danielson and Gesch 2011), state/province, and country of origin (Hijmans et al. 2018) as well as biome (Ellis et al. 2010) and ecoregion classifications (Olson et al. 2001; Dinerstein et al. 2017). The interactive map displays this information in a sidebar and as global raster layers (Figure 2). We convert the list of species names provided during submission to species specific hyperlinks that reference occurrence and distribution data on GBIF (GBIF 2020). We apply the R package 'plotbiomes' (Stefan and Levin 2020) to plot the location of the photo on a Whittaker biome diagram defined by mean annual temperature and precipitation (Whittaker 1970). We use the R package 'climatol' (Guijarro 2019) to create Walter and Leith climate diagrams of historic and recent climates for that location (Breckle 2002). Figure 2 illustrates the layout of the online map interface after selecting a photo point. The pop-up to the left of the sidebar contains a thumbnail of the user submitted photo. The sidebar on the right is comprised of three tabs that shows photo metadata (detailed above), climate diagrams, and spatial filters.

Spatial filters and comparative climate diagrams enhance the education value of the map interface by providing a means for active learning. We give users the option to filter observations by precipitation (mm/yr), temperature (°C), elevation (m), and biome at present and intend to expand these options to include all user inputs from the data entry application. These queries will be invaluable for educators seeking photos for their lectures and the general public who are curious about vegetation in their region. We also provide users the ability to compare climate diagrams based on the most recent decade of data (2010–2018) to historic averages (1961–2009) to demonstrate recent climate change at the location of each photo.

We released the beta version of the Global Vegetation Project in October 2020 and have had 2,011 unique visitors as of February 15, 2021. At present, 240 users have contributed 1,043 photos spread across 14 biomes (100% of terrestrial biomes) and 196 ecoregions (~23% of ecoregions classified in Dinerstein et al. 2017). Users have



Tropical lowland evergreen Amazonian forest

Tropical & Subtropical Moist Broadleaf Forests

GONZALO NAVARRO (Date: 18 Jul, 2005)

Location: Bolivia, Cochabamba department, Chapare region, between San Antonio de Moleto and Moleto river. (Cochabamba, Bolivia)
Ecoregion: Bolivian Yungas
Dominant species: Aspidosperma rigidum, Dypterix micrantha, Eschweilera coriacea, Ficus trigona, Geonoma deversa, Geonoma macrostachys, Guarea macrophylla, Iriartea deltoidea, Poulsenia armata, Sapium marmieri, Terminalia oblonga,
Comments: Well-preserved high Amazon forest of the Andean foothills, on deep well-drained soils.
Naturalness: NA
Vegetation classification system: NA
Associated DOI: NA

Figure 2. Screen shot of the online map application at http://gveg.wyobiodiversity.org illustrating a photo from a tropical lowland evergreen Amazonian forest in Bolivia (photo by Gonzalo Navarro, used with permission) within the pop up feature (on the left) and the photo metadata on right (**A**). Whereas (**B**) illustrates the historic and recent climate of the area in a Walter and Leith climate diagram and its location in a Whittaker biome diagram. Note that users can turn on additional global layers, including mean annual temperature and precipitation, elevation, aridity (MAP:PET ratio), biomes, and ecoregions. For clarity, we do not display the spatial filters tab here.

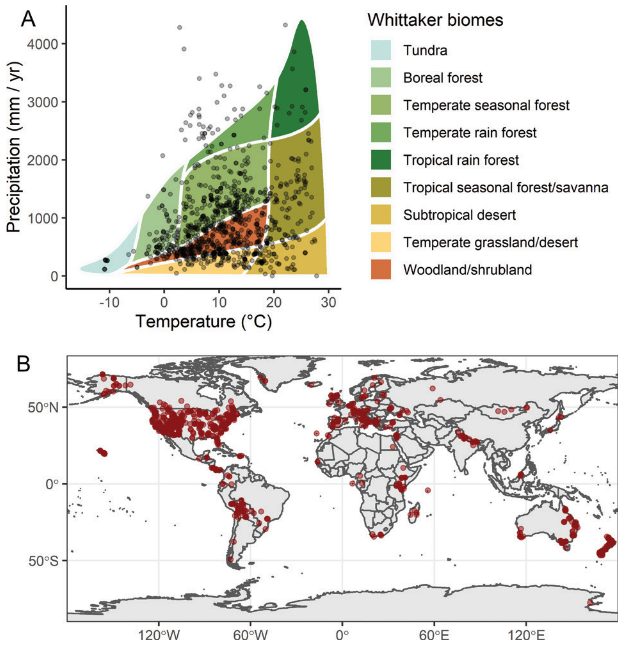


Figure 3. A Location of current photos in the database in a Whittaker biome diagram defined by mean annual temperature and mean annual precipitation. **B** Point locations of current photos.

submitted photos from 64 countries, on every continent, and across a wide range of climate conditions (Figure 3). However, like many ecological surveys, there are apparent gaps in tropical and temperate rain forests, tundra, and hot deserts, representing the extremes in climate space (Figure 3a). We hope that contributions from the global community of vegetation ecologists and community scientists will fill the map with photos (Figure 3b).

Plans for the future

Our goal is to enhance online ecology education and serve the global community of vegetation scientists. The Global Vegetation Project will evolve to match the needs of vegetation scientists and ecology educators. We have several additions in the pipeline to improve the functionality of both applications and we are in discussions with vegetation scientists to meet the needs of the research community.

We have plans to add additional global data layers to the mapping application, such of land cover, disturbance regimes, canopy height, soil properties, and other globally mapped factors that relate to vegetation distributions. We will use these layers in conjunction with preexisting features in educational modules that we will develop for primary, secondary, and post-secondary education levels. These modules will be geared toward teaching concepts such as functional convergence, vegetation-climate relationships, and climate change. We have expanded our database by integrating photos and their metadata from other scientific and open-access databases such as PhenoCam (http://phenocam.us) (Richardson et al. 2018). New features and educational support tools will be released as they are developed through the coming years.

With the help of contributions from a global community, the Global Vegetation Project aims to improve online vegetation science and education. We encourage vegetation scientists to use this resource in their classrooms and to contribute photos of vegetation to grow this valuable resource for the world.

Author contributions

J.R.F., D.H.A., S.A.W., S.E.A., N.W.C., and D.C.L. conceptualized the idea. N.W.C. and S.E.A. developed the geodatabase and web API. J.R.F. developed the R-Shiny apps with contributions from all other authors. J.R.F. and D.C.L. prepared the original draft manuscript. All authors contributed to review and editing. D.C.L. acquired all funding.

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RESEARCH PAPER

Syntaxonomy of the xero-mesophytic oak forests in the Republic of Tatarstan (Eastern Europe)

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Abstract

Aims: To develop a syntaxonomic classification of the xero-mesophytic broad-leaved oak forests of the Republic of Tatarstan with a preliminary analysis of their unique ecological features. **Study area:** The Republic of Tatarstan (European part of the Russian Federation). **Methods:** A total of 91 relevés were processed. Most of them (73.6%) were sampled in Tatarstan during 2016 and 2017, the remaining ones (26.4%) were historical published data. They were classified by means of a modified TWINSPAN algorithm using total inertia as a heterogeneity measure. Diagnostic, constant, and dominant species were identified using analytical tools in the JUICE 7.0 program. **Results:** The xero-mesophytic forests of the study area were assigned to four clusters. We describe two of them as new associations: *Astragalo ciceri-Quercetum roboris* ass. nova and *Sanguisorbo officinalis-Quercetum roboris* ass. nova. We classify them within the class *Quercetea pubescentis*. **Conclusions:** Our study is the first attempt to classify thermophilous and xero-mesophytic oak forests of the Republic of Tatarstan using the Braun-Blanquet system.

Taxonomic reference: Czerepanov (1995).

Syntaxonomic reference: Mucina et al. (2016) unless stated otherwise in the text.

Abbreviations: GIVD = Global Index of Vegetation-Plot Databases; NMDS = Non-metric multidimensional scaling.

Keywords

Aceri tatarici-Quercion, *Lathyro pisiformis-Quercion*, oak forest, *Quercetalia pubescenti-petraeae*, *Quercetea pubescentis*, Republic of Tatarstan, xero-mesophytic forest

Introduction

The xero-mesophytic broad-leaved forests of the Republic of Tatarstan (hereafter referred to as Tatarstan) are of interest for several reasons. These forests are characterized by high biodiversity and host many rare and protected plant species. *Quercus robur*, a canopy-forming tree species of these ecological communities, is found here near the northeastern boundary of its native range (Gorchakovskij 1968). The communities of this type form an ecotone between forest and steppe, which has long attracted researchers, starting with the works of Korzhinsky (1888) and Markov (1935).

Xero-mesophytic broad-leaved forests occupy a large area within the forest-steppe zone of Central and Eastern Europe. Communities of this type occur eastward as a gradually tapering belt that extends to the following territories of Eastern Europe: Ukraine (Goncharenko 2003; Onyshchenko et al. 2007; Solomakha 2008; Semenishchenkov and Panchenko 2012; Panchenko 2013); Crimea (Korzhenevskij et al. 2003); the regions of Bryansk (Bulokhov and Solomeshch 2003), Kursk, Tula, Belgorod (Semenishchenkov and Poluyanov 2014), Voronezh, Tambov, Penza, Saratov, Samara, and Ulyanovsk (Blagoveshchenskij 2005); the Republics of Mordovia, Chuvashia, Tatarstan (Markov 1935), and Bashkortostan (Yamalov et al. 2004); and the Orenburg region.

Until recently, the classification of plant communities of Tatarstan has been performed using the dominance approach (Rogova and Shajhutdinova 2000; Pozdnyak 2005). The syntaxonomic position of the xero-mesophytic oak forests of Tatarstan in the Braun-Blanquet system is still unclear.

The westerly distributed analogues have been attributed to the alliance *Aceri tatarici-Quercion* (Semenishchenkov and Poluyanov 2014) and the eastern analogues to the alliance *Lathyro pisiformis-Quercion roboris* (Yamalov et al. 2004; Willner et al. 2016). However, Semenishchenkov and Panchenko (2012) suggested that some associations previously assigned to the *Aceri tatarici-Quercion* should be classified in the *Quercion petraeae*. They also pointed out that the xero-mesophytic oak forests of Tatarstan are distinct from both of the aforementioned alliances. In a recent revision of the thermophilous oak forests of the steppe and forest-steppe zones of Ukraine and Russia, Goncharenko et al. (2020) described the eastern part of the *Aceri tatarici-Quercion* as a new alliance *Scutellario altissimae-Quercion roboris* and the eastern part of the *Quercion petraeae* as *Betonico officinalis-Quercion roboris.*

The aim of this article is to address the following research questions: 1. Are there communities in Tatarstan that may be assigned to the order *Quercetalia pubescenti-petraeae*? 2. To which lower-level syntaxa can they be assigned? 3. What are the compositional, ecological, and chorological characteristics of these syntaxa?

Study area

The Republic of Tatarstan is located in the eastern part of the East European Plain at the confluence of the largest European river Volga with the rivers Kama and Belaya (Figure 1). The northwesternmost point is approximately 56.67°N, 047.26°E, the southeasternmost one 53.97°N, 054.27°E. The total area is 67,600 km^2. The territory is divided by the rivers into clearly separated natural and geographical parts: Cis-Volga region (west and south of the Volga valley), Cis-Kama region (north of the Kama and Volga valleys), Trans-Kama region (south of the Kama valley) (Butakov 1994).

Large uplands alternate with lowland areas across the study area. The lowest elevation in the territory is along the line of the Kuibyshev Reservoir with an average of 53 m, while the maximum elevation of 380 m is reached in the south-east of the study area (Butakov 1994). Being located within the Sarmatian mixed forests and the East European forest-steppe (Dinerstein et al. 2017), the study area has high biodiversity, particularly regarding its vegetation cover (Bakin et al. 2000). The heterogeneity of site conditions due to climatic and soil characteristics, as well as the long-term human impact on vegetation (Bakin et al. 2000), has determined the complexity and diversity of the vegetation cover. The territory is comprised of 18% forests, 21.5% grasslands and 6% water bodies (Shadrikov 2019). The remaining 54.5% of the territory is agricultural and urban land. Young forest stands prevail in the forest vegetation (secondary birch, aspen, and lime coppice), whereas the ancient forests

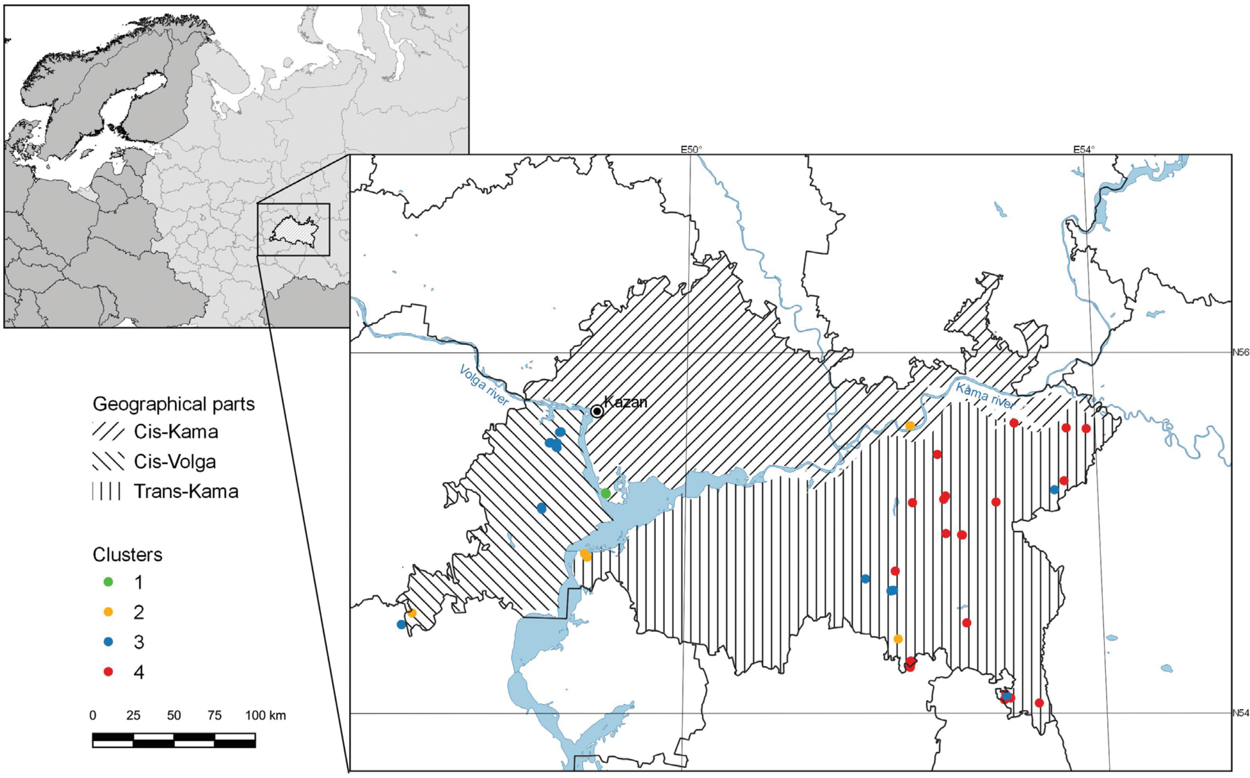

Figure 1. Study area and plot location.

are small and fragmented. Steppe communities occupy very small territories. They are represented by meadow steppes along the edges of deciduous forests and gentle slopes. The steep slopes of southern exposure in the southeastern part of the Tatarstan are occupied by petrophytic steppes (Bakin et al. 2000).

Methods

Vegetation data

All relevés of the oak forests of Tatarstan were previously classified and analyzed to exclude hygrophytic and mesophytic communities (Kozhevnikova et al. 2018). For the present study, a total of 91 relevés of xero-mesophytic oak forests were compiled from the study area. The majority of relevés (n = 67), was sampled in the field during the field seasons of 2016 and 2017, with the aim of investigating the communities of thermophilous oak forests following the construction of a model of their potential distribution (Kozhevnikova et al. 2019). Further 24 relevés were historical data retrieved from the literature (Markov 1935).

The newly collected relevés were sampled using the standard phytosociological methodology (Dengler et al. 2008). In most cases, the plot size was 400 m^2. For each vegetation plot, all vascular plant species were recorded with indications of their layer and abundance based on the Drude scale (Drude 1896). In addition, the geographical coordinates, altitude, exposition, and slope were recorded for each relevé.

The published relevés of Markov (1935) include information on all species of vascular plants, their abundance on the Drude scale and the geographical position, which we georeferenced with an accuracy of 200 m.

To compare the newly sampled relevés with the previously described associations, we used published relevés assigned to the *Aceri tatarici-Quercion* from the Belgorod and Kursk regions (Semenishchenkov et al. 2013; Semenishchenkov and Poluyanov 2014): *Chamaecytiso ruthenici-Quercetum roboris* Semenishchenkov et al. 2014, *Pyro pyrastris-Quercetum roboris* Semenishchenkov et al 2014, *Vicio pisiformis-Quercetum roboris* Semenishchenkov et al. 2014, *Lathyro nigri-Quercetum roboris* Bulokhov et Solomeshch 2003. We also analyzed the published relevés of the *Lathyro pisiformis-Quercion roboris* from Southern Urals (Gorchakovskij 1972; Schubert et al. 1979; Solomeshch et al. 1989; Martynenko et al. 2005, 2008): *Filipendulo vulgaris-Quercetum roboris* Martynenko et al. 2008, *Omphalodo scorpioidis-Quercetum roboris* Martynenko et al. 2008, *Brachypodio pinnati-Quercetum roboris* Grigorjev in Solomeshch et al. 1989, *Aconogono alpini-Quercetum roboris* Gorczakovskij ex Solomeshch et al. 1989, *Calamagrostio epigei-Quercetum roboris* Gorczakovskij ex Solomeshch et al. 1989, *Carici macrourae-Quercetum roboris* Gorczakovskij ex Solomeshch et al. 1989, *Pruno-Quercetum roboris* Solomeshch et al. 1989, *Bistorto majoris-Quercetum roboris* Martynenko et Zhigunov, 2005. All processed relevés are included in the information system “Flora” (Rogova et al. 2010), which contains data from Tatarstan (Prokhorov et al. 2017) and adjacent territories.

Analysis

The relevés of xero-mesophytic communities were exported from the information system “Flora” with simultaneous translation of the Drude abundance grades into cover percentage (soc – 95%, cop$_3$ – 75%, cop$_2$ – 50%, cop$_1$ – 25%, sp – 3%, sol – 2%, un – 0.5%). This file was then imported into the JUICE 7.0 program (Tichý 2002) with the transformation of cover percentage into the Braun-Blanquet scale. The relevés were classified by applying the modified TWINSPAN algorithm (Roleček et al. 2009). For optimizing the number of clusters, the procedure OptimClass proposed by Tichý et al. (2010) was used. The resulting clusters were analyzed by calculating the species frequency and by identifying diagnostic, constant and dominant species. The following threshold values were used: for diagnostic species, a phi value > 0.6, for constant species, a frequency > 60%, and for dominant species, average cover > 80%.

The resulting clusters were compared with the aforementioned associations of the alliances *Aceri tatarici-Quercion* and *Lathyro pisiformis-Quercion* by combining them into a single constancy table. For all vegetation units, the frequency sum of diagnostic species of the following syntaxa was calculated: *Lathyro pisiformis-Quercion roboris*, *Betonico officinalis-Quercion roboris*, and *Scutellario altissimae-Quercion roboris*. Diagnostic species follow Goncharenko et al. (2020).

The names of classes, orders and alliances follow Mucina et al. (2016), except for those newly described in Goncharenko et al. (2020). The newly described associations follow the ICPN, 4th edition (Theurillat et al. 2021). Biogeographic characteristics of the species are given according to Bakin et al. (2000).

The TWINSPAN clusters were compared with the other associations by calculating a distance matrix. As a distance metric we used 1 – Jaccard coefficient following the recommendations of Legendre and De Cáceres (2013). As vectors for paired comparison, we used the species list of each group and the frequency of the species. The results are visualized using a “heat map” combined with a dendrogram, which is computed by complete-linkage clustering method. We also used non-metric multidimensional scaling (NMDS) as a “dimensional reduction” method (Kraemer et al. 2018).

Results

TWINSPAN classification

The OptimClass procedure resulted in four clusters (Table 1, Suppl. material 1).

Cluster 1 contained five relevés located at the single site on the high and steep slope of the Volga terrace. Species identified as diagnostic for this cluster included ruderal and meadow plants (*Asparagus officinalis*, *Crepis tectorum*, *Melandrium album*, *Phleum phleoides*, *Polygonatum odoratum*, *Rumex acetosella*, *Tanacetum vulgare*), which indicates the derivative nature of these communities.

Cluster 2 also contained a small number of relevés (seven) and a mixture of ruderal, meadow and shade-tolerant nemoral species as diagnostic (*Fragaria vesca*, *Glechoma hederacea*, *Tilia cordata*, *Trifolium hybridum*, *Veronica chamaedrys*).

Cluster 3 contained 37 geographically widespread plots, which indicates a regular occurrence of this community type. Only one species was identified as diagnostic – *Laser trilobum*. When the phi value threshold was decreased from 0.6 to 0.3, *Astragalus cicer*, *Adonis vernalis*, *Campanula rapunculoides*, and *Xanthoselinum alsaticum* also became diagnostic.

Cluster 4 contained 42 relevés. Diagnostic species included forest, forest-meadow and steppe plants (*Adenophora lilifolia*, *Aegopodium podagraria*, *Crepis sibirica*, *Dactylis glomerata*, *Euphorbia semivillosa*, *Geranium sylvaticum*, *Heracleum sibiricum*, *Lathyrus vernus*, *Pteridium aquilinum*, *Pulmonaria mollis*, *Rubus saxatilis*, *Sanguisorba officinalis*, *Viola mirabilis*).

In the following, we describe clusters 3 and 4 as new associations. We refrain from describing clusters 1 and 2 formally as new syntaxa because of the small number of relevés and their presumable derivative nature.

Description of new syntaxa

Astragalo ciceri-Quercetum roboris ass. nova

Diagnostic species: *Adonis vernalis*, *Astragalus cicer*, *Campanula rapunculoides*, *Laser trilobum*, *Xanthoselinum alsaticum.*

Geographical range: Communities assigned to this association are found in the southeast of Tatarstan, Cis-Volga region, and the western part of Tatarstan. The most typical of these communities were described from the Central Cis-Volga region, Kamskoe Ust'e and Apastovo districts (a distribution map and a photo of the community are provided in Suppl. material 3).

Floristic composition: These communities represent a sparse open forest. The first tree layer is dominated exclusively by *Quercus robur*, which also occurs in the shrub layer. In the second tree layer, *Betula pendula*, *Tilia cordata* and *Sorbus aucuparia* are found along with oak. The shrub layer is not dense and mainly consists of *Euonymus verrucosa*, *Corylus avellana*, *Rhamnus cathartica*, *Sorbus aucuparia*, and *Lonicera xylosteum*. The proportion of shrubs in these communities increases if there are signs of fire impacts. In case of intensive grazing, the undergrowth density is reduced, and the proportion of herbs increases. The floristic composition is homogeneous; only 94 plant species were recorded at the 37 plots of this association (with most commonly 20–30 species per plot). The composition of dominant species is determined by quite high light availability. Among the dominant species, *Brachypodium pinnatum*, *Carex muricata*, *Fragaria viridis* and *Laser trilobum* prevail.

Habitat characteristics: These communities grow on the middle parts of gentle (5–15°) slopes of southwestern exposure at altitudes less than 150 m a.s.l. The flat surfaces adjacent to the tops of these slopes are usually plowed up or, more rarely, occupied by meadow steppes with a large number of grasses (including *Stipa* species) and legumes. The lower parts of the slopes are most often occupied by a strip of shrubby vegetation with *Cerasus fruticosus*, *Genista tinctoria* and *Spiraea* species. The soils are generally rich in nutrients. The parent rocks are characterized by high content of calcium.

Typus relevé:

Database ID 13,119

20 Jul 2016; Kuralovo; 55.65813°N, 048.77161°E; 97 m; plot size 400 m^2; species richness: 45.

Tree layer: *Quercus robur* 3; shrub layer: *Euonymus verrucosa* r, *Corylus avellana* r, *Prunus spinosa* r, *Rhamnus cathartica* r, *Sorbus aucuparia* r, *Lonicera xylosteum* r; herb layer: *Laser trilobum* 4, *Brachypodium pinnatum* 3, *Vincetoxicum hirundinaria* +, *Galium mollugo* +, *Ranunculus polyanthemos* +, *Crepis praemorsa* +, *Medicago falcata* +, *Pimpinella saxifraga* +, *Pyrethrum corymbosum* +, *Carex rhizina* +, *Viola collina* +, *Campanula rapunculoides* +, *Geranium sanguineum* +, *Carex muricata* +, *Asparagus officinalis* +, *Astragalus cicer* +, *Centaurea pseudophrygia* +, *Stachys officinalis* +, *Adonis vernalis* +, *Viscaria vulgaris* +, *Carex tomentosa* +, *Poa angustifolia* +, *Galium boreale* +, *Silene nutans* +, *Campanula persicifolia* +, *Asarum europaeum* +, *Convallaria majalis* +, *Viola mirabilis* +, *Vicia pisiformis* +, *Rubus saxatilis* +, *Cichorium intybus* +, *Picris hieracioides* +, *Trifolium medium* +, *Vicia tenuifolia* +, *Inula salicina* +, *Serratula coronata* +, *Centaurea scabiosa* +.

Sanguisorbo officinalis-Quercetum roboris ass. nova

Diagnostic species: *Adenophora lilifolia*, *Heracleum sibiricum*, *Pulmonaria mollis*, *Sanguisorba officinalis.* .

Geographical range: The communities assigned to this association occur in the southeast of Tatarstan, within the western slope of the Bugulma-Belebey Upland at the territories of the Bugulma, Leninogorsk, Bavly, Aznakaevo and Almetyevsk districts of Tatarstan (a distribution map and photos of the community are provided in Suppl. material 3).

Floristic composition: The communities are characterized by an extremely high species diversity. The total number of species is 293, while the average number of species per relevé is 50. In the tree layer, *Betula pendula*, *Pinus sylvestris*, *Populus tremula*, *Tilia cordata* and *Ulmus glabra* are found in addition to the dominant *Quercus robur*. Trees are distributed unevenly within the plots: some of them grow close to each other, while others are separated and form open areas (meadows) with sparse tree stands. In the meadow areas, heliophytes are abundant. The shrub layer is not dense, being characterized by high species diversity (total number of species 21) without any clear dominance among them. The most abundant species is *Euonymus verrucosa*. The herb layer is multilayered, polydominated, with tall forest-steppe herbs (*Campanula trachelium*, *Euphorbia semivillosa*, *Heracleum sibiricum*, *Lilium pilosiusculum* and *Pleurospermum uralense*).

Habitat characteristics: In Tatarstan, the communities of this type occur at altitudes of 250–300 m a.s.l. They occupy areas near the water divide and middle parts of the gentle (up to 5°) slopes of mostly southeastern exposure. The soils are leached and typical chernozems. The parent material can be Permian bed rocks, Permian eluvial clays and loams, deluvial deposits on the gentle slopes, and post-Pliocene loess-like loams.

Typus relevé:

Database ID 13,057

21 May 2016; Leninogorsk district, near Tuktarovo-Urdala village; 54.39278°N, 052.15631°E; 262 m a.s.l.; plot size 400 m^2; species richness: 43.

Tree layer: *Quercus robur* 3, *Betula pendula* 1, *Acer platanoides* 1; shrub layer: *Acer platanoides* 1, *Padus avium* +, *Populus tremula* +, *Sorbus aucuparia* +, *Ulmus laevis* +; herb layer: *Calamagrostis arundinacea* 2, *Carex montana* 1, *Adenophora lilifolia* +, *Aegopodium podagraria* +, *Angelica sylvestris* +, *Campanula persicifolia* +, *Carex rhizina* +, *Centaurea pseudophrygia* +, *Convallaria majalis* +, *Crepis sibirica* +, *Dracocephalum ruyschiana* +, *Euphorbia semivillosa* +, *Filipendula vulgaris* +, *Galium boreale* +, *Galium tinctorium* +, *Geranium sylvaticum* +, *Heracleum sibiricum* +, *Lathyrus pisiformis* +, *Lathyrus vernus* +, *Lilium pilosiusculum* +, *Phlomoides tuberosa* +, *Poa pratensis* +, *Pteridium aquilinum* +, *Pulmonaria mollis* +, *Pyrethrum corymbosum* +, *Quercus robur* +, *Rubus saxatilis* +, *Sanguisorba officinalis* +, *Serratula coronata* +, *Silene nutans* +, *Stellaria holostea* +, *Thesium ebracteatum* +, *Trommsdorfia maculata* +, *Veronica chamaedrys* +, *Vicia tenuifolia* +, *Viola mirabilis* +.

Comparison with associations in other regions

The comparison of the identified syntaxa and previously described associations of the *Lathyro pisiformis-Quercion* and *Aceri tatarici-Quercion* (sensu lato) are given in Table 1. The analysis of the table reveals significant differences in both floristic composition and combinations of characteristic species between identified syntaxa and previously described associations.

Table 1. Percentage synoptic table of xero-mesophytic broad-leaved oak forests of Eastern Europe. Only species with a frequency ≥ 40% in one column or ≥ 20% in at least two columns are shown. Diagnostic taxa follow Goncharenko et al. (2020). **BQ** –*Betonico officinalis-Quercion roboris*; **SQ** –*Scutellario altissimae-Quercion roboris*; **LQ** –*Lathyro pisiformis-Quercion roboris*. Diagnostic species of the alliances are shaded in grey.

Cluster/association	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Alliance					**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**BQ**	**BQ**	**BQ**	**SQ**
Number of relevés	**5**	**7**	**37**	**42**	**23**	**6**	**54**	**5**	**10**	**9**	**14**	**7**	**17**	**24**	**18**	**10**
Tree layer 1:																
Quercus robur (BQ, SQ, LQ)	100	100	100	93	100	.	.	100	100	100	100	100	.	100	.	100
Tilia cordata	20	86	.	7	17	.	.	80	100	100	100	.	.	13	.	.
Betula pendula	.	43	5	76	39	.	46	100	100	56	21	.	24	13	.	.
Acer platanoides	.	.	.	5	9	.	.	100	100	.	.	86	.	.	.	.
Ulmus glabra	.	.	.	2	.	.	.	60	60	78	.	.	.	.	.	.
Populus tremula	.	.	.	10	.	.	.	40	.	33	.	.	.	25	.	.
Pinus sylvestris	.	43	.	5	.	33	.	.	.	.	7	.	.	8	.	.
Rubus idaeus	.	.	.	.	.	.	.	.	.	.	.	43	.	.	.	.
Sorbus aucuparia	.	.	.	.	.	.	.	.	.	.	.	43	.	.	.	.
Abies sibirica	.	.	.	.	.	.	.	40	.	.	.	.	.	.	.	.
Tree layer 2:																
Quercus robur (BQ, SQ, LQ)	.	.	16	7	78	.	20	.	.	.	.	.	6	83	.	.
Betula pendula	.	14	5	10	13	.	2	.	.	.	.	.	24	13	.	50
Sorbus aucuparia	.	.	.	.	.	.	.	.	.	.	.	.	.	79	.	.
Padus avium	.	.	.	.	13	.	.	.	.	.	.	.	.	46	.	.
Malus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	58	.	.
Shrub layer:																
Rosa majalis (LQ)	.	14	19	12	61	.	.	.	10	33	71	43	.	.	.	.
Caragana frutex (LQ)	.	.	.	.	43	.	.	.	.	33	.	.	.	.	.	.
Chamaecytisus ruthenicus (BQ)	20	.	8	7	57	.	24	.	20	.	.	.	.	83	.	.
Cerasus fruticosa (SQ)	60	29	46	17	65	.	.	.	10	33	71	.	.	.	.	.
Acer tataricum (SQ)	.	.	3	.	.	.	.	.	.	.	.	.	.	4	.	90
Prunus spinosa (SQ)	20	.	3	.	.	.	.	.	.	.	.	.	.	.	.	60
Quercus robur (BQ, SQ, LQ)	20	71	43	38	78	83	22	.	.	.	.	.	29	46	.	80
Sorbus aucupari	.	57	24	48	17	50	33	100	100	33	21	.	59	75	.	20
Euonymus verrucosa	60	100	76	24	.	83	.	.	.	78	100	.	.	4	.	80
Acer platanoides	40	43	32	40	22	.	22	.	.	.	.	.	24	25	.	70
Rubus idaeus	.	.	.	.	13	33	22	60	100	44	.	.	.	.	.	.
Rhamnus cathartica	.	71	41	17	22	.	.	.	.	.	50	.	.	.	.	50
Tilia cordata	.	43	8	7	43	.	.	.	.	.	.	.	.	33	.	70
Padus avium	.	.	14	12	22	.	.	60	.	78	.	.	.	.	.	.
Viburnum opulus	.	.	11	2	.	.	.	20	10	22	36	.	.	.	.	20

Cluster/association	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Alliance					**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**BQ**	**BQ**	**BQ**	**SQ**
Number of relevés	**5**	**7**	**37**	**42**	**23**	**6**	**54**	**5**	**10**	**9**	**14**	**7**	**17**	**24**	**18**	**10**
Malus sylvestris	.	.	14	.	.	.	.	.	.	.	.	.	.	63	.	20
Lonicera xylosteum	.	14	5	.	.	50	.	20	.	.	7	.	.	.	.	.
Acer campestre	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	90
Euonymus europaea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	90
Pyrus pyraster	.	.	.	.	.	.	.	.	.	.	.	.	.	29	.	50
Ulmus glabra	.	.	.	5	22	.	.	.	.	.	.	.	.	.	.	50
Corylus avellana	.	.	59	7	.	.	.	.	.	.	.	.	.	.	.	.
Frangula alnus	.	.	3	2	.	.	.	.	10	.	50	.	.	.	.	.
Fraxinus excelsior	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50
Ulmus laevis	.	43	.	5	.	.	.	.	.	.	.	.	.	.	.	.
Herb layer:																
Brachypodium pinnatum	.	86	51	48	87	.	93	60	100	56	79	43	.	33	.	.
Heracleum sibiricum (LQ)	.	.	16	62	65	.	.	60	70	100	71	.	.	17	.	.
Lathyrus pisiformis (LQ)	.	.	46	55	70	.	.	.	90	22	.	43	.	.	.	.
Phlomoides tuberosa (SQ)	20	29	57	55	74	.	.	.	10	.	.	.	.	.	.	70
Pyrethrum corymbosum	.	29	81	88	91	.	.	.	.	.	.	.	.	13	.	.
Pleurospermum uralense (LQ)	.	.	3	31	13	.	.	80	90	33	.	.	.	.	.	.
Seseli libanotis (LQ)	20	14	.	19	78	.	.	.	.	44	.	14	.	.	.	.
Geranium sylvaticum (LQ)	.	.	14	74	22	.	.	60	.	.	.	.	.	.	.	.
Lathyrus gmelinii (LQ)	.	.	.	.	.	.	.	60	40	22	.	14	.	.	.	.
Lathyrus sylvestris (LQ)	.	.	14	5	.	.	.	.	30	67	.	.	.	.	.	.
Carex macroura (LQ)	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.	.
Lathyrus litvinovii (LQ)	.	.	.	.	61	.	.	.	.	.	.	.	.	.	.	.
Cerasus fruticosa (SQ)	20	.	8	5	.	.	.	.	.	.	.	.	.	.	.	.
Origanum vulgare (BQ)	100	57	24	43	96	100	59	.	10	56	.	86	53	17	.	.
Veronica chamaedrys (BQ)	.	100	11	52	30	.	26	.	.	33	14	.	76	58	78	90
Campanula persicifolia (BQ)	20	.	5	36	52	.	37	.	.	.	14	14	35	83	72	.
Digitalis grandiflora (BQ, LQ)	.	.	.	2	52	.	.	60	90	78	.	71	.	.	.	.
Viola hirta (BQ)	20	.	3	17	65	.	.	20	30	78	.	.	.	8	.	70
Vincetoxicum hirundinaria (BQ)	80	.	27	12	.	.	.	.	.	44	.	.	18	21	.	60
Melampyrum nemorosum (BQ)	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.	.
Campanula bononiensis	40	.	.	17	43	.	.	.	.	.	.	.	.	.	.	.
Chamaecytisus ruthenicus (BQ)	40	.	.	2	.	.	15	.	.	.	.	43	.	.	.	.
Trifolium alpestre (BQ)	.	.	.	21	.	.	.	.	.	.	.	.	.	75	.	.
Securigera varia (BQ)	.	.	.	2	.	.	.	.	.	.	.	.	.	58	.	.
Allium oleraceum (BQ)	.	.	.	.	.	.	.	.	.	.	.	.	.	46	.	.
Turritis glabra (BQ)	.	.	3	2	22	.	.	.	.	11	.	.	.	.	.	.
Serratula tinctoria (BQ)	.	.	8	.	.	.	.	.	.	.	.	.	.	21	.	.
Potentilla alba (BQ)	.	.	.	.	.	.	.	.	.	.	.	.	.	21	.	.
Vicia pisiformis (SQ)	.	.	41	2	.	.	.	.	.	.	.	.	.	.	.	90
Euphorbia semivillosa (SQ)	.	.	38	64	.	.	.	.	.	11	.	.	.	.	.	.
Crataegus rhipidophylla (SQ)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100
Acer tataricum (SQ)	.	.	.	.	.	.	.	.	.	.	.	.	.	79	.	10
Ajuga genevensis (BQ)	40	.	8	.	.	.	.	.	.	.	.	.	.	29	.	.
Vicia sepium (BQ, LQ)	.	29	3	40	26	.	39	60	50	56	14	29	41	17	.	.
Betonica officinalis (BQ)	20	14	19	60	52	.	.	.	10	.	.	57	.	63	.	40
Quercus robur (BQ, SQ, LQ)	.	.	14	43	.	.	2	.	.	.	.	.	.	21	33	.
Lathyrus vernus	.	14	8	79	78	83	87	80	100	100	100	43	65	4	50	20
Poa nemoralis	40	43	11	12	70	.	63	40	100	56	57	100	.	58	83	100
Calamagrostis arundinacea	20	.	.	33	100	50	81	100	100	100	50	100	6	67	22	.
Rubus saxatilis	.	14	16	83	83	50	74	100	100	100	86	71	6	.	.	.
Viola mirabilis	.	.	38	69	52	83	74	100	80	100	100	.	.	17	50	.
Aegopodium podagraria	.	.	24	86	43	67	69	80	100	100	71	.	.	17	56	.
Stellaria holostea	.	14	5	43	91	.	.	60	40	89	100	100	.	4	22	100
Polygonatum odoratum	100	29	5	36	57	67	48	.	10	22	79	14	18	88	17	20
Melica nutans	.	29	14	26	26	.	67	100	.	78	57	57	71	63	.	20
Fragaria vesca	60	100	38	31	30	67	30	.	30	.	.	.	71	33	28	30
Calamagrostis epigeios	40	14	3	33	87	33	26	.	80	33	7	71	24	63	33	.
Solidago virgaurea	.	.	14	29	57	67	41	80	50	.	36	71	12	63	.	.
Galium boreale	.	29	41	71	87	.	.	.	70	.	71	.	53	4	.	30
Dactylis glomerata	.	.	3	45	74	.	50	80	100	.	.	43	.	38	.	20
Asarum europaeum	.	.	11	2	.	50	39	100	60	67	50	29	12	.	22	.
Glechoma hederacea	.	86	5	14	13	.	.	40	10	33	100	14	12	29	11	30
Galium verum	100	100	32	31	52	17	15	.	.	11	.	.	6	25	.	.
Pteridium aquilinum	.	.	3	57	.	.	19	80	100	33	21	.	41	.	33	.
Urtica dioica	.	.	5	21	17	67	13	20	10	56	57	.	47	25	44	.
Geum urbanum	.	.	11	38	48	67	28	.	.	11	.	.	47	50	.	70
Convallaria majalis	40	29	35	52	.	.	.	.	.	.	.	.	94	50	22	40
Hypericum perforatum	80	.	14	24	17	.	.	.	10	44	7	.	41	42	.	80
Galium odoratum	.	.	.	17	26	33	50	100	100	22	.	.	.	.	.	.

Cluster/association	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Alliance					**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**BQ**	**BQ**	**BQ**	**SQ**
Number of relevés	**5**	**7**	**37**	**42**	**23**	**6**	**54**	**5**	**10**	**9**	**14**	**7**	**17**	**24**	**18**	**10**
Scrophularia nodosa	.	.	3	10	.	.	39	40	60	67	.	57	.	42	.	30
Pulmonaria obscura	.	14	.	12	.	33	19	100	30	78	.	.	.	4	.	50
Hieracium umbellatum	20	.	3	36	65	17	26	.	.	.	21	14	47	79	.	.
Bupleurum longifolium	.	.	.	7	30	.	.	80	100	44	.	29	.	.	.	.
Fragaria viridis	20	.	46	29	74	.	.	.	.	33	.	29	12	4	39	.
Poa angustifolia	20	14	24	40	26	.	.	.	.	.	.	.	6	96	39	20
Crepis sibirica	.	.	5	48	.	.	.	80	100	44	.	.	.	.	.	.
Achillea millefolium	20	.	3	21	61	33	28	.	.	.	21	14	24	42	.	.
Hylotelephium triphyllum	.	.	.	10	39	50	24	.	.	22	.	100	6	.	.	.
Geranium sanguineum	60	.	54	40	.	.	.	.	.	.	7	.	.	88	.	.
Silene nutans	20	.	30	29	48	33	11	.	.	.	7	.	12	58	.	.
Milium effusum	.	.	.	5	.	.	22	100	80	22	.	14	.	.	.	.
Filipendula vulgaris	.	43	49	48	87	.	.	.	.	.	.	.	.	4	.	.
Angelica sylvestris	.	.	.	14	.	.	9	80	90	.	.	.	24	.	.	.
Vicia tenuifolia	60	.	30	48	74	.	.	.	.	.	.	.	.	.	.	.
Thalictrum minus	80	.	22	26	65	.	.	.	.	.	.	14	.	.	.	.
Asparagus officinalis	100	29	30	5	17	.	4	.	.	.	.	.	12	.	.	.
Agrimonia eupatoria	20	14	49	40	.	.	.	.	.	.	.	.	.	4	.	70
Polygonatum multiflorum	.	.	.	7	.	33	4	80	.	22	.	.	18	4	28	.
Chelidonium majus	.	43	8	.	9	.	17	.	.	33	50	.	.	33	.	.
Carex muricata	.	.	5	.	43	.	.	.	.	56	64	14	.	.	11	.
Clinopodium vulgare	.	.	16	5	.	.	.	.	70	.	.	.	.	50	.	50
Veronica teucrium	.	14	27	43	83	.	.	.	.	.	.	.	.	21	.	.
Aconogonon alpinum	.	.	3	5	70	.	.	.	10	.	.	100	.	.	.	.
Chamaenerion angustifolium	.	.	.	.	22	.	.	80	70	.	.	.	.	13	.	.
Trifolium medium	.	43	8	24	70	.	.	.	10	.	.	.	.	.	.	20
Inula salicina	.	43	35	36	52	.	.	.	.	.	.	.	6	.	.	.
Galium mollugo	.	14	8	14	.	.	.	.	.	.	.	.	59	25	50	.
Viola collina	.	57	46	2	26	.	17	.	.	.	.	.	.	.	17	.
Aconitum lycoctonum	.	.	.	5	.	.	9	80	70	.	.	.	.	.	.	.
Elytrigia repens	20	.	3	7	35	.	.	.	.	.	.	.	24	42	33	.
Fallopia convolvulus	.	.	.	2	22	17	15	.	10	22	36	.	6	.	.	30
Anthriscus sylvestris	.	.	3	26	.	.	.	.	.	67	.	.	.	33	.	30
Vicia cracca	.	43	14	10	22	.	.	.	.	22	29	.	.	.	17	.
Carex praecox	40	.	5	5	74	.	.	.	.	.	.	.	.	29	.	.
Pulmonaria mollis	.	.	30	69	43	.	11	.	.	.	.	.	.	.	.	.
Campanula latifolia	.	.	.	.	.	.	.	40	90	22	.	.	.	.	.	.
Veronica spicata	40	.	11	7	13	17	9	.	.	11	14	29	.	.	.	.
Lysimachia vulgaris	.	.	3	10	.	.	.	.	40	.	.	43	47	8	.	.
Asperula tinctoria (*BQ*)	20	.	30	17	30	.	.	.	.	.	.	.	.	46	.	.
Lilium martagon	.	.	.	19	26	.	33	.	50	.	.	14	.	.	.	.
Carex rhizina	.	14	5	5	13	.	15	.	.	.	.	.	.	.	.	90
Taraxacum officinale	.	.	16	17	13	.	.	.	.	.	.	.	.	42	28	20
Sanguisorba officinalis	.	.	14	76	35	.	.	.	10	.	.	.	.	.	.	.
Primula macrocalyx	.	.	.	10	57	.	.	20	.	33	.	14	.	.	.	.
Viscaria vulgaris	40	43	11	5	.	.	6	.	.	.	.	.	12	17	.	.
Lysimachia nummularia	.	.	.	.	.	.	.	.	.	.	.	.	24	4	56	50
Galeopsis bifida	.	.	.	.	22	.	.	.	.	.	.	100	.	8	.	.
Bistorta major	.	.	.	.	26	.	.	.	.	.	.	100	.	.	.	.
Euonymus verrucosa	.	.	3	12	.	.	2	.	.	.	.	.	.	96	.	10
Geranium pseudosibiricum	.	.	.	.	.	.	.	.	.	22	.	100	.	.	.	.
Pimpinella saxifraga	.	71	32	19	.	.	.	.	.	.	.	.	.	.	.	.
Torilis japonica	.	.	.	.	.	.	.	.	.	.	.	.	.	42	.	80
Viola canina	.	.	.	7	39	.	.	.	20	11	.	43	.	.	.	.
Adenophora lilifolia	.	.	3	62	22	.	.	.	30	.	.	.	.	.	.	.
Brachypodium sylvaticum	.	.	.	2	.	.	.	.	.	44	.	.	.	.	.	70
Linaria vulgaris	20	.	5	10	30	.	2	.	.	.	7	14	.	25	.	.
Cicerbita uralensis	.	.	.	.	.	.	.	40	70	.	.	.	.	.	.	.
Campanula rapunculoides	20	.	68	7	.	.	.	.	.	.	.	.	.	13	.	.
Dryopteris filix-mas	.	.	.	7	.	.	.	60	40	.	.	.	.	.	.	.
Anemonoides ranunculoides	.	.	3	2	.	.	.	.	.	100	.	.	.	.	.	.
Carex pilosa	.	14	.	7	.	.	.	60	.	22	.	.	.	.	.	.
Phleum phleoides	80	.	3	10	.	.	.	.	.	.	.	.	.	8	.	.
Anomodon viticulosus	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.	.
Veronica longifolia	40	.	.	2	35	.	.	.	10	.	.	.	12	.	.	.
Verbascum nigrum	.	.	.	12	30	.	.	.	.	56	.	.	.	.	.	.
Dicranum scoparium	.	.	.	.	.	.	.	.	90	.	7	.	.	.	.	.
Frangula alnus	.	.	.	.	.	.	2	.	.	.	.	.	6	83	6	.
Astragalus glycyphyllos	.	.	11	2	.	.	.	.	.	.	.	.	.	4	.	80
Paris quadrifolia	.	.	.	5	.	.	.	60	30	.	.	.	.	.	.	.

Cluster/association	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Alliance					**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**LQ**	**BQ**	**BQ**	**BQ**	**SQ**
Number of relevés	**5**	**7**	**37**	**42**	**23**	**6**	**54**	**5**	**10**	**9**	**14**	**7**	**17**	**24**	**18**	**10**
Carex contigua	.	.	8	26	.	.	.	.	.	.	.	.	.	.	.	60
Campanula glomerata	.	.	.	19	.	.	.	40	20	.	.	14	.	.	.	.
Hylotelephium maximum	60	.	.	2	.	.	.	.	.	.	.	.	.	.	.	30
Adonis vernalis	.	.	51	26	13	.	.	.	.	.	.	.	.	.	.	.
Geranium robertianum	.	.	.	.	.	.	.	20	40	.	.	.	.	.	.	30
Knautia arvensis	20	29	3	21	.	.	.	.	.	.	.	.	.	17	.	.
Trifolium montanum	.	43	14	19	.	.	.	.	.	.	.	.	.	13	.	.
Conioselinum tataricum	.	.	.	2	.	.	.	.	.	.	.	86	.	.	.	.
Peucedanum oreoselinum	.	.	.	.	.	.	.	.	.	.	.	.	.	88	.	.
Melandrium album	80	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.
Tanacetum vulgare	60	.	.	2	.	.	.	.	.	.	.	.	24	.	.	.
Laser trilobum	.	.	65	17	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis tenuis	.	.	3	.	.	.	.	.	.	.	7	.	.	71	.	.
Viola epipsila	.	.	.	.	.	.	.	80	.	.	.	.	.	.	.	.
Poa pratensis	.	.	5	5	13	.	15	.	.	.	.	.	41	.	.	.
Cirsium heterophyllum	.	.	.	7	.	.	.	40	30	.	.	.	.	.	.	.
Dracocephalum ruyschiana	.	.	.	21	30	.	13	.	.	.	.	.	.	13	.	.
Melampyrum cristatum	.	.	.	14	.	.	.	.	60	.	.	.	.	.	.	.
Valeriana wolgensis	.	.	.	.	13	.	.	.	50	11	.	.	.	.	.	.
Serratula gmelinii	.	.	5	24	43	.	.	.	.	.	.	.	.	.	.	.
Knautia tatarica	.	.	.	.	.	.	.	20	50	.	.	.	.	.	.	.
Festuca valesiaca	20	.	14	7	9	.	.	.	.	.	.	.	.	.	.	20
Campanula trachelium	.	.	14	29	26	.	.	.	.	.	.	.	.	.	.	.
Artemisia vulgaris	.	29	3	14	22	.	.	.	.	.	.	.	.	.	.	.
Valeriana officinalis	.	.	.	7	.	.	.	60	.	.	.	.	.	.	.	.
Anemonoides altaica	.	.	.	.	.	.	.	.	.	67	.	.	.	.	.	.
Trommsdorfia maculata	20	.	5	17	.	.	.	.	.	.	.	.	.	25	.	.
Stellaria graminea	.	.	3	17	.	.	4	.	.	.	.	.	.	42	.	.
Serratula coronata	20	.	22	24	.	.	.	.	.	.	.	.	.	.	.	.
Vincetoxicum albowianum	.	.	.	.	22	.	.	.	.	.	.	43	.	.	.	.
Moehringia trinervia	.	.	.	.	.	.	.	.	.	.	.	.	.	54	11	.
Nepeta pannonica	.	.	11	24	30	.	.	.	.	.	.	.	.	.	.	.
Lamium album	.	.	.	.	.	.	.	20	.	44	.	.	.	.	.	.
Stachys sylvatica	.	.	5	10	.	.	4	.	.	44	.	.	.	.	.	.
Verbascum lychnitis	20	29	3	7	.	.	.	.	.	.	.	.	.	4	.	.
Veronica spuria	.	.	.	5	57	.	.	.	.	.	.	.	.	.	.	.
Euphorbia virgata	20	29	8	5	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia armeniaca	.	.	.	.	61	.	.	.	.	.	.	.	.	.	.	.
Ranunculus polyanthemos	.	.	22	26	.	.	.	.	.	.	.	.	.	13	.	.
Genista tinctoria	20	.	.	2	.	.	.	.	.	.	.	.	.	17	22	.
Ptarmica cartilaginea	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis tectorum	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veratrum lobelianum	.	.	.	.	.	.	.	60	.	.	.	.	.	.	.	.
Sorbus aucuparia	.	.	3	7	.	.	.	.	.	.	.	29	.	21	.	.
Euphorbia caesia	.	.	.	.	.	.	.	.	.	.	.	57	.	.	.	.
Lathyrus pratensis	.	14	.	21	22	.	.	.	.	.	.	.	.	.	.	.
Carex caryophyllea	40	.	.	2	13	.	.	.	.	.	.	.	.	.	.	.
Maianthemum bifolium	.	.	.	.	.	.	.	20	.	.	.	.	35	.	.	.
Medicago falcata	20	.	24	10	.	.	.	.	.	.	.	.	.	.	.	.
Festuca rubra	.	.	.	2	.	.	.	.	.	.	.	.	.	50	.	.
Padus avium	.	.	.	.	.	.	.	.	.	.	.	.	.	46	6	.
Carex montana	.	.	16	7	.	.	.	.	.	.	.	.	.	29	.	.
Pulsatilla patens	40	.	.	5	.	.	6	.	.	.	.	.	.	.	.	.
Helictotrichon pubescens	.	.	.	5	.	.	.	.	.	.	.	.	.	46	.	.
Lactuca serriola	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30
Hypericum maculatum	.	.	.	.	.	.	.	.	20	.	.	.	29	.	.	.
Populus tremula	.	.	.	7	.	.	.	.	.	.	.	.	6	25	11	.
Euphorbia gmelinii	.	.	.	.	48	.	.	.	.	.	.	.	.	.	.	.
Rumex acetosa	40	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.
Dracocephalum thymiflorum	40	.	3	2	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia campestris	40	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.
Ficaria verna	.	.	.	.	.	.	.	.	.	44	.	.	.	.	.	.
Aristolochia clematitis	20	.	.	.	.	.	.	.	.	.	.	.	24	.	.	.
Scorzonera purpurea	40	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Galatella biflora	.	.	.	.	43	.	.	.	.	.	.	.	.	.	.	.
Myosotis sylvatica	.	.	3	.	.	.	.	40	.	.	.	.	.	.	.	.
Senecio schvetzovii	.	.	3	.	.	.	.	40	.	.	.	.	.	.	.	.
Campanula sibirica	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Brachytheciastrum velutinum	.	.	.	.	.	.	.	40	.	.	.	.	.	.	.	.
Lathyrus niger	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40

Compared to the *Chamaecytiso ruthenici-Quercetum roboris*, *Pyro pyrastris-Quercetum roboris*, *Vicio pisiformis-Quercetum roboris* and *Lathyro nigri-Quercetum roboris* associations, the *Astragalo ciceri-Quercetum roboris* has a higher proportion of Euro-West Asian species (41.5% against 30% in the above-listed associations, on average) and a lower number of European species (9.6% against 16%).

Based on the floristic composition, the *Sanguisorbo officinalis-Quercetum roboris* is most similar to the *Filipendulo vulgari-Quercetum roboris*, but it differs from the latter by the absence of such characteristic species as *Galatella biflora* and *Artemisia armeniaca*, as well as because of the lower proportion of *Carex praecox*, *Veronica spuria* and *Campanula bononiensis*. Compared to the *Sanguisorbo officinalis-Quercetum roboris*, the *Filipendulo vulgari-Quercetum roboris* has a much lower proportion of European species (3.4% against 8.5%) and more Eurasian species (23.3% against 19%).

An analysis of "heat maps" shows that all associations have a low similarity. The largest number of pairs being compared has a distance between 0.4 and 0.8 (Figure 2).

The newly identified associations are clustered in the dendrogram into one group with the associations of the *Aceri tatarici-Quercion*. This clustering is generally consistent with the analysis of the composition of diagnostic species. Cluster 2 was grouped with the new associations from the territory of the Republic of Tatarstan, and cluster 1 was grouped with the association *Vicio pisiformis-Quercetum roboris*.

However, the NMDS ordination (Figure 3) shows that the *Sanguisorbo officinalis-Quercetum* is intermediate between the *Lathyro pisiformis-Quercion* and *Aceri tatarici-Quercion* and is closer to the *Filipendulo vulgaris-Quercetum* than to the newly described *Astragalo ciceri-Quercetum roboris*. The left group of points unites the "western" (in relation to the territory of the Republic of Tatarstan) associations of the *Aceri tatarici-Quercion*. Clusters 1 and 2 adjoin them, together with the *Astragalo ciceri-Quercetum roboris*. The right part unites the "eastern" associations of the *Lathyro pisiformis-Quercion*. It is also noticeable that the "eastern" associations are less homogeneous and may require a revision of their syntaxonomic position.

Cluster 1 also has a higher frequency sum of diagnostic species of the *Betonico officinalis-Quercion roboris* alliance (or *Aceri tatarici-Quercion* in the previous concept).

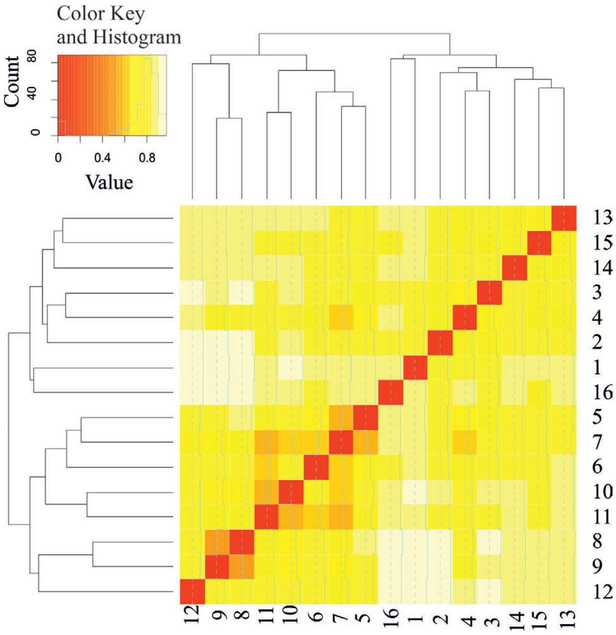

Figure 2. "Heat map" of distance matrix combined with a dendrogram. 1 – cluster 1, 2 – cluster 2, 3 – cluster 3 (*Astragalo ciceri-Quercetum roboris*), 4 – cluster 4 (*Sanguisorbo officinalis-Quercetum roboris*), 5 – *Filipendulo vulgari-Quercetum roboris*, 6 – *Omphalodo scorpioidis-Quercetum roboris*, 7 – *Brachypodio pinnati-Quercetum roboris*, 8 – *Aconogono alpini-Quercetum roboris*, 9 – *Calamagrostio epigei-Quercetum roboris*, 10 – *Carici macrourae-Quercetum roboris*, 11 – *Pruno-Quercetum roboris*, 12 – *Bistorto majoris-Quercetum roboris*, 13 – *Lathyro nigri-Quercetum roboris*, 14 – *Chamaecytiso ruthenici-Quercetum roboris*, 15 – *Pyro pyrastris-Quercetum roboris*, 16 – *Vicio pisiformis-Quercetum roboris*.

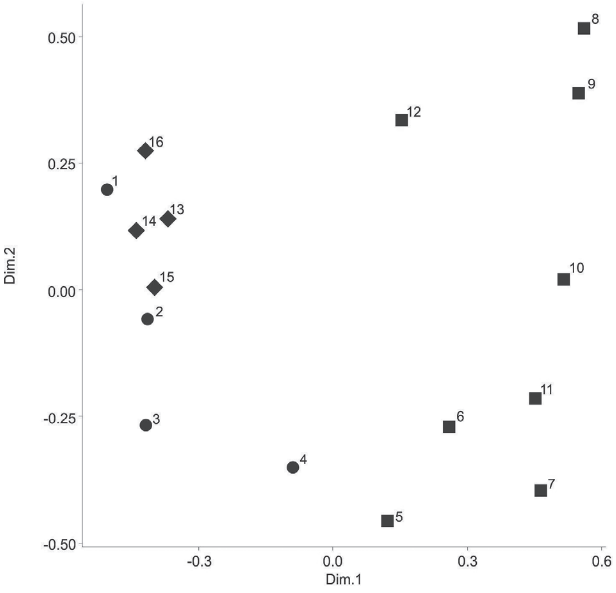

Figure 3. Non-metric multidimensional scaling (NMDS) of the communities similarity matrix. 1 – cluster 1, 2 – cluster 2, 3 – cluster 3 (*Astragalo ciceri-Quercetum roboris*), 4 – cluster 4 (*Sanguisorbo officinalis-Quercetum roboris*), 5 – *Filipendulo vulgari-Quercetum roboris*, 6 – *Omphalodo scorpioidis-Quercetum roboris*, 7 – *Brachypodio pinnati-Quercetum roboris*, 8 – *Aconogono alpini-Quercetum roboris*, 9 – *Calamagrostio epigei-Quercetum roboris*, 10 – *Carici macrourae-Quercetum roboris*, 11 – *Pruno-Quercetum roboris*, 12 – *Bistorto majoris-Quercetum roboris*, 13 – *Lathyro nigri-Quercetum roboris*, 14 – *Chamaecytiso ruthenici-Quercetum roboris*, 15 – *Pyro pyrastris-Quercetum roboris*, 16 – *Vicio pisiformis-Quercetum roboris*. circle – newly described associations; diamond – associations of the *Aceri tatarici-Quercion*; square – associations of the *Lathyro pisiformis-Quercion*.

Table 2. Frequency sum (in %) of diagnostic species of the alliances *Betonico officinalis-Quercion roboris*, *Scutellario altissimae-Quercion roboris* and *Lathyro pisiformis-Quercion roboris* in clusters 1–4 (this paper) and previously described associations. 1 – cluster 1, 2 – cluster 2, 3 – cluster 3 (*Astragalo ciceri-Quercetum roboris*), 4 – cluster 4 (*Sanguisorbo officinalis-Quercetum roboris*), 5 – *Filipendulo vulgari-Quercetum roboris*, 6 – *Omphalodo scorpioidis-Quercetum roboris*, 7 – *Brachypodio pinnati-Quercetum roboris*, 8 – *Aconogono alpini-Quercetum roboris*, 9 – *Calamagrostio epigei-Quercetum roboris*, 10 – *Carici macrourae-Quercetum roboris*, 11 – *Pruno-Quercetum roboris*, 12 – *Bistorto majoris-Quercetum roboris*, 13 – *Lathyro nigri-Quercetum roboris*, 14 – *Chamaecytiso ruthenici-Quercetum roboris*, 15 – *Pyro pyrastris-Quercetum roboris*, 16 – *Vicio pisiformis-Quercetum roboris*.

Number of cluster (association name)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Betonico officinalis-Quercion roboris	440	371	284	470	651	183	220	240	290	456	142	400	258	867	183	440
Scutellario altissimae-Quercion roboris	240	229	369	324	395	83	44	100	120	144	171	100	35	333	33	600
Lathyro pisiformis-Quercion roboris	140	228	288	481	747	83	83	480	570	688	256	314	76	284	33	180

In clusters 2, 3 and 4, the frequency sum of the diagnostic species of the *Lathyro pisiformis-Quercion* is higher than the frequency sum of the diagnostic species of the *Betonico officinalis-Quercion roboris* and *Scutellario altissimae-Quercion roboris* alliances (Table 2).

Discussion

The NMDS ordination diagram shows distinct floristic and ecological composition of the identified syntaxa (Figure 3).

The *Astragalo ciceri-Quercetum roboris* is close to some associations within the *Betonico officinalis-Quercion* alliance, but they are found under more continental conditions. It comprises the following diagnostic species of this alliance (Goncharenko et al. 2020): *Asperula tinctoria*, *Betonica officinalis*, *Campanula persicifolia*, *Origanum vulgare*, *Veronica chamaedrys*, and *Vincetoxicum hirundinaria.*,. However, important species characteristic of *Betonico officinalis-Quercion*, such as *Anthericum ramosum*, *Clematis recta*, *Digitalis grandiflora*, *Melampyrum nemorosum*, *Potentilla alba* and *Trifolium alpestre*, are absent.

Our results suggest that the communities of the *Sanguisorbo officinalis-Quercetum roboris* are close to the group of associations of the *Lathyro pisiformis-Quercion roboris* alliance. However, they differ from the latter by their preference for warmer sites with more light availability. *Sanguisorbo officinalis-Quercetum roboris* includes the diagnostic species of this alliance (Willner et al. 2016) such as *Geranium sylvaticum*, *Heracleum sibiricum*, *Lathyrus pisiformis*, *L. sylvestris*, *Pleurospermum uralense*, *Rosa majalis*, *Seseli libanotis*. Some of diagnostic species of *Lathyro pisiformis-Quercion* are absent: *Caragana frutex*, *Carex macroura*, *Lathyrus gmelinii*, and *L. litvinovii*.

We conclude that the xero-mesophytic oak forests in the Republic of Tatarstan can be assigned to the alliance *Betonico officinalis-Quercion roboris* (ass. *Astragalo ciceri-Quercetum roboris*), and to the alliance *Lathyro pisiformis-Quercion roboris* (ass. *Sanguisorbo officinalis-Quercetum roboris*). However, a syntaxonomic revision of the entire phytocoenotic material of xero-mesophytic oak forests in Europe, including the European part of Russia, is necessary to clarify the exact delimitation of these alliances.

Data availability

The original plot records are included in Suppl. material 1.

Author contributions

Both authors have equally planned the study, conducted field sampling, performed taxonomic considerations, and contributed to writing the article.

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Supplementary material

Supplementary material 1
Ordered table of individual relevés (*.xlsx)
Link: https://doi.org/10.3897/VCS/2021/39583.suppl1

Supplementary material 2
Diagnostic, constant and dominant species of the four clusters. (*.pdf)
Link: https://doi.org/10.3897/VCS/2021/39583.suppl2

Supplementary material 3
Distribution maps and photos of the newly described associations. (*.pdf)
Link: https://doi.org/10.3897/VCS/2021/39583.suppl3

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 2: 59–63
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LONG DATABASE REPORT ECOINFORMATICS

SWEA-Dataveg: a vegetation database for sub-Saharan Africa

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Abstract

SWEA-Dataveg is a vegetation-plot database collecting observations mainly in sub-Saharan Africa but also open to the rest of the African continent. To date this database contains more than 5,500 plot observations provided by 47 sources (projects, monographs, and articles). While the database is stored in PostgreSQL (including the PostGIS extension), the R-package "vegtable" implements a suitable exchange format. In this article we assess the current content of SWEA-Database and introduce its history and future as a repository of data for syntaxonomic assessments and macroecological research.

Keywords

ecoinformatics, plant biodiversity, taxlist, syntaxonomy, vegetation ecology, vegtable

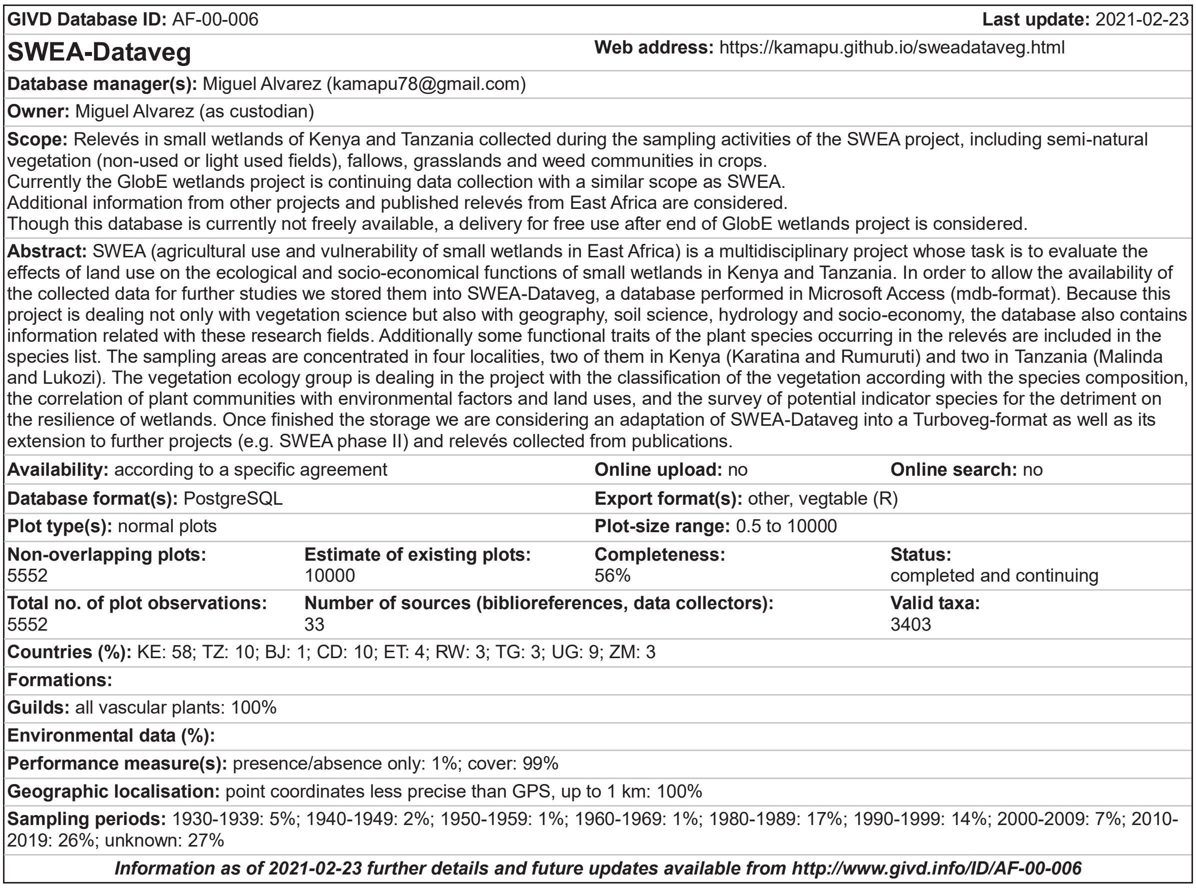
Introduction

In sub-Saharan Africa as elsewhere, documenting and classifying vegetation has become an urgent task to enable the proper assessment of endangered ecosystems (Jansen et al. 2016). With an increasing number of research projects dealing with vegetation ecology in the region, there is a vast amount of information of high scientific value that could be made accessible to the wider research community. At the same time, knowledge accumulated in past research programs can also provide the basis for constructive research into vegetation history, biogeography and conservation. Database structures such as vegetation-plot databases may serve as important repositories for data curation and ensure research repeatability and meta-analysis in the context of macroecological and biogeographical studies (Dengler et al. 2011; Bruelheide et al. 2019).

The database SWEA-Dataveg (Alvarez et al. 2012b) was initiated as a repository for ongoing projects in East Africa, specifically for the SWEA project (Agricultural use and vulnerability of small wetlands in East Africa). At its genesis the database was focusing on the collection of data from wetland ecosystems in Kenya and Tanzania (see Alvarez et al. 2012a). Through follow-up projects and collaboration activities with the ETH-Zürich (Switzerland) and the East African Herbarium (Kenya), the database was expanded to all vegetation formations and included data from additional African countries.

This report briefly displays the current status of the vegetation-plot database SWEA-Dataveg (GIVD AF-00-006) and its applications in the research of vegetation ecology and biogeography in sub-Saharan Africa.

GIVD Fact Sheet



GIVD Database ID: AF-00-006			**Last update:** 2021-02-23
SWEA-Dataveg		**Web address:** https://kamapu.github.io/sweadataveg.html	
Database manager(s): Miguel Alvarez (kamapu78@gmail.com)			
Owner: Miguel Alvarez (as custodian)			
Scope: Relevés in small wetlands of Kenya and Tanzania collected during the sampling activities of the SWEA project, including semi-natural vegetation (non-used or light used fields), fallows, grasslands and weed communities in crops. Currently the GlobE wetlands project is continuing data collection with a similar scope as SWEA. Additional information from other projects and published relevés from East Africa are considered. Though this database is currently not freely available, a delivery for free use after end of GlobE wetlands project is considered.			
Abstract: SWEA (agricultural use and vulnerability of small wetlands in East Africa) is a multidisciplinary project whose task is to evaluate the effects of land use on the ecological and socio-economical functions of small wetlands in Kenya and Tanzania. In order to allow the availability of the collected data for further studies we stored them into SWEA-Dataveg, a database performed in Microsoft Access (mdb-format). Because this project is dealing not only with vegetation science but also with geography, soil science, hydrology and socio-economy, the database also contains information related with these research fields. Additionally some functional traits of the plant species occurring in the relevés are included in the species list. The sampling areas are concentrated in four localities, two of them in Kenya (Karatina and Rumuruti) and two in Tanzania (Malinda and Lukozi). The vegetation ecology group is dealing in the project with the classification of the vegetation according with the species composition, the correlation of plant communities with environmental factors and land uses, and the survey of potential indicator species for the detriment on the resilience of wetlands. Once finished the storage we are considering an adaptation of SWEA-Dataveg into a Turboveg-format as well as its extension to further projects (e.g. SWEA phase II) and relevés collected from publications.			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): PostgreSQL		**Export format(s):** other, vegtable (R)	
Plot type(s): normal plots		**Plot-size range:** 0.5 to 10000	
Non-overlapping plots: 5552	**Estimate of existing plots:** 10000	**Completeness:** 56%	**Status:** completed and continuing
Total no. of plot observations: 5552	**Number of sources (biblioreferences, data collectors):** 33		**Valid taxa:** 3403
Countries (%): KE: 58; TZ: 10; BJ: 1; CD: 10; ET: 4; RW: 3; TG: 3; UG: 9; ZM: 3			
Formations:			
Guilds: all vascular plants: 100%			
Environmental data (%):			
Performance measure(s): presence/absence only: 1%; cover: 99%			
Geographic localisation: point coordinates less precise than GPS, up to 1 km: 100%			
Sampling periods: 1930-1939: 5%; 1940-1949: 2%; 1950-1959: 1%; 1960-1969: 1%; 1980-1989: 17%; 1990-1999: 14%; 2000-2009: 7%; 2010-2019: 26%; unknown: 27%			
Information as of 2021-02-23 further details and future updates available from http://www.givd.info/ID/AF-00-006			

History

The idea of establishing a vegetation-plot database started during a visit to the 8th Meeting on Vegetation Databases, held at the University of Greifswald, Germany, in 2009. The project was officially launched in 2010 and the first report was published in 2012 with a small collection of 206 plots originally stored in a Microsoft-Access database (Alvarez et al. 2012b). Since then, this database has been affiliated with research activities at the University of Bonn, Germany, in collaboration with diverse academic and research institutions in Eastern Africa.

In 2015, and in the context of a collaborative activity between the SWEA-Project and the ETH-Zürich, Switzerland, SWEA-Dataveg migrated to the software Turboveg (Hennekens and Schaminée 2001) and the first trials for data exchange and processing using R-images and R-scripts were carried out. At that time, export of Turboveg to R was completed using the package “vegdata” (Jansen and Dengler 2010).

After the first releases of the packages “taxlist” and “vegtable” at CRAN in 2017 (see Alvarez and Luebert 2018), the database migrated again, this time to PostgreSQL including the PostGIS extension for handling the location of plots in a Geographical Information System (GIS). During this development, SWEA-Database became larger and more complex, and partially interlinked with the database “sudamerica” (former CL-Dataveg, GIVD SA-CL-001; Alvarez et al. 2012c).

Content of the database

Currently, the database contains 5,552 plot observations (relevés) collected from 47 sources, including projects, journal articles and monographs. These observations contain records of 3,530 plant species belonging to 1,318 genera and 216 families. The dominant families are *Leguminosae* (402 species; 10.4%), *Poaceae* (393 species; 10.2%), *Compositae* (290 species; 7.5%), and *Cyperaceae* (212 species; 5.5%).

According to record date and year of publication, the oldest observations are from 1937 (Lebrun 1947, 1960), while the most recent records are from 2020 (unpublished data). Plot sizes comprise < 1 m^2 (37 plots, 0.7%); 1–10 m^2 (1,168 plots, 21.0%); 10–100 m^2 (1,289 plots, 23.2%); 100–1,000 m^2 (616 plots, 11.1%); 1,000–10,000 m^2 (84 plots, 1.5%); and for 2,358 observations (42.5%) the plot size is unknown. A total of 1,822 plot observations (32.8%) were collected in projects affiliated to SWEA-Dataveg.

The current version of SWEA-Dataveg is stored in a PostgreSQL database, including the PostGIS extension for geo-referenced information. Plot observations are organized in a table called "header" and linked to several tables analogous to the popup tables of Turboveg (Hennekens and Schaminée 2001). A taxonomic list is also integrated into this database, following the structure used by the R-package "taxlist" (Alvarez and Luebert 2018). Data export is preferentially designed in SQL language and assigned to a "vegtable" object in R (see https://github.com/kamapu/vegtable). Further process and assessment can be done either in R or exporting to any spreadsheet application for analysis. Additionally, export to the software Juice (Tichý 2002) is carried out by a function called "write_juice()".

All plots included in the database are geo-referenced. A logical variable called "validation_coordinates" indicates whether these coordinates were provided by the authors as coordinate values or in a detailed map ("true"), or if they are inferred from the description of locality ("false"). Observations have been undertaken in 12 countries with 2,804 plots (51%) sampled in Kenya, 986 (18%) in the Democratic Republic of the Congo, 467 (8%) in Ethiopia, and 425 (8%) in Tanzania. The rest of the plots were collected in Uganda, Togo, Rwanda, South Africa, Burundi, Congo-Brazzaville, Benin, and Zambia (see Figure 1).

Figure 1. Geographical distribution of plot observations (black dots) stored in SWEA-Dataveg.

SWEA-Dataveg attempts to collect as much of the information originally published with plot observations as possible. Besides information on plot size, recording dates and locations (coordinates and descriptions of localities), additional data on slope inclination, exposition, elevation, total vegetation cover, soil physical and chemical properties and remarks, if provided by the sources, are digitized and stored. From all observations, 79% are stored with a sampling date, 64% with coordinates, 58% with information on plot size, and 21% with information on soil physical or chemical properties (Figure 2). Furthermore, original pages and table number as well as assignment to a specific plant community is also documented.

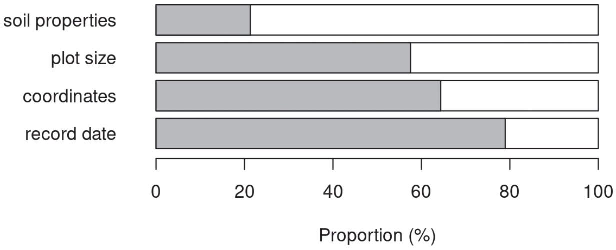


Figure 2. Completeness of important information within the plots stored in SWEA-Dataveg. Grey areas represent the proportion of observations containing any data for the respective variables.

The associated taxonomic list is supported by five sources referred to as taxon views (see Alvarez and Luebert 2018). This module contains information on taxonomic ranks, parent-child relationships (e.g. indication of the parent genus for a species) and taxon attributes (e.g. life forms, chorology and functional traits). The later information is usually collected from secondary references, including on-line databases, and complements specific project objectives.

Additional features

All data sources are supported by a private soft copy of the relevant published article to enable cross-validation of fidelity of data stored in the database. Digitization procedures strive to resemble the data published in the original source.

Projects attempting to derive critical assessments of classifications in the context of the Braun-Blanquet approach (e.g. Alvarez 2017) are also catered for with a collection of syntaxonomic nomenclatures and Cocktail algorithms stored as "expert systems" (see Landucci et al. 2015).

Besides all of these features, the development of the R-packages "taxlist" and "vegtable" (Alvarez and Luebert 2018) are strongly dependent on the assessment of data contained in SWEA-Dataveg and are used as the main mechanisms for data sharing and publication. The implementation of R-scripts in the assessment of data assure the repeatability of statistics while the current efforts to integrate r-markdown in some functions enables the possibility of producing automatic updates of summaries such as lists of data per syntaxa and publications or check lists of plant species.

At present, data is accessible only after special agreements with the custodian. While data stored from ongoing projects are highly restricted at least during the lifespan of the respective projects, we expect to be able to make data freely available from already published works. The preferred format for exchange is an R-Image including a vegtable object (Alvarez and Luebert 2018). Further alternative formats are Juice tables, SQL dump files for freeware relational database systems (e.g. PostgreSQL, MySQL, LibreOffice Base), and spreadsheets in xlsx, odt and csv formats. In all of these cases, the content of the requested files requires correspondence with the custodian.

Resulting publications

From its origins, SWEA-Dataveg focused on a preliminary classification of wetland vegetation in East Africa (Alvarez et al. 2012a). This work was followed by a classification of aquatic and semi-aquatic vegetation using observations collected in 2012 in Kenya and Tanzania and addressing the Braun-Blanquet approach (Alvarez 2017).

In the specific case of Kenya, a model describing plant biodiversity and spatial conservation prioritization was performed for the Kenyan subset and included a pool of bioclimatic, macroecological and economic factors as explanatory variables (Scherer et al. 2017a, b). This work inferred locations in the country that are most suitable for the expansion of protected areas in order to meet national targets for biodiversity conservation and estimated the required funding to achieve this.

SWEA-Dataveg also supported the design of ecological assessment and monitoring methods, such as an adaptation of the WET-Health approach by Beuel et al. (2016), and the use of physiognomic properties of the vegetation for the estimation of the biological integrity completed by Behn et al. (2018). In both works, the information included in the database was used for the calibration of regression models and the evaluation of outcomes.

Ongoing projects are dealing with distribution models of invasive species in Eastern Africa, in particular on *Prosopis juliflora* (Sw.) DC. (Alvarez et al. 2019) and *Parthenium hysterophorus* L. (no publications to date).

In addition to inclusion in the Global Index of Vegetation-Plot Databases (Dengler et al. 2011; Alvarez et al. 2012b), this database also contributed to the sPlot initiative (Bruelheide et al. 2019).

The way forward

The implementation of a multiple-taxon views approach, for instance considering discrepancies among different projects involved in the African Plant Database (https://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php) and some regional floras (e.g. Flora of Tropical East Africa, Beentje et al. 1952–2012; Flora of Ethiopia and Erithrea, Hedberg et al. 1989–2009), will make this database more versatile. This will also allow it to expand areas of coverage and to integrate other databases under the same database model, such as the database “sudamerica” (Alvarez et al. 2012c).

We also seek to integrate an electronic document library, which is at present housed in a separated database formatted as a BibTeX file and linked to respective data sources as well as taxonomic and syntaxonomic authorities.

Acknowledgements

The database is currently maintained in the context of the project “Future Invasions” within the Collaborative Research Centre “Future Rural Africa” (http://www.futureruralafrica.de/). We thank Mrs. Emilia Lösche for her support accessing the valuable collections of the Library of the Geographical Department at the University of Bonn in Germany. Several students have supported the work of digitizing data and testing assessments by the developed R-packages, to whom we are very thankful.

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VEGETATION CLASSIFICATION AND SURVEY
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NOMENCLATURAL PROPOSAL PHYTOSOCIOLOGICAL NOMENCLATURE

Proposals (26–27): to conserve the names *Nanocyperetalia* Klika 1935 and *Isoetetalia* Braun-Blanquet 1936

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Abstract

After a nomenclatural revision of the higher rank syntaxa of the class *Isoeto-Nanojuncetea*, the conservation of the order name *Nanocyperetalia* against *Nanocypero-Polygonetalia* and a conserved type for the order *Isoetetalia* are proposed.

(26) *Nanocyperetalia* Klika 1935: 292, nom. cons. propos.
Typus: *Nanocyperion flavescentis* Koch 1926: 20–28 (holotypus)
(≡) *Nanocypero-Polygonetalia* Koch 1926: 20, nom. rejic. propos.

(27) *Isoetetalia* Braun-Blanquet 1936a: 142, typus cons. propos.
Typus: *Isoetion* Braun-Blanquet 1936a: 141 (typus cons. propos.)

Taxonomic reference: Euro+Med (2020).

Syntaxonomic reference: Mucina et al. (2016).

Abbreviations: ICPN = International Code of Phytosociological Nomenclature.

Keywords

conserved name, conserved type, ICPN, *Isoeto-Nanojuncetea*, nomenclature, phytosociology, temporary ponds, vegetation

Introduction

The pioneer vegetation of temporary ponds and other periodically flooded soils has claimed the attention of European phytosociologists for almost a century and, therefore, has a complex syntaxonomic and nomenclatural history. This is the case of the three orders described for this type of vegetation (class *Isoeto-Nanojuncetea*) during the 1920s and 1930s, whose nomenclatural vicissitudes are analysed below under the rules of the 4th edition of the ICPN (Theurillat et al. 2021).

Nanocypero-Polygonetalia Koch 1926

In his study on the vegetation of the Linth Plain ("Linthebene"), Koch (1926: 20) introduced the order *Nanocypero-Polygonetalia [‘Nanocypereto-Polygonetalia’]* with two alliances ("Assoziationsverband"): *Nanocyperion flavescentis* and *Polygono-Chenopodion polyspermi*. The diagnosis of the *Nanocyperion* includes three new associations present in the Linth Plain (*Eleocharitetum ovato-at-*

ropurpureae [*'Eleocharetum ovato-purpureae'*], *Centunculo-Anthocerotetum punctati* [*'Centunculo-Anthoceretum punctati'*] and *Cyperetum flavescentis*) and references to other associations described from different areas that the author considers as belonging to the new alliance (Koch 1926: 21, 28). The *Eleocharitetum ovato-atropurpureae* is invalid because (1) only a species list is given in Koch; (2) the reference to *'Archidietum [phascoidis]* Jäggli 1922 p.p.' is not accepted as a sufficient diagnosis according to Art. 7, and (3) the other references (Schröter and Wilczek 1902 [recte: 1904], Hayek 1923) contain only species lists. Koch does not provide relevés for the *Centunculo-Anthocerotetum punctati*. On pages 24–25, he discusses its affinities with the wetter aspects of a community validly described by Allorge (1922b) with a synoptic table under the name 'Association des moissons siliceuses [siliceous crops] à *Chrysanthemum segetum* et *Myosurus minimus*', concluding that the latter is a different association not belonging to the *Nanocyperion flavescentis*. Therefore, the name *Centunculo-Anthocerotetum punctati* Koch 1926 is a nomen nudum (Art. 2b), and the *Chrysanthemo segetum-Myosuretum minimi* Allorge 1922 is to be excluded from the original diagnosis of the alliance. It should be noted that Allorge (1922b) is an explicit reprint in book format of the previous publications of Allorge (1921, 1922a) in the Revue Générale de Botanique.

With respect to the *Cyperetum flavescentis*, Koch does not provide relevés but unambiguously refers to the *'Juncus compressus-Parvo-Cyperus*-Assoziation' validly published by Braun-Blanquet (1922: 20) with a relevé containing both *Cyperus flavescens* and *C. fuscus*. Therefore, the *Cyperetum flavescentis* Koch 1926 is a valid name that is automatically the type of the alliance *Nanocyperion flavescentis* (Art. 20). However, it is a superfluous name (Art. 29c) for the *Junco compressi-Parvo-Cyperetum* Braun-Blanquet 1922 (Mucina et al. 2016: 178).

In the description of the *Cyperetum flavescentis*, Koch also recognizes, as floristically related but syntaxonomically independent unit, the 'Association à *Cicendia filiformis* et *Stereodon arcuatus*' described by Allorge, with direct bibliographic references to Allorge (1922b), Gadeceau (1909) and Gaume (1924). Allorge's original diagnosis of the association contains 14 presence-absence relevés of vascular plants (table XXI) that would meet Art. 7. Nevertheless, *Stereodon arcuatus* Lindb. (*Calliergonella lindbergii* (Mitt.) Hedenäs in modern floras) is absent from the table XXI because bryophyte species "present in the association" are listed separately in the text, without an indication of their frequency meeting Art. 7 or a statement about their presence in table XXI. Therefore, the name *Cicendio filiformis-Stereodontetum arcuati* Allorge 1922 is invalid according to Art. 3f Note 1, which requires that the name-giving taxa must be present in the relevés or synoptic tables. Allorge also uses the form 'association à *Cicendia filiformis*' in the text, always in descriptive sentences and in most cases close to sentences in which the form used is 'association à *Cicendia filiformis* et *Stereodon arcuatus*', the latter being the form used in the header of the section describing the association and in the header of table XXI. Therefore, it is clear that the double name is the one really proposed by Allorge, and the form 'association à *Cicendia filiformis*' is a literary shortcut to refer to the community, not a true alternative name in the sense of Art. 30a. Gadeceau (1909: 117–118), cited for the association both by Allorge (1922a) and Koch (1926), contains only a species list under the name *'Pusillaejuncetum'* that is invalid according to Arts. 2a and 2b. Gaume (1924: 169), for his part, provides a synoptic table under the name 'Association à *Cicendia filiformis* (*Cicendietum*)', validating in this way Allorge's association to whom reference is made, and whose correct name is, therefore, *Cicendietum filiformis* Allorge ex Gaume 1924. Finally, the '*Isolepis-Stellaria uliginosa*-Assoziation' introduced by Koch (1926: 28) is another nomen nudum (Art. 2b).

The diagnosis of the *Polygono-Chenopodion polyspermi*, the second alliance of the order, contains (1) the association *Bidentetum tripartitae* Koch 1926, validly published with a relevé on page 29, and unambiguous bibliographical references to (2) the 'association à *Bidens tripartita* et *Brassica nigra*', validly described by Allorge (1921) with a synoptic table; (3) to Gaume (1924) who described an 'association à *Bidens tripartita*' with a species list (Art. 2b); and (4) to Braun-Blanquet (1921, 1923) who introduced the nomen nudum '*Panico-Chenopodietum polyspermi*' (Art. 2b). However, because the valid elements of the alliance (*Bidentetum tripartitae* Koch 1926 and *Bidenti tripartitae-Brassicetum nigrae* Allorge 1921) do not contain *Chenopodium polyspermum*, the name *Polygono-Chenopodion polyspermi* is invalid according to Art. 3f (Mucina et al. 2016: 205).

In conclusion, the original diagnosis of the order *Nanocypero-Polygonetalia* Koch 1926 includes only the *Nanocyperion flavescentis* as a valid alliance. Among the valid elements of the alliance, *Polygonum* species are lacking in the original diagnosis of the *Cyperetum flavescentis*. However, in the original diagnosis of the *Cicendietum filiformis* Allorge ex Gaume 1924, *Polygonum hydropiper* occurs in Gaume's synoptic table; besides, *P. minus* is also present in table XXI of Allorge (1922b) to whom Gaume refers. Therefore, Koch validly published the order's name according to Art. 3f, and its holotype is the *Nanocyperion flavescentis* Koch 1926.

Nanocyperetalia Klika 1935

In a study about the Central European vegetation on temporarily flooded soils, Klika (1935) revised the alliance *Nanocyperion flavescentis* with unambiguous bibliographical references to Koch (1926) on pages 298–299 and 301, subordinating it to the order '*Nanocyperetalia*' as the sole alliance on page 292. No rationale is given for the new name of the order. The renaming was probably due to a change of the syntaxonomic concept since Klika subordinated the alliance *Polygono-Chenopodion polyspermi* to a different order (*Chenopodietalia*). In any case, the *Nanocyperetalia* Klika 1935 is a valid name and its holotype is the *Nanocyperion flavescentis* Koch 1926. However, the order's name is superfluous since it contains the type of the earlier *Nanocypero-Polygonetalia* Koch 1926 (Art. 29c). According to the indication provided on the front page of the issue 2/3 of Beihefte zum botanischen Centralblatt volume 53, Klika's paper was published in May 1935.

Isoetetalia Braun-Blanquet 1936

The order *Isoetetalia* was validly published by Braun-Blanquet in volume 47 of the Bulletin de la Société d'Étude des Sciences Naturelles de Nîmes (Braun-Blanquet 1936a) as well as in the Communication 42 of the SIGMA (Braun-Blanquet 1936b). Text and format are identical in both publications, except for the page numbering. The Communication is dated 'January 1936' on the cover page and contains a reference to the Bulletin on the last page: 'Extrait du [reprint from] Bulletin de la Société d'Étude des Sciences Naturelles de Nîmes, t. XLVII, 1930–35'. An additional evidence that the Communication is a reprint of the Bulletin is that in both publications a reference to the 'Communication de la Station Intern. de Géobotanique Méditerranéenne et Alpine N° 40' is given under the title on the first page, but the actual number of the Communication series is 42, suggesting that it was postponed until the Bulletin was published, leading to an earlier publication of volumes 40 and 41 of the Communications that are dated 1935 and 1936, respectively. The precise date of publication of volume 47 of the Bulletin is unknown. However, on page 252, there is a reference to a meeting of the Société held on 29 November 1935. Hence, it is very unlikely that the volume could have been printed and distributed before 1936 (D. Kania, personal communication). Although in many publications, including the EuroVegChecklist (Mucina et al. 2016), Braun-Blanquet's publication is dated 1935, in the 4th edition of the ICPN (Theurillat et al. 2021) the date has been corrected to 1936. The order *Isoetetalia* had been mentioned in previous publications (Braun-Blanquet 1931, Moor 1935), but without a sufficient original diagnosis (Art. 2b).

The original diagnosis of the order in Braun-Blanquet (1936a) contains three alliances. One is the *Isoetion* Braun-Blanquet 1936 whose description covers almost the entire publication. It includes six valid associations together with one provisional association. The second alliance, the *Preslion cervinae*, is a nomen nudum (Art. 2b) validated later by Moor (1937) (see Silva et al. 2021). The third alliance is the *Nanocyperion flavescentis* Koch 1926, with an unambiguous bibliographical reference to Koch (1926) on p. 142. Since the *Nanocyperion flavescentis* is the type of the earlier name *Nanocypero-Polygonetalia*, the name *Isoetetalia* is superfluous (Art. 29c). Consequently (Art. 18b), the alliance *Nanocyperion flavescentis* Koch 1926 is the type of the name *Isoetetalia*.

Conservation of the order names *Nanocyperetalia* and *Isoetetalia*

Until now, it was considered that the *Nanocypero-Polygonetalia* was an invalid name (Mucina et al. 2016), or a name to be rejected due to its heterogeneous content (Moor 1935, 1937, Braun-Blanquet 1936a). Currently, the alliance *Nanocyperion flavescentis* is included in the class *Isoeto-Nanojuncetea* while the original valid content of Koch's *Polygono-Chenopodion polyspermi* would belong to the *Bidentetea* (Mucina et al. 2016). Authors that recognize only one order in the *Isoeto-Nanojuncetea* have given priority to *Isoetetalia* over *Nanocyperetalia* following Moor (1937). However, the majority of authors after 1970 recognizes two or more orders (see Brullo and Minissale 1998 for a synopsis of the different syntaxonomic systems), including the EuroVegChecklist (Mucina et al. 2016). According to such a syntaxonomic concept, the Mediterranean communities flowering in spring and early summer are included in the order *Isoetetalia,* assuming that its nomenclatural type would be automatically the *Isoetion* according to Art. 20, while the temperate European and Mediterranean communities flowering in late summer and autumn are included in the order *Nanocyperetalia*. However, both names *Nanocyperetalia* Klika 1935 and *Isoetetalia* Braun-Blanquet 1936 are homotypic superfluous names because their original diagnoses include the nomenclatural type of the *Nanocypero-Polygonetalia* Koch 1926. This name cannot be considered an ambiguous name (Art. 36) because it has been rarely used, nor a dubious name (Arts. 37 and 38) because the nomenclatural type of its type alliance, the *Cyperetum flavescentis* (for which the correct name is *Junco compressi-Parvo-Cyperetum*), has been widely accepted and used.

Accepting the consequences of the strict application of the nomenclatural rules would imply important changes, because a new syntaxon name would be needed for the traditional concept of the *Isoetetalia*. Moreover, it would make the future understanding of almost a century of phytosociological literature on this type of vegetation extremely difficult, because *Isoetetalia* and *Nanocyperetalia* are nomenclatural synonyms of *Nanocypero-Polygonetalia*, a name disused for the last 90 years. Brullo and Minissale (1998) list 130 papers dealing with the syntaxonomy of *Isoeto-Nanojuncetea*, a number that has probably multiplied in the last 20 years given the relevance of this habitat type for biodiversity conservation (Foucault 2013a, b, Šumberová and Hrivnák 2013). Conserving the name *Nanocyperetalia* against *Nanocypero-Polygonetalia* would not solve the problem of the *Isoetetalia* for which a new name should be published. However, the introduction of the new Art. 53 in the ICPN (Theurillat et al. 2021) allows preserving the common use of a name by choosing a nomenclatural type other than the one determined by the application of the rules. Therefore, we propose here to conserve the name *Isoetetalia* Braun-Blanquet 1936 with a conserved type, the *Isoetion* Braun-Blanquet 1936 that has been traditionally considered the type of that order. At the same time, we propose to conserve the name *Nanocyperetalia* Klika 1935 against the disused name *Nanocypero-Polygonetalia* Koch 1926.

Author contributions

All authors have contributed to the nomenclature research and the critical revision of the manuscript.

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NOMENCLATURAL PROPOSAL
PHYTOSOCIOLOGICAL NOMENCLATURE

Requests (1–2) for a binding decision on the name-giving taxa in the names *Isoeto-Cicendietum* Br.-Bl. 1967 and *Verbeno-Gnaphalietum* Rivas Goday 1970

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Abstract

We propose to complete two association names of the class *Isoeto-Nanojuncetea* by selecting the name-giving taxa according to Art. 40 of the International Code of Phytosociological Nomenclature.

Taxonomic reference: Euro+Med (2021).

Keywords

binding decision, Isoeto-Nanojuncetea, nomenclature, phytosociology

(1) Request for a binding decision on the name-giving taxon in the name *Isoeto longissimae-Cicendietum* Br.-Bl. 1967 nom. corr.

Original form of the name: *Isoeto-Cicendietum*

Syn.: *Isoeto velatae-Cicendietum* Br.-Bl. 1967 nom. inept. (Art. 44)

Typus: Braun-Blanquet 1967: 29 (holotypus).

Braun-Blanquet (1967: 29) published this Galician-Portuguese syntaxon with only one relevé from Braga (Minho province, Portugal), which is therefore the holotype. The only *Isoetes* in the original diagnosis is *Isoetes velata* A. Braun. However, as this is an illegitimate name (Troia and Greuter 2014), the correct name of the name-giving taxon of the association is *Isoetes longissima* Bory, and the name of the syntaxon must be corrected (Art. 44, Theurillat et al. 2021).

Braun-Blanquet did not indicate from which of the two *Cicendia* species present in the original diagnosis the association name was formed, *C. filiformis* or *C. pusilla* (= *Exaculum pusillum*; Euro+Med 2021). However, *C. filiformis* is more abundant in the type relevé (cover-abundance value 1) than *C. pusilla* (value +). As far as we can ascertain, no other relevés assigned to this association have been published (see, e.g., Brullo and Minissale 1998). Thus, we propose to select *Cicendia filiformis* as the name-giving taxon.

(2) Request for a binding decision on the name-giving taxon in the name *Gnaphalio-Verbenetum supinae* Rivas Goday 1970 nom. invers.

Original form of the name: *Verbeno-Gnaphalietum*

Syn.: “com. prov. *Gnaphalium luteo-album-Verbena supina*” Rivas Goday 1956 (Art. 3b, 3c)

Typus: Rivas Goday 1970: 270–271, table 8, rel. 1 (lectotypus designated by Silva et al. 2021: 8).

The provisional community “*Gnaphalium luteo-album-Verbena supina*” was published by Rivas Goday in Rivas Goday et al. (1956: 370) together with seven relevés. Later, Rivas Goday (1970: 273) validated the syntaxon under the name “*Verbeno-Gnaphalietum* Rivas Goday 1955”, giving an unambiguous reference to his older work (though with the wrong year 1955; see Izco (1975) for information about the correct publication date) and publishing another table with ten relevés. The only *Verbena* species in the original diagnosis is *V. supina*, but there are two species of *Gnaphalium*: *G. luteoalbum* and *G. uliginosum*. Rivas Goday et al. (1956) used *G. luteoalbum* in the name of their provisional community, and this species is also more frequent and abundant in the original diagnosis than *G. uliginosum*. We therefore propose to select *G. luteoalbum* as the name-giving taxon of the *Verbeno-Gnaphalietum*.

In the type relevé, *Verbena supina* has a cover-abundance value of 2, whereas *G. luteoalbum* has a 1 and *G. uliginosum* a +. Therefore, the name ‘*Verbeno-Gnaphalietum*’ must be inverted (Arts. 10b and 42, Theurillat et al. 2021). If our proposal is accepted, the correct name of the association will be ‘*Gnaphalio luteoalbi-Verbenetum supinae* Rivas Goday 1970 nom. invers.’.

Author contributions

Both authors have contributed to the nomenclature research and writing the manuscript.

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REVIEW AND SYNTHESIS

Terrestrial biomes: a conceptual review

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Abstract

Aims: We attempt to review the conceptualisation, science and classification of biomes and propose to limit the definition of a biome to potential natural vegetation as determined by general environmental variables.

Results: Classifying the distribution and abundance of vegetation types on earth has been a central tenet of vegetation science since Humboldt's classic studies in the early 1800s. While the importance of such classifications only grows in the wake of extreme changes, this review demonstrates that there are many fundamentally different approaches to define biomes, hitherto with limited efforts for unifying concepts among disciplines. Consequently, there is little congruence between the resulting maps, and widely used biome maps fail to delimit areas with consistent climate profiles.

Conclusions: Gaps of knowledge are directly related to research avenues, and suggestions for defining and classifying biomes, as well as modelling their distributions, are provided. These suggestions highlight the primary importance of the climate, argue against using anthropogenic drivers to define biomes and stabilize the concept of biome to escape from the current polysemy. The last two decades have seen an emergence of new approaches, e.g., using satellite imagery to determine growth patterns of vegetation, leading to defining biomes based on the objective, observable qualities of the vegetation based on current reality.

Keywords

climate, climax vegetation, ecozone, formation, global, potential natural vegetation, terrestrial, typology, vegetation classification, zonal

Introduction

Mapping and classifying the distribution and abundance of the world's organisms, and shifts in their distribution and abundance, is the only means to understand species' response to numerous factors stressing those organisms (climate change, pollution, habitat loss, etc.). Examining species' distributions has been a central tenet of the organismal sciences for 200 years, with the understanding that distributions follow rules and that if we can model those rules, we can predict responses to changes as well as look back historically (e.g., shifts during the Pleistocene, Davis and Shaw 2001; Loidi et al. 2012). Concepts like biomes (developed throughout this review and defined under **Final remarks**), ecozones, and formations have described such distributions at the regional and global scale due to the importance of this global scale for conservation biology (Chytrý et al. 2020) and answering basic ecological questions (Mucina 2019). For example, the biome concept has been used to examine diversity-productivity (Madrigal-González et al. 2020) and species-area (e.g., see Dengler et al. 2020) relationships, quantify temporal dynamics (Wang and Fensholt 2017), model historical distributions and shifts following climate change (Rowland et al. 2016), and identify areas most affected by human impact and showing evolutionary convergence in plant form and function (Ringelberg et al. 2020). Indeed, our need for understanding regional distributions is growing quickly as we struggle to understand the effects of a rapidly changing climate, land use changes and other anthropogenic impacts on ecosystems (Shukla et al. 2019). While some of the major drivers of distributions (i.e., 'the rules') have been identified (e.g., climate factors and phylogeny), and those drivers have been related to certain biota (e.g., southern hemisphere taxa) and biotic traits (e.g., life form, growth form and life history), an accepted classification and map are lacking (Moncrief et al. 2015; Higgins et al. 2016). That is, we have yet to define these regional distributions with metrics and subsequently map the world's biomes, despite the obvious and pressing need. One reason is that the knowledge and tools for such work have recently exploded and a concerted effort to incorporate these many new ideas has not been achieved (although see Mucina 2019 and Procheş 2020). Toward that goal, we attempt to review here the history, science and classification of biomes and biome-like concepts and propose a conceptual frame in order to build a global biome classification usable for mapping.

Vegetation biomes: a conceptual review

We first show the development of the biome concept, then the historical antagonism between the two main approaches to delineating biomes (floristics and physiognomy), and then focus on the development of the physiognomical approach and from that approach to the concept of a biome.

Initial steps – from phytogeography to the biome concept

A biome is a complex concept with no exact definition, some have argued that the varying traditions and usages of 'biome' and its synonyms are ambiguous and therefore of little empirical use (Kreft and Jetz 2010). However, the term is continually being adapted and re-invented (Griffith et al. 2019; Keith et al. 2020), and others suggest that much use can come from this flexibility of definition (Pennington et al. 2004). Although the earliest endeavors did not use the term biome, phytogeography, and vegetation science in general, attempts to find general patterns that explain the distribution and interactions of living organisms with the physical and non-physical world. Though not conceptualized at the time as we understand biomes today these early phytogeographical concepts underpin the earliest attempts at biome like concepts. This process involves the discovery of universal laws that govern their lives, imposing an order upon the huge number of species and diverse life forms at different scales. Since the inception of phytogeography, Alexander von Humboldt showed an obsession for finding these patterns and laws (in contrast with systematic Botany and Zoology). The idea of unity in the universe (Cosmos) underlies all his work, so that the multitude of life forms are subject to a unified system of laws that order and govern them in harmony with the physical environment.

"*Die Natur ist für die denkende Betrachtung Einheit in der Vielheit, Verbindung des Mannigfaltigen in Form und Mischung, Inbegriff der Naturdinge und Naturkräfte, als ein lebendiges Ganzes. Das wichtigste Resultat des sinnigen physischen Forschens ist daher dieses: in der Mannigfaltigkeit die Einheit zu erkennen; von dem Individuellen alles zu umfassen, was die Entdeckungen der letzteren Zeitalter uns darbieten; die Einzelheiten prüfend zu sondern und doch nicht ihrer Masse zu unterliegen: der erhabenen Bestimmung des Menschen eingedenk, den Geist der Natur zu ergreifen, welcher unter der Decke der Erscheinungen verhüllt liegt.*"

"*For the thinking consideration, nature is unity in the multiplicity, the connection of the manifold in form and mixture, the embodiment of natural things and forces of nature, as a living whole. The most important result of sensible physical research is therefore this: to recognize unity in diversity; to embrace of the individual all that the discoveries of the latter ages present to us; to scrutinize the details, and yet not to succumb to their masses: remembering the sublime destiny of man to grasp the spirit of nature, which lies hidden under the cover of the apparitions.*" (Humboldt 1855: 5–6).

Consistently, in his comments about plant geography, he addresses:

"*La géographie des plantes fournit des matériaux précieux pour ce genre de recherches: elle peut, jusqu'á un certain point, faire reconnoître les îles qui, autrefois réunis, ce sont sépareés les unes des autres; elle announce la séparation de l'Afrique de l'Amérique méridionale s'est faite avant le dévelopemant des êtres organisés. C'est encores cette science qui montre quelles plantes sont comunes à l'Asie orientale et aux côtes du Mexique et de la Californie;* ".

"*The geography of plants provides valuable materials for this kind of research: it can, up to a certain point, make known the islands which once united are separated from each other; it announces the separation of Africa from South America was made before the development of organized beings. It is still this science which shows what plants are common in East Asia and the coasts of Mexico and California; …*" (Humboldt and Bonpland 1805: 19).

Biome and biome-like systems such as found in many biogeographic or ecoregional classifications attempt to divide and explain the distribution of the world's biota at large scales, allowing global predictions, agreements and assessments, and to act as templates for research and enquiry. While the definition of a biome and its wider usage has a relatively recent history, biome-like schemas extend back to Humboldt's passionate beginnings and inform how we conceptualise the term today.

Historically, biome and biome-like concepts have both variously separated and combined vegetation and fauna into different, but often parallel schema. Within this review, we concentrate primarily on vegetation, and a schematic presentation of the different contributions along the history related to the biome concept is provided in Table 1. The earliest attempts at a biome vegetation classification were simply to aid in the description of the world's vegetation, to better comprehend where, and potentially why, vegetation occurred in that precise context. Predating Darwin, some tried to explain differences through concepts such as special creations (Egerton 2018). From these descriptive beginnings, however, global schemas have evolved to incorporate our increased understanding of the complexity of abiotic influences on flora. These include climate, soil and disturbance effects (fire, top-down grazing and extreme weather events such as cyclones) as well as human-induced change, and of course natural selection factors driving evolution: phylogenetic constraints, plate tectonics, past climates and disturbance, plus the theoretical importance of scale and feedback mechanisms between the biotic and abiotic realms (Levin 1992).

Evolution works in two key ways to determine the distribution and abundance of organisms: 1) speciation where organisms more geographically adjacent tend to be taxonomically similar (e.g., floristic regions and phytogeography; Burbidge 1960; Takhtajan 1961; Cox 2001; Kreft and Jetz 2010), and convergent evolution that determines traits specific to environmental influences (e.g., physiognomy specific to a certain climate; Humbodlt and Bonpland 1805) which is characteristic of biomes. Takhtajan (1961), for instance, developed the concept of 'Phytochoria' based on taxonomic and phylogenetic information with reference to endemism, harking back to the original works of De Candolle (1855) and Drude (1884) (phytochoria and flora kingdoms were later revised by Cox (2001). We agree with the approach of Procheş (2020) who clearly separated the phytogeographical approach from that the biome approach (convergent evolution), but the historical development of the biome concept starts with a combination of these approaches to map global distributions and thus there is a need to review the history of phytogeography in the conceptualization of biomes.

The earliest vegetation schema – floristics vs physiognomy (1805)

One of the earliest attempts at a large-scale vegetation schema was a map of the distribution of the flora of France by Lamarck and De Candolle (1805). They used floristic composition, climate and terrain to produce floristic regions or provinces for mapping (see Ebach and Goujet 2006). Different approaches used to create a schema are thus present from the earliest days of the concept, with Lamarck and De Candolle's method diverging from Humboldt and Bonpland (1805), who used the physiognomic traits of major dominant plants rather than composition to describe large-scale phytogeographic units. Humboldt and Bonpland tried to establish generic categories that grouped living beings (particularly plants) according to their physiognomic characteristics (morphologic features also used to classify them taxonomically). They addressed physiognomy as having the unifying value of representing adaptive morphological traits occurring in different lineages, which could then be classified into common categories:

"*quelle différence de physionomie distingue les plantes de l'Afrique de celles de nuveau continent?*

Quelle analogie des formes unit les végétaux alpins des Andes à ceux des hautes cimes des Pyrénées?"

"*What difference in physiognomy distinguishes the plants of Africa from those of the new continent?*

What analogy of forms unites the alpine plants of the Andes with those of the high peaks of the Pyrenees?" (Humboldt and Bonpland 1805: 31).

They finally dare to describe a short number of physiognomic groups that could be used to classify most of the vegetation types on earth:

"*Dans la variété des végétaux qui couvrent la charpente de notre planète, on distingue sans peine quelques formes générales auxquelles se réduisent la plupart des autres, et que présentent autant des familles ou groupes plus ou moins analogues entre eux. Je me borne à nommer quinze de ces groupes, dont la physionomie offre un étude importante au peintre paysagiste.* ".

"*In the variety of plants which cover the frame of our planet, we can easily distinguish some general forms, to which most others are reduced, and which are presented as much by families or groups more or less analogous to each other. I limit myself to naming fifteen of these groups, whose physiognomy offers an important study to the landscape painter*. ... (nominates 15 physiognomic types for plants)" (Humboldt and Bonpland 1805: 31) which are later more widely described in a specific paper (Humboldt 1806).

The development of the physiognomic approach

The concept of formation, initially introduced by Grisebach in 1838, defined as "*a major kind of plant community on a given continent, characterized by physiognomy and a range of environments to which that physiognomy is a response*" (Beard 1978), is related to environmental conditions and can even be considered as an expression of them. It can be considered an antecedent of the concept of biome, due to its geographical transversality. For instance, grassland is an herbaceous vegetation dominated by grasses or grass-like plants, and there are several types of them in the world, e.g., tropical C_4 grassland (savanna), temperate dry C_3 grassland (steppe) or alpine meadows. The differences among them rely on the climatic conditions they live, not in the physiognomy, which can be quite similar. At broad scales, climate is the main driver and under similar climatic conditions in different parts of the world, dominant vegetation can be expected to have the same physiognomic types. In fact, the convergence in physiognomy of major vegetation types is now expected to occur if they live under similar broad environmental conditions.

Table 1. Historical development of vegetation-based biome and biome-like concepts.

Author	Biome concept	Conceptualisation	Hierarchical
Lamarck (1778)	Floristic region	Floristic composition (within France)	No
Humboldt and Bonpland (1805)	Phytogeography	Physiognomy of dominants	No
Lamarck and de De Candolle (1805)	Floristic province	Floristic composition, climate and terrain (within France)	No
De Candolle (1820)	Biogeographic region	Composition, endemism and climate.	No
Grisebach (1838)	Formation	Physiognomy	No
Henfrey (1852)	Phytogeography	Composition, taxonomy and geology	No
De Candolle (1855)	Station	Composition, taxonomy, endemism and climate	No
Humboldt (1855)	Phytogeography	Physiognomy	No
Engler (1879)	Kingdom, realm	Composition and climate	Yes
Drude (1884)	Kingdom	Endemic plant families	No
Grisebach (1884)	Formation	Physiognomy	No
Tate (1889)	Bioregionalisation	Taxonomy and climate	No
Merriam (1892)	Life zone, habitation and regions	Distribution of biota, climate and terrain	No
Warming (1895)	Phytogeography	Physiognomy	No
Schimper (1903)	Formation	Physiognomy and climate	No
Diels (1908)	Realm	Physiognomy and climate	Yes
Brockman-Jerosch and Rübel (1912)	Formation, Class	Physiognomic	Yes
Rübel (1930)	Formation, Class	Physiognomic	Yes
Köppen (1931)	Climatic zone	Climate but influenced by distribution of vegetation	No
Tansley (1935)	Biome and Ecosystem	Only biotic – all organisms Ecosystem includes biotic and abiotic	Yes
Carpenter (1939)	Biome	Biotic components	No
Clements and Shelford (1939)	Biome	Composition	Yes
Richards et al. (1940)	Phytogeography	Physiognomy	No
Holdridge (1947)	Formation	Vegetation, temperature, precipitation and evaporation	Yes
Burbidge (1960)	Phytogeographic zone and interzone	Taxonomic (family/genera), climate in particular rainfall seasonality	Yes
Walter (1964)	Vegetation zone	Main vegetation within main climatic zones	No
Crowley (1967)	Ecoregion	Ecologically homogenous region containing a single biome	No
Dashmann (1972)	Phytogeography	Physiognomy of climax vegetation	Yes
Udvardy (1975)	Biome	Physiognomy of climax vegetation, though major biome disjunctions based on flora and fauna	Yes
Box (1981)	Biome	Plant functional types based on climatic limits (expert knowledge)	No
Polunin (1984)	Ecobiome	Biotic, edaphic and climate	No
Walter (1985)	Zonobiome	Biotic, climate	No
Bailey and Hogg (1986)	Macroecosystem	Macroclimate, physiognomy of climax vegetation, landform, attitude	No
Takhtajan et al. (1986)	Phytochoria	Phylogenetic. Taxonomy (orders, families, subfamilies and tribes), endemism	Yes
Prentice et al. (1992)	Biome	Mechanistic tolerances of a small number of lifeforms. Cold, heat and moisture	No
Cox (2001)	Phytochoria	Re-evaluation of Takhtajan (1986)	Yes
Olson et al. (2001)	Biome – Ecoregional	Based on compilation of preexisting units and expert opinion	Yes
Pennington et al. (2004)	Biome	Physiognomy	No
Woodward et al. (2004)	Biome	Physiognomy and phenology as assessed by remote sensing. Climate envelopes and geography	No
Box and Fujiwara (2005)	Biome	Physiognomic	No
Bond et al. (2005)	Biome	Fire as a controlling factor of physiognomy	No
Abell et al. (2008)	Ecoregion	Vegetation type, physiography and climate	No
Crisp et al. (2009)	Biome	Phylogenetic	No
Ellis and Ramankutty (2008)	Anthrome	Inclusion of anthropogenic disturbances	No
Kreft and Jetz (2010)	Bioregionalisation	Species turnover and taxonomic distinctiveness	Yes
Reu et al. (2011)	Dynamic Global Vegetation Model	Plant functional and species richness. Functional type derived from demonstrated trade-offs	No
Scheiter et al. (2013)	Dynamic Global Vegetation Model	Modification of DGVM to include community assembly and coexistence theory	No
Pfadenhauer andKlötzli (2014)	Formation	Physiognomic	No
González-Orozco et al.(2014)	Phytogeography	Climate and vegetation.	No
Moncrieff et al. (2015)	Biome	Physiognomy and phenology	Yes
Moncrieff et al. (2016)	Biome	Physiognomy and phenology modified by local, disturbance and biogeographic history	Yes
Buitenwerf and Higgins (2016)	Phenome and Biogeographic Realm	Physiological habitat classes, evolutionary history and taxonomic composition	Yes
Jiang et al. (2017)	Biome	Physiognomy and phenology, temperature, rainfall and climate predictability	No
Mucina (2019)	Biome	Climatic, physiognomy, common selective pressures, evolutionary assembly	Yes

The early use of physiognomic vs floristic traits marked a distinct divergence in methodology that still exists today. Humboldt's (1806) idea of building a general world classification based on the physiognomy of dominant plants strongly influenced European Geobotany as it unfolded during the 19th century.

Developed by the likes of Joseph Dalton Hooker, Arthur Henfrey, Asa Gray and Alphonse De Candolle, early 1800's publications increased the overall understanding of global plant and vegetation distribution (Egerton 2018). De Candolle (1820) created biogeographic kingdoms based on a more complex understanding of composition that included areas of taxonomic endemism within species and genera (with reference to climate); however, no maps were produced. After De Candolle, German phytogeographer August Grisebach made an important step by coining the term *formation*: "*I give the name of phytogeographical formation to a group of plants, such as a meadow or a forest, that has a fixed physiognomic character* (Grisebach 1838)". This purely physiognomic concept could be applied at different scales, including the global scale, as he did later in his synthesis of the vegetation of the world (Grisebach 1884). The formation concept was accepted by the German-Central European geobotanical tradition throughout the 19th and early 20th century, and synthesis at the global scale continues.

Following the floristic-physiognomic divide, systems were created, with occasional meetings of both.

While Grisebach (1838) and Humboldt (1855) continued the new tradition of using physiognomic criteria, Henfrey (1852) in producing the vegetation of Europe, and De Candolle (1855) in creating his two-volume treatise on plant geography, continued to emphasize floristic composition with reference to climate and geology. In 1879, Engler took a Darwinian perspective to De Candolle's (1855) climate and floristic criteria, adding physiognomic criteria to create four global 'Realms' with 32 regions. Drude (1884) also continued De Candolle's tradition, but concentrated on endemic families to define phytogeographic kingdoms, rather than genera and species. Tate (1889) created the first bioregionalization using taxonomic distributions and climate. While in 1892, Merriam followed, using a systematic method to create a map of life zones based on the composition of the biota, climate and terrain. This allowed for the creation of 'habitations' and 'regions' in a similar fashion to the 'floristic provinces' of Lamarck and De Candolle (1805) and De Candolle's (1855) 'stations'. Drude (1887, 1890) defined the worlds "zones of vegetation", emphasizing that "*Die Vegetationszonen vereinigen die physiognomischen Hauptgenossenschaften der Pflanzen*", "*The vegetation zones unite the main physiognomic associations of plants*".

As a result of this 19th century European work, the formation idea was applied generally to create large-scale units characterized by the physiognomy of the dominant plants. These units could be used to synthesize vegetation at a global scale by describing potential natural vegetation in a broad sense, and correlated with the corresponding broadly defined climatic types. Schimper used Grisebach's (1884) physiognomic 'formations' to produce a map of the globe based on three main levels of vegetation formation: woody, grassy and desertic (Schimper 1898; Schimper and von Faber 1935) (see also Diels 1908). Additionally, these post-'origin of the species' plant geographers were freed from issues associated with vastly different species occurring in different regions of world, which had made comparisons among regions difficult. This change in understanding allowed later physiognomic plant geographers to contemplate more directly on convergence of functional traits.

At the turn of the 20th century, Warming (1895), Schimper (1903) and Diels (1908) moved away from these compositional and taxonomic traditions and emphasised physiognomy over floristics (phytosociology), which was to be the major focus for several decades. Warming, who had re-defined the formation as "*an expression of certain defined conditions of life and is not concerned with floristic differences*" (Warming 1909), was the first to separate floristic composition from physiognomy. This meant that taxonomically distant plants could bear physiognomic traits in common and a vegetation type could be defined by the physiognomy of the dominant species. The formation concept, in this physiognomic sense, was then also adopted by French and Spanish plant geographers and vegetation scientists (Flauhaut 1901: Huguet del Villar 1929; Font Quer 1953; Rivas-Martínez 1996).

Continuing into the 20th century, Brockmann-Jerosch and Rübel (1912), later amended and completed by Rübel (1930), grouped basic units into three main structural levels called associations, but also made *formation classes* (*Formationsklassen*) to highlight their physiognomic nature. Rübel's (1930) description of world vegetation into 'formations' was based on the climatic limits of the main structural elements, which was the first attempt to set limits on the climatic ranges of the types described (Box and Fujiwara 2005). This system, in which units are strongly linked to climate, is included in a series of Botany teaching books by Strasburger (Ehrendorfer 1971) and in the Spanish textbook by Losa et al. (1974). A more recent valuable approach for world-scale formations is that of Schmithüsen (1976), which has been adopted in the last versions of the Strasburger book (Körner 2002). In recent years, these concepts were applied in a new map of the world by Pfadenheuer and Klötzli (2014) with an accurate typology fitting the climatic boundaries. All the vegetation typologies used in these contributions are inescapably based on physiognomy. Today, the formation concept is still important, and one of the largest units in the European, American, Asian and Australian vegetation classification systems (Peet and Roberts 2013; Bolton et al. 2017).

Mid-1900 physiognomic traditions still held a highly deterministic climate-vegetation worldview, without taking into account the evolutionary history of a region (Moncrieff et al. 2016). This was despite the different patterns of existing formations in the northern and southern hemispheres, which had already been noted almost 100 years earlier (Wildenow 1811). Köppen (1931) developed climatic zones of the world based on major vegetation boundaries in relation to seasonality. Meanwhile Holdridge (1947) built on Rübel (1930) and Köppen (1931) to determine the climatic limits of biological processes associated with major plant forms. Using three climatic parameters, biotemperature, mean annual precipitation and potential evapotranspiration ratio, he defined 39 'life zones' (Holdridge 1947). However, as discussed by Moncrieff et al. (2015), climate was often considered in a circular way, both being part of the definition while also used to determine the limits and responses of vegetation. Interestingly, the EcoVeg approach has the top three levels of the hierarchy based on formation concepts, the lowest of those three levels with the name Formation (Faber-Langendoen et al. 2012). This Formation concept integrates growth form and global climates as modified by regional edaphic factors, attempting to satisfy some of the issues discussed above.

"Formation: A vegetation classification unit of high rank (3rd level) defined by combinations of dominant and diagnostic growth forms that reflect global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions". (Faber-Langendoen et al. 2012).

From physiognomy to biomes

Clements was the first to use the term 'biome' as early as 1916 in a meeting of the Ecological Society of America (Clements 1917), initially meaning only a biotic community excluding climate and edaphic components (Pennington et al. 2004), but later it was upgraded to encompass large geographical scale, was largely based on plant formations, and included animals, particularly "influent" animals (Shelford and Olson 1935). Similarly, Tansley (1935) equated biomes to only the biotic components and used biotic and abiotic elements to help differentiate the lower strata of 'ecosystems' within biomes. It was therefore Schimper (1903) who was the first to develop a concept closest to a modern conceptualisation of biomes, when he based his classification on climates selecting for a similar plant form. This first use of the term was somewhat different to many of the later circumscriptions and it was only widely utilised after Clements and Shelford (1939). In contrast to this early definition of a biome, the term has since come to commonly incorporate physiognomic rather than taxonomic or geographical components, and to include climate as the principal determinant of global vegetation distribution (Neilson et al. 1992; Pennington et al. 2004).

Vegetation units at the world-scale are therefore made by grouping together similar formations from different continents, and have been termed formation or biome-types (Beard 1978).

Differences within defined biomes became a major source of contention within the 1970s with Dashmann (1972) defining types based on the physiognomy of the potential climax vegetation, also called potential natural vegetation. This concept was also used by Udvardy (1975) and also by Bailey and Hogg (1986). Extending this, Walter (1985) modified the formation system and coined the concept "*Zonobiome*", of which only nine are recognized globally. Walters large-scale units are basically defined by the climatic zones of the world and act as containers for the existing ecosystems.

One of the major issues, apart from the generalised attempts of Holdridge (1947), is that these high-level classifications have been expert-based and deterministic in approach. The reliance on intuition and personal experiences of the creators of each system greatly limits our ability to compare schema and to perform statistical stratifications testing theory (Moncrieff et al. 2014). In a comparison of different biome classifications, Moncrieff et al. (2014) discovered that different biomes in different continents had different environmental envelopes and that these could vary more within than between biomes, potentially due to past histories. To provide a sounder underpinning to biome creation, a more functional approach in which underlying processes are emphasised became the focus in recent decades (Griffith et al. 2019).

Challenges to a Global Biome Classification

This conceptual review demonstrates that there are many fundamentally different ways to define biomes, hitherto with limited efforts for unifying concepts among disciplines. Consequently, there is little congruence between the resulting maps (Higgins et al. 2016), and widely used biome maps fail to delimit areas with consistent climate profiles (Moncrieff et al. 2015). The approach of the formation concept by Faber-Langendoen et al. (2012), EcoVeg, integrates growth form and global climates as modified by regional edaphic factors but is not yet in a form that can be modelled. The highly clarifying contribution of Procheș (2020) establishes the concept of biome clearly separate from biogeographic concepts such as phytochoria.

Other recent challenges to the biome concept include the finding that vegetation structure and function of the same biome on different continents can differ substantially; for example, savannas (Lehmann et al. 2014; Moncrieff et al. 2016; Muldavin et al. 2021). Moreover, under the same climatic conditions, different plant formations such as savannas and tropical deciduous forests are possible. These alternative states are modulated by complex interactions between climate, soil conditions, herbivores or disturbances such as fire (Breckle 2002; Bond et al. 2005; Moncrieff et al. 2016; Langan et al. 2017). In the case of alternate states under the same climate, one also needs to decide whether these two formations represent one or several biomes. An additional dilemma is that there is no agreement regarding which kinds of edaphic, hydrological, orographic or disturbance-driven deviations should be considered important enough to count them as separate biomes. For example, Olson et al. (2001) recognize mangroves as a biome but not riparian forests. Likewise, mountain areas with their compressed sequence of vegetation belts are not treated consistently and are often simply overlooked (Woodward 2004) or included into a general category (Mucina 2019) most likely due to spatial representation. Lastly, as humans have shifted the biosphere into a new geological epoch, one can question whether it still is appropriate to consider only the potential natural vegetation in a biome map (Ellis et al. 2010; Ellis 2011). The idea of Ellis (2011) to add degree and type of human alterations as an additional dimension to a revised biome concept is appealing.

It has become apparent that a close one-to-one relationship between climate type and physiognomic types has some weaknesses, as different floras show disparity from predicted convergence. For example, the asymmetry between Northern and Southern Hemispheres was initially pointed out by Willdenow (1811), who focused primarily on the floristic differences between hemispheres, rather than on vegetation *sensu stricto*. This dissimilarity was extensively addressed by Troll (1948) who published his famous average continent, and later by Box (2002), who argued that under similar climatic envelopes, particularly under non-tropical conditions, the physiognomy of vegetation is often different between the latitudes. This dissimilarity is more pronounced in extratropical areas and is in contradiction with the principle of 'similar-climate, similar-physiognomy'. Thus, climatic differences between the halves of the planet do not sufficiently explain vegetational divergences, and it is likely that a long period of separation and evolutionary history plays a major role in floristic-phylogenetic dissimilarities (Hopper 2009).

The necessity to consider physiology and plant functional types became apparent. Box (1981) attempted to define more precisely the physiological limits of major plant forms and developed an understanding of plant functional types based on physiological limits imposed (largely) by climate. He defined one hundred plant functional types based on climatic filters and used to create biome types based on a culmination of the types available within zones. The advancements in physiological classifications using plant functional types and climate were still, however, formalised within a deterministic framework largely informed by expert opinion (Ni 2001; Bunce et al. 2002; Reu et al. 2011; Lehmann et al. 2011; Moncrieff et al. 2015). Additionally, in spite of these developments in our understanding of physiological tolerances and functional types, a resurgence of purely floristic and compositional approaches also occurred around this period (1980's).

In recent studies, the importance of phylogeny and floristic divergence in producing different physiognomic profiles within similar climatic envelopes has been highlighted (Pennington et al. 2004; Moncrieff et al 2014, 2015). Plant traits are not only determined by current environmental conditions, but are also the result of inherited ancestral adaptations to past conditions, i.e. "niche conservatism" (Donoghue 2008; Crisp et al. 2009; Loidi 2018). The divergent physiognomy observed in the altitudinal belts of mountains between different geographical areas provides an example. Zonation in tropical mountains does not match the well-known model for temperate and Mediterranean mountains, as initially pointed out by Humboldt. While climatic differences due to latitude could explain part of these differences, we cannot ignore the floristic-phylogenetic divergences (Troll 1961: Stocker 1963) and that additional abiotic and biotic interactions are likely important in driving the evolutionary pattern.

Beyond evolution

The underlying principles of strict relationships between climate and vegetation used to develop the majority of earlier schema have been re-evaluated by a number of researchers. Bond et al. (2005) showed that fire was a controlling factor in the distribution of physiognomic types across large areas of the world and this helped to explain some of the anomalies encountered under purely deterministic approaches. Crisp et al. (2009) showed that phylogenetic history and continental movements constrained the expression of plant functional types limiting the direct relationships between climate and functional types. Phylogenetic lineages were rarely found to colonise new biomes (Crisp et al. 2009). Montcrieff et al. (2016) highlighted that not only did evolutionary and biogeographic history limit functional convergence, but that ecosystem engineering could occur due to feedbacks between vegetation and climate along with disturbance, thus altering the conditions for plant function influencing the expression of traits. Top-down pressure from large herbivores was shown to alter the combination of traits expressed beyond the effects of climate or local edaphic conditions (Lehmann et al. 2011).

Anthropogenic influences were also considered important to the extreme they severely influence a majority of terrestrial ecosystems of the world. The term "anthromes" has been coined to designate human influenced systems (Ellis and Ramankutty 2008). Clark et al. (2010) suggested that natural selection factors or competition could exceed the influence imposed by climate on composition and expression of functional traits. Further, Jiang et al. (2017) proposed the importance of climatic fluctuations and predictability, and their complexity, as being highly relevant to the structure and functioning of vegetation types, which could also explain divergences based on average climate records. Plants require different strategies and tactics to cope with differing levels of predictability within their environment (Jiang et al. 2017). The non-deterministic nature of plant functional responses provided evidence that alternative stable states of biomes may occur within the same location and under the same climatic conditions, dependent on historical and current influences (Bond et al. 2005; Lehmann et al. 2011; Buitenwerf and Higgins 2016; Moncrieff et al. 2016).

With improved access to geographical information systems and higher computing power over the last two decades, an emergence of more top-down approaches to defining the boundaries of major vegetation types and biomes became a possibility. Such approaches were able to use satellite imagery to determine growth patterns of vegetation, for example NDVI, leading to defining biomes based on the objective, observable qualities of the vegetation (Pennington et al. 2004). Woodward et al. (2004) assessed physiognomic and phenological types based on climate envelopes using remote sensing. Such approaches were viewed as a progress as they allowed interpretation without circularity, but also placed the focus on existing vegetation compared to potential. With global databases, satellite imagery and GIS abilities, more intensive and complex interrogation of global patterns and species functional responses have become achievable. Dynamic Global Vegetation Models (DGVM) were first used by Prentice et al. (1992), who argued that models based on deterministic considerations would be more robust than those based on correlations. Reu et al. (2011) extended the DGVM concept by investigating the survival of plant functional trade-offs across a range of global conditions and regional climatic constraints. Scheiter et al. (2013) proposed that, in order to move away from the fixed plant functional type paradigm, DGVMs should be based in community assembly, competition and coexistence theory.

Final remarks

In this section we offer a summarized conceptual proposal of the term Biome. The proposal combines historic evolution with more recent contributions to the concept, trying to safeguard a necessary stability in the use of the term in order to prevent a "babelization" which we consider entirely inconvenient. In science, concepts can evolve, while avoiding change to the original conceptual underpinnings (semantic area). Similar to the term "species", which has been used for centuries while the information carried in it has increased enormously (from morphology to current genetics), but we apply it to the same objects as the ancient botanists. If there is a horizontal displacement, i.e., a change in the group of objects included within the concept, excluding some objects and including new objects, that is a change in the meaning (semantic area) and confusion is likely. Science has to stick to the highest terminological accuracy so that the well-known concepts can be enriched but not changed. If there are new concepts, new terms have to be coined to name them. In the case of biome, the most recent version of this term appearing in the literature is that of the Global Ecosystem Typology, issued by the IUCN (Keith et al. 2020). In it, the term biome (functional biome) is used for level 2 of the proposed classification and is based on an imprecise definition with conditions such as "main ecological drivers" and "main ecological functions". Of the seven biomes recognized for the terrestrial domain (1-tropical-subtropical forests, 2-temperate-boreal forests and woodlands, 3-shrublands and shrubby woodlands, 4-savannas and grasslands, 5-deserts and semi-deserts, 6-polar-alpine, 7-intensive land-use systems), only four, 1, 2, 5 and 6, are determined by climate in a very loose way. Two others are largely miscellaneous units composed by vegetation types representing seral stages associated with disturbance regimes, often fires, and the last one is the unstable and heterogeneous "biome" of intensive land use systems. This conception of biomes is far from the ones based on a climatic or on stable environmental factors determinism. Additionally, different criteria are adopted for the biome definitions (Keith et al. 2020): climate, disturbances, human influence, and that could be considered a source of inconsistency. If a new conceptual entity is proposed, perhaps a new name should be proposed to avoid confusion.

The inclusion of human influences in the conceptual framework of biome has the following objections:

Human influence is relatively new, with notable influences on terrestrial ecosystems beginning approximately 11,000 years ago when the Neolithicum age started and agriculture and cattle raising arose (Lubbock 1913). Before that point, the impact of humans was that of a medium-sized mammal. After that time, these activities expanded throughout the world at very different paces and intensities, transforming the territories in numerous ways, but global change has only occurred in the last few hundred years. In any case, human influence in terrestrial ecosystems has been and is enormous, and manifests in a complexity of ways, depending on geographical conditions, technology and cultural variability.

In addition, the way in which humans have influenced ecosystems has also been heavily influenced by the natural conditions inherent to them. This has to do with profitability of the environment in question; with humans particularly concentrating modifications within highly fertile environments and leaving highly infertile landscapes much less disturbed (YODFELS as opposed OCBILS of Hopper 2009; Hopper et al. 2021). For example, compare and contrast human occupation and use within deserts with the seasonal tropical forest, or on the tundra with the Mediterranean evergreen sclerophyllous forest areas. Modern technology is pushing towards a homogenization of the land uses and species composition and thus of the ways that humans transform natural ecosystems. We can nearly grow tomatoes in the Arabian desert by means of intensive irrigation and we can grow oranges in the tundra if we provide a formidable greenhouse and fertilizers. Thus, human influence is very diverse and is changing with technology, population growth and time and space. We therefore propose that human influence should not be considered as a defining element for biomes and that the creation of Anthromes is counterproductive (Ellis and Ramankutty 2008; Ellis 2013). Concepts that include the influence of humans within a definition of a biome such as anthromes are likely to have a blurring effect that will only be temporary in nature as technology and human uses advance and change over the decades. The biome should be a concept restricted to nature in the first instance. If we do so, we can use the biome concept to assess the degree and type of human alteration on a given site just by comparing with the corresponding biome. This has been also argued in favour of the Potential Natural Vegetation concept (Loidi and Fernández-González 2012).

Another point is disturbances as a main factor in defining biomes. This is also ill-defined because many of these disturbances are human induced (e.g. grazing, browsing, etc.) or the disturbance regime was altered. We need to take particular care if considering the use of disturbances as separating nature versus human disturbances can be highly complex.

The numerous challenges for developing a global biome classification are synonymous with understanding the diversity of life on earth, which essentially point to knowledge gaps, but those challenges also point to opportunities. In simply trying to understand the diversity of life on earth, Hortal et al. (2015) lists seven shortfalls: (i) Linnean shortfall (not all species have been discovered), (ii) Wallacean shortfall (lack of knowledge of species geographical distributions, especially less common species), (iii) Prestonian shortfall (lack of knowledge about species dynamics in space and time), (iv) Darwinian shortfall (lack of knowledge about evolutionary lineage of species and traits), (v) Raunkiaeran Shortfall (lack of knowledge of ecologically relevant species traits), (vi) Hutchinsonian Shortfall (lack of knowledge about species' tolerances), and (vii) Eltonian Shortfall (lack of knowledge about species' interactions). These gaps of knowledge are directly related to research avenues for defining and classifying biomes, as well as modelling their distributions. Models provide one way to move the concept of biomes forward in testing the concept – testing the importance of variables like climate, disturbance, and phylogeny. Therefore, refining models of biomes toward prediction will allow the concept of a biome to be tested and ultimately define a biome.

In basic agreement with Mucina (2019), a biome is a large-scale container concept that includes a series of elements that belong to these three categories:

- A biome encapsules all the biological diversity that can be found within its limits: plants, animals, fungi, etc.
- A biome encompasses all the forms of assemblages of these species: populations, communities (coenoses), landscapes.
- A biome encompasses the processes taking place in the frame of the two aforementioned components: ecosystem functioning, dynamic processes, evolutionary processes, disturbances, etc.

The limits of a given biome in comparison with neighbouring biomes are given by:

- Physiognomy, dominant life-forms. Deciduous forests vs. evergreen forests, steppe vs. desert, etc.
- Regional climate or climatic zone. Ever rainy tropical vs. seasonally rainy tropical, boreal vs. temperate, summer rainy vs. winter rainy, etc.
- Ecological factors. Soil fertility, natural disturbance regime, etc.

As an integrative concept, the biome should in first principles be defined by natural features: natural biota (flora, fauna, etc.), natural ecosystems, natural landscapes. Natural is considered when human influence is less apparent at the level of noticeable ecosystem modification.

Author contributions

JL and JTH wrote much of the initial draft but all authors JL, JTH, SF and SL contributed greatly to the writing and construction of the final document.

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RESEARCH PAPER CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC

Syntaxonomy of steppe depression vegetation of Ukraine

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Abstract

Aims: To revise the syntaxonomy of the vegetation of steppe depressions (*pody*), in particular (1) to identify the associations and to reveal their environmental, structural and compositional peculiarities; (2) to assign the associations to higher syntaxa; and (3) to correct nomenclatural aspects according to the ICPN.

Study area: Steppe zone of Ukraine, Left-Bank of the Lower Dnieper basin.

Methods: 641 relevés were included in the final analysis in the PCOrd program integrated into Juice software. Two expert systems (EVC and EUNIS-ESy) were used to assign relevés to vegetation classes and to EUNIS units.

Results: The analysis resulted in nine clusters, which were interpreted as *Festuco-Brometea* (two units), *Molinio-Arrhenatheretea* (three units), *Isoëto-Nanojuncetea* (three units) and one derivate community of the *Festuco-Puccinellietea*. Detailed characteristics of the species composition, structure, distribution, and environmental conditions are provided for each unit. According to the DCA ordination, the leading factors of the syntaxa differentiation are soil moisture and fluctuating water level.

Conclusions: We could clarify the placement of steppe depression vegetation in the system of syntaxonomic units of Europe. The previously described syntaxa of the rank of alliance (*Myosuro-Beckmannion eruciformis*), suballiance (*Galio ruthenici-Caricenion praecocis*), and six associations are validated. Two associations and two subassociations are described as a new to science.

Taxonomic references: Euro+Med PlantBase (https://www.emplantbase.org), except Mosyakin and Fedoronchuk (1999) for *Phlomis scythica* Klokov & Des.-Shost. and *Tulipa scythica* Klokov & Zoz.

Syntaxonomic references: Mucina et al. (2016) for syntaxa from alliance to class level; Dubyna et al. (2019) for associations.

Abbreviations: DCA = Detrended Correspondence Analysis; DES = Didukh Ecological Scales; EUNIS = European Nature Information System; EVC = EuroVegChecklist; GIVD = Global Index of Vegetation-Plot Databases; ICPN = International Code of Phytosociological Nomenclature.

Keywords

Althaeion officinalis, Bern Convention, Didukh ecological scales, EUNIS, expert system, grasslands, *Myosuro-Beckmannion eruciformis*, steppe depressions, syntaxonomy, wetlands

Introduction

Steppe depressions (*pody* in Ukrainian) are large closed depressions, up to 16,000 ha in area, elliptical or round in shape with gentle slopes and flat bottoms, periodically flooded by meltwater and characterized by Planosol soils and peculiar ephemeral mesic to wet grassland phytocenoses. These depressions accumulate natural runoff in poorly drained steppe plains within the periglacial area of the Quaternary glaciation. In Ukraine, the largest depressions are concentrated on the Left Bank of the Lower Dnieper (Kherson and Zaporizhia administrative oblasts), while sporadic, smaller depressions and steppe "saucers" occur on the Right Bank of the Dnieper (Kherson, Mykolaiv, rarely Odessa oblasts). In the Russian Federation, similar depressions are common in the Lower Don River and Lower Volga River regions (Molodykh 1982; Evdokimova and Bykovskaya 1985; Marinich et al. 1985; Shapoval 2007; Zakharov 2018).

Following the flooding of depressions, over the entire area of the shallow basin, there is an "explosive" formation of ephemeral hydrophilic cenoses. They exist for a short period, being rapidly replaced by xeromorphic flora and finally become steppic when the depression dries. The average duration of the period between severe floods is, according to various estimates, from 7 to 12 years (Shapoval and Zvegintsov 2010). During periods of flooding and subsequent drying, distinctive alternating phytocenoses with wide ecological amplitude are observed, which consist of plants that withstand drought well and «explosively» increase in number during floods, i.e. are adapted to significant fluctuations in water levels. During short-term floods, the vegetation of depressions is characterized by high values of aboveground phytomass. For example, after the floods of 2003, the average values on the hayfields of the «Black Valley» depression was 12892 ± 518.0 kg/ha in the dry state. However, these values decline rapidly during periods of drought. Also, their productivity decreases due to overgrazing. In particular, in the post-flood period, the value of aboveground phytomass of the adjacent intensively grazed «Sugakli» depression was only 912 ± 239.2 kg/ha, which is significantly less than similar values of hayfields with better moderate grazing management. In general, the stocks of aboveground phytomass in the studied *pody* under different landuse regimes vary in a wide range from 588 to 14788 kg/ha in the dry state (Shapoval 2004). During the latter, the dominant species become low, sparse, some hydrophytes disappear from the phytocenosis, enduring a prolonged drought in a latent state (seeds formed under a favorable moisture regime, or underground perennial organs such as caudex, rhizomes, etc.).

Vegetation types of depressions are separated in time and space, as actual phytocenoses are scattered territorially (some are confined to the deepest, wettest areas of a depression bottom, others tend to its dry periphery), and they are delimited in time (open water surface overgrown with wetland vegetation, which is later replaced by mesic and semi-dry grasslands). At the same time, the boundaries between these phytocenoses are often blurred, and the spatial transitions among them are very gradual.

The problem of the origin of the depressions still has no unambiguous solution; many issues remain problematic and debatable. During the long history of studying the loess cover of the lowland steppes of the Southern Ukraine, many hypotheses and theories of the origin of steppe *pody* have been put forward. They were considered as remnants of the ancient hydrographic network (Krokos 1927; Lichkov 1927; Zamoriy 1934; Sambur et al. 1956; Mulika 1961; Bulavin 1972) or relict elements of the periglacial area of the Quaternary glaciation (Dokuchaev 1892; Dostovalov 1952; Velichko 1965; Molodykh 1982). According to the results of the recent studies of the morphology and genesis of the large depression relief of the Eastern Azov Sea region (Zakharov 2018) it is established that the existing *pody* lie in the thickness of loess sediments and do not affect the underlying sediments of sea and river terraces, therefore, they are of aeolian origin and are large deflationary basins, which was assumed earlier (Tutkovskiy 1910; Levengaupt 1932). However, it seems most probable that these geomorphological structures represent a polygenetic group, and their development is caused by a complex of subsidence-suffusion, fluvial and aeolian transformations.

Unfortunately, in Ukraine most of the steppe depressions are plowed, and the surviving remnants are exploited, mainly as hayfields and pastures without compliance with rational management standards, including nature conservation. The only steppe depression that has a national conservation status is the Great Chapelsky *pid*, as part of the natural core of the Biosphere Reserve «Askania-Nova» (2,376 hectares). Steppe depressions are the sole localities of local and regional endemics in the region of the Left Bank of the Lower Dnieper (*Elytrigia repens* subsp. *pseudocaesia*, *Phlomis scythica*, *Tulipa scythica*).

The syntaxonomy of these unique complexes is still poorly known and needs to be thoroughly revised. The first attempt to develop a classification of the steppe depression vegetation was made by a team led by Solomakha (Solomakha et al. 2005) in the study of coenotic affinity of *Allium regelianum* and *Ferula orientalis*. It was proposed to include such communities in a new alliance *Carici praecocis-Elytrigion pseudocaesiae* of the new order *Carici praecocis-Elytrigietalia pseudocaesiae*, which was assigned to the class *Festuco-Limonietea* (= *Festuco-Puccinellietea*). In this case, the dataset used for the analysis was only 34 relevés, selected by the criterion of the presence of two target species. The following year, a study on the syntaxonomy of the steppe depression vegetation based on 367 relevés was published (Shapoval 2006). In this article, the author proposed another syntaxonomic solution: the wettest communities are classified within the class *Isoëto-Nanojuncetea*, order *Nanocyperetalia* and two alliances – *Eleocharition ovatae* and newly described *Myosuro-Beckmannion eruciformis*. Mesic communities of depressions were included in the class *Molinio-Arrhenatheretea*, order *Molinietalia* and a new alliance *Lythro virgati-Elytrigion pseudocaesiae*. Xero-mesic communities, common in small, shallow depressions, were included in the class *Festuco-Brometea*, order *Festucetalia valesiacae*, alliances *Amygdalion nanae* and *Festucion valesiacae*. However, given the distinctiveness of the depression vegetation, it was proposed to distinguish two suballiances – *Cerastio ucrainici-Festucenion valesiacae* and *Galio ruthenici-Caricenion praecocis* within the alliance *Festucion valesiacae*. All the associations described by Shapoval (2006) were new to science. To date, the latter work remains the most complete overview of the vegetation and syntaxonomic interpretation of the phytocenotic diversity of steppe depressions of the Left Bank of Ukraine. However, the status of many syntaxa remains controversial. Thus, from the above new syntaxa of alliance rank, only the *Myosuro-Beckmannion eruciformis* is accepted in Mucina et al. (2016). Also, Mucina et al. (2016) mention the order «*Myosuro-Beckmannietalia eruciformis* Shapoval 2006 (2b, 5)» as synonymous of the *Nanocyperetalia*. However, the *Myosuro-Beckmannion eruciformis* with the single association *Myosuro-Beckmannietum eruciformis* from the beginning was assigned to the classical order *Nanocyperetalia*, and the order *Myosuro-Beckmannietalia eruciformis* was not described by Shapoval (2006) and is not mentioned in any other sources, except in Mucina et al. (2016); therefore it should obviously be considered as a phantom name. Finally, the order *Carici praecocis-Elytrigietalia pseudocaesiae* is considered by Mucina et al. (2016) as a syntaxonomic synonym of the *Galietalia veri*, and the alliances *Carici praecocis-Elytrigion pseudocaesiae* and *Lythro virgati-Elytrigion pseudocaesiae* are considered as synonyms of the *Agrostion vinealis*. The latter decision seems insufficiently justified because the alliance *Agrostion vinealis* is described from the forest zone of Ukraine with completely different climatic conditions (Sypailova et al. 1985), and practically none of its diagnostic species, except the widespread *Poa angustifolia* and *Carex praecox*, have been found in the steppe depression communities.

Adding to syntaxonomic incertainty, in the recently published Prodromus of Vegetation of Ukraine (Dubyna et al. 2019) the order *Carici praecocis-Elytrigietalia pseudocaesiae* as well as alliances *Carici praecocis-Elytrigion pseudocaesiae* and *Poo angustifoliae-Ferulion orientalis* are accepted, but are considered within the class *Festuco-Puccinellietea*; also, alliance *Lythro virgati-Elytrigion pseudocaesiae* is considered as a synonym for alliance *Carici praecocis-Elytrigion pseudocaesiae*, and alliance *Myosuro-Beckmannion eruciformis* assigned as synonyms of the alliance *Beckmannion eruciformis* of the class *Festuco-Puccinellietea*. All the associations described in Solomakha et al. (2005) and Shapoval (2006) are also mentioned in the Prodromus, some as accepted names, some as synonyms. In particular, the association *Carici praecocis-Elytrigietum pseudocaesiae* is assigned as synonym of the *Pycreo flavescenti-Arabidopsietum toxophyllae*, *Herniario glabrae-Poetum angustifoliae* as synonym of the *Achilleo micranthoidis-Poetum angustifoliae*, as well as *Potentillo orientalis-Caricetum melanostachyae* and *Euphorbio virgati-Caricetum melanostachyae* as synonyms of the *Galio ruthenici-Caricetum praecocis*. The Prodrome also states that all syntaxa described in the two mentioned publications (Solomakha et al. 2005; Shapoval 2006) are invalid because their typification does not meet the requirements of art. 5 ICPN (Weber et al. 2000; Theurillat et al. 2021), i.e., the Latin word '*typus*' ('*holotypus*', '*lectotypus*', '*neotypus*') was not used *expressis verbis* for the designation of the type of a syntaxon name, although the nomenclature type itself was designated.

The above review has shown that many questions remain unresolved in the syntaxonomy of the steppe depression vegetation. And the biggest, quite objective problem of syntaxonomic analysis of *pody* vegetation is the availability of representative data because the object of study is quite ephemeral. The precondition for its occurrence is a flood. Due to the exceptional rarity of this phenomenon, it is possible to observe and describe the *pody* phytocenoses in very limited periods of time, and the interval between the favorable seasons for the mentioned ephemeral vegetation can be decades. Only after the major flooding in 2010 was sufficiently representative data for the current analysis available for collection.

Given this, our aim was to revise the syntaxonomy of the steppe depressions (*pody*) vegetation, in particular (1) to identify the associations and to reveal their environmental, structural and compositional peculiarities; (2) to assign the associations to higher syntaxa; and (3) to correct nomenclatural aspects according to the ICPN.

Study area

In accordance with the modern administrative-territorial structure of Ukraine, the studied *pody* are located within Kakhovka and Henichesk districts of Kherson oblast and Melitopol district of Zaporizhia oblast. Great Chapelskyi *pid*, as well as Staryi *pid* and a number of small depressions within "Southern" site are components of the natural core of the Askania-Nova Biosphere Reserve (Figure 1, Table 1). The altitudinal range of the studied pody is from 10 m (Novotroitsky and Syvasky) to 45 m (Garbuzy).

In accordance with the Worldwide Bioclimatic Classification System the study area is located on the border of Temperate xeric steppic and Mediterranean pluviseasonal continental steppic variants, Supra-submediterranean and Supramediterranean variants within the Dobrujo-Crimean subregion of the Eurosiberian biogeographic region (Rivas-Martínez et al. 2004). The climate is characterized as aride, steppe, cold (Beck et al. 2018).

According to the agro-meteorological station Askania-Nova, the average annual temperature is 11.3°C. The average annual precipitation is 400 mm. Most precipitation (37% of the annual amount) falls in the summer in a form of showers and short-term rains. During the period of moisture accumulation (November-March) the amount of precipitation does not exceed 100 mm. Evaporation is 900–1000 mm, and in the summer months it exceeds precipitation by 5–7 times (Figure 2).

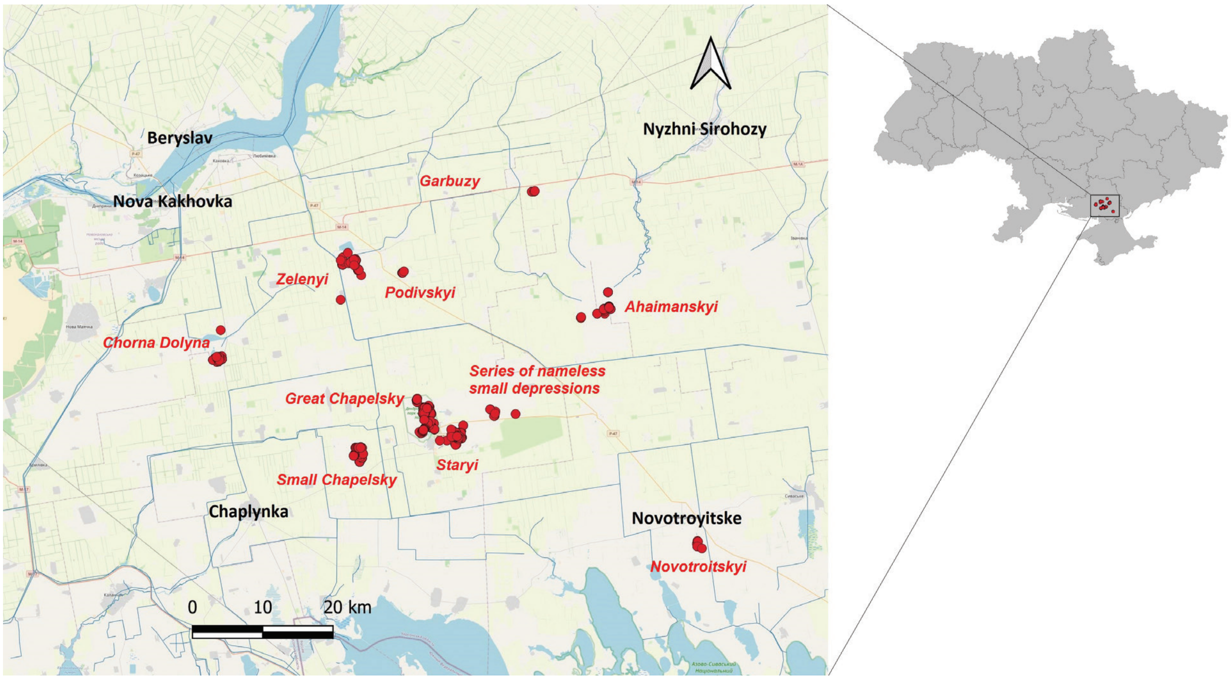

Figure 1. Locations of the vegetation plots (red dots) used for the analysis (region of the Left Bank of the Lower Dnieper).

Table 1. Characteristics of the studied steppe depressions (*pody*).

Name	Coordinates of the conditional central point	Administrative location	Preserved area (pristine land and perennial fallows), hectares	Size (bottom and slopes forming a closed «bowl» of the depression), km	Protection
Great Chapelsky	46.484630° 33.850533°	near Askania Nova, Kakhovka district, Kherson oblast	2376	4,5×6	natural core of the Askania-Nova Biosphere Reserve
Staryi	46.456985° 33.918434°	near Askania Nova, Kakhovka district, Kherson oblast	140	0.3×0.5	natural core of the Askania-Nova Biosphere Reserve
Series of nameless small depressions	46.465470° 34.007211°	near Askania Nova, Kakhovka district, Kherson oblast	up to 300 (in total)	–	natural core of the Askania-Nova Biosphere Reserve
Small Chapelsky	46.427852° 33.731158°	outskirts of Khrestivka and Dolynske villages, Kakhovka district, Kherson oblast	1022	5,5×6,5	Emerald site UA0000372
Barnashivsky	46.547296° 33.977308°	near the Maryanivka village, Kakhovka district, Kherson oblast	738	2.5×4	Emerald site UA0000367
Chorna Dolyna (Black Valley)	46.554197° 33.474011°	near the Chorna Dolyna village, Kakhovka district, Kherson oblast	494	3×6	Emerald site UA0000368
Zeleny (Green)	46.670855° 33.717165°	outskirts of Zeleny *pid* and Zelena Rubanivka villages, Kakhovka district, Kherson oblast	1580	5,5×8	Emerald site UA0000370
Podivsky	46.664349° 33.825659°	near Podivka village, Kakhovka district, Kherson oblast	258	1.5×2.4	–
Garbuzy	46.768667° 34.053785°	near Stepne village, Henichesk district, Kherson oblast	152	1.2×1.7	Emerald site UA0000383
Ahaimansky	46.670501° 34.193323°	near Ahaimany village, Henichesk district, Kherson oblast	4849	10×16	Emerald site UA0000366
Koianly	46.690165° 34.482390°	near Shotivka village, Henichesk district, Kherson oblast	148	5,5×11	–
Domuzlynsky	46.603908° 34.728707°	near Zeleny Hai village, Henichesk district, Kherson oblast and Trudove village с. Трудове, Melitopol district, Zaporizhzhia oblast	4743	9×13	Emerald site UA0000369
Novotroitsky	46.319373° 34.360386°	near Novotroitse urban village, Henichesk district, Kherson oblast	97	3.5×4	–
Syvasky	46.349037° 34.529281°	Near Syvaske village Henichesk district, Kherson oblast	1549	6×8,5	Emerald site UA0000371

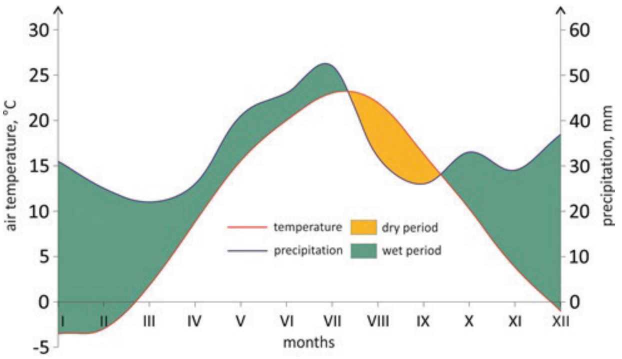

Figure 2. Climate diagram of the Askania Nova region.

Depressions in lowland steppes are represented by two structural and genetic forms – steppe saucers and *pody*. Steppe saucers are small, with depth up to 0.5 m and diameter 2–150 (up to 600) m. Their density is 30–120 saucers per 1 km^2, depending on erosional dissection and inclination of the terrain. Almost all of them are plowed today. Depressions with a depth of 3–5 (sometimes 10–15) m and a total area of more than 1 ha (up to 16,000 ha), with erosive slopes, catchment basins and flat bottoms represent the second group of depressions – *pody*. In the interfluve of the Dnieper and Molochna rivers, small depressions with a diameter of up to 1000 m and a depth of about 0.5–3 m are common. Most of depressions are plowed due to their easy accessibility; pristine vegetation is preserved only in the small depressions within the territory of the Biosphere Reserve «Askania-Nova». Other interfluve *pody* have significant size (see Table 1). The depths of these depressions (relative elevations of watersheds above the bottoms) vary from 1.5–2 m (Small Chapelsky) to 10–15 m (Agaymansky, Great Chapelsky, Sivashsky, Domuzlynsky). The slopes and periphery of the bottoms of these large depressions are plowed, with the exception of the Great Chapelsky. Some depressions (Sugakli, Mustapa, Oleksandrivsky, Rubanovsky, Timoshivsky, etc.) are completely plowed.

In general, *pody* is a key typological unit of macro- and mesorelief forms of the Steppe zone, and expresses the geomorphological, hydrographic, edaphic, and biotic identity of the whole catchment. The actual concept of steppe depressions (*pody*) means a complex formation, which includes the following elements: a bottom (perfectly flat surface delineated by the lowest closed horizontal), the slopes, which form a closed depression bowl (its sides) and, finally, the estuaries of a ravine catchment, cut into the general slopes (Shapoval and Zvegintsov 2010) (Figure 3). Only a few depressions have a circle shape, the rest are more or less ellipsoidal, elongated from north to south. The average inclination of slopes is about 2°. The slopes of southern and eastern exposures are steeper (up to 4–6°) and have more pronounced excess of a depression edge over its bottom. This kind of asymmetry of *pody* is due to the general tendency of lowering the relief in the direction to the Black Sea. In large depressions, slopes are complicated by catchment hollows, and temporary watercourses have produced erosive leaks where these depressions occur in floodplains. The width of such catchment hollows is 500–1000 m, and the length is 7–9 km. Deeper ravines can reach more than 60 km in length (Chekmenchi ravine, which flows into the Ahaimansky *pid*). In places of transition from a hollow to a bottom, the soil deposits brought by water are formed. These are peculiar deltas that are clearly identified by the steppe nature of vegetation. The slopes of some depressions (Ahaimansky and Sivashsky *pody*) are terraced. Sometimes there are several bottoms within the large depression, due to generalization of a series of smaller depressions.

The most common and typical soils of the studied region are Luvic Planosol or gleyosolod in the traditional Ukraininan soil classification (Polupan et al. 2005). Their formation is determined by periodic stagnation of melt and rainwater, processes of gleying and sweetening (hydrolysis). This soil type is well diagnosed by numerous iron-manganese nodules. In general, soil varieties in the *pody* are localized by strips with concentrically closed contours. The width of the strips is determined by an exposure of the slope, a depth of depression, an intensity and nature of moistening, and so on (Anon 1984).

There are two seasonal types of depression flooding: winter-spring, caused by melting snow during thaw, and extremely rare summer-autumn – caused by heavy rains (Drohobych and Polishchuk 2003). A key role in winter-spring floods is played by the snow factor, which accumulates and retains water reserves until the melting period. In addition, heavy rainfall in the previous moisture accumulation period, deep freezing of the soil and the formation of a "frost lock" that prevents infiltration of water; crust and rapid warming are also the key to severe flooding. According to the analysis of well-known dates of flooding in 19–21 centuries, the average duration of the period between severe floods is 7–12 years (Shapoval and Zvegintsov 2010). Occasionally flooding is observed for two or three years in a row, much more often with intervals of 15–17 years or more. In the past, the flooding of the depressions of the Black Sea steppe was much larger (Shalyt 1930) and therefore on old maps they were marked as lakes.

Currently, due to the over-regulation of the catchment area, with much plowing and crossing by various communications (water supply canals, highways, etc.), the frequency and duration of floods have decreased significantly, causing xerophytization of these habitats. Modern heavy floods begin in February and last until the beginning of June (the last small puddles in the depths of the bottom may last until the end of July). The area of flooding can reach 3–4 thousand hectares with the water depth up to 20–40 cm in the center of the depression.

Polygenetics, different sizes, differentiation of microrelief and soil cover of depressions together with sporadic hydrogenic fluctuations, historical and current management determine the nature and dynamics of their vegetation. In fact, it is a unique dynamic complex of hydro-, meso- and xeromorphic communities, which, of course, complicates its study.

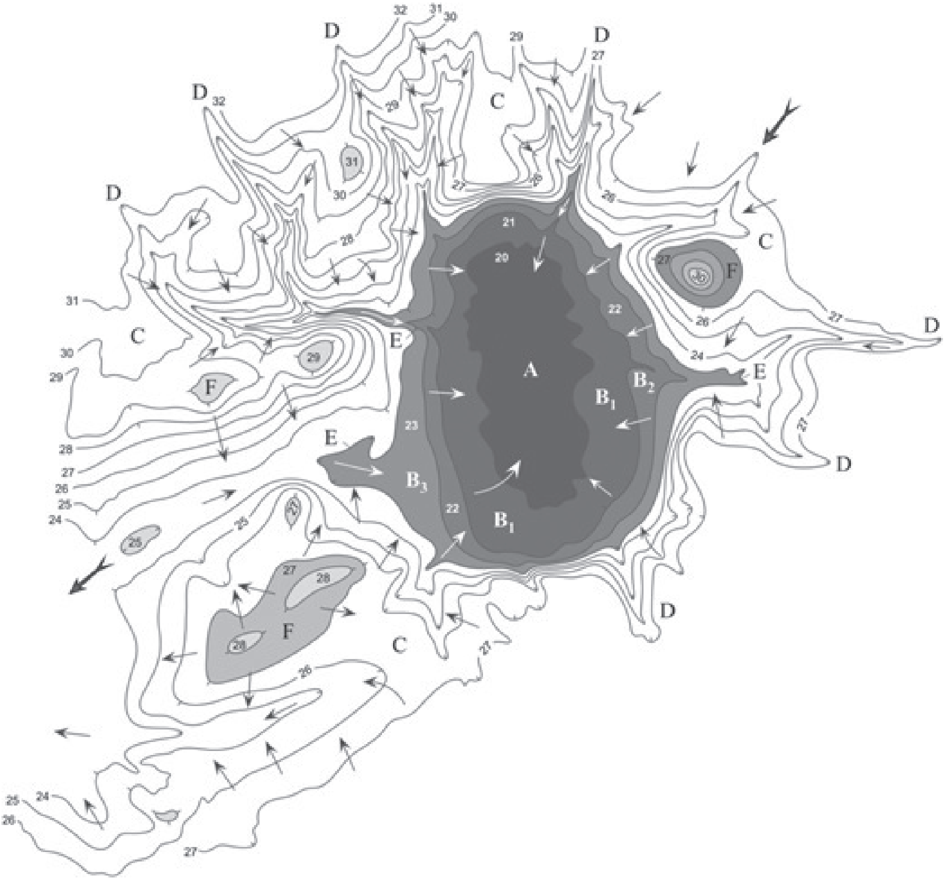

Figure 3. Relief of the hydrographic network of the basin of the Great Chapelsky *pid*, fragment (Shapoval and Zvegintsov 2010). A: bottom, B1–B3: closed slopes of depression, B: general slopes with indented watershed hollows (D), C: ravine estuaries, F: plakor (slightly convex or almost flat elevated area); 20–32: altitudes; arrows indicate direction of the runoff (bold arrows: general regional runoff).

Methods

The materials for the study were 1897 vegetation plots made by V.V. Shapoval, O.P. Goffman, N.Y. Drohobych, N.A. Dotsenko, N.S. Shestakova, A.A. Kuzemko and I.I. Moysienko in the depressions of the Steppe zone of Ukraine in the period from 1967 to 2019. Plots are stored in the Turboveg format (Hennekens and Schaminée 2001) as a part of the Ukrainian Grassland Database (Kuzemko 2012), registered as EU-UA-0001 in GIVD (https://www.givd.info/ID/EU-UA-001). These vegetation plots covered most of the large steppe depressions within the Kherson region (see Figure 1). The relevés were made according to the standard method of the Braun-Blanquet school on plots from 9 and 16 m^2 (relevés of small spots of hydrophilic vegetation in 2010 and some relevés of 2019) to 100 m^2 (the rest of relevés). Different plot sizes are due to the specifics of spatial differentiation of *pody* vegetation. “Small” plots (9–16 m^2) are mostly timed to small microrelief forms (saucer depths, road tracks, trampled cattle tracks, shores of the arches, etc.) with different moisture conditions and small sizes of vegetation contours. All “large” plots have a standard area of 100 m^2 and characterize relatively homogeneous vegetation. The vast majority of the relevés did not include cryptogam species, which are very poorly represented in steppe depressions and mostly have no diagnostic value. For historical relevés, georeferences were determined by the original characteristics of their location in the quarter network of the natural core of the Askania-Nova Biosphere Reserve, corrals of the Great Chapelsky *pid* or other landmarks – position in relief, adjacency with settlements or economic objects. The new relevés were georeferenced with GPS-navigators Lowrance iFinder and Garmin eTrex 20X, coordinate system WGS-84. A graphical summary of the catena of depression vegetation was completed in the form of an idealized transect, which was constructed based on the results of generalized analysis of vegetation plots and visualization of the results of ordination and territorial differentiation of syntaxa. Images of typical plants were obtained by scanning herbarium specimens of plants collected directly in steppe depressions.

Since the aim of our work was the syntaxonomic analysis of mesic and wet communities of steppe depressions, we deliberately removed from the analysis all vegetation plots of typical steppes, which according to a preliminary phytoindication assessment received an average score 7 or less on the moisture scale based on the DES (Didukh 2011). We also removed from the analysis vegetation plots with cover of shrub layer more than 15%. All taxa identified to the genus level were removed from the species list. The resulting dataset of 641 vegetation plots containing 261 species was analyzed in the Juice software (Tichý 2002). We tested several variants of cluster analysis (both divisive and agglomerative), but the best results in terms of separation and sharpness of vegetation units were obtained with the agglomerative cluster analysis in PCOrd (McCune and Mefford 2006) with the following parameters: square root transformation of species data, Relative Sørensen index as distance measure, flexible Beta -0.25 as group linkage method. Phytoindication assessment of syntaxa was performed using DES for flora of Ukraine (Didukh 2011) in the Juice program. In one case, we rearranged the plots manually between units 7 and 8, for a clearer separation of the two subassociations, moving all plots with presence of *Damasonium alisma* to a cluster where this species had a much greater frequency. Diagnostic taxa for vegetation units were determined based on their fidelity values calculated with phi coefficient (Chytrý et al. 2002) with Fisher's exact test at $p > 0.001$ and standardisation of relevé groups to equal size. The threshold value of the phi coefficient for diagnostic species for syntaxa of all ranks was 0.3. For the assignment of communities to syntaxonomical classes and to EUNIS units we used two expert systems: EVC, which allows with a fairly high degree of reliability to determine the affiliation of vegetation plots to vegetation classes and is based on a recent review of the European vegetation (Mucina et al. 2016) and EUNIS-ESy (Chytrý et al. 2020). Both expert systems were used in the Juice program environment.

Results

Description of vegetation units

As a result of the classification, we obtained nine units (Table 1, Suppl. materials 1, 2). Below we provide characteristics of their distribution, environmental conditions, structure and composition.

Cluster 1 "Ferulo euxinae-Caricetum praecocis» (Table 2, column 1)

Distribution. Small shallow depressions of the natural core of the Askania-Nova Biosphere Reserve.

Environmental conditions. Communities characterized by clear signs of succession with accumulation of a thick litter. The territory is kept in a completely protected regime ('absolut zapovednost"). Here, the ecosystem is not grazed by wild ungulates which contributes to growth of vegetative-mobile mesophytic species and impoverishment of phytodiversity. Soils are meadow-chestnut gleyed sweetened and gley-sweet Planosol. These small depressions are almost not flooded, although they usually have better moisture conditions compared to the adjacent steppe. Sometimes during snowy winters, there may be short-term puddles on the bottoms in February-March, but heavy floods are not observed and the water completely disappears before the period of active vegetation.

Structure and composition. Total cover varies in a wide range – from 19 to 100%, an average of 75,3%, litter – from 5 to 70%. In general, phytocenoses are quite dynamic and are characterized by various combinations of mesomorphic rhizome species and rotations of their coenotic positions depending on different changes in the environment. Dominant species are *Bromopsis inermis*, *Elytrigia repens*, *Carex praecox*, *Poa angustifolia*, rarely *Bromopsis riparia* (Figure 4). *Elytrigia repens* subsp. *pseudocaesia*, *Alopecurus pratensis* and *Carex melanostachya*, which are the most mesophytic components, occur sporadically. Turf-forming xeromorphic species (*Stipa capillata* and *Agropyron cristatum* subsp. *pectinatum*) are rare. The herb layer has clear vertical differentiation. The first layer is formed by tall forbs (*Ferula euxina*, *Peucedanum ruthenicum*, *Asparagus officinalis*) and grasses – *Bromopsis inermis* and *Elytrigia repens*, sporadically *Stipa capillata*, *Rumex crispus*, *Sisymbrium altissimum*. In the second layer, *Carex praecox* and *Poa angustifolia* dominate, *Falcaria vulgaris*, *Galium ruthenicum*, *Vicia villosa* are common. The third layer is formed by *Viola kitaibeliana*, *Lamium amplexicaule* var. *orientale*, *Cruciata pedemontana*, *Veronica arvensis*. Some synanthropic plants are present in the floristic composition, even among the characteristic species of the syntaxon, due to sporadic zoogenic soil disturbances – anthills (*Lasius*) or vole's colonies (*Microtus*), which are optimal stations for weeds. *Sisymbrium altissimum* and *Salsola tragus* spread in bulk after fires; *Falcaria vulgaris*, *Eryngium campestre*, *Atriplex oblongifolia*, *Lactuca serriola* are also common.

Figure 4. Phytocenoses of the association *Ferulo euxinae-Caricetum praecocis* at the bottom of the «Old» depression (natural core of the Askania-Nova Biosphere Reserve, «Southern» massif, quarter №44) with the aspect of *Bromopsis inermis*, 16.06.2005.

Table 2. Synoptic table of the steppe depression vegetation. Taxa percentage frequency (constancy) and modified fidelity index (phi coefficient × 100) superscripted are shown. Species within units are arranged in descending order of fidelity index; the table shows only diagnostic species; diagnostic species with percentage frequency values more than 30% and constant species with percentage frequency more than 30% are indicated in bold.

Group No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
No. of releves	**140**	**85**	**32**	**122**	**52**	**54**	**95**	**44**	**18**
Bromopsis inermis	**82**^{71}	7	31	1	.	.	.	.	.
Viola kitaibeliana	**52**^{55}	25^{21}	.	.	.	.	.	.	.
Vicia villosa	**74**^{53}	**48**^{28}	12	11	10	2	.	.	.
Elytrigia repens	24^{40}	1	.	5	.	.	.	.	.
Lamium amplexicaule var. *orientale*	17^{39}	.	.	.	.	.	.	.	.
Phlomis herba-venti subsp. *pungens*	**34**^{38}	27^{29}	.	.	.	.	.	.	.
Salsola tragus	16^{35}	.	.	.	2	.	.	.	.
Dianthus guttatus	19	**65**^{53}	.	**30**^{17}	.	.	.	5	.
Thesium arvense	.	20^{42}	.	1	.	.	.	.	.
Carex melanostachya	9	**74**^{42}	**31**	29	15	9	20	20	6
Linaria biebersteinii	15	**47**^{41}	3	**31**^{23}	.	2	.	.	.
Seseli tortuosum	10	27^{38}	.	4	.	.	.	.	.
Eryngium planum	12	**35**^{36}	3	16	.	.	3	2	.
Euphorbia seguieriana	2	16^{34}	.	1	.	.	.	.	.
Tragopogon dasyrhynchus	7	19^{32}	.	2	.	.	.	.	.
Allium flavum subsp. *tauricum*	8	18^{30}	.	3	.	.	.	.	.
Veronica arvensis	19^{5}	9	**94**^{79}	10	.	.	.	.	.
Artemisia austriaca	2	8	**88**^{76}	26^{13}	.	.	.	.	.
Cerastium pumilum	2	10	**75**^{74}	8	.	.	.	.	.
Carex spicata	.	1	**56**^{72}	.	.	.	.	.	.
Trifolium retusum	.	1	**81**^{70}	7	.	33^{20}	.	.	.
Poa bulbosa	.	1	**66**^{67}	20^{12}	.	.	.	.	.
Festuca valesiaca	.	6	**56**^{57}	21^{15}	.	.	.	.	.
Lepidium draba	5	3	**50**^{57}	10^{3}	.	.	.	.	.
Vicia lathyroides	.	15^{10}	**50**^{56}	4	.	.	.	.	.
Capsella bursa-pastoris	6	.	**41**^{52}	7	.	.	.	.	.
Taraxacum sect. *Taraxacum*	7	7	**62**^{50}	21^{8}	19	4	1	2	.
Medicago minima	.	.	28^{47}	.	4	.	.	.	.
Crepis ramosissima	9	17	**62**^{45}	**36**^{20}	17	.	1	.	.
Cruciata pedemontana	17^{8}	26^{19}	**47**^{43}	.	.	.	.	.	.
Arenaria leptoclados	.	3	**41**^{38}	20^{13}	8	13	.	.	.
Trifolium arvense	4	1	25^{36}	9^{8}	.	.	.	.	.
Stellaria graminea	3	14	**38**^{32}	15^{6}	21^{13}	.	.	.	.
Allium regelianum	1	8	.	**66**^{59}	15	.	11	5	.
Herniaria glabra	.	.	.	**45**^{47}	.	28^{25}	2	.	.
Artemisia santonicum	.	3	.	**71**^{47}	**38**^{17}	**35**^{14}	14	5	6
Plantago lanceolata	.	2	25^{20}	**44**^{44}	.	2	4	2	.
Ventenata dubia	.	2	.	20^{39}	.	.	1	.	.
Lepidium ruderale	.	.	.	12^{33}	.	.	.	.	.
Potentilla argentea	1	**51**^{21}	**34**	**65**^{33}	2	7	25	**39**	.
Polycnemum arvense	.	.	.	11^{32}	.	.	.	.	.
Cyperus flavescens	.	3	.	8	**58**^{48}	.	**36**^{25}	7	.
Lathyrus nissolia	.	.	6	.	**31**^{48}	.	.	.	.
Armoracia rusticana	.	.	.	.	19^{37}	.	4	.	.
Crepis sancta	2	1	.	2	19^{36}	.	.	.	.
Lathyrus tuberosus	.	.	.	3	17^{36}	.	.	.	.
Phalacrachena inuloides	.	7	19	16^{7}	**38**^{32}	.	6	10	.
Lotus angustissimus	.	1	.	**43**^{23}	12	**93**^{68}	15	.	.
Myosurus minimus	1	15	3	28$^{6.0}$	.	**98**^{67}	28^{7}	10	6
Mentha pulegium	.	.	.	.	.	39^{57}	3	.	.
Lythrum virgatum	.	5	.	**34**^{5}	17	**91**^{49}	**54**^{20}	**56**^{22}	.
Chaiturus marrubiastrum	.	.	.	2	.	**31**^{43}	13^{12}	.	.
Polygonum aviculare	.	20	9	**57**^{8}	23	**100**^{40}	**45**	**61**^{12}	**83**^{28}
Erigeron canadensis	2	.	.	10^{6}	8	**31**^{39}	.	.	.
Xanthium orientale subsp. *riparium*	.	.	.	5	.	22^{33}	9^{10}	.	.
Aegilops cylindrica	.	.	.	.	.	11^{32}	.	.	.
Lythrum borysthenicum	.	.	.	12^{12}	.	.	**31**^{41}	2	.
Elatine hungarica	.	.	.	1	12^{10}	.	24^{31}	10	.
Damasonium alisma	.	5	.	2	.	.	.	**100**^{97}	.
Elatine alsinastrum	.	5	.	11	.	.	25^{12}	**80**^{69}	.
Butomus umbellatus	.	.	.	28^{8}	**37**^{16}	.	**41**^{20}	**66**^{42}	.
Rumex crispus	9	24	9	**30**	**40**^{14}	.	**42**^{15}	**61**^{30}	.
Rorippa brachycarpa		**30**	6	**31**	**52**^{15}	**48**^{12}	**54**^{16}	**71**^{29}	.
Puccinellia distans	.	.	.	1	.	.	.	.	**67**^{79}

Group No.	1	2	3	4	5	6	7	8	9
Rumex ucranicus	.	.	.	2	.	.	.	.	**67**^{79}
Juncus gerardi	.	1	.	.	.	.	.	.	**61**^{76}
Juncus bufonius	.	.	.	9	.	.	2	.	**67**^{73}
Plantago major	.	1	.	3	.	**30**^{18}	.	.	**78**^{70}
Ranunculus sceleratus	.	.	.	.	.	.	7	5	**61**^{68}
Bolboschoenus maritimus	.	.	.	1	.	.	.	.	**50**^{68}
Veronica anagallis-aquatica	.	.	.	.	.	.	.	.	**44**^{65}
Petrosimonia triandra	.	.	.	.	.	.	.	.	**39**^{60}
Echinochloa crus-galli	.	.	.	1	.	.	.	.	**39**^{59}
Atriplex prostrata	.	.	.	.	.	.	.	.	**33**^{56}
Crypsis schoenoides	.	.	.	1	.	.	.	5	**39**^{55}
Taraxacum besarabicum	.	2	.	.	.	.	.	.	33^{53}
Setaria pumila	.	.	.	2	.	2	.	.	22^{41}
Persicaria maculosa	.	.	.	.	.	4	9^{8}	.	28^{39}
Juncus compressus	.	.	.	1	.	.	.	.	17^{38}
Xanthium spinosum	.	.	.	2	.	.	.	.	17^{36}
Plantago tenuiflora	.	2	.	12^{2}	2	.	15^{5}	22^{14}	**39**^{33}
Falcaria vulgaris	**81**^{61}	**51**^{33}	.	14	.	4	.	.	.
Galium ruthenicum	**79**^{55}	**66**^{44}	6	13	.	.	.	.	.
Carex praecox	**83**^{47}	**95**^{58}	.	29	13	.	1	2	.
Poa angustifolia	**87**^{32}	**90**^{34}	**75**^{23}	**59**	2	2	15	**56**	.
Alopecurus pratensis	8	**42**^{8}	**100**^{52}	27	.	6	18	**71**^{29}	17
Achillea micranthoides	.	3	**47**^{42}	**39**^{33}	.	4	1	.	.
Gypsophila muralis	.	10	.	**69**^{38}	10	**100**^{64}	22	.	.
Inula britannica	1	27	.	**56**^{16}	**81**^{34}	**87**^{39}	24	29	6
Eleocharis palustris	.	.	.	25	**35**	**100**^{44}	**53**^{10}	**46**^{5}	**94**^{40}
Gratiola officinalis	.	17	.	**41**^{6}	10	**80**^{36}	**63**^{23}	**83**^{38}	.
Beckmannia eruciformis	.	8	.	2	6	**76**^{35}	31	**61**^{23}	**94**^{49}
Juncus atratus	.	6	.	3	.	.	**37**^{32}	**44**^{40}	.
Pulicaria vulgaris	.	2	.	16^{3}	.	**31**^{19}	13	17	**39**^{27}

Cluster 2 «Diantho guttati-Caricetum melanostachyae» (Table 2, column 2)

Distribution. Small depressions of the natural core of the Askania-Nova Biosphere Reserve and sporadically on the slopes and dry bottom of the Great Chapelsky *pid*.

Environmental conditions. Communities are mostly localized along the bottom edge and at lower slopes (on the verge of flooding) or in local depressions, surrounded by more xerophytic phytocenoses, so they occur in depressions with preserved slopes and adjacent pristine steppe. During strong floods they give way to more hydrophytic communities; during severe droughts they are in a depressed state, lose hygromesophytic elements, and are replaced by more dry communities. The conditions of this association are perfectly suited to *Carex melanostachya*, which can resist extreme changes in moisture conditions, growing both in a dry steppe and among ephemeral shallow-water vegetation.

Structure and composition. The total cover varies in a wide range from 40 to 100%, occasionally 10–25%, on average 73%. Communities are more mesophytic than the *Ferulo-Caricetum praecocis*, which is manifested primarily in the strong phytocenotic position of the dominant *Carex melanostachya* and *Elytrigia repens* subsp. *pseudocaesia*, increase in the occurrence and total proportion of *Alopecurus pratensis*, presence of *Eryngium planum* (which tends in the Ascanian steppe to depressions with saline soils and sufficient moisture) as well as *Hypericum perforatum*, *Veronica spicata*, *V. barrelieri*, *Gagea transversalis*, *Euphorbia esula* subsp. *tommasiniana*, *Ferula euxina* and *Rumex crispus*, and sometimes a significant admixture of annual plants, confined to short-term wetlands (“saucers”, puddles), namely *Gypsophila muralis*, *Cyperus flavescens*, *Myosurus minimus* and *Rorippa brachycarpa* and *Phalacrachena inuloides* as characteristic element of the mesophytic forbs of steppe depressions. Another typical mesophytic species of these communities is *Sibbaldianthe bifurca* subsp. *orientalis*, which is found in watershed hollows and depressions with semi-dry or mesic grassland vegetation. Thus, the phytocenoses of this unit show a more mesomorphic character, although they are accompanied by many xerophytic steppe elements (*Seseli tortuosum*, *Euphorbia seguierana*, *Sisymbrium polymorphum*, *Festuca valesiaca*, *F. pseudovina*, *Agropyron cristatum* subsp. *pectinatum*, *Phlomis herba-venti* subsp. *pungens*, and very rarely *Stipa capillata* and *S. ucrainica*), which generally reveals the mixed, transition nature of these communities.

Cluster 3 «Vicio lathyroidis-Alopecuretum pratensis» (Table 2, column 3)

Distribution. Peripheral part of the Great Chapelsky *pid* bottom.

Environmental conditions. The territory is grazed by wild ungulates, mostly in a state of modest overgrazing.

Structure and composition. Litter is almost absent. Sometimes, where there is considerable aboveground phytomass, strands of coarse dry biomass from common rhizome grasses can be present. Total cover of herb layer is 70–100% (average 80.3%). Phytocenoses are characterized by an absolute dominance of rhizome-turf mesophytic grass *Alopecurus pratensis* (Figure 5). Sometimes,

Figure 5. Phytocenoses of the association *Vicio lathyroidis-Alopecuretum pratensis* in the corral №6 of the Great Chapelsky *pid* (peripheral part of the bottom) after flooding, aspect of *Alopecurus pratensis* with an admixture of *Phlomis scythica*, 27.05.2010.

Poa angustifolia is codominant. Occasional species include *Elytrigia repens* subsp. *pseudocaesia*, *Bromopsis inermis*, *Carex spicata* and *Carex melanostachya*; *Festuca valesiaca* s.l. is quite common; it generally tolerates short-term flooding well and, if soaked, restores coenotic positions during the xerotic series. Forbs are represented by *Achillea micranthoides*, *Convolvulus arvensis*, *Ferula euxina*, *Phalacrachena inuloides*, *Phlomis scythica*, *Plantago lanceolata*, *Potentilla argentea* and several legumes: *Vicia lathyroides*, *V. hirsuta*, *V. tetrasperma*, *V. villosa*, *Lathyrus nissolia*, *Trifolium arvense*.

Long-term grazing regime of this community leaves an imprint on the structure of herb layer and is marked by a significant participation of *Artemisia austriaca* (the number of individuals increases markedly in dry periods with increasing grazing pressure), *Poa bulbosa*, *Capsella bursa-pastoris*, *Cardaria draba*, *Polygonum aviculare*, *Senecio vernalis*, *Lactuca serriola*, *L. tatarica*, *Lamium amplexicaule*, *Erodium cicutarium*, *Euphorbia esula* subsp. *tommasiniana*, *Taraxacum* sect. *Taraxacum* etc. However, trampling and fragmentary exposure of soil contributes to spreading of many annual plants including *Trifolium retusum*, *Arenaria leptoclados*, *Cerastium pumilum*, *Crepis ramosissima*, *Cruciata pedemontana*, *Draba verna*, *Medicago minima*, *Myosotis stricta*, *Veronica arvensis* etc. In general, these phytocenoses are characterized by low floristic richness and insignificant physiognomic variability due to an admixture of meadow forbs, and dominance of *Alopecurus pratensis*.

Cluster 4 “Herniario glabrae-Poetum angustifoliae” (Table 2, column 4)

Distribution. Slopes and dry bottoms of Zeleny, “Black Valley”, Ahaimansky, Garbuzy, Small Chapelsky *pody*, nameless depressions from the outskirts of the village Podivka and the village Novotroyitske, on the slopes of the Great Chapelsky *pid*, as well as known from old relevés (1970s) from the natural core of the Biosphere Reserve «Askania-Nova» («Southern» site). Today, due to reservogenic succession (i.e. succession caused by the protected regime of the territory, with an unbalanced or incomplete structure), accompanied by the accumulation of abundant litter, these phytocenoses have disappeared from the «Southern» site and are replaced mainly by monodominant communities of *Poa angustifolia* belonging to cluster 1.

Environmental conditions. This vegetation unit includes the most common phytocenoses, distributed in dry small depressions and in concentric strips on non-flooded edges of major depressions, which are used as pastures and periodic hayfields (under favorable vegetation conditions). Communities are confined to meadow-chestnut residual saline sweetened gley heavy loam soils. At the same time, they are characterized by a relatively stable floristic composition, which in general is maintained in scattered depressions with a similar landuse regime.

Structure and composition. Total cover varies from 25 to 95%, averaging 78.4%. Dominants are *Poa angustifolia*, *Elytrigia repens* subsp. *pseudocaesia*, *Ventenata dubia*, *Artemisia santonicum* and *A. austriaca*, in some places *Festuca valesiaca*, *Alopecurus pratensis*, *Carex praecox* and *C. melanostachya*. Extremely bright and colorful aspects are formed by the large and coenotically strong contribution of forbs (Figure 6), especially *Achillea micranthoides*, *Allium regelianum*, *Dianthus guttatus*, *Ferula euxina*, *Inula britannica*, *Linaria biebersteinii*, *Lythrum virgatum*, *Phlomis scythica*, sporadically *Vicia villosa*, *Phalacrachena inuloides*, *Eryngium planum*, and *Lathyrus tuberosus*. Phytocenoses are characterized by high floristic richness and pronounced vertical structure. Due to periodic flooding and grazing, numerous bare inter-turf plots are observed, which serve as temporary habitats for a rich group of low-growing annual plants: *Herniaria glabra*, *Juncus bufonius*, *Myosurus minimus*, *Lotus angustissimus*, *Lythrum thymifolia*, *Gypsophila muralis*, *Scleranthus annuus*, *Elatine hungarica*, *Lythrum borysthenicum*, *Rorippa brachycarpa*, *Arenaria leptoclados*, etc.

The heterogeneous nature of these communities is visualized by the combination of xeromorphic plants, such as *Festuca valesiaca*, *F. pseudovina*, *Koeleria macrantha*, *Limonium sareptanum*, *Medicago romanica*, *Ventenata dubia*, *Polycnemum arvense*, *Filago arvensis*, *Seseli tortuosum* with hydrophilic species like *Butomus umbellatus*, *Elatine alsinastrum*, *Eleocharis palustris*, *E. uniglumis*, *Gratiola officinalis*, *Lythrum virgatum*, *Plantago tenuiflora*, *Pulicaria vulgaris*, *Rorippa austriaca*, occasionally *Beckmannia eruciformis*.

Finally, the condition and structure of the communities are significantly affected by grazing, which is manifested in sporadic distribution of *Ambrosia artemisiifolia*, *Artemisia austriaca*, *Cardaria draba*, *Centaurea diffusa*, *Consolida orientalis*, *Descurainia sophia*, *Eryngium campestre*, *Euphorbia esula* subsp. *tommasiniana*, *Polygonum aviculare*, *Tripleurospermum inodorum*, *Xanthium orientale* subsp. *riparium*, etc.

In general, these phytocenoses are relatively open, so in between beds of grasses, it is easy to see the whitish-dusty dried soil with iron-manganese nodules (beans) common on the surface, sometimes quite large (up to 1.5–2 cm in diameter, 20–30 pcs./m^2).

Cluster 5 «Lathyro nissoliae-Phalacrachenetum inuloidis» (Table 2, column 5)

Distribution. Along the edge of Ahaimanskyi *pid* bottom, including the old fallows, which were plowed in inter-flood periods. Sporadic spots and rather large closed massifs are observed in the lower part of the catchment basins and in the northern part of the Great Chapelsky *pid* bottom.

Structure and composition. Sparse communities with a total cover of 50–90% (average 66%), with three herbal layers. The first layer is formed by tall *Elytrigia repens* subsp. *pseudocaesia* and *Rumex crispus*, sporadically *Armoracia rusticana*, *Lythrum virgatum*, *Schoenoplectus lacustris* and *Butomus umbellatus* (in the first stages of post-hydrogeneous succession). In the second layer *Phalacrachena inuloides* prevails (Figure 7), mixed with *Inula britannica*, *Artemisia santonicum*, *Pseudoarabidopsis toxophylla*, *Eleocharis palustris*, *Gratiola officinalis*, *Vicia hirsuta*. The lower layer is formed by *Cyperus flavescens*, *Lotus angustissimus*, *Polygonum aviculare*, *Gypsophila muralis*, *Rorippa brachycarpa*, *Stellaria graminea*, which are typical for bare, temporarily wet, bottom areas. In general, these bottoms are floristically poor, low-productive communities with unstable composition, depending on various disturbances, moisture regime, cover of the dominant *Phalacrachena inuloides*, etc.

Figure 6. Phytocenoses of the association *Herniario glabrae-Poetum angustifoliae*. Small Chapelsky *Pid*, peripheral part of the bottom, public pasture of cattle (near the village of Dolynsky), communities dominated by *Poa angustifolia* with *Artemisia santonica*, *Allium regelianum*, *Achillea micranthoides*, *Diantus guttatus*, *Plantago lanceolata*, 26.06.2010.

Figure 7. Phytocenoses of the association *Lathyro nissoliae-Phalacrachenetum inuloidis* on the bottom of the Ahaimansky *pid* (near the village of Podove), aspect of *Phalacrachena inuloides*, single shoots of *Rumex crispus* and *Beckmannia eruciformis* visible in the background, 6.06.2008.

*Cluster 6 «Myosuro-Beckmannietum eruciformis» (*Table 2, column 6)

Distribution. Large depressions during heavy flooding (Ahaimansky, Domuzlynsky, Great Chapelsky, Zeleny *pody*).

Environmental conditions. These communities have a fluctuating nature. The ecological optimum is realized during severe floods and in the short post-hydrogenous period.

Structure and composition. Phytocenoses are formed by polycarpic biomorphs and hemicryptophytes, which are dominants (predominate numerically or by mass) and edificators (determine the structure and functioning of the community, form a specific environment); namely, *Beckmannia eruciformis*, *Gratiola officinalis*, *Elytrigia repens* subsp. *pseudocaesia*, *Lythrum virgatum* etc. The proportion of therophytes is 60–80%. These syntaxa are related to the previous cluster 5, but are more hydrophilic and tend to more wet habitats.

The total cover varies in the range of 65–97%, averaging 82.2%. Litter is not developed – up to 4%, sometimes 10-20%, due to soaked strands of the previous year's vegetation that floated with the flowing water. Phytocenoses are distributed sporadically in local concavities of the bottom, sometimes merging into large integral massifs, characterized by distinct layers and sparse synusia. The first layer is dominated by perennial hemicryptophytes and cryptophytes: the characteristic dominant *Beckmannia eruciformis* (cover up to 80%), *Elytrigia repens* subsp. *pseudocaesia*, *Lythrum virgatum*, *Schoenoplectus lacustris*, occasionally *Alopecurus pratensis* (Figure 8). The second layer is quite dense and closed, and it is formed mostly by rhizome vegetative-mobile species *Gratiola officinalis*, *Eleocharis palustris*, *Inula britannica*, *Mentha pulegium*, *Carex melanostachya*, *Rorippa austriaca*, *Artemisia santonicum*, as well as annuals *Chaiturus marrubiastrum*, *Pulicaria vulgaris* and *Vicia hirsuta*. The lowest layer consists of characteristic therophytes of drying habitats: *Myosurus minimus*, *Lotus angustissimus*, *Gypsophila muralis*, *Rorippa brachycarpa*, *Herniaria glabra*, sporadically *Lythrum tribracteatum*, *Trifolium retusum*, *Scleranthus annuus* and *Myosotis stricta*.

Due to combined mowing and grazing land-use in the «Black Valley» *pid*, synanthropic elements are abundant: *Aegilops cylindrica*, *Ambrosia artemisiifolia*, *Centaurea diffusa*, *Erigeron canadensis*, *Lactuca serriola*, *L. tatarica*, *Plantago major*, *Polygonum aviculare*, *Xanthium orientale* subsp. *riparium*.

Cluster 7 «Elatino-Butometum umbellati typicum» (Table 2, column 7)

Distribution. Large depressions: Great Chapelsky, Ahaimanskyi, Zeleny, "Black Valley" *pody*.

Environmental conditions. Hydrophilous coenoses formed during heavy flooding. Concentrated in local concavities and furrows, or occurs sporadically in the depression bottoms.

Structure and composition. Total cover is 35–97%, in average 78.7%. Quite diverse, mosaic communities with a wide range of dominants and codominants, and combined in different variants based on the forms of microrelief, soil disturbances, and degree of flooding: *Butomus umbellatus*, *Schoenoplectus lacustris*, *Elytrigia repens* subsp. *pseudocaesia*, *Eleocharis palustris*, *E. uniglumis*, *Cyperus flavescens*, sporadically in dry places *Inula britannica* (Figure 9). Other characteristic dominants and edificators of wet grasslands are less common and have low cover: *Alopecurus pratensis*, *Carex melanostachya*, *Beckmannia eruciformis*, *Lythrum virgatum*, *Gratiola officinalis*. The structure is generally similar to the phytocenoses described above. The fraction of tall hygromesophilic forbs is composed by *Rumex crispus*, *Pulicaria vulgaris*, *Persicaria maculata*, *Armoracia rusticana*. Low-growing annual plants are widespread in the exposed fragments of drying soil: *Rorippa brachycarpa*, *Gypsophila muralis*, *Pholiurus pannonicus*, *Myosurus minimus*, *Lythrum tribracteatum*, *Lotus angustissimus*, *Elatine alsinastrum*, as well as diagnostic species of this subassociation – *Lythrum borysthenicum*, *Juncus atratus*, *Elatine hungarica*. *Polygonum aviculare* occurs with high constancy and considerable abundance; *Plantago tenuiflora*, *Alisma plantago-aquatica*, *Allium regelianum*, *Juncus atratus*, *Ranunculus sceleratus*, *Typha angustifolia*, *Verbena supina* are sporadic.

Cluster 8 «Elatino-Butometum umbellati damasonietosum alismae» (Table 2, column 8)

Distribution. Phytocenoses of the Great Chapelsky *pid* with the presence of rare species *Damasonium alisma* (Figure 10). Outside this depression, *D. alisma* grows only near the village of Sofiyivka, Novotroitske district, Kherson oblast, in a gulley that connects the basins of the Barnashivka site and the Ahaimansky *pid*, on both sides of the former sewage sump, near the Kherson – Henichesk highway (Shapoval 2012). In other depressions, no specimen of *D. alisma* was found, despite the similar ecological and coenotic parameters and related floristic composition of these habitats.

Environmental conditions. Phytocenoses of the subassociation tend to occur in shallow water, often with open water gaps. In general, the described phytocenoses are extremely rare and exist ephemerally, with an exceptionally favorable flooding regime. In insufficiently wet seasons, such hydrophilic communities are transformed into mesic grasslands, preserving the core of dominant plants that are able to resist of moisture deficiency. But a whole complex of water demanding ephemeral species of depression disappear and are replaced by the more resistant mesophytic species.

Structure and composition. Total cover varies in the range of 65–97%, averaging 87.5%. The first herbal layer is formed by tall dominants and edificators, generally typical for bottom of depressions during periods of flooding: *Elytrigia repens* subsp. *pseudocaesia* and *Lythrum virgatum* with an admixture of *Beckmannia eruciformis*, *Alopecurus pratensis*, *Butomus umbellatus*, *Rumex crispus*, *Poa angustifolia* and *Juncus atratus*. The second layer is composed of dominants *Eleocharis palustris*, *Carex melanostachya* and *Gratiola officinalis*, with a significant proportion of *Euphorbia esula* subsp. *tommasiniana*, *Phlomis scythica* and sporadically *Inula britannica*, *Rorippa austriaca*, *Phalacrachena inuloides*.

Figure 8. Hygrophytic cenoses of the association *Myosuro-Beckmannietum eruciformis*, flooded bottom of the Zeleny *pid*, aspect of *Lythrum virgatum* with admixture of *Inula britanica*. 7.07.2010.

Figure 9. Phytocenoses of the subassociation *Elatino-Butometum umbellati typicum*, concentrated in the center of the newly dried bottom of the Ahaimansky *pid*, aspect *Butomus umbellatus*, *Schoenoplectus lacustris*, *Elytrigia repens* subsp. *pseudocaesia*, 9.06.2010.

Figure 10. Phytocenoses of the *subassociation Elatino-Butometum umbellati damasonietosum alismae* in the central part of the bottom of the Great Chapelsky *pid* during flooding, flowering individuals of *Damasonium alisma* among vegetative shoots of *Butomus umbellatus* and *Elytrigia repens* subsp. *pseudocaesia*, 17.05.2010.

Finally, as the water recedes the damp soil is covered by *Damasonium alisma*, *Rorippa brachycarpa*, *Elatine alsinastrum*, rarely *Elatine hungarica*, *Lotus angustissimus*, *Lythrum thymifolia*, *Lythrum borysthenicum*, *Myosurus minimus*, *Pholiurus pannonicus*, *Plantago tenuiflora*, *Polygonum aviculare* (due to trampling), *Potentilla argentea* (numerous seedlings and juveniles), *Gypsophila muralis*, *Cyperus flavescens*. Sometimes, under optimal moisture conditions, *Damasonium alisma* reach 40–60 cm in height and extends into to the second layer.

Cluster 9 Derivative community «Rumex ucranicus+-Puccinellia distans» (Table 2, column 9)

Distribution. Great Chapelsky *pid.*

Environmental conditions. Fragmentary cenoses, confined to the trampled shores of artificial watercourses, which are flooded all year round and filled with artesian water (ditches for watering wild ungulates). Localized in a narrow strip along a watercourse. Characterized by clear signs of salinity.

Structure and composition. The total cover varies from 30 to 90%. The most common species are *Rumex ucranicus*, *Taraxacum bessarabicum*, *Plantago tenuiflora*, *Pholiurus pannonicus*, *Petrosimonia triandra*, *Myosurus minimus*, *Juncus bufonius*, and *J. compressus*. On the edge of a water pool *Veronica anagallis-aquatica*, *Ranunculus sceleratus*, *Persicaria maculata* grow. Due to significant trampling, species that spread include *Polygonum aviculare*, *Plantago major*, *Echinochloa crus-galli*, *Setaria pumila*, *Ambrosia artemisiifolia*, *Lactuca tatarica*, *Xanthium spinosum*. The most common dominants are *Beckmannia eruciformis*, *Bolboschoenus maritimus*, *Eleocharis palustris*, *Elytrigia repens* subsp. *pseudocaesia*, *Juncus gerardii*, *Pulicaria vulgaris*, *Puccinellia distans*, and sporadically *Schoenoplectus lacustris*.

Ordination and territorial differentiation of vegetation units

The DCA ordination of the identified units (Figure 11) showed that they are distributed along the first ordination axis from the driest (cluster 1) to the wettest (cluster 9). Xerophytic and mesoxerophytic units 1–3 are located in the right part of the ordination diagram and units 4–9, which are characteristic for wetter conditions, are located in the left part of the diagram. Clusters 3–5 are concentrated in the central part, which indicates their mesic nature, not only by moisture, but also by other closely correlated edaphic factors, including soil aeration, fluctuating water level, nitrogen content in soil and salt regime of the soil. Units 1 and 9 are located at the extremes of the first ordination axis, while the remaining units are separated into two rows along the second ordination axis. In the lower part of the diagram are units 3, 4 and 6, and in the upper part are units 2, 5 and 7. Probably the leading factors of differentiation along the second axis are climatic – first of all, thermal regime and light. Almost all units are well separated from each other, with the exception of units 7 and 8, which we have interpreted as subassociations of one association. Regardless of the number of vegetation plots in these units, which varies widely, the amplitude of the units is approximately the same.

Peculiarities of ecological differentiation of steppe depression syntaxa can be traced on the transect across the conditional (model) depression, which has well-preserved natural slopes and bottom and is periodically flooded (Figure 12). Xero-mesophytic and mesic communities of syntaxa 1, 2 and 4 are formed at the edges of the depression, its slopes are occupied by communities belonging to units 3 (upper part of a slope) and 5 (lower part of a slope), and communities of units 6, 7 and 8 at the bottom as well as unit 9 (the latter in the presence of a shallow artificial watercourse constantly filled with artesian water). The abrupt change of ecological values on the slopes and especially on the bottom of a depression are clearly visible. In addition to a sharp increase of moisture, there is an increase in the variability of dampness, soil aeration, soil pH and salt regime and a decrease in the carbonates content of the soil. At the same time indicators of climatic factors do not change.

Identification of vegetation units by expert systems

The classification of vegetation plots by the expert system EVC (Suppl. material 3: Fig. A) showed a predominance of plots belonging to the class *Festuco-Brometea* within units 1–2, although a significant portion of the plots also belonged to the *Molinio-Arrhenatheretea* class. In addition, the plots assigned to the class *Molinio-Arrhenatheretea* represented a significant portion in cluster 3, although the predominant portion of the plots assigned in that cluster by the expert system belonged to

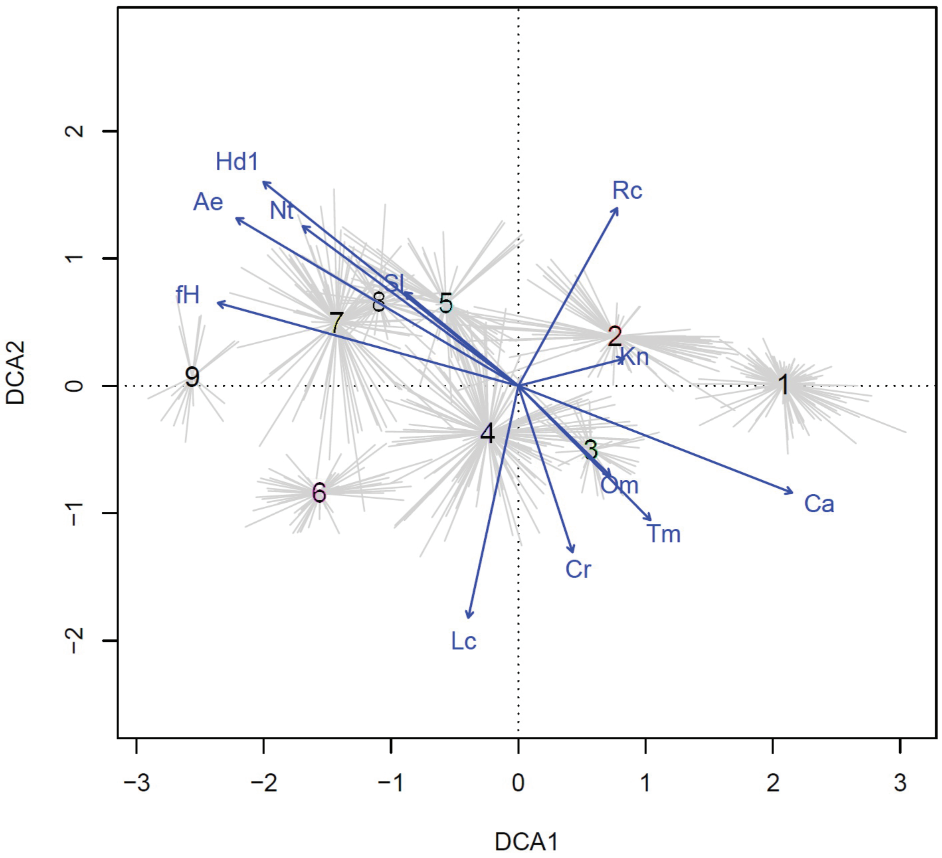

Figure 11. DCA-ordination of the resulted vegetation units. Numbers in the centroids correspond to the unit number in the text. Environmental verctors of DES: Hd – moisture, fH – variability of damping, Rc – soil acidity, Sl – salt regime of a soil, Ca – carbonate content in a soil, Nt – nitrogen content in a soil, Ae – soil aeration, Tm – thermal regime, Om – humidity of climate (ombroregime), Kn – continentality of climate, Cr – cryoregime, Lc – light. Eigenvalues: 1st axis (DCA1) 0.6533, 2nd axis (DCA2) 0.2723.

the class *Sedo-Scleranthetea*. In the clusters 4–8 there was a clear predominance of plots assigned to the class *Molinio-Arrhenatheretea*, although in cluster 7 there was also a significant portion of plots assigned to the classes *Isoëto-Nanojuncetea* and *Phragmito-Magnocaricetea*. Cluster 9 clearly shows the predominance of plots assigned by the expert system to Festuco-Puccinellietea class.

The interpretation of vegetation plots by the expert system EUNIS-ESy in units of the EUNIS habitat classification (Suppl. material 3: Fig. B) showed that most plots of unit 1 were classified as anthropogenic habitat, which can probably be explained by the large number of therophytes in xerophytic communities of the steppe depressions, which are also characteristic for xerophytic anthropogenic vegetation. Within the units 2–6 the plots assigned to grassland habitats prevailed. A significant part of those units was identified only to the first level of the hierarchy (R). Clusters 2 and 3 contained a considerable proportion of plots of dry and mesic grasslands, cluster 5 largely contained plots of wet and subhalophytic meadows, and plots in cluster 4 were distributed evenly to grassland habitats and anthropogenic habitats, and somewhat less commonly to wetlands. The latter clearly predominated in clusters 7–9. Cluster 8 also showed a high proportion of plots assigned to freshwater habitats, in particular to type C35b (periodically exposed shore with stable mesotrophic sediments with pioneer vegetation).

Discussion

Syntaxonomy

The obtained results of the vegetation classification, in particular the list of diagnostic, constant and dominant species of the syntaxa (Suppl. material 4), supported by the results of their phytoindication analysis, distribution in relief, as well as the interpretation by two expert systems, allowed us to develop an ecologically sound syntaxonomic system of the steppe depression vegetation of Ukraine. We then attempted to fit these units into the existing system of syntaxa in Europe (Mucina et al. 2016). Cluster 1 (*Ferulo euxinae-Caricetum praecocis*) occupies an intermediate position between the classes *Festuco-Brometea* and *Artemisietea vulgaris* (*Agropyretalia intermedio-repentis*). Communities of this association are characterized by a significant participation of synanthropic species. However, these species do not form clear diagnostic blocks, and

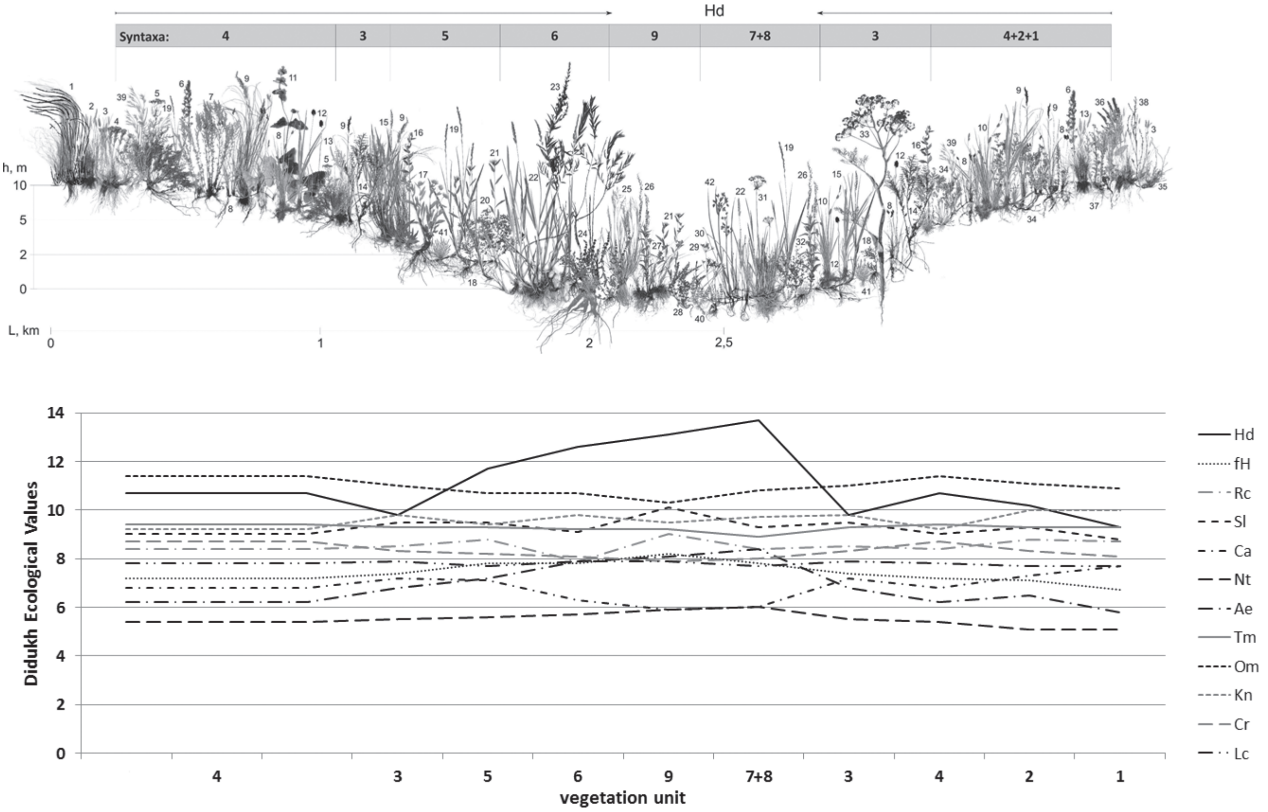

Figure 12. Ecological and coenotic profile of model steppe depressions of the Left Bank of the Lower Dnieper. The central part of the bottom is occupied by wetland communities, which change along the slopes by wet, mesic and xero-mesic phytocenoses. The transectshows the difference in absolute height between the bottom of the depression and its slope, the length and asymmetry of the «body» of the depression along the line: slope-bottom. Species: 1 – *Stipa ucrainica*, 2 – *Koeleria macrantha*, 3 – *Agropyron cristatum* subsp. *pectinatum*, 4 – *Galatella villosa*, 5 – *Achillea micranthoides*, 6 – *Atriplex oblongifolia*, 7 – *Artemisia austriaca*, 8 – *Carex praecox*, 9 – *Poa angustifolia*, 10 – *Carex melanostachya*, 11 – *Phlomis scythica*, 12 – *Allium regelianum*, 13 – *Festuca valesiaca*, 14 – *Artemisia santonicum*, 15 – *Alopecurus pratensis*, 16 – *Chaiturus marrubiastrum*, 17 – *Inula britannica*, 18 – *Rorippa brachycarpa*, 19 – *Elytrigia repens* subsp. *pseudocaesia*, 20 – *Lotus angustissimus*, 21 – *Phalacrachena inuloides*, 22 – *Beckmannia eruciformis*, 23– *Lythrum virgatum*, 24 – *Mentha pulegium*, 25 – *Puccinellia distans*, 26 – *Gratiola officinalis*, 27 – *Juncus atratus*, 28 – *Rumex ucranicus*, 29 – *Damasonium alisma*, 30 – *Eleocharis palustris*, 31 – *Butomus umbellatus*, 32 – *Pulicaria vulgaris*, 33 – *Ferula euxina*, 34 – *Sibbaldianthe bifurca* subsp. *orientalis*, 35 – *Bassia prostrata*, 36 – *Salvia nemorosa* subsp. *tesquicola*, 37 – *Tanacetum millefolium*, 38 – *Polygonum patulum*, 39 – *Ventenata dubia*, 40 – *Elatine alsinastrum*, 41 – *Myosurus minimus*, 42 – *Schoenoplectus lacustris*. For the two-letter abbreviations of environmental factors – see Figure 11.

secondly, the communities are formed naturally, not due to human activities, which does not allow them to be classified within synanthropic vegetation syntaxa e.g., to assign them to the *Agropyretalia intermedio-repentis* order. Therefore, at this stage, we assign these communities, as in the original publication (Shapoval 2006), to the class *Festuco-Brometea*, order *Festucetalia valesiacae* and alliance *Festucion valesiacae*. Whereas these comunities are somewhat different from the typical communities of the alliance, we consider them as a separate suballiance *Galio ruthenici-Caricenion praecocis*. It is quite possible that in the future this suballiance will get the rank of alliance, but so far the lack of their own character species does not allow to consider them in the rank of a separate alliance. Cluster 2 (*Diantho guttati-Caricetum melanostachyae*) can be included in the same suballiance, although this association is slightly more mesophytic according to the results of phytoindication assessment, but according to the expert systems, it contains the most plots of the *Festuco-Brometea* class and true steppe habitat type – R1B. In addition, its floristic composition is quite similar to the previous association. Earlier these coenoses were described as association *Potentillo orientalis-Caricetum melanostachyae*; however, a significant increase in the plots used in our dataset revealed the sporadic nature of *Sibbaldianthe bifurca* subsp. *orientalis* (syn. *Potentilla orientalis*) in this syntaxon. Instead, *Dianthus guttatus* has a higher diagnostic value for this association (see Table 1). These features of the floristic composition, as well as nomenclature changes in relation to *Sibbaldianthe bifurca* subsp. *orientalis*, prompted us to reject the previous invalid name and describe these communities as a new association.

Units 3–5 obviously represent mesic grasslands and their mesophytic character was shown by the results of phytoindication. According to the results of the analysis using the EVC expert system, a significant number of plots are assigned to the class *Molinio-Arrhenatheretea*, which is also confirmed by the results of the analysis using the expert system EUNIS-ESy, which assigned these plots to mesic grassland habitats. Therefore, we classify them within the *Molinio-Arrhenatheretea* class. Among the higher-ranking syntaxa recognized in EuroVegCheklist, these communities are the most similar to the order *Althaeetalia officinalis* and its alliance *Althaeion officinalis*. Although the diagnosis of the order and alliance in the original publication (Golub 1995) is not clearly defined, its definition as "Tall-herb periodically flooded meadows of the steppe and semi-desert zones of Eastern Europe" in Mucina et al. (2016) is fully consistent with the steppe depression vegetation. Thus, we synonymize the previously described alliances of the mesic vegetation of the steppe depressions, *Carici praecocis-Elytrigion pseudocaesiae*, *Poo angustifoliae-Ferulion orientale*, and *Lythro virgati-Elytrigion pseudocaesiae*, as was done in a previous publication (Shapoval 2006), and consider them within the *Althaeion officinalis* alliance.

The wettest associations of depression bottoms (clusters 6–8) showed some inconsistency in their interpretation by expert systems – on the one hand, the EVC expert system assigned most of their plots to the *Molinio-Arrhenatheretea* class, and on the other hand the EUNIS-ESy expert system interpreted most of their plots as C (Surface waters) and Qb (Wetlands) groups. But this inconsistency is quite understandable given the ephemeral and complex nature of these habitats and irregularity of flooding. In view of this, we propose that the nature of these communities best fits the class *Isoëto-Nanojuncetea*, defined as "Pioneer ephemeral dwarf-cyperaceous vegetation in periodically freshwater flooded habitats of Eurasia" in Mucina et al. (2016). We include these units (two associations and one additional subassociation) to an alliance of steppe depression vegetation, which is currently accepted in the EVC – *Myosuro-Beckmannion eruciformis* – within the order *Nanocyperetalia*. The floristic composition of these communities is quite unique and differs significantly from other alliances of this order, such as the *Verbenion supinae* alliance, which includes pioneer ephemeral communities in the nemoral zone in habitats flooded with fresh water without signs of salinity or sweetening. Moreover, the fluctuating nature of ephemeral communities of *pody* hardly makes it possible to consider them as pioneer.

Cluster 9, according to the list of diagnostic species and the analysis using expert systems, can be assigned to the class *Festuco-Puccinellietea*. This is the only community that has a pronounced halophytic character, which distinguishes it from all other analyzed units. This difference, both floristic and ecological, might explain the erroneous attribution of the steppe depression vegetation in general to the halophytic type. This unit should probably be attributed to the order *Scorzonero-Juncetalia gerardi*. However, the transitional nature of the communities as well as the source of the chloride salinity does not currently allow them to be attributed to any of the existing alliances.

The obtained results once again showed that the vegetation of steppe depressions (*pody*) is indeed rather complex, but not «mosaic», because it was not possible to isolate phytocenoses of annual (ephemeral) plants characteristic for the class *Isoëto-Nanojuncetea*, and separate them spatially or in time from grassland or wetland communities of perennial plants. Even in the plots of small size in small depressions and bottom depressions with the longest duration of flooding, both ephemeral annual and perennial species were present. Of course, the increase in the plot size slightly changed the proportions of individual and total cover, but in no way affected the homogeneity and integrity of the studied plant communities. It can be assumed that with sufficiently long floods and increasing depth of a water body, some mesophytic or xeromesophytic plants, which are common in dry, non-flooded depressions, would disappear from the communities. Then we would probably get localized occurrences of ephemeral annual vegetation, confined to drying puddles. But irregular and short-term flooding of depressions (every 7–10 yrs, sometimes 20 yrs, lasting only 2–3 months), as well as the shallowness of temporary standing water (about 30–40 cm deep at the peak of the flood and then becoming shallow, 5–10cm) do not adversely affect perennial mesophytic species. It is worth noting that the closed bottoms of the depressions in the natural intact state is a perfectly flat surface, so the edaphic conditions, moisture regime and other abiotic parameters are almost identical throughout a flooded bottom. Thus, when the depressions are flooded and then begin to dry in the same season, peculiar combinations of ephemeral annual aquatic plants and perennial grassland and wetland plants are observed. These plants grow in different layers, but within the same phytocenosis. Such an original complex of hydrophytic vegetation ("ephemeretum") is indivisible either territorially or chronologically.

When interpreting the obtained units, we tried to compare them with the units described in the very first work on the *pody* vegetation (Solomakha et al. 2005). However, we did not succeed, since the diagnostic species of those associations were in most cases not concentrated in one cluster but distributed among different units in the dataset. We believe that the reason for this is that these units were identified using insufficiently representative data. With the increase in the number of vegetation plots from 34 to 367 (Shapoval 2006), and in the present work to 641, the blocks of diagnostic species have been dissolved. Therefore, we can say that, although they are somewhat similar to our associations, we cannot synonymize them. For example, we can assume that the association *Achilleo micranthoides-Poetum angustifoliae* is close to *Herniario glabrae-Poetum angustifoliae*; however, from the three species that are listed as diagnostic for *Achilleo micranthoidis-Poetum angustifoliae*, *Achillea micranthoides* has a fairly high fidelity in our clusters 3 and 4, *Poa angustifolia* in clusters 1 and 2, and *Potentilla argentea* in clusters 2 and 4, which may indicate their diagnostic significance for syntaxa of a higher rank than the association.

Our testing of two expert systems showed that they can be used as an additional tool for interpreting the results of vegetation classification, especially for assigning associations to syntaxa of a higher hierarchical rank. However, for such complex communities, and, accordingly, complex habitat types, the use of expert systems has limitations, since their nature is such that communities can contain species of different ecological groups, different vegetation classes, and, accordingly, different discriminant or functional species groups, which often overlap. These features prevent the correct interpretation of the relevés by an expert system.

Nomenclatural notes

Taking into account that all previously described units of the steppe depression vegetation are invalid, because the nomenclature type was not indicated using *expressis verbis* the Latin words '*typus*' or '*holotypus*'(ICPN Art. 5, par.3), we validly describe the syntaxa of the steppe depression vegetation which we accepted, according to the analysis presented in this paper. When validating the previously described syntaxa, we have kept all their nomenclature types, which are also presented in this article in the Suppl. material 1, but we have slightly modified the lists of diagnostic species of these syntaxa, in accordance with the taxonomic nomenclature used in this paper and the results of calculating their fidelity on the basis of the phi coefficient (Chytrý et al. 2002).

Suballiance ***Galio ruthenici-Caricenion praecocis***
Shapoval ex Shapoval et Kuzemko suball. nov. hoc loco

Validated name: *Galio ruthenici-Caricenion praecocis* Shapoval 2006 nom. inval. (Art. 5).

Holotypus hoc loco: ass. *Ferulo euxinae-Caricetum praecocis* Shapoval ex Shapoval et Kuzemko hoc loco.

Diagnostic taxa: *Bromopsis inermis*, *Carex praecox*, *Convolvulus arvensis*, *Cruciata pedemontana*, *Dianthus guttatus*, *Falcaria vulgaris*, *Galium ruthenicum*, *Galium spurium*, *Phlomis herba-venti* subsp. *pungens*, *Poa angustifolia*, *Seseli tortuosum*, *Veronica spicata*, *Vicia hirsuta*, *Vicia villosa*, *Viola kitaibeliana.*

Association ***Ferulo euxinae-Caricetum praecocis***
Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco

Validated name: *Ferulo euxinae-Caricetum praecocis* Shapoval 2006 nom. inval. (Art. 5).

Holotypus hoc loco: Shapoval (2006: table 13, relevé 12), or the same relevé in the Suppl. material 1, relevé 1010 (this paper):

V. Shapoval, 16.05.2005, 46.462707°N, 33.91405°E, plot size 9 m^2, total cover 90%, litter 70%.

Species (with cover of the Braun-Blanquet scale): *Bromopsis inermis* 3; *Carex praecox* 3; *Falcaria vulgaris* 2; *Galium ruthenicum* 2; *Ferula euxina* 2; *Poa angustifolia* 2; *Vicia hirsuta* 1; *Viola kitaibeliana* 1; *Vicia villosa* +; *Eryngium campestre* r; *Eryngium planum* r; *Limonium sareptanum* r.

Diagnostic taxa: *Bromopsis inermis*, *Carex praecox*, *Elytrigia repens*, *Falcaria vulgaris*, *Galium ruthenicum*, *Lamium amplexicaule* var. *orientale*, *Phlomis herba-venti* subsp. *pungens*, *Poa angustifolia*, *Salsola tragus*, *Vicia villosa*, *Viola kitaibeliana*

Association ***Diantho guttati-Caricetum melanostachyae***
ass. nov. hoc loco

Synonym: *Potentillo orientalis-Caricetum melanostachyae* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Shapoval (2006: table 14, relevé 4), or the same relevé in the Suppl. material 1, relevé 871 (this paper):

V. Shapoval, 12.07.2004, 46.456164°N, 33.918493°E, plot size 100m^2, total cover 95%, litter 5%.

Species: *Poa angustifolia* 4; *Carex praecox* 2; *Falcaria vulgaris* 2; *Galium ruthenicum* 2; *Sibbaldianthe bifurca* subsp. *orientalis* 2; *Veronica spicata* 2; *Allium flavum* subsp. *tauricum* 1; *Artemisia austriaca* 1; *Bromopsis inermis* 1; *Carex melanostachya* 1; *Convolvulus arvensis* 1; *Dianthus guttatus* 1; *Elytrigia repens* subsp. *pseudocaesia* 1; *Phlomis herba-venti* subsp. *pungens* 1; *Vicia hirsuta* 1; *Vicia villosa* 1; *Euphorbia esula* subsp. *tommasiniana* +; *Hylotelephium maximum* +; *Eryngium campestre* r; *Lactuca serriola* r; *Lepidium perfoliatum* r; *Rumex crispus* r; *Sisymbrium altissimum* r; *Tragopogon dasyrhynchus* r.

Diagnostic taxa: *Allium flavum subsp. tauricum*, *Carex melanostachya*, *Carex praecox*, *Dianthus guttatus*, *Eryngium planum*, *Euphorbia seguieriana*, *Falcaria vulgaris*, *Galium ruthenicum*, *Linaria biebersteinii*, *Poa angustifolia*, *Seseli tortuosum*, *Thesium arvense*, *Tragopogon dasyrhynchus*

Association ***Vicio lathyroidis-Alopecuretum pratensis***
Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco

Validated name: *Vicio lathyroidis-Alopecuretum pratensis* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Shapoval (2006: table 12, relevé 2), or the same relevé in the Suppl. material 1, relevé 1085 (this paper):

V. Shapoval, 17.05.2005, 46.476654°N, 33.862878°E, plot size 9m^2, total cover 80%, litter 5%.

Species: *Alopecurus pratensis* 3; *Poa angustifolia* 3; *Bromopsis inermis* 2; *Festuca valesiaca* 2; *Artemisia austriaca* 1; *Cerastium pumilum* 1; *Convolvulus arvensis* 1; *Lepidium draba* 1; *Medicago minima* 1; *Poa bulbosa* 1; *Taraxacum* sect. *Taraxacum* 1; *Veronica arvensis* 1; *Vicia lathyroides* 1; *Capsella bursa-pastoris* +; *Achillea micranthoides* r; *Crepis ramosissima* r; *Plantago lanceolata* r.

Diagnostic taxa: *Achillea micranthoides*, *Alopecurus pratensis*, *Arenaria leptoclados*, *Artemisia austriaca*, *Capsella bursa-pastoris*, *Carex spicata*, *Cerastium pumilum*, *Crepis ramosissima*, *Cruciata pedemontana*, *Festuca valesiaca*, *Lepidium draba*, *Medicago minima*, *Poa bulbosa*, *Stellaria graminea*, *Taraxacum sect. Taraxacum*, *Trifolium arvense*, *Trifolium retusum*, *Veronica arvensis*, *Vicia lathyroides.*

Association ***Herniario glabrae-Poetum angustifoliae*** *Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco*

Validated name: *Herniario glabrae-Poetum angustifoliae* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Suppl. material 1, relevé 932 (this paper):

V. Shapoval, 18.07.2004, 46.437786°N, 33.740333°E, plot size 100m^2, total cover 65%, litter 1%.

Species: *Inula britannica* 3; *Artemisia santonicum* 2; *Euphorbia esula subsp. tommasiniana* 2; *Holosteum umbellatum* 2; *Lotus angustissimus* 2; *Myosurus minimus* 2; *Poa angustifolia* 2; *Polycnemum arvense* 2; *Polygonum aviculare* 2; *Potentilla argentea* 2; *Trifolium retusum* 2; *Veronica arvensis* 2; *Achillea micranthoides* 1; *Carex praecox* 1; *Elytrigia repens* subsp. *pseudocaesia* 1; *Filago arvensis* 1; *Gypsophila muralis* 1; *Herniaria glabra* 1; *Linaria biebersteinii* 1; *Allium regelianum* +; *Crepis ramosissima* r; *Erysimum repandum* r.

Diagnostic taxa: *Achillea micranthoides*, *Allium regelianum*, *Artemisia santonicum*, *Gypsophila muralis*, *Herniaria glabra*, *Lepidium ruderale*, *Plantago lanceolata*, *Polycnemum arvense*, *Potentilla argentea*, *Ventenata dubia.*

Association ***Lathyro nissoliae-Phalacrachenetum inuloidis*** *Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco*

Validated name: *Lathyro nissoliae-Phalacrachenetum inuloidis* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Shapoval (2006: table 6, relevé 9)), or the same relevé in the Suppl. material 1, relevé 805 (this paper):

V. Shapoval, 27.05.2004, 46.618698°N, 34.198073°E, plot size 100m^2, total cover 50%, litter 40%.

Species: *Elytrigia repens* subsp. *pseudocaesia* 3; *Cyperus flavescens* 2; *Inula britannica* 2; *Phalacrachena inuloides* 2; *Rorippa brachycarpa* 2; *Eleocharis palustris* 1; *Lathyrus nissolia* 1; *Stellaria graminea* 1; *Vicia hirsuta* 1; *Senecio leucanthemifolius* subsp. *vernalis* +; *Crepis sancta* r.

Diagnostic taxa: *Armoracia rusticana*, *Crepis sancta*, *Cyperus flavescens*, *Inula britannica*, *Lathyrus nissolia*, *Lathyrus tuberosus*, *Phalacrachena inuloides*

Alliance ***Myosuro minimi-Beckmannion eruciformis*** *Shapoval ex Shapoval et Kuzemko all. nov. hoc loco*

Validated name: *Myosuro-Beckmannion eruciformis* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: ass. *Myosuro-Beckmannietum eruciformis* Shapoval ex Shapoval et Kuzemko hoc loco

Diagnostic taxa: *Butomus umbellatus*, *Chaiturus marrubiastrum*, *Damasonium alisma*, *Elatine alsinastrum*, *Gratiola officinalis*, *Juncus atratus*, *Lythrum virgatum*, *Mentha pulegium*, *Myosurus minimus*, *Rorippa brachycarpa*

Association ***Myosuro minimi-Beckmannietum eruciformis*** *Shapoval ex Shapoval et Kuzemko ass. nov. hoc loco*

Validated name: *Myosuro-Beckmannietum eruciformis* Shapoval 2006 nom. inval. (Art. 5)

Holotypus hoc loco: Shapoval (2006: table 5, relevé 10), or the same relevé in the Suppl. material 1, relevé 982 (this paper):

V. Shapoval, 12.08.2004, 46.557254°N, 33.472972°E, plot size 100m^2, total cover 80%, litter 2%.

Species: *Beckmannia eruciformis* 3; *Lotus angustissimus* 3; *Eleocharis palustris* 2; *Herniaria glabra* 2; *Myosurus minimus* 2; *Polygonum aviculare* 2; *Carex melanostachya* 1; *Elytrigia repens* subsp. *pseudocaesia* 1; *Gratiola officinalis* 1; *Gypsophila muralis* 1; *Inula britannica* 1; *Lythrum virgatum* 1; *Mentha pulegium* 1; *Rorippa brachycarpa* 1; *Trifolium retusum* 1; *Ambrosia artemisiifolia* +; *Plantago major* +.

Diagnostic taxa: *Aegilops cylindrica*, *Beckmannia eruciformis*, *Chaiturus marrubiastrum*, *Eleocharis palustris*, *Erigeron canadensis*, *Gratiola officinalis*, *Gypsophila muralis*, *Inula britannica*, *Lotus angustissimus*, *Lythrum virgatum*, *Mentha pulegium*, *Myosurus minimus*, *Polygonum aviculare*, *Xanthium orientale subsp. riparium*

Association ***Elatino hungaricae-Butometum umbellati*** *ass. nov. hoc loco*

Holotypus hoc loco: Suppl. material 1, relevé 675 (this paper):

V. Shapoval, 25.06.2010, 46.433217°N, 33.7257°E, plot size 100m^2, total cover 80%, litter 0%.

Species: *Butomus umbellatus* 4; *Chaiturus marrubiastrum* 1; *Elatine hungarica* 1; *Lythrum borysthenicum* 1; *Pholiurus pannonicus* 1; *Polygonum aviculare* 1; *Pulicaria vulgaris* 1; *Gratiola officinalis* +; *Plantago tenuiflora* +; *Rorippa austriaca* +; *Rorippa brachycarpa* +.

Diagnostic taxa: *Elatine hungarica*, *Juncus atratus*, *Lythrum borysthenicum*,

Subassociation ***Elatino-Butometum umbellati damasonietosum alismae*** *subass. nov. hoc loco*

Holotypus hoc loco: Suppl. material 1, relevé 641 (this paper):

V. Shapoval, 24.06.2010, 46.487017°N, 33.8533°E, plot size 100m^2, total cover 80%, litter 0%.

Species: *Eleocharis palustris* 3; *Elytrigia repens* subsp. *pseudocaesia* 3; *Butomus umbellatus* 1; *Damasonium alisma* 1; *Elatine alsinastrum* 1; *Euphorbia esula* subsp. *tommasiniana* 1; *Juncus atratus* 1; *Rorippa brachycarpa* 1; *Gratiola officinalis* +; *Lythrum virgatum* +; *Rorippa austriaca* +; *Rumex crispus* +.

Diagnostic taxa: *Alopecurus pratensis*, *Butomus umbellatus*, *Damasonium alisma*, *Elatine alsinastrum*, *Gratiola officinalis*, *Juncus atratus*, *Rorippa brachycarpa*, *Rumex crispus.*

Thus, the classification scheme of the steppe depression vegetation of Ukraine in accordance with our results has the following form:

Cl. *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947
Ord. *Festucetalia valesiacae* Soó 1947
All. *Festucion valesiacae* Klika 1931
Suball. *Galio ruthenici-Caricenion praecocis* Shapoval ex Shapoval et Kuzemko hoc loco
    Ass. *Ferulo euxinae-Caricetum praecocis* Shapoval ex Shapoval et Kuzemko hoc loco
    Ass. *Diantho guttati-Caricetum melanostachyae* Shapoval et Kuzemko hoc loco
Cl. *Molinio-Arrhenatheretea* Tx. 1937
Ord. *Althaeetalia officinalis* Golub et Mirkin in Golub 1995
All. *Althaeion officinalis* Golub et Mirkin in Golub 1995
    Ass. *Vicio lathyroidis-Alopecuretum pratensis* Shapoval ex Shapoval et Kuzemko hoc loco
    Ass. *Herniario glabrae-Poetum angustifoliae* Shapoval ex Shapoval et Kuzemko hoc loco
    Ass. *Lathyro nissoliae-Phalacrachenetum inuloidis* Shapoval ex Shapoval et Kuzemko hoc loco
Cl. *Isoëto-Nanojuncetea* Br.-Bl. et Tx. in Br.-Bl. et al. 1952
Ord. *Nanocyperetalia* Klika 1935
All. *Myosuro-Beckmannion eruciformis* Shapoval ex Shapoval et Kuzemko hoc loco
    Ass. *Myosuro-Beckmannietum eruciformis* Shapoval ex Shapoval et Kuzemko hoc loco
    Ass. *Elatino-Butometum umbellati* Shapoval et Kuzemko hoc loco
    Subass. *Elatino-Butometum umbellati typicum*
    Subass. *Elatino-Butometum umbellati damasonietosum alismae* Shapoval et Kuzemko hoc loco
Cl. *Festuco-Puccinellietea* Soó ex Vicherek 1973
Ord. *Scorzonero-Juncetalia gerardi* Vicherek 1973
All.?
    D.c. *Rumex ucranicus+Puccinellia distans*

Conservation values

We have noted 21 taxa in the depression communities that have a protected status, including nine species protected at the regional level in the Kherson oblast (Andriyenko and Peregrym 2012, Anon. 2013), six species from the Red Book of Ukraine (Didukh 2009), two species from the European Red List (Bilz et al. 2011), one species from the IUCN list (Anon. 2020) and three species having several protection statuses (Table 3). *Elytrigia repens* subsp. *pseudocaesia*, which is protected at the regional level and is found in all syntaxa of the *pody* vegetation, has the greatest frequency in the dataset. Among the species of national and international protection status, *Allium regelianum* has the highest frequency and is present in six units. In cluster 4, it has a constancy of 65.6%. This cluster, which we interpret as the association *Herniario glabrae-Poetum angustifoliae*, is characterized by the largest number of red listed species, 13 in all (see Table 3). It should also be not-

Table 3. Distribution of rare and endangered vascular plant taxa in nine units of *pody* vegetation (the cluster numbers correspond to their numbers in the text, see Section 4.1). Status of red-listed species: RBU – Red Data Book of Ukraine (Didukh 2009), RLKhO – Red List of Kherson oblast (Andriyenko and Peregrym 2012; Anon. 2013); Bern – Annex I of the Resolution 6 of Bern Convention (Anon. 2011); IUCN RL – The IUCN Red List of threatened species (Anon. 2020), Eu RL (Bilz et al. 2011); category correspond to IUCN categories. For each taxon, percentage frequency for all relevés (= Total) and per association are given.

Taxon	Status (category)	Total	Clusters								
			1	2	3	4	5	6	7	8	9
Achillea micranthoides	RLKhO	10.6		3.5	46.9	38.5		3.7	1.1		
Alisma gramineum	IUCN RL (dd)	0.3								4.7	
Allium regelianum	RBU (r), Bern, Eu RL (dd)	16.8	0.7	8.2		65.6	15.4		10.5	4.7	
Beckmannia eruciformis	Eu RL (dd)	19.3		4.7		1.6	5.8	75.9	30.5	65.1	94.4
Bellevalia speciosa	RLKhO	0.2	0.7								
Damasonium alisma	RBU (en), Eu RL (nt)	7.2		2.4		1.6				97.7	
Elatine alsinastrum	Eu RL (nt)	11.7		2.4		11.5			25.3	81.4	
Elatine hungarica	RBU (vu), RLKhO, Eu RL (dd)	5.1				0.8	11.5		24.2	7.0	
Elytrigia repens subsp. *pseudocaesia*	RLKhO	52.9	10.7	96.5	28.1	57.4	92.3	79.6	38.9	62.8	44.4
Ferula caspica	RLKhO	0.3	0.7	1.2							
Juncus sphaerocarpus	RBU (en)	2.2				5.7			7.4		
Lathyrus nissolia	RLKhO	2.8			6.3		30.8				
Lythrum thymifolia	RBU (vu)	7.3				20.5			22.1	2.3	
Peucedanum ruthenicum	RLKhO	3.3	12.1	4.7							
Phalacrachena inuloides	RLKhO	9.7		7.1	18.8	16.4	38.5		6.3	9.3	
Phlomis scythica	RBU (ne)	13.1	16.4	8.2	9.4	19.7			13.7	32.6	
Pholiurus pannonicus	RLKhO	6.1				9.8	3.8		21.1		27.8
Prunus tenella	RLKhO	0.2	0.7								
Stipa capillata	RBU (ne)	1.7	7.1	1.2							
Stipa ucrainica	RBU (ne)	0.2		1.2							
Tulipa scythica)	RBU (en)	0.6				3.3					
Total number of red listed taxa per vegetation unit		21	8	12	5	13	7	3	11	10	3

ed that the species protected at the national level, *Damasonium alisma*, has a clear coenotic confinement to cluster 8 (*Elatino-Butometum umbellati damasonietosum alismae*), in which its constancy reaches 97.7%.

Given the floristic, coenotic and habitat specificity of steppe depressions, as well as the absence of such units in the existing EUNIS hierarchy, and accordingly to Resolution 4 of the Bern Convention (Anon 1997), which makes it impossible to protect this habitat type in the Emerald Network of Ukraine, we have prepared proposals to include them into Resolution 4 (Kuzemko et al. 2017). In 2018, our proposals were adopted by the Steering Committee of the Bern Convention, and the depressions (*pody*) of the steppe zone of Ukraine were included as a complex type X36 to Resolution 4, accordingly, to the EUNIS classification (https://eunis.eea.europa.eu/habitats/8009), which requires a comprehensive study and protection of this habitat type. In 2019, we prepared proposals for the inclusion of seven new sites to the Emerald Network of Ukraine specifically for the preservation of the X36 habitat type. All these sites were officially recognized at the end of 2019 and included in the existing Emerald network. Taking into account their international conservation status, as well as the high proportion of red listed taxa, which was also confirmed by our research, the next step should be to develop effective management plans for the protection and maintenance of these communities and habitat types. The most important task is the maintenance of the optimal moisture regime, as well as the limits on land issues related to the current land reform in Ukraine; namely that it be impossible to plow them further.

Conclusions

Our analysis allowed us to propose an updated syntaxonomic system of mesic and wet grassland vegetation of the steppe depressions, which reflects their ecological and territorial differentiation, to restore a syntaxonomic status of a number of syntaxa that were considered doubtful, and to find a proper place of the steppe depression vegetation in the syntaxonomic system of the European vegetation (Mucina et al. 2016). Our study confirmed the existence of at least eight associations of the *pody* vegetation. We tried to correct nomenclatural aspects according to the current addition of the ICPN, and we have validated all syntaxa of the steppe depression vegetation of Ukraine, the existence of which has been proven by a comprehensive analysis using currently accepted methods of phytosociological research. The results of our study will contribute to further inventory of the steppe depression vegetation, organization of proper management and effective protection, which will preserve these unique habitats and provide a system of phytocenotic monitoring of their current state, structure, functional organization and dynamic trends.

Data availability

The data used in the paper are available as Supplementary material in *.xlsx format and in *.csv format.

Author contributions

V.S. formulated the idea of the paper, prepared the dataset for the analysis (85% of the relevés are his own), reviewed the literature, wrote a description of the obtained vegetation units and interpreted them at the level of associations, subassociations and alliances. A.K. planned the research, made all analyzes and interpreted the obtained units at the level of orders and classes. The authors jointly prepared the manuscript.

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Supplementary material

Supplementary material 1
Ordered relevé table of the steppe depression vegetation of Ukraine (*.xlsx)
Link: https://doi.org/10.3897/VCS/2020/62825.suppl1

Supplementary material 2
Ordered relevé table of the steppe depression vegetation of Ukraine (*.csv)
Link: https://doi.org/10.3897/VCS/2020/62825.suppl2

Supplementary material 3
Results of analyzes using expert systems EVC (A) and EUNIS-ESy (B) in units of steppe depression vegetation of Ukraine (*.pdf)
Link: https://doi.org/10.3897/VCS/2020/62825.suppl3

Supplementary material 4
Diagnostic, constant, and dominant species of the steppe depression vegetation of Ukraine (*.pdf)
Link: https://doi.org/10.3897/VCS/2020/62825.suppl4

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 2: 109–116
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LONG DATABASE REPORT ECOINFORMATICS

First vegetation-plot database of woody species from Huíla province, SW Angola

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Abstract

Angola is a country in south-central Africa, particularly rich in biodiversity. Despite the efforts recently made to document its biodiversity, there is a need for standardized sampling methods to document and compare the variety of ecosystems and plants occurring in the country. With this database report we aim to document the abundance and diversity of woody species in the woodlands of Huíla province. The database hosts the results of a standardised plot-based vegetation survey, consisting of 448 vegetation plots distributed throughout the 14 municipalities and Bicuar National Park. In total, 40,009 individuals belonging to 44 plant families were recorded and measured, belonging to 193 woody species. Species richness per municipality ranged from 32 to 126. The mean stem diameter (DBH) was 10.9 cm ± 7.5 cm. Small-size classes are increasingly dominated by few species, while the largest trees come from a wider range of species; miombo key-species dominated almost all size classes. Our study represents the first plot-based vegetation survey of any Angolan province and constitutes a useful source of information for conservation and management. Additionally, may constitute a powerful dataset to support future studies on biodiversity patterns and vegetation change over time and facilitate the elaboration of vegetation maps.

Taxonomic reference: Checklist of Angolan Plants (Figueiredo and Smith 2008), The African Plant Database (version 3.4.0) and A new classification of *Leguminosae* (LPWG 2017).

Abbreviations: DBH = Diameter at Breast Height; GIVD = Global Index of Vegetation-Plot Databases; LUBA = Acronym of the Herbarium of Lubango

Keywords

Angola, *Baikiaea-Burkea* woodland, database, Huíla province, miombo, woodlands/forests, woody species, vegetation survey

GIVD Fact Sheet: Vegetation-Plot Database of Woody Species from Huíla Province

GIVD Database ID: AF-AO-001			**Last update:** 2021-05-17
Vegetation-Plot Database of Woody Species from Huíla Province		**Web address:** http://www.givd.info/ID/AF-AO-001	
Database manager(s): Francisco Gonçalves (francisco.goncalves@isced-huila.ed.ao); António Chisingui (valter.chissingui@isced-huila.ed.ao); José Tchamba (jose.tchamba@isced-huila.ed.ao)			
Owner: ISCED-Huíla, Rua Sarmento Rodrigues, N.º 2, C.P. 230, Lubango-Angola			
Scope: The database contains information on diversity, abundance and diameter (DBH>5 cm) of woody species from the woodlands of Huíla province, Angola. The species were locally identified based on familiarity of team members with local/regional flora or using the available field guides.			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): Excel		**Export format(s):** Excel, CSV file	
Plot type(s): nested plots		**Plot-size range (m^2):** 100 to 1000	
Non-overlapping plots: 448	**Estimate of existing plots:** 448	**Completeness:** 100%	**Status:** completed and continuing
Total no. of plot observations: 448	**Number of sources (biblioreferences, data collectors):** 0		**Valid taxa:** 193
Countries (%): AO: 100			
Formations: Forest: 100% = Terrestrial: 100%			
Guilds: woody vascular plants: 100%			
Environmental data (%): altitude: 100 slope inclination: 100; surface cover other than plants (open soil, litter, bare rock etc.): 100; land use categories: 100; soil depth: 100; other attributes: At least one soil sample per plot was collected, depth depends on soil characteristic.			
Performance measure(s): presence/absence only: 100%; number of individuals: 100%; measurements like diameter or height of trees: 100%			
Geographic localization: GPS coordinates (precision 25 m or less): 100%			
Sampling periods: 2010-2019: 100%			
Information as of 2021-05-17; further details and future updates available from http://www.givd.info/ID/AF-AO-001			

Introduction

Africa's total forest area is estimated at 675 Mha, or about 23% of land area (PROFOR 2012). Globally, the value of forests to society is becoming increasingly evident, as they play an important role in the livelihoods and economic development of many communities and countries which depend on intact forests (Mayaux et al. 2005, FAO and UNEP 2020). Despite the global importance of forests and woodlands, there is an increasing pressure on forest resources and the situation in Angola is no exception. Replacement of forests by agriculture, urbanisation, or construction of infrastructure, charcoal production, timber exploitation of valuable tree species and human-ignited fires are among others the main causes for deforestation and forest degradation in Africa. Together, these drivers of change have contributed to an estimated loss of 13.7% of intact forests in Angola over the last decade (Schneibel et al. 2016, Potapov et al. 2017).

According to the preliminary results of the National Forest Inventory, Angola has an estimated forest cover of about 69.3 Mha, corresponding to 55.6% of the national territory (FAO 2018). Unfortunately, this document only provides a general overview of the state of forest resources in Angola; important data to understand the social-ecological dynamics of the woodland ecosystems are still lacking. Adding to that are unpredictable effects of climate change, which is expected to bring more frequent and intense droughts to some parts the country (Catarino et al. 2020). In fact, the southern and south-eastern parts of Angola are currently experiencing severe droughts, posing additional threats to forest resources, as local populations are driven to explore the available natural resources even more to meet their daily needs.

In Angola, several vegetation studies have been conducted, aiming to document the diversity of plants and to map the vegetation (Gossweiler and Mendonça 1939, Barbosa 1970, Stellmes et al. 2013). However, most of the early studies lack detailed descriptions of the species composition and plant diversity (Revermann et al. 2016). An approach based on the quantitative analysis of woody species was introduced by Monteiro (1970); this study conducted on the Bié plateau provided an excellent first overview of the composition of woody species in the woodlands of the Bié province. Over the last decade, relevant research projects in Angola have adopted plot-based surveys in their vegetation studies; most of them rely on standard plot sizes of either 10 × 10 m or 20 × 50 m, e.g., the Future Okavango Project (TFO) and the Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL). Other initiatives, however, have introduced other survey approaches,

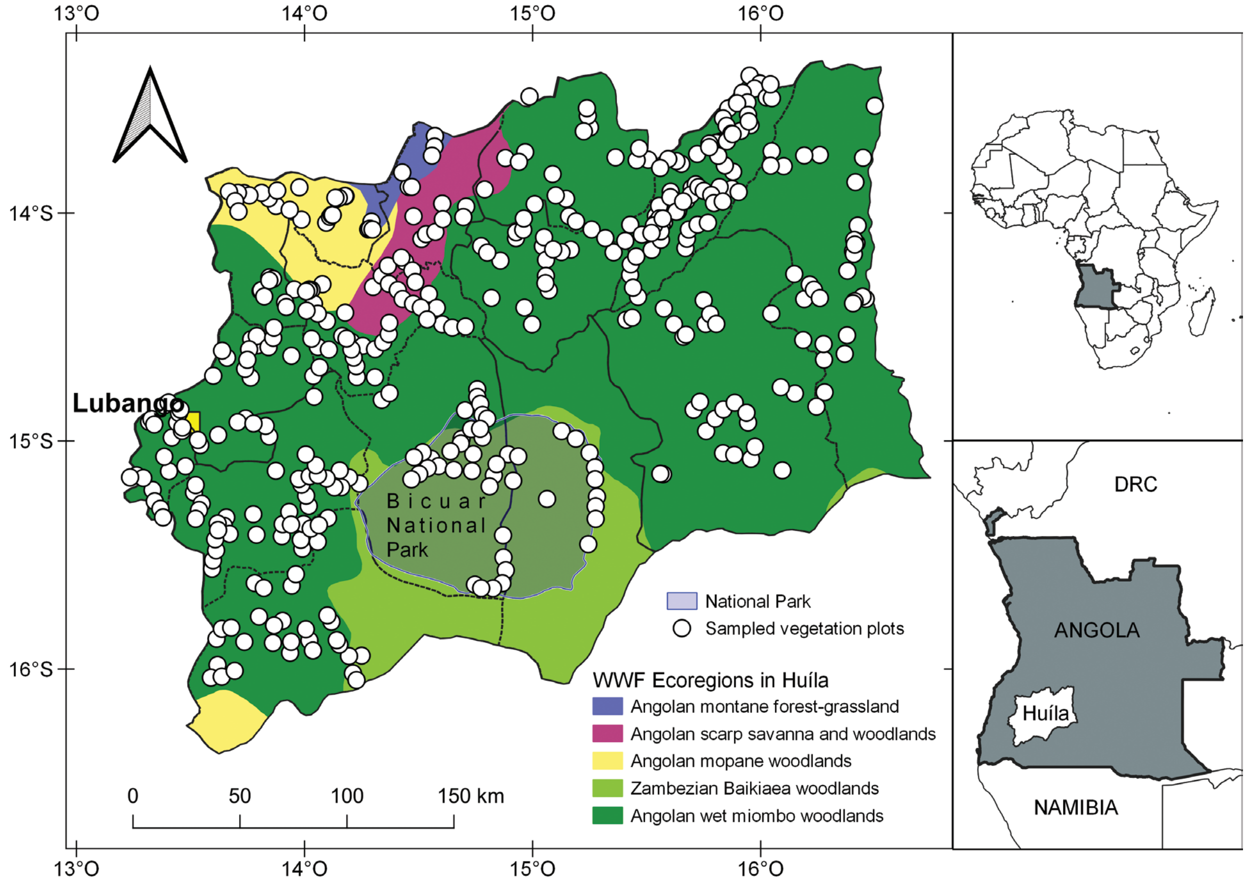

Figure 1. Map of Huíla province with municipalities (sub-polygons), ecoregions (color surfaces), and the location of the vegetation relevés (white dots) stored in the database.

looking in more detail at vegetation structure and strata, in order to allow for structural and functional analyses of these woodlands (FAO 2009, SEOSAW partnership 2021).

The studies which resulted from the mentioned research initiatives have greatly contributed to understand the diversity and composition of species at national and regional scale and provided powerful datasets (Revermann et al. 2016, Godlee et al. 2020). Despite these pioneer studies, systematic biodiversity surveys based on a standard plot design are still lacking for large parts of the forests and woodlands in Angola. Therefore, further plot-based vegetation surveys are of crucial importance to quantify forest resources and to provide data to support a sustainable management and conservation of woodland resources in Angola.

Our study represents the first vegetation-plot database of Huíla province, Angola, and contains data on diversity, abundance and DBH of woody species in the woodlands of the region. Using the data from this vegetation database, we provided the first classification of the woodlands of the Huíla province (Chisingui et al. 2018) and a comparative assessment of above-ground biomass in the western miombo region (Sichone et al. 2018).

Study area

The database covers the entire territory of Huíla province located in the highlands of southwest Angola. The province is divided into 14 municipalities and has an area of 78,879 km^2. The region falls within the Dry Winter Temperate bioclimate (Cwb) according to the Köppen-Geiger classification, being predominantly characterized by a warm temperate climate with a dry winter (Kottek et al. 2006). Mean annual temperature varies between 18 and 20°C and mean annual precipitation varies from about 700 mm in the southwest to ca. 1000 mm in the east. The province is inhabited by approximately 2.4 million people, belonging to various ethnic groups, being the second most populated province of Angola, after the capital province of Luanda (INE 2016). Apart from agriculture and livestock, extractive industries and tourism are the principal socio-economic activities (CESO 2010). Barbosa (1970) described eight vegetation units within Huíla province, while Chisingui et al. (2018) recently reported 14.

Data collection

The database comprises data about the woody vegetation sampled in 448 vegetation plots, distributed in the five ecoregions which extend into Huíla (Dinerstein et al. 2017) (Figure 1).

Vegetation sampling was based on the plot design adapted from the BIOTA Biodiversity Observatories (Jürgens et al. 2012). Each plot had a rectangular design of 20

× 50 m with one 10 m × 10 m nested subplot in the centre (Figure 2).

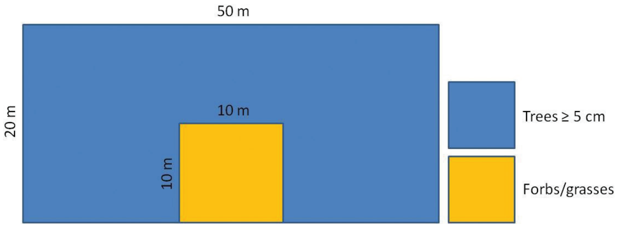

Figure 2. Plot design used in the vegetation surveys of the woodlands of Huíla province, note that we used the entire 1000 m^2 plot for tree measurements.

The vegetation relevés were carried out over approximately four years (2014–2018), mostly during the rainy season to ensure correct identification of plants, as many of the woody species in the region are deciduous. Since we had no a priori knowledge about the occurring woodland types (and associated plant communities), we aimed to standardise the sample coverage, trying to locate a comparable number of plots per municipality. Additionally, a slightly greater sampling effort was made in remote and sparsely populated areas, like Bicuar National Park, to integrate woody vegetation of little disturbed areas in our approach.

Plots were sited in areas of homogenous vegetation, the plots location was occasionally adjusted due to problems of accessibility, habitat fragmentation and dense or thorny vegetation. Plots were located at least 5 km apart, to minimize spatial autocorrelation and to capture spatial variation. In the entire 1000 m^2 plot, all tree species with DBH ≥ 5 cm were measured and identified on site to species or at least genus level, using the expertise on regional flora of the team members, and available field guides (Palgrave 2005). If on-site identification was not possible, a voucher was collected for identification at the Herbarium of Lubango [LUBA], based on other specimens deposited there, and on online resources (e.g. http://coicatalogue.uc.pt/; http://powo.science.kew.org/; http://theplantlist.org/; http://www.worldfloranoline.org/). Using the extended Braun-Blanquet cover-abundance scale (Dengler 2017), we estimated the cover for each woody as well as forb and grass species within the 100 m^2 subplot for the description of the overall plant community. Besides DBH, we also measured canopy height of the tallest and smallest tree using digital clinometers (Haglöf Vertex). Other environmental and site characteristics, including soil samples were also collected in each vegetation plot.

Database content

The vegetation-plot database of woody species from Huíla province **AF-AO-001** is registered at the GIVD – Global Index of Vegetation Databases (http://www.givd.info/ID/AF-AO-001). Overall, the database contains a total of 40,009 individuals of 193 tree species (incl. eight subspecies and five varieties), 40 tree taxa were only identified to genus, while 42 are yet to be confirmed. For consistency in the taxonomy of plants we used the Checklist of Angolan Plants as reference (Figueiredo and Smith 2008). To clean the data and to avoid any errors in the general database we used the “OpenRefine” tool (http://openrefine.org). To avoid misspelling of scientific plant names we standardized the names using the package “Taxonstand” version 2.2 (Cayuela et al. 2019) in R v3.4.3 (R Development Core Team 2021). Some tree species were preliminarily identified by their local names and we used various bibliographical sources to assign the scientific name (dos Santos 1972, Figueiredo and Smith 2012, Gonçalves et al. 2019). The family names followed mostly the African Plants Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php). However, we decided in some cases to adopt recent changes in family assignments, in particular for *Aloe – Asphodelaceae*; *Cochlospermum – Bixaceae*; *Bridelia*, *Hymenocardia*, *Phyllanthus*, *Pseudolachnostylis*, and *Uapaca – Phyllanthaceae*; *Adansonia* and *Grewia – Malvaceae* and *Ptaeroxylon – Rutaceae*. Similarly, we adopted the most recent classification of the *Fabaceae* subfamilies (LPWG 2017).

The municipalities of Matala and Quipungo show fewer plot numbers, as most of their administrative territories falls within Bicuar National Park. The heavily fragmented woodlands in the municipality of Caluquembe made it difficult to allocate vegetation plots and are, thus, also represented by fewer plots. In Humpata woodlands are very patchy since geoxyle grasslands dominate vast areas, so that we only assessed the 100 m^2 subplots. A total of 44 families of vascular plants (including *Fabaceae* subfamilies) were recorded. The ten most dominant families in terms of individual records were: *Fabaceae*, subfamilies *Detarioideae* (58%), *Papilionoideae* (6%) and *Caesalpinioideae* (5%), followed by *Combretaceae* (13%), *Phyllanthaceae* (5%), and *Euphorbiaceae* (5%) other families showed only few individuals (Figure 3).

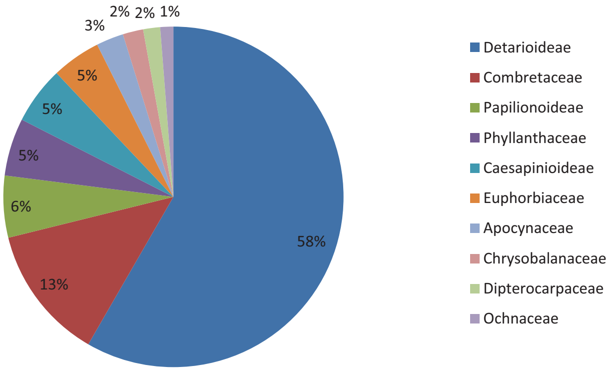

Figure 3. The ten most abundant families of vascular plants in the woodlands of Huíla.

Table 1. The ten most abundant woody species in terms of numbers of recorded individuals, including the families they belong to, municipalities in which they have been recorded and their respective mean DBH in cm plus Standard deviation (mean±sd).

Species (No. of Individuals)	Botanical family	Sites (municipalities)	DBH (cm)
Julbernardia paniculata (6691)	Detarioideae*	All municipalities, except in Gambos	11.5 ± 5.8
Brachystegia spiciformis (4547)	Detarioideae*	Except in Bicuar, Chicomba, Cuvango, Gambos, Humpata, and Matala	14.7 ± 10.6
Brachystegia longifolia (2259)	Detarioideae*	Except in Bicuar, Cacula, Chibia, Gambos, Humpata, and Matala	10.5 ± 5.2
Brachystegia boehmii (2133)	Detarioideae*	All municipalities	11.4 ± 6.1
Combretum collinum (1628)	Combretaceae	All municipalities	8.5 ± 4.1
Cryptosepalum exfoliatum subsp. *pseudotaxus* (1520)	Detarioideae*	Except in Bicuar, Cacula, Caluquembe, Chicomba, Gambos, Humpata, Matala, and Quipungo	9.2 ± 5.1
Colophospermum mopane (1369)	Detarioideae*	Recorded in Chibia, Gambos and Quilengues only	12.3 ± 8.4
Spirostachys africana (1222)	Euphorbiaceae	Except in Caconda, Caluquembe, Chicomba, Chipindo, Cuvango, Jamba, Matala, and Quipungo	9.6 ± 6.2
Pteleopsis anisoptera (1010)	Combretaceae	All municipalities, except in Caconda	9.4 ± 5.4
Diplorhynchus condylocarpon (930)	Apocynaceae	Recorded in all municipalities, except in Gambos, Humpata, and Matala	11.4 ± 9.4

*refers to the subfamily (*Detarioideae*) of the larger *Fabaceae* family.

Trees belonging to the *Fabaceae* subfamily *Detarioideae* were the most frequent across the sites. *Brachystegia spiciformis* exhibited the highest mean DBH, while *Combretum collinum* had the lowest mean DBH (Table 1).

Tree species richness calculated from the total number of taxa per municipality varied between 32 in Matala and 126 in Quilengues. The overall Shannon-Wiener diversity index (H'), calculated from the abundance of tree species per municipality, revealed also highest diversity of tree species in the municipality of Quilengues compared to others. The exceptional diversity of tree species found in Quilengues can be explained by the fact that this municipality includes parts of four important ecoregions and, thus, harbours many different vegetation units and species (Table 2).

Table 2. Overview of the study sites (the 14 municipalities and Bicuar NP), number of plots per site, total number of individuals, number of taxa and diversity (H') calculated from the abundance of tree species.

Municipalities	No. of plots	Taxa	No. Individuals	Shannon diversity (H')
Bicuar National Park	34	53	1782	2.71
Caconda	20	63	2760	2.54
Cacula	36	94	1744	3.15
Caluquembe	16	69	1498	3.08
Chibia	40	100	3124	3.29
Chicomba	20	78	2858	2.83
Chipindo	80	103	9465	2.93
Cuvango	34	86	4187	2.68
Gambos	30	57	2547	2.42
Humpata	15	60	1109	2.43
Jamba	30	51	2940	2.57
Lubango	31	99	2367	3.23
Matala	9	31	619	2.64
Quilengues	39	125	2690	3.79
Quipungo	14	56	714	2.85

It is a well-known phenomenon that the species richness increases with increasing sampling effort. This is particularly true for the municipality of Chibia for instance. However, in some places like Caluquembe also exhibited high-species richness, although the number of plots was lower due to fragmentation, caused by expanding agriculture. The influence of habitat fragmentation on biodiversity has been discussed by ecologists for a long time (Fahrig 2003). Recent studies indicate that habitat loss and fragmentation may have complex effects on species diversity, suggesting that variation in species diversity can be influenced by the total amount of habitat (Rybicki et al. 2020). Aguirre-Gutiérrez (2014) argues that the effect of fragmentation is dependent on the vegetation type and that these are not strongly related to species richness and diversity. From our point of view, the high species richness observed in Caluquembe can also be related to vegetation plots covering forest patches of the scarp savanna and woodlands ecoregion, considered of high diversity of vegetation types and significant levels of endemism (Goyder and Gonçalves 2019).

The mean DBH in the vegetation plots was 10.9 cm (±7.5), ranging from 5 cm to 218.7 cm. Small-size classes are increasingly dominated by few species, the five most dominant tree species are different for each size class, except for *Julbernardia paniculata* and *Brachystegia spiciformis*, which occur everywhere and in every size class (Figure 4). In general key-species of miombo woodlands were the most dominant trees across size classes, only interrupted by the presence of *Baikiaea plurijuga* and *Colophospermum mopane* in the intermediate and larger size classes. Size classes (+50 cm) were mostly dominated by individuals of *Brachystegia spiciformis* recorded in Gambos and Quilengues, and *Diplorhynchus condylocarpon* together with *Adansonia digitata* all from the woodlands of Quilengues, *B. plurijuga*, recorded only in the less disturbed areas of Bicuar and Gambos, exhibited also larger diameter.

Conclusion

The Huíla vegetation plot database (AF-AO-001) represents the first plot-based dataset of woody species in Huíla province. It comprises information from all 14 municipal-

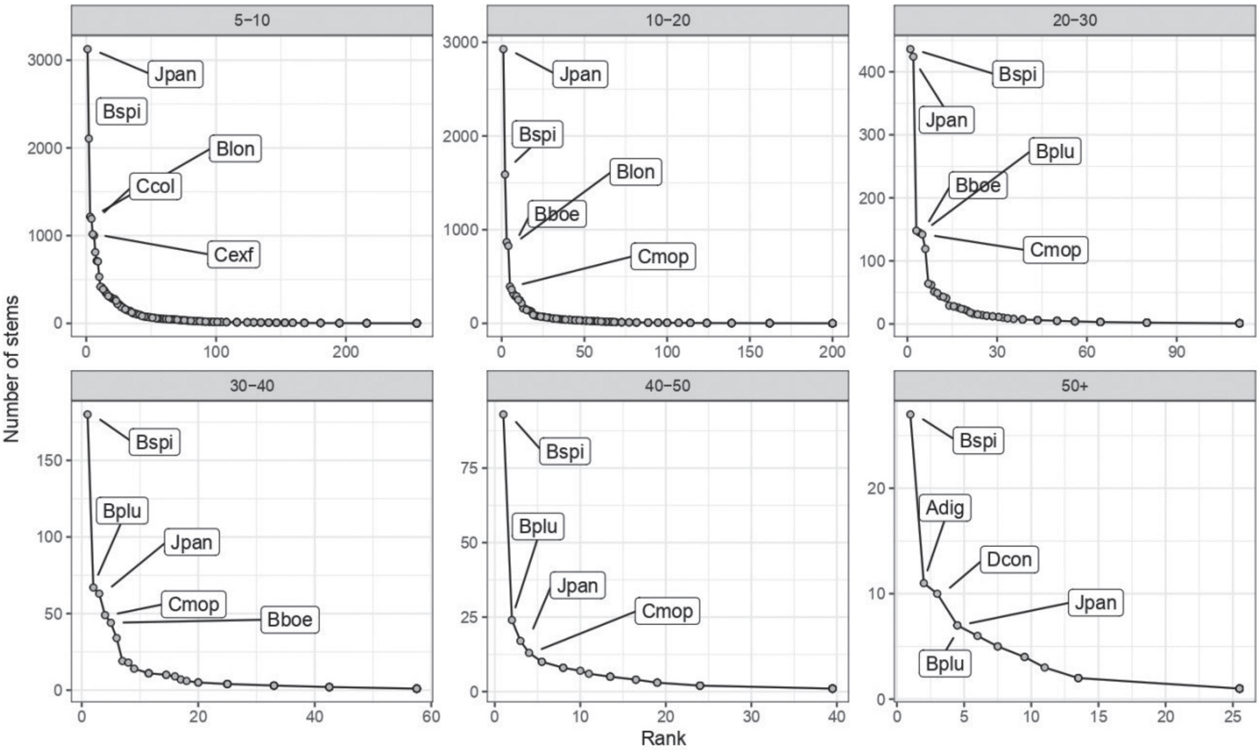

Figure 4. Rank abundance curve for the ten most abundant tree species per size class, as shown on the curves by their abbreviaton: *Adansonia digitata* (Adig), *Baikiaea plurijuga* (Bplu), *Brachystegia boehmii* (Bboe), *B. longifolia* (Blon), *B. spiciformis* (Bspi), *Colophospermum mopane* (Cmop), *Combretum collinum* (Ccol), *Cryptosepalum exfoliatum* subsp. *pseudotaxus* (Cexf), *Diplorhynchus condylocarpon* (Dcon) and *Julbernardia paniculata* (Jpan).

ities and Bicuar National Park. The information provided here constitutes a useful tool for management and conservation actions and may serve as a baseline for subsequent studies to analyse biodiversity patterns and assess changes in vegetation.

Future perspectives

This database may also provide the foundation for the elaboration of an envisaged vegetation map of this region. In addition to this work, we intend to explore additional information related to shrub and herbaceous plants, based on the identification of the botanical vouchers, field notes and photograph records collected during the field campaigns, to produce a preliminary checklist of the vascular plants of Huíla. The database of woody species from Huíla province may also be used for comparable studies with other plot data, using the same standard sampling plots in the African continent.

Authors contribution

F.M.P.G. conducted field work (incl. data collection, collection and identification of plants), conceptualized the MS and provided overall supervision to assure the quality of the database. A.V.C. conducted field work, project and database management. J.C.L. and M.F.F.R. conducted field work, conception and curation of the database. J.J.T. conducted field work combined with plant identification, J.L.M.A. helped with the conceptual design of the manuscript. H.D.J., I.M.C.C., B.R.B., M.D.G.C. and M.J.C. did field work and data collection. S.K.A.M. participated in the conceptualization and curation of the database. M.F. and P.M. helped with data collection in Bicuar National Park and with data analysis, N.J. contributed to study design, R.R. participated in field work in the municipalities of Cuvango and Jamba. All authors critically revised the final manuscript.

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VEGETATION CLASSIFICATION AND SURVEY

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RESEARCH PAPER

Long term changes of the inner-alpine steppe vegetation: the dry grassland communities of the Vinschgau (South Tyrol, Italy) 40–50 years after the first vegetation mapping

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Abstract

Aims: The Vinschgau is the driest inner-alpine valley in the Eastern Alps and harbours a unique steppe vegetation. We studied these dry grassland communities and aimed to answer the following questions: Which plant communities can be found currently? Do the syntaxa described by Braun-Blanquet in the 1960s still prevail in the area? Has there been any change in species composition over the last 40–50 years? **Study area:** Along an approximately 40 km transect, the south-facing slopes of the Vinschgau valley (South Tyrol, Italy) from Mals to Plaus were investigated. **Methods:** For the classification, 92 relevés were sampled in 2019 and compared with 76 relevés from the 1960s and ´70s by means of vegetation tables and ordinations (Detrended Correspondence Analysis). **Results:** Based on our investigation, the majority of dry grassland communities can be classified as *Festuco-Caricetum supinae*. Three subassociations were defined by the dominant species *Stipa capillata*, *Bothriochloa ischaemum* and *Stipa pennata* agg. The comparison of new and old relevés shows an increase in species from the class *Sedo-Scleranthetea* (e.g. *Trifolium arvense*, *Erodium cicutarium*) and the association *Artemisieto-Agropyretum*. In addition, ruderal elements (e.g. *Erigeron annuus*, *Convolvulus arvensis*) have also migrated into dry grasslands. A shift in the dominance over time can be recognized as well. In particular, *Festuca rupicola* and to some extent also *Stipa capillata*, have increased in abundance and frequency. **Conclusions:** We suggest to include the investigated closed dry grasslands in the alliance *Festucion valesiacae*. The rank of the character species at association, alliance and order level should be re-analysed. In order to obtain a better syntaxonomic overview of western and eastern alpine dry grassland communities in relation to Eastern European dry grasslands, a comprehensive study is absolutely necessary. Furthermore, long-term vegetation dynamics and vegetation change need to be studied in more detailed future studies.

Taxonomic reference: Fischer et al. (2008).

Syntaxonomic references: Mucina et al. (2016) for syntaxa from alliance to class level; Braun-Blanquet (1961) for associations.

Abbreviations: agg. = aggregate; cf. = confer (means 'compare'); DCA = Detrended Correspondence Analysis; s. lat. = sensu lato; s. str. = sensu stricto

Keywords

biodiversity, *Festuco-Brometea*, *Festucetalia valesiacae*, inner-alpine steppes, syntaxonomy, vegetation change

Introduction

The Eurasian steppe belt is the largest steppe region and stretches from the Amur in the east to the Hungarian basin in the west (Hurka et al. 2019). Generally, the Eurasian steppe vegetation harbours a unique and species-rich flora (Dengler et al. 2012; Wilson et al. 2012) and is a key habitat for several animal species (cf. Calaciura and Spinelli 2008; Zulka et al. 2014), especially for insects such as butterflies (WallisDeVries and van Swaay 2009), as well as wild bees, grasshoppers and beetles (WallisDeVries et al. 2002). At the same time, steppes are highly threatened mainly by land use change, e.g. agricultural intensification or abandonment (Habel et al. 2013; Török et al. 2016). A further impact by the ongoing environmental and climate change can be assumed as well (Janssen et al. 2016; Wesche et al. 2016). In contrast to the Eastern steppes, which depend on macroclimate, the Central European steppe vegetation is primarily determined by special edaphic and microclimatic factors. In Central Europe, hence, xerophytic vegetation often has a small expansion and disjunct distribution. These inherently small-scale dry grasslands can be considered as “primary” dry grasslands. The anthropogenic transformation of the landscape, in particular through deforestation of thermophilic woodlands followed by grazing or mowing, led to an area expansion of these “primary” dry grasslands. These dry grasslands, created by anthropogenic influence, make up a significant proportion of the current area of the steppe vegetation in Europe and can be referred to as “secondary” dry grasslands. The exact distinction between primary and secondary dry grasslands is not always possible, however, and this classification is subject to debate (Pott 1996; Ellenberg and Leuschner 2010; Hurka et al. 2019). Outside the Eurasian steppe belt, therefore, there are only azonal islands of steppe vegetation, for instance in central and southern Germany, in Lower Austria and in the inner-alpine dry valleys in the Central Alps (Hurka et al. 2019). The steppe vegetation in these valleys was defined as ”Inneralpiner Trockengürtel”, i.e. inner-alpine dry belt, by Braun-Blanquet (1961, Figure 1) extending from the Durance valley (France) near the Provence across the Vinschgau (South Tyrol, Italy) northeast to Styria (Austria). These valleys harbour a unique steppe flora. Beside (sub)mediterranean species which occur widely in these dry grasslands, especially Eastern steppe species can reach very far to the west in the inner-alpine dry valleys and often have their western-most occurrences in the region (Braun-Blanquet 1936, 1961; Wagner 1941; Ellenberg and Leuschner 2010; Dengler et al. 2020). The origin and evolution of the extra-zonal steppe vegetation is much discussed (Hurka et al. 2019). A recent study (Kirschner et al. 2020), however, pointed out, that some inner-alpine steppe species are phylogenetically largely independent from their eastern relatives so that these steppes can be seen as a relict steppe vegetation. Within the inner-alpine dry belt, the valleys differ in the strength of the continental climate so that there are extreme and more moderate dry valleys (Figure 1), hence, the flora and plant communities differ between the valleys as well (Braun-Blanquet 1961; Schwabe and Kratochwil 2004). In the driest valley of the Eastern Alps, the Vinschgau, dry grasslands mostly occur along the south-west to south-east facing slopes, the so-called “Vinschgauer Leiten”, over approximately 40 km from Mals to Naturns-Plaus (Braun-Blanquet 1961). In addition to the special climatic conditions (Schenk 1949, 1951), especially the lower precipitation on the south-facing slopes, grazing is a primary factor for the occurrence and distribution of these highly diverse communities (Braun-Blanquet 1961; Strimmer 1968; Ellenberg and Leuschner 2010). The interest of botanists for the unique steppe vegetation in South Tyrol resulted into a number of scientific studies at the beginning of the 20th century (citations in Peer 1980). However, apart from the general syntaxonomic overview of the entire inner-alpine dry vegetation by Braun-Blanquet (1961), which still represents the most comprehensive classification of the inner-alpine xerophytic vegetation so far, and the more recent and more ecologically focused overview by Schwabe and Kratochwil (2004, 2012), there are only few phytosociological studies on a regional scale. Recently, inner-alpine dry grasslands in Switzerland were studied (Dengler et al. 2019, 2020) and new syntaxonomical classifications on the European level for the class *Festuco-Brometea* were published (Willner et al. 2017, 2019). However, none included data from the Vinschgau.

In the past, three local scientists were concerned with vegetation mapping and ecophysiological investigations (Strimmer 1968, 1974; Florineth 1973, 1980; Köllemann 1979, 1981), building up the most comprehensive description for the steppe vegetation of Vinschgau. Several other publications were dedicated to selected communities (e.g. Staffler and Karrer 2001; Wilhalm et al. 2008) or floristical research (e.g. Wilhalm 2007; Wilhalm et al. 2007; Zippel and Wilhalm 2009).

Due to the essential impacts on vegetation, such as climate change (Gobiet et al. 2014), land use change (Lüth et al. 2011) and atmospheric nitrogen input (Willner et al. 2019), it is doubtful whether the actual Vinschgau dry grassland communities still correspond to the syntaxa described by Braun-Blanquet (1961) and to the communities outlined by the three local scientists 40 to 50 years ago. Already Schwabe and Kratochwil (2004) have noticed ruderalization trends. Therefore, considerable alterations of the communities may be expected.

In the present study we aimed to repeat the relevés performed in the 1960s and 1970s by the three local authors Strimmer (1968), Florineth (1973) and Köllemann (1979). We visited the sites together with them and they identified quite precisely the localities of their relevés in the field and on their vegetation maps. A total of 76 old relevés of typical dry grasslands were then selected and repeated in 2019.

First, we were interested to check if the character species of the syntaxa described by Braun-Blanquet (1961) are still valid. Second, we compared old and new relevés by means of vegetation tables and ordinations and

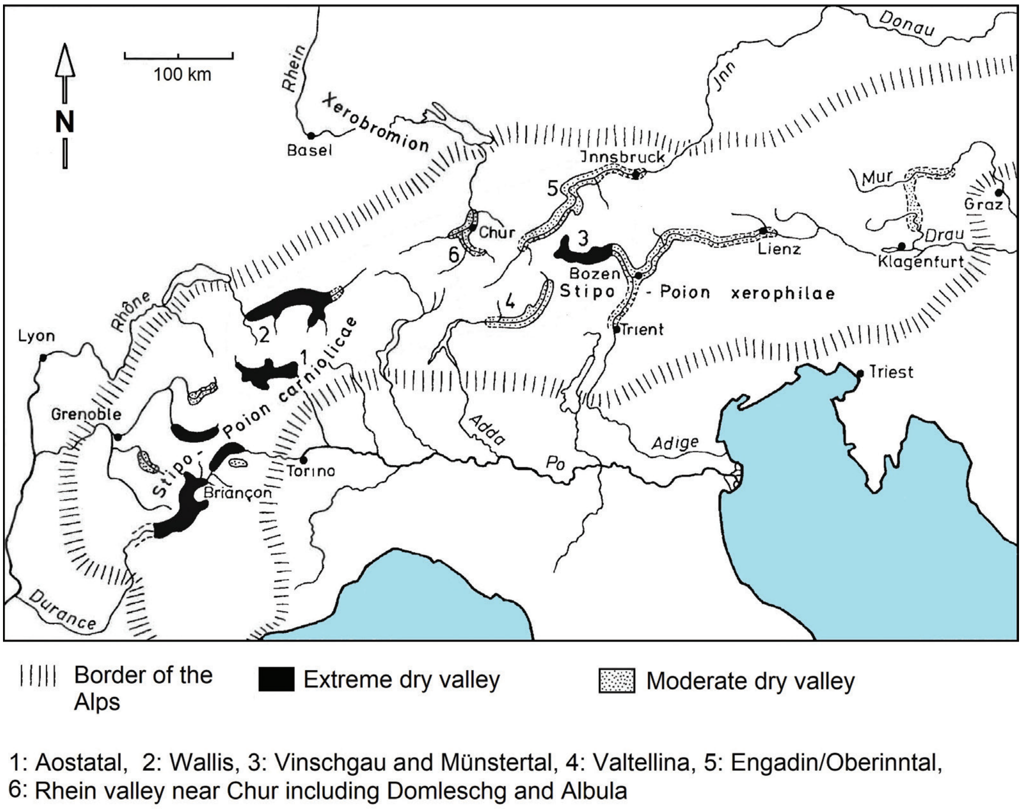

Figure 1. Distribution of the inner-alpine dry valleys (with friendly permission by Angelika Schwabe-Kratochwil, according to Braun-Blanquet (1961), modified by M. Lübben) and the two alliances (*Stipo-Poion carniolicae* and *Stipo-Poion xerophilae*) described by Braun-Blanquet (1961, see also Mucina et al. 2016).

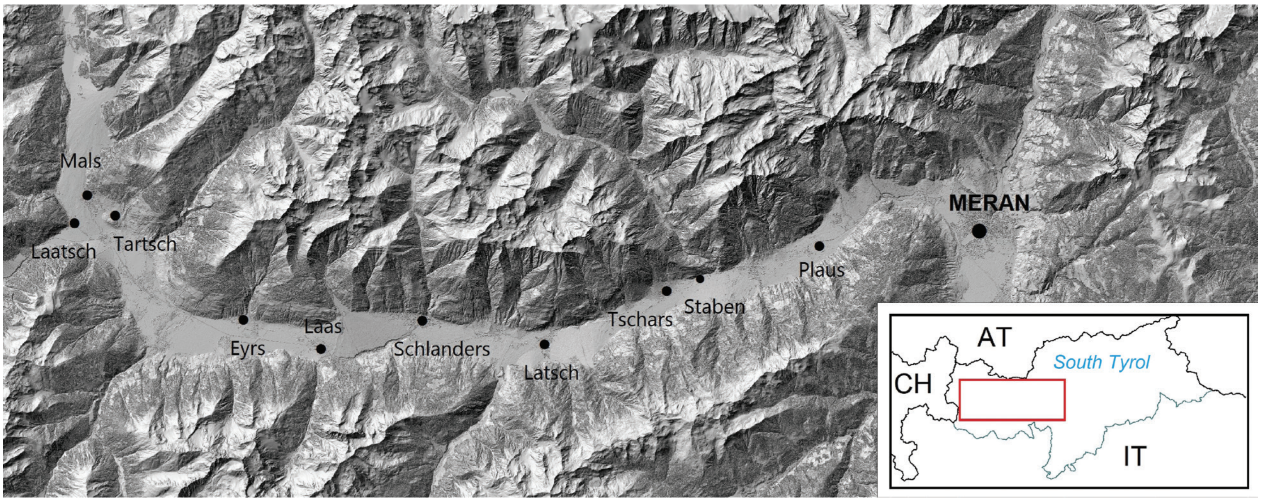

Figure 2. The investigated study area in the Vinschgau (South Tyrol, Italy) at the south-facing slopes from Mals and Laatsch to Plaus, spanning a length of approximately 40 km (Source: Office for Geology and Building Materials Testing of the Autonomous Province of Bolzano and ISPRA (big map); Eurostat (https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units) EuroGeographics for the administrative boundaries (small map)).

analysed the species composition qualitatively as well as quantitatively. The following hypotheses were outlined: (i) Species composition changed considerably in the last 40–50 years; (ii) The number of ruderal elements (Schwabe and Kratochwil 2004) further increased; (iii) Succession tendencies towards shrub vegetation are visible.

Study area

Over the approximately 40 km long transect from Mals to Plaus (Figure 2) the valley bottom of the study area slopes down from approximately 1,000 m to 550 m above sea level (Strimmer 1968). Also, the steepness of the slopes increases continuously from west to east. This leads to the fact that dry grasslands in Vinschgau continuously give way to a bush forest (*Fraxinus ornus*, *Quercus pubescens*) as well as afforestations by *Pinus nigra* and *Robinia pseudacacia* (Köllemann 1979). Precipitation is very low (Schenk 1949, 1951); it amounts to around 500 mm in Schlanders (Figure 3). Geologically, the south-facing slopes belong to the "Austroalpine unit" ("Ostalpin" in German), which consists of various metamorphic rocks such as mica schists and paragneisses. Quartz phyllites, amphibolites, orthogneisses, and marbles also occur (Mair 2010; Keim et al. 2017). The soils consist essentially of sandy clay sediments and typically form pararendzines with predominantly neutral or slightly basic pH (Strimmer 1968; Florineth 1973; Staffler et al. 2003).

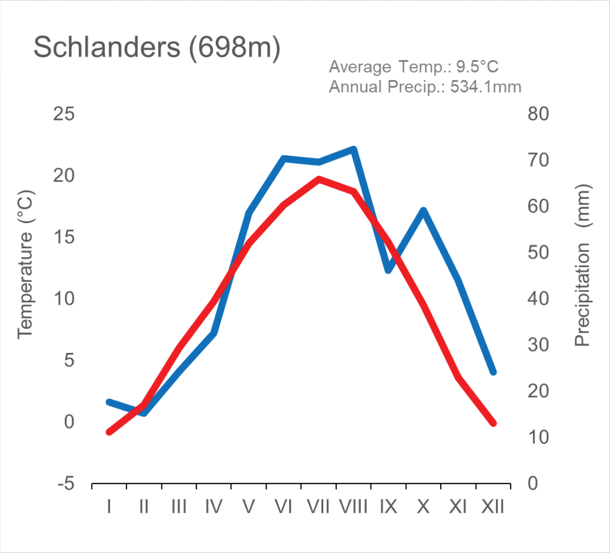

Figure 3. Climate diagram from Schlanders (1981–2010) based on data from the 3PCLIM-project (Source: www.3pclim.eu). The red line shows the monthly mean temperature and the blue line the precipitation. Overall, there is an average temperature of 9.5°C and an annual precipitation rate of approximately 530 mm.

In the 1960s and ´70s mostly all of the lower slopes in Vinschgau were used as pastures (Braun-Blanquet 1961; Strimmer 1968). Due to a change in agricultural policy, including the afforestation of dry grassland sites (Strimmer 1968; Feichter and Staffler 1996; Staffler and Karrer 2005, 2009; Wilhalm et al. 2008), the areal extent of dry grasslands has decreased. The remaining dry grassland areas are still used as pastures for goats, sheep and even cattle.

Methods

Field sampling

Together with Dr. Strimmer, Prof. Dr. Florineth and Dr. Köllemann, 76 relevés were selected from their studies, relocated in spring 2019, and new relevés were sampled in June 2019. Since it became apparent during the field inspections that there are currently only a few dry grassland occurrences in Dr. Köllemann's study area and that these were hardly accessible, only the area between Mals and Staben was investigated. Due to the lack of GPS information, a congruent resurvey was not possible. The old relevés could not be spatially assigned exactly to one plot but to larger areas or slopes, thus, a "one-to-one" comparison of old and new plots was not possible. The comparison, therefore, was more focused on the vegetation type so that all 92 new relevés from June 2019 were compared with the 76 old ones in order to investigate the general changes in the species spectrum. Our relevés were sampled using the same cover scale as the three initial investigators (i.e. Braun-Blanquet 1951) to ensure methodological consistency and to compare the relevés as best as possible. As mentioned above, because of the lack of GPS data for the old relevés, the comparison of old and recent relevés does not have the rank of a permanent plot study. Nevertheless, despite some uncertainties in plot relocation, resurveys are a robust enough method to assess vegetation changes over time (cf. Kopecký and Macek 2015).

Mosses and lichens were not recorded. In the first mapping, plots of 100 m² were used for the Vinschgau dry grasslands (according to Mueller-Dombois and Ellenberg 1974). In this work we decided to use the same plot size in order to be able to compare the plots as well as possible and to minimize uncertainties in plot relocation. In some cases, the size of the plots had to be reduced because of the topography (e.g. rocks, hedges and shrubs, afforestation) and in order to ensure best possible homogeneity. GPS coordinates were recorded from the plot centre by using a Garmin Etrex 10. The elevation (m above sea level) was noted simultaneously to the GPS coordinates. In addition, the upper left and lower right corners (viewed up the slope) of each plot were also marked using a steel plate (10 cm × 10 cm). The inclination (°) was determined with a Suunto PM-5/360 PC clinometer and the exposition (°) with a Recta Type DP 10 compass.

Vegetation classification

The raw table with the relevés from 2019 was sorted iteratively using the frequency of the species as a phytosociological characteristic. Relevés with similar floristic composition form a group which is characterized by character and differential species (Braun-Blanquet 1964; Dierschke et al. 1973; Dierschke 1994). Since all site factors find expression in the floristic composition of the plant community, such table can be interpreted floristically, syndynamically, and synecologically (Tüxen 1970, 1974). More importance was given to the higher cover values of *Bothriochloa ischaemum*, *Stipa capillata* and *S. pennata* agg. which reflect mainly physiognomic and structural aspects, when sorting the table. These species mainly characterize different ecological and physiognomical "formations" of dry grasslands in the study area (Figure 4).

Therefore, the term “subassociation” was defined more widely in this work by taking greater account of these physiognomical and structural aspects (cf. Westhoff 1967; Hurka et al. 2019). The sorted relevé table with subdivisions below association level is shown in Suppl. material 1, according to which a synoptic table (Table 1) was compiled (Dierschke 1994). The raw table is provided in Suppl. material 2 and Suppl. material 3. Similarly, an individual relevé table with the entire dataset (new and old relevés) was sorted to highlight the floristic differences between 2019 and the 1960s/70s. Based on this dataset, a synoptic table (Table 2) was created. Species groups with diagnostic value were listed and indicated by D1, D2.... in all tables to characterize variants of the plant communities below the association level.

Statistical analysis

In addition to the vegetation tables, a Detrended Correspondence Analyses (DCA) was performed in R (R Core Team 2020) version 4.0.3 by using the VEGAN package (Oksanen et al. 2020) in order to analyse the relevés quantitatively. To minimize the problem of an unduly high influence of rare species on the results, a downweighting was carried out by using the function ‘decorana ()’ with the value iweigh = 1 (Leyer and Wesche 2008; Dormann and Kühn 2011; Oksanen 2015). The Braun-Blanquet scale was converted into the mean abundance values (r → 0.01, + → 0.5, 1 → 2.5, 2 → 15.0, 3 → 37.5, 4 → 62.5) following Dierschke (1994). For further interpretation of the DCA ordination axes, the environmental parameters altitude, aspect and slope inclination were analysed and fitted via the function ‘envfit ()’ with permutations = 999 (VEGAN package). Only significant parameters were added post hoc on the scatter plot.

Floristical nomenclature and syntaxonomy

The nomenclature of the plant species follows Fischer et al. (2008). If possible, plants were identified at the species or subspecies level. Because of the fact that many species showed only vegetative parts or were in an inadequate condition for proper identification, some (sub)species were grouped into aggregates in case of doubt (marked with ‘agg.’ in the tables). The following aggregates were used: *Verbascum chaixii* agg. (*Verbascum chaixii* subsp. *chaixii*, *V. chaixii* subsp. *austriacum*), *Thymus praecox* agg. (*Thymus praecox* subsp. *praecox*, *T. praecox* subsp. *polytrichus*), *Thymus pulegioides* agg. (*Thymus pulegioides* subsp. *pulegioides*, *T. pulegioides* subsp. *carniolicus*), *Hieracium pilosella* agg. (*Hieracium pilosella* s.str., *H. pilosella* subsp. *velutinum*), *Stipa pennata* agg. (*Stipa pennata* s. str., *S. eriocaulis* subsp. *eriocaulis*, *S. eriocaulis* subsp. *austriaca*, *S. epilosa*), *Veronica verna* agg. (*Veronica verna* s.str., *V. dillenii*).

Due to a few floristic peculiarities in the Vinschgau, some taxa should be considered closer: *Festuca valesiaca* (2n = 2x = 14) and *Festuca rupicola* (2n = 6x = 42) belong to the *Festuca valesiaca* aggregate. *F. valesiaca* s. str. is, in addition to the microscopic sclerenchyma features, characterized vegetatively by hair-thin and darker blue-green, frosted leaves. The leaf of *F. rupicola* usually has a larger leaf cross-section (typically 0.6–0.7 mm), which can be practiced relatively quickly visually and haptically. Furthermore, it is often characterized by a comparatively warmer shade of green (although a blue-green colour, as is mandatory for *F. valesiaca*, is common). In the Vinschgau also higher-ploidy forms occur which can differ significantly from these two types in their vegetative characteristics. In addition to the number of chromosomes these characteristics primarily concern height, leaf width, leaf cross section and spikelet dimensions. In dry grasslands of lower and middle locations, the two octoploid species *F. bauzanina* (s. str.) and *Festuca bauzanina* subsp. *rhaetica* occur as well (Thomas Wilhalm, pers. comm.; Kiem 1987; Wilhalm et al. 2006; Fischer et al. 2008). However, these “atypical” *Festuca* species were not investigated further. In general, the identification of the *Festuca* species was based on macroscopic and often (by necessity) on mentioned vegetative characteristics and collected herbaria material.

From the *Stipa pennata* complex four elements occur in South Tyrol: *Stipa pennata* s. str. (quite common), *Stipa eriocaulis* (by far the most common species, with subspecies subsp. *eriocaulis* and subsp. *austriaca*), *S. epilosa* (very rare). The taxonomic value of these clades is the subject of current research (Thomas Wilhalm, pers. comm.; Wilhalm et al. 2006). According to Florineth (1973) only *Stipa eriocaulis* occurs in Vinschgau from the aggregate *Stipa pennata*. Schwabe and Kratochwil (2004) indicate *Stipa austriaca* as well as transitional forms to *S. eriocaulis*. Since an exact species identification within this complex was not always possible without any doubt, in this study the species and subspecies are therefore listed under *Stipa pennata* agg.

The delimitation between the (sub)species within the genus *Thymus* is not clear in every case. In our investigation this particularly concerns e.g. the alliance character species *Thymus serpyllum* subsp. *carniolicum* (= *T. pulegioides* subsp. *carniolicus*) (WFO 2021). Generally, hybrids are also very common in the genus *Thymus*, so that the identification is quite difficult (Fischer et al. 2008; Jäger 2017). In many cases it was not possible to identify subspecies so that the two aggregates *Thymus pulegioides* agg. and *T. praecox* agg. are used in this study.

According to Fischer et al. (2008), *Scabiosa columbaria* s. str. is missing in South Tyrol and in the Inner Alps. Plants that correspond to *S. columbaria* in terms of identification or combinations of characteristics are thus to be interpreted here as primary hybrids between *S. triandra* and *S. lucida* and listed under *S. columbaria* s. lat.

Hieracium pilosella s. str. and *Hieracium velutinum* are included in the *Hieracium pilosella* agg. (Fischer et al. 2008). In general, this aggregate is very rich in form and includes hybrid populations (Wilhalm et al. 2006). According to Dengler et al. (2019), *H. velutinum* differs also from *Hieracium pilosella* s. str. ecologically, as it occurs on much drier sites. In this work the species is listed as *Hieracium pilosella* agg.

Syntaxonomy and classification were essentially based on Braun-Blanquet (1961), Mucina and Kolbek (1993a) and Schwabe and Kratochwil (2004). The mentioned character species in the Suppl. material 1 and in Table 1 as well as the nomenclature of the associations are based essentially on Braun-Blanquet (1961). The nomenclature of the high rank syntaxa followed Mucina et al. (2016).

Results

Syntaxonomy of the new relevés

Based on the character species *Astragalus exscapus*, *Carex liparocarpos*, *Festuca rupicola*, *F. valesiaca*, *Oxytropis xerophila*, *Petrorhagia saxifraga*, *Potentilla pusilla*, *Pulsatilla montana*, *Silene otites* and *Stipa capillata* dry grassland communities recorded in 2019 (Table 1 and Suppl. material 1) can be assigned to the order of continental dry grasslands, *Festucetalia valesiacae* in the *Festuco-Brometea* class. Furthermore, from the alliance *Stipo-Poion xerophilae* only the relatively constant *Centaurea stoebe* can be mentioned. *Poa molinerii* (= *Poa xerophila*) occurred only in one relevé. At the association level, the *Festuco-Poetum xerophilae* and the *Festuco-Caricetum supinae* were identified.

The ***Festuco-Poetum xerophilae*** could be documented in only five relevés from the northwest of the study area, near Laatsch (Figure 2). It extends between approximately 1,000 m and 1,100 m a.s.l. on relatively steep, east to south-east exposed slopes. The association can be characterized by *Achillea nobilis* and, to a lesser extent, *Thesium linophyllon*. The species group *Anthoxanthum odoratum*, *Bromus erectus*, *Pimpinella saxifraga*, *Potentilla argentea* (D1, Table 1) as well as some taller shrubs such as, *Prunus spinosa* and *Rosa* sp. distinguished this association from the other investigated dry grasslands. *Poa molinerii* was not present in this community.

The ***Festuco-Caricetum supinae*** (87 relevés) occurred on the south-west to south-facing slopes from Tartsch near Mals approximately to Staben-Plaus (Figure 2) with an elevation range between 560 m and 1,400 m a.s.l. These areas were almost all identified as pastures that are still used or were used in the past, extending on more even areas (e.g. at Laas). The *Festuco-Caricetum supinae* can be divided into three subassociations (Table 1): with *Stipa capillata* (*stipetosum capillatae*), with *Bothriochloa ischaemum* (*bothriochloetosum ischaemi*), and with *Stipa pennata* agg. (*stipetosum pennatae*). The DCA (Figure 5) clearly shows the correlation of inclination for the *stipetosum pennatae* and of altitude for the two other associations, particularly for the *bothriochloetosum ischaemi*. It also highlights "outlier relevés", which can be seen as transitional stages between subassociations.

Table 1. Synoptic table of the dry grassland communities in the Vinschgau (South Tyrol, Italy) with all relevés from 2019. Values are percentage frequencies. Only companion species with frequency > 15% are stated. I = *Festuco-Poetum xerophilae* (col. 1); II = *Festuco-Caricetum supinae*; II.1 = subassociation *stipetosum capillatae* (cols. 2–4); II.2 = subassociation *bothriochloetosum ischaemi* (cols. 5, 6); II.3 = subassociation *stipetosum pennatae* (cols. 7, 8). The name giving species *Stipa capillata*, *Bothriochloa ischaemum* and *Stipa pennata* agg. are indicated in bold. Variants (D1–D7, cols 2–8) were identified based on the similarity of the species composition: *Veronica verna*-variant (cols. 2, 5), typical variant (cols. 3, 6, 8), species-poor variant (col. 4), *Melica ciliata*-variant (col. 7). Abbreviations: AC = association character species, agg. = aggregate, cf. = confer (means 'compare'), juv. = juvenile, KC = class character species, OC = order character species, s. lat. = sensu lato, sp. = species, ssp. = subspecies, VC = alliance character species.

Vegetation type	I	II.1			II.2		II.3	
Column number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Number of relevés	5	12	25	8	13	8	9	12
AC1: *Festuco-Poetum xerophilae*								
Achillea nobilis	100	–	–	–	–	–	–	–
Thesium linophyllon	80	33	12	–	31	–	–	8
D1								
Bromus erectus	60	25	16	–	8	13	11	8
Pimpinella saxifraga	80	–	4	–	8	–	–	–
Prunus spinosa	60	8	–	–	–	–	–	–
Potentilla argentea	40	8	–	–	8	–	–	–
Anthoxanthum odoratum	40	–	–	–	–	–	–	–
AC2: *Festuco-Caricetum supinae*								
Astragalus onobrychis	20	92	84	13	100	88	100	58
Carex supina	–	67	80	25	100	75	78	33
Achillea tomentosa	–	67	28	50	77	38	11	25
D2								
Artemisia absinthium	–	75	8	–	38	–	–	–
Buglossoides incrassata	20	58	4	–	31	–	–	–
Erodium cicutarium	–	50	4	13	38	–	–	–
Convolvulus arvensis	–	50	4	–	8	13	–	–
D3								
Veronica verna agg.	20	92	44	63	77	38	11	8
Trifolium arvense	100	75	12	88	85	13	11	25
Trifolium campestre	–	50	–	13	77	13	11	–
Plantago lanceolata	–	58	8	–	46	13	–	–
Turritis glabra	40	50	12	–	69	–	–	8
D4								
Silene nutans	–	–	16	–	–	13	–	–
Plantago media	–	8	16	–	–	13	–	–
Carduus nutans	20	–	20	–	8	–	–	–
Achillea cf. *collina*	–	–	8	–	–	13	–	–
Trifolium repens	–	–	8	–	–	–	–	–
D5								
Erigeron annuus	–	–	–	75	–	13	–	8
Chondrilla juncea	–	25	16	50	–	–	11	8
Quercus pubescens juv.	–	–	–	38	–	–	–	8
Prunus mahaleb	–	–	8	38	8	13	–	–
Filago arvensis	20	17	12	50	8	–	–	8
D6								
Melica ciliata	40	42	8	13	15	13	100	–
Allium sphaerocephalon	100	25	8	25	23	13	67	8
D7								
Scorzonera austriaca	–	–	8	–	–	–	–	25
Ephedra helvetica	–	–	–	–	–	–	–	17
Telephium imperati	–	–	–	–	–	–	–	17
Seseli pallasii	–	–	–	38	–	13	–	17
Kengia serotina	–	–	–	13	–	–	–	25
VC: *Stipo-Poion xerophilae*								
Centaurea stoebe	80	67	52	100	85	50	44	42
Thymus pulegioides agg.	–	17	–	–	31	–	11	–
Verbascum chaixii agg.	–	–	4	–	–	–	–	17

Vegetation type	I		II.1		II.2		II.3	
Column number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Number of relevés	5	12	25	8	13	8	9	12
Poa molinerii	–	–	–	–	–	13	–	–
OC: *Festucetalia valesiacae*								
Potentilla pusilla	100	83	96	75	100	100	100	83
Festuca valesiaca	80	83	84	88	92	88	78	83
Festuca rupicola	80	58	88	100	69	100	89	83
Stipa capillata	80	100	100	100	62	88	44	25
Petrorhagia saxifraga	80	75	36	88	77	75	100	75
Silene otites	100	58	56	75	85	63	56	42
Carex liparocarpos	20	33	32	63	8	13	22	33
Pulsatilla montana	40	8	8	–	23	–	–	8
Astragalus exscapus	–	8	16	–	15	13	–	–
Oxytropis xerophila	–	–	4	–	–	25	–	–
KC: *Festuco-Brometea*								
Veronica spicata	100	17	16	25	69	38	–	17
Galium lucidum	100	42	44	25	15	–	44	58
***Stipa pennata* agg.**	100	33	16	50	8	25	100	100
Artemisia campestris	80	100	92	88	100	88	100	100
Phleum phleoides	100	92	88	88	85	75	78	75
Koeleria macrantha	80	83	84	75	100	50	100	67
Thymus praecox agg.	100	67	96	63	77	100	67	67
Verbascum lychnitis	60	67	76	63	54	63	44	25
Alyssum alyssoides	60	83	56	25	85	50	89	50
Arenaria serpyllifolia	60	83	52	50	92	63	67	–
Bothriochloa ischaemum	20	75	40	88	100	88	78	50
Stachys recta subsp. *recta*	60	50	40	13	8	38	78	50
Carex humilis	60	42	16	13	15	50	22	33
Lotus corniculatus	20	42	32	–	31	–	–	8
Astragalus glycyphyllos	–	25	4	–	–	–	–	–
Fumana procumbens	–	8	44	50	23	75	22	50
Helianthemum nummularium subsp. *obscurum*	20	–	24	75	8	13	33	58
Medicago minima	40	42	32	38	23	25	11	17
Clinopodium acinos	20	33	4	–	62	13	33	17
Companion species								
Sempervivum arachnoideum	100	50	56	75	85	88	67	92
Hieracium pilosella agg.	100	50	68	25	54	100	44	50
Teucrium chamaedrys	100	42	56	75	23	13	44	67
Erysimum rhaeticum	60	83	40	13	77	63	44	25
Sempervivum tectorum	40	25	32	63	46	38	78	92
Dianthus sylvestris	80	42	36	25	46	75	44	67
Plantago strictissima	80	58	44	–	46	63	22	–
Sedum montanum s. lat.	100	58	12	25	31	25	78	33
Scabiosa columbaria s. lat.	–	25	36	50	38	38	56	17
Teucrium montanum	20	25	40	–	23	50	44	42
Berberis vulgaris	60	50	40	–	15	50	11	33
Chenopodium album	–	33	24	38	54	13	11	8
Medicago falcata	40	58	28	25	8	–	–	17
Juniperus communis	–	25	28	–	23	13	33	25
Sedum sexangulare	20	17	12	–	38	25	–	17
Lactuca perennis	40	17	12	–	8	13	22	25
Euphorbia cyparissias	–	8	8	38	15	13	22	8
Tragopogon dubius	20	33	8	–	23	–	22	–
Carex caryophyllea	20	17	16	25	15	–	–	–
Saponaria ocymoides	–	8	12	–	15	–	33	17
Veronica prostrata	–	25	4	–	31	–	–	–
Arabidopsis thaliana	60	8	4	–	15	13	–	–
Anthericum liliago	–	–	4	13	15	–	22	17
Viola cf. *kitaibeliana*	–	33	4	–	15	–	–	–
Rosa cf. *micrantha*	20	8	8	–	–	13	11	–
Rosa sp.	20	8	4	–	15	–	11	–
Allium lusitanicum	–	–	12	–	–	13	–	17
Asplenium septentrionale	40	8	–	25	–	13	–	–
Fraxinus ornus juv.	–	–	–	13	8	–	22	17
Phelipanche bohemica	20	17	–	–	–	–	22	–
Securigera varia	20	–	4	–	15	–	11	–
Bromus japonicus	–	–	–	25	15	–	–	–
Robinia pseudacacia juv.	–	–	–	–	–	–	11	25
Poa angustifolia	20	8	4	–	–	–	–	8
Astragalus vesicarius subsp. *pastellianus*	–	–	–	–	–	–	11	25
Descurainia sophia	–	25	–	–	8	–	–	–
Echium vulgare	–	17	–	–	8	–	–	–
Torilis arvensis	–	–	–	25	8	–	–	–
Hypericum maculatum	–	–	–	–	23	–	–	–
Calina acaulis	–	17	4	–	–	–	–	–
Verbascum nigrum	–	17	–	–	–	–	–	–
Silene vulgaris	20	–	–	–	–	–	11	–
Linaria angustissima	20	–	–	–	–	–	–	8
Trifolium alpestre	20	–	–	–	–	13	–	–
Cuscuta epithymum	40	–	–	–	–	–	–	–
Vicia tetrasperma	–	–	–	25	–	–	–	–
Geum montanum	20	–	–	–	–	–	–	–

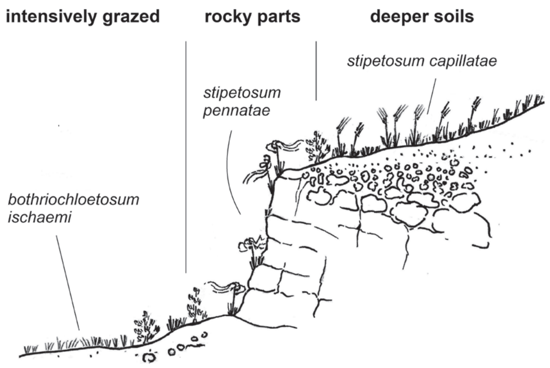

Figure 4. Idealised scheme of the ecological occurrence of the three subassociations of the *Festuco-Caricetum supinae* (cf. Strimmer 1974). The *bothriochloetosum ischaemi* occurs mainly in intensively grazed areas, very often on the foot slopes, especially near the village Mals, and sometimes on terraces as well. The *stipetosum pennatae* characterize the rockier slopes, rocky pulpits and occurs sometimes on rocky parts within the plain areas. The subassociation *stipetosum capillatae* mostly occur on deeper soils, often on terraces and form very often dense vegetation layers. (Created by M. Lübben).

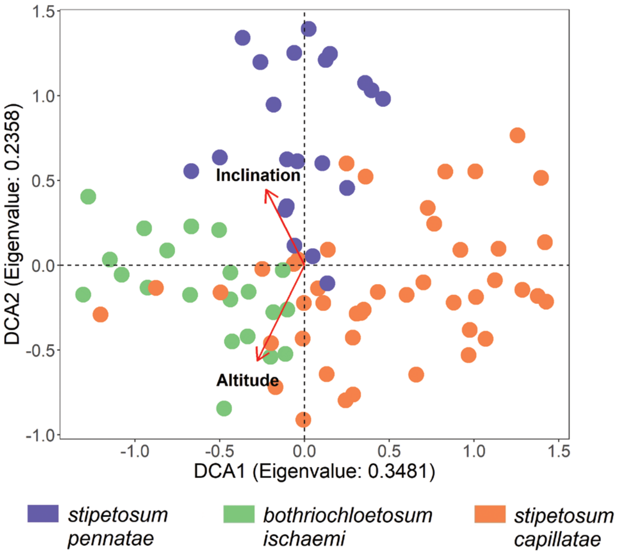

Figure 5. Ordination (DCA) of the *Festuco-Caricetum supinae*. Three subassociations are shown, characterized by the dominant species *Stipa capillata*, *Bothriochloa ischaemum*, and *Stipa pennata* agg. Transitions between the subassociations are visible.

Subassociation *stipetosum capillatae*

The subassociation with *Stipa capillata* was found on low mountain terraces and lower slopes with deeper soils. The community was grass-rich and very often contained tall herbs (Figure 6). Beside *Stipa capillata*, a particularly high abundance of *Festuca rupicola* and *F. valesiaca* was obvious. The character species of the *Festuco-Brometea* class, such as *Artemisia campestris*, *Koeleria macrantha* and *Phleum phleoides*, were also frequently present. Three variants were identified: the variant with *Veronica verna*, a typical variant and a species-poor variant in which the association character species were less frequent. In the *Veronica verna*-variant *Artemisia absinthium*, *Convolvulus arvensis* or *Plantago lanceolata* and some annuals such as *Buglossoides incrassata*, *Trifolium arvense* and *Veronica verna* itself occurred (D2, D3 in Table 1). The typical variant was mainly characterised by the high abundance of grass species such as *Festuca rupicola*, *F. valesiaca*, and *Stipa capillata*. In few relevés of this variant more mesophilic species such as *Achillea* cf. *collina*, *Trifolium repens* and *Plantago media* occurred. In the species-poor variant almost all character species of the *Festuco-Caricetum supinae* were lacking. In addition, ruderal species such as *Chondrilla juncea*, *Erigeron annuus* and *Filago arvensis* occurred with high abundance (D5 in Table 1). It has to be mentioned that *Bothriochloa ischaemum* occurred with higher abundance and frequency in this variant as well (Table 1).

Figure 6. Subassociation *stipetosum capillatae* (Photo: M. Lübben).

Subassociation *bothriochloetosum ischaemi*

This subassociation dominated on the heavily grazed areas of the terraces and the lowest slopes, especially near Mals. The more open and very low-growing vegetation was dominated by *Bothriochloa ischaemum*, *Festuca valesiaca*, *Potentilla pusilla* and *Thymus praecox* agg. (Figure 7). *Alyssum alyssoides*, *Arenaria serpyllifolia* and *Artemisia campestris* were also recorded. Overall, the herb layer of this subassociation was open. Even here two variants were identified. The *Veronica verna*-variant was represented by *Trifolium arvense*, *T. campestre*, *Veronica verna* and to some extent also by *Plantago lanceolata*, *Turritis glabra* (D3 in Table 1). *Artemisia absinthium*, *Buglossoides incrassata* and *Erodium cicutarium* (D2 in Table 1) were still present but not very dominant. In the typical variant, almost all species from the *Veronica verna*-variant were absent or occurred less frequently. Only *Festuca rupicola*, *Fumana procumbens*, *Hieracium pilosella* agg. and *Thymus praecox* agg. were more frequent. *Poa molinerii* was present only in this variant.

Figure 7. Subassociation *bothriochloetosum ischaemi* (Photo: M. Lübben).

Subassociation *stipetosum pennatae*

The subassociation *stipetosum pennatae* characterized the rockier slopes, which were at great risk of erosion, and on rocky outcrops so that the canopy layer showed more gaps (Figure 8). The highly dominant *Stipa pennata* agg. separated the community from the other subassociations (Figure 5, Table 1). The character species of the order, i.e. *Festuca rupicola*, *F. valesiaca* and *Potentilla pusilla* were present. *Artemisia campestris*, *Koeleria macrantha*, *Phleum phleoides*, and *Thymus praecox* agg. were also frequent. *Stipa capillata* was found a few times and with low cover values. *Bothriochloa ischaemum* occurred just as frequently, but with barely abundance as well. Two variants were identified: the *Melica ciliata*-variant and the typical variant. Within the *Melica ciliata*-variant (D6 in Table 1) *Melica ciliata* and *Allium sphaerocephalon* were highly dominant. In the typical variant these two species were missing, and the character species *Astragalus onobrychis* and *Carex supina* of the *Festuco-Caricetum supinae* were significantly

Figure 8. Subassociation *stipetosum pennatae* (Photo: M. Lübben).

less abundant than in the *Melica ciliata*-variant. In addition, in some relevés of this variant *Kengia serotina*, *Scorzonera austriaca* and *Seseli pallasii* occur (D7 in Table 1).

Vegetation change over the last 40–50 years

The comparison of new and old relevés showed a clear vegetation change. Over the last 40–50 years, a large group of species newly immigrated (D1 in Table 2). The following species achieved a higher constancy in the immigrating group: *Chenopodium album*, *Erodium cicutarium*, *Plantago lanceolata* and *Trifolium campestre* (Table 2, cols. 1–2). Together with these species, a number of sporadically occurring species were also new, such as *Astragalus glycyphyllos*, *Descurainia sophia* (Table 2, cols. 1–2), *Erigeron annuus* (Table 2, cols. 2–4) and *Silene nutans* (Table 2, col. 3) together with a bunch of species with very low occurrence. Some species such as *Arenaria serpyllifolia*, *Artemisia absinthium*, *Buglossoides incrassata*, *Festuca rupicola*, *Trifolium arvense*, *Turritis glabra* and *Veronica verna* agg. (D2, Table 2) showed a higher constancy in the new relevés and appeared rarely in the old ones. Among them, *F. rupicola* with its highest constancy clearly separated the new and old relevés. The species group only present or dominating in the old relevés contained grassland species and a few shrubs (D3, Table 2). The diagnostic species of inner-alpine dry grasslands were found with slightly diverging constancy (D4, Table 2) or with equal constancy (D5, Table 2) in the new and old relevés.

The quantitative analysis of the relevés (DCA ordination) confirmed the discrimination of old and new relevés (Figure 9). The separation basically follows DCA axis 1, reflecting the floristic differences.

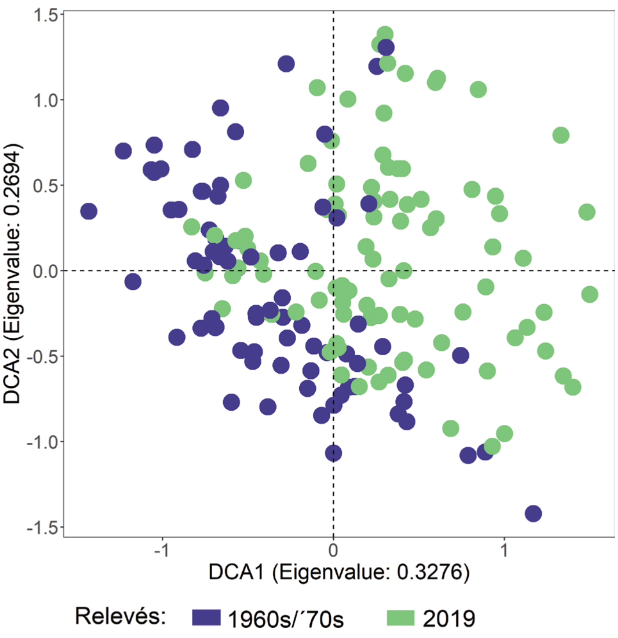

Figure 9. Ordination (DCA) of the old relevés (1960s / ´70s) and new relevés (2019).

Table 2. Synoptic table of the dry grassland communities in the Vinschgau (South Tyrol, Italy) from 2019 in comparison to the 1960s/´70s. Values are percentage frequencies. The columns 1 to 9 show the different relevé groups based on the similarity of the species (2019, cols. 1-5; 1960s/70s, cols. 6–9). Different species groups (D1 – D5) were identified which separate the new and old relevés. The floristical shift over time is illustrated by these groups. In D5 species are stated which do not show a clear change over time in their frequencies. Only species with frequency > 15% are stated in this group. Abbreviations: agg. = aggregate, cf. = confer (means "compare"), juv. = juvenile, s. lat. = sensu lato, sp. = species.

Sampling period	**2019**					**1960/70**			
Column number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Number of relevés	17	16	19	17	23	15	24	26	11
D1									
Camelina microcarpa	6	–	–	–	–	–	–	–	–
Lolium perenne	6	–	–	–	–	–	–	–	–
Medicago sativa	6	–	–	–	–	–	–	–	–
Geum montanum	6	–	–	–	–	–	–	–	–
Reseda luteola	6	–	–	–	–	–	–	–	–
Silene vulgaris	6	6	–	–	–	–	–	–	–
Descurainia sophia	18	6	–	–	–	–	–	–	–
Astragalus glycyphyllos	18	6	–	–	–	–	–	–	–
Bromus japonicus	12	13	–	–	–	–	–	–	–
Linaria angustissima	6	–	–	6	–	–	–	–	–
Papaver dubium	6	6	–	6	–	–	–	–	–
Torilis arvensis	6	6	–	6	–	–	–	–	–
Viola cf. *kitaibeliana*	29	6	–	–	4	–	–	–	–
Plantago lanceolata	65	19	11	–	–	–	–	–	–
Erodium cicutarium	59	13	5	–	–	–	–	–	–
Trifolium campestre	59	44	–	6	4	–	–	–	–
Chenopodium album	47	50	21	–	13	–	–	–	–
Arabidopsis thaliana	18	6	5	6	9	–	–	–	–
Anthericum liliago	6	13	5	18	4	–	–	–	–
Rosa cf. *micrantha*	6	–	11	12	4	–	–	–	–
Plantago media	6	–	21	–	4	–	–	–	–
Taraxacum laevigatum	6	–	16	–	4	–	–	–	–
Phelipanche bohemica	12	–	–	6	9	–	–	–	–
Poa angustifolia	12	–	–	6	4	–	–	–	–
Asplenium septentrionale	6	–	–	18	9	–	–	–	–
Prunus spinosa	12	–	–	–	9	–	–	–	–
Lactuca serriola	6	–	5	12	–	–	–	–	–
Erigeron annuus	–	25	5	18	–	–	–	–	–
Quercus pubescens	–	13	–	6	4	–	–	–	–
Sanguisorba minor	–	13	–	–	4	–	–	–	–
Senecio inaequidens	–	13	–	6	–	–	–	–	–
Vicia tetrasperma	–	13	–	–	–	–	–	–	–
Orobanche artemisiae-campestris	–	6	–	–	–	–	–	–	–
Ononis spinosa	–	6	–	–	–	–	–	–	–
Salvia pratensis	–	6	5	–	–	–	–	–	–
Veronica fruticans	–	–	5	6	4	–	–	–	–
Silene nutans	–	–	26	–	–	–	–	–	–
Achillea cf. *collina*	–	–	16	–	–	–	–	–	–
Trifolium repens	–	–	11	–	–	–	–	–	–
Myosotis stricta	–	–	5	–	–	–	–	–	–
Carlina vulgaris	–	–	5	–	–	–	–	–	–
Anchusa arvensis	–	–	5	–	–	–	–	–	–
Cynoglossum officinale	–	–	5	–	–	–	–	–	–
Lonicera xylosteum	–	–	5	–	–	–	–	–	–
Cerastium semidecandrum	–	–	5	–	–	–	–	–	–
Kengia serotina	–	–	–	24	–	–	–	–	–
Viscaria vulgaris	–	–	–	18	–	–	–	–	–
Quercus petraea	–	–	–	6	–	–	–	–	–
Ulmus minor	–	–	–	6	–	–	–	–	–
Carduus defloratus	–	–	–	6	–	–	–	–	–
Trifolium alpestre	–	–	–	6	4	–	–	–	–
Cuscuta epithymum	–	–	–	–	9	–	–	–	–
Bromus tectorum	–	–	–	–	9	–	–	–	–
Anthoxanthum odoratum	–	–	–	–	9	–	–	–	–
Telephium imperati	–	–	–	–	9	–	–	–	–
Aster alpinus	–	–	–	–	4	–	–	–	–
Ononis natrix	–	–	–	–	4	–	–	–	–

Sampling period	**2019**						**1960/70**		
Column number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Number of relevés	17	16	19	17	23	15	24	26	11
D2									
Artemisia absinthium	71	–	–	6	13	–	4	–	9
Buglossoides incrassata	76	–	–	–	–	–	–	–	9
Turritis glabra	59	38	11	–	13	–	8	–	–
Chondrilla juncea	18	19	5	35	–	–	4	–	9
Trifolium arvense	82	88	–	41	22	7	38	12	9
Sedum sexangulare	29	6	21	–	22	–	–	15	9
Veronica verna agg.	76	100	32	18	22	–	4	–	–
Arenaria serpyllifolia	82	75	74	24	39	7	–	–	–
Festuca rupicola	71	69	89	88	91	13	–	27	36
D3									
Saponaria ocymoides	18	6	5	12	17	47	33	4	9
Rosa sp.	6	13	–	–	13	60	38	4	9
Oxytropis pilosa	–	–	–	–	–	13	4	–	–
Onosma helvetica subsp. *tridentata*	–	–	–	–	–	13	13	–	–
Asparagus officinalis	–	–	–	–	–	7	13	–	–
Orobanche gracilis	–	–	–	–	–	7	–	–	9
Veronica teucrium	–	–	–	–	–	7	–	–	–
Phelipanche arenaria	–	–	–	–	–	–	8	–	–
Cirsium sp.	–	–	–	–	–	–	4	–	–
Clinopodium alpinum	–	–	–	–	–	–	4	–	–
Medicago lupulina	–	–	–	–	–	–	4	–	–
D4									
Stipa pennata agg.	24	38	–	82	74	73	8	35	27
Alyssum alyssoides	82	69	42	29	87	47	29	15	36
Achillea tomentosa	76	63	21	29	17	53	54	19	55
Berberis vulgaris	35	6	53	6	52	93	79	4	9
Juniperus communis	24	6	32	–	39	80	92	12	9
Hieracium pilosella agg.	65	25	79	29	87	73	92	81	9
Dianthus sylvestris	47	31	37	41	74	80	83	81	36
Plantago strictissima	65	13	53	–	52	67	88	92	64
Teucrium montanum	29	13	42	24	48	80	88	62	–
Thymus praecox agg.	71	75	100	59	91	87	75	88	82
Stipa capillata	82	81	100	59	65	80	83	88	82
Bothriochloa ischaemum	71	94	42	71	57	93	92	81	64
Centaurea stoebe	88	75	47	47	57	87	92	88	73
D5									
Artemisia campestris	94	100	95	88	96	100	96	85	100
Potentilla pusilla	88	88	95	94	96	93	83	96	100
Festuca valesiaca	82	88	95	71	87	73	100	96	100
Astragalus onobrychis	82	69	89	59	78	100	79	85	82
Phleum phleoides	94	94	79	82	74	73	79	69	64
Sempervivum arachnoideum	71	69	58	71	87	80	96	65	36
Koeleria macrantha	88	88	68	100	70	80	75	46	36
Petrorhagia saxifraga	71	88	47	76	65	100	83	62	45
Silene otites	71	75	42	47	78	93	88	50	27
Carex supina	71	69	74	47	65	33	50	50	64
Erysimum rhaeticum	88	50	32	24	57	80	67	23	18
Carex humilis	35	13	26	24	35	67	58	85	36
Verbascum lychnitis	59	63	89	35	48	53	25	8	27
Sempervivum tectorum	35	31	16	88	70	93	33	12	18
Teucrium chamaedrys	41	38	47	53	65	73	50	4	18
Galium lucidum	29	31	26	24	74	67	58	15	27
Scabiosa columbaria s. lat.	47	25	26	41	30	53	75	38	–
Fumana procumbens	18	38	37	53	35	73	54	27	–
Stachys recta subsp. *recta*	29	25	47	47	48	73	38	4	9
Veronica spicata	41	38	11	18	39	20	29	46	45
Sedum montanum s. lat.	53	13	11	41	61	60	33	12	–
Helianthemum nummularium subsp. *obscurum*	6	25	11	65	30	73	50	15	9
Medicago falcata	53	13	32	6	13	27	46	31	36
Allium sphaerocephalon	24	25	–	29	43	40	33	8	18
Lotus corniculatus	53	19	21	6	9	13	50	27	–
Carex liparocarpos	35	38	26	24	22	–	–	31	36
Clinopodium acinos	41	31	5	18	17	40	33	4	18
Melica ciliata	35	19	–	24	39	40	17	8	18
Medicago minima	29	31	37	29	17	–	13	–	9
Tragopogon dubius	29	19	–	18	4	27	25	8	18
Bromus erectus	29	13	11	6	17	33	17	–	9
Thesium linophyllon	41	13	11	–	22	7	17	4	9
Carex caryophyllea	29	19	11	6	–	–	4	31	18
Astragalus exscapus	6	13	16	–	9	–	4	38	9
Euphorbia cyparissias	12	13	11	12	17	13	17	–	–
Filago arvensis	12	19	11	18	9	–	13	8	9
Carduus nutans	12	–	26	–	–	7	33	4	9
Lactuca perennis	6	13	5	24	26	13	4	–	–
Verbascum nigrum	6	6	–	–	–	–	–	42	27
Galium verum	6	6	5	–	–	27	25	8	9
Thymus pulegioides agg.	24	13	–	–	4	13	13	12	–
Allium lusitanicum	–	6	11	6	9	27	13	4	–
Pulsatilla montana	12	13	11	–	13	–	–	15	–
Pimpinella saxifraga	12	–	5	–	13	–	21	8	–
Seseli pallasii	–	6	–	24	4	20	13	–	9
Calina acaulis	12	–	5	–	–	–	8	19	18
Oxytropis xerophila	–	–	11	–	4	–	13	19	9
Astragalus vesicarius subsp. *pastellianus*	–	–	–	6	13	13	21	4	–
Convolvulus arvensis	35	–	–	6	9	7	4	–	9
Prunus mahaleb	–	19	11	–	9	–	17	–	–
Securigera varia	6	6	5	–	9	7	17	–	–
Veronica prostrata	24	13	5	–	4	–	–	4	9
Potentilla argentea	6	–	–	–	13	7	4	4	18
Scorzonera austriaca	–	6	–	12	9	27	–	–	–
Fraxinus ornus juv.	6	–	–	18	9	–	–	–	9
Robinia pseudacacia	–	–	–	18	4	7	4	–	9
Lappula squarrosa	6	–	16	6	–	–	4	–	–
Achillea nobilis	6	–	–	–	17	–	–	–	9
Echium vulgare	18	–	–	–	–	–	–	–	9

Discussion

Validity of Braun-Blanquet's (1961) syntaxonomy

Following Braun-Blanquet (1961), our relevés from 2019 were clearly included in the order *Festucetalia valesiacae* (class *Festuco-Brometea*). The alliance affiliation (*Stipo-Poion xerophilae*) was less justifiable, because only one character species – *Centaurea stoebe* – connected the relevés to this alliance. Even if we consider the order character species *Festuca rupicola* (cf. Mucina and Kolbek 1993a) as a character species for the alliance *Stipo-Poion xerophilae*, doubts on the validity of the *Stipo-Poion xerophilae* may be raised. Dengler et al. (2019) defined it as "rocky grassland alliance". In our study, *Poa xerophila* (valid species name = *Poa molinerii*) was recorded in only one relevé. Therefore, we suggest to skip this alliance for most of Vinschgau dry grasslands and to classify them as *Festucion valesiacae*, similarly to Mucina et al. (2016) and Dengler et al. (2019, 2020). These authors outlined the Eastern European *Festucion valesiacae* as "non rocky grassland of the Swiss inner-alpine valley" and we highly agree to use this definition also for the investigated Vinschgau' dry grasslands.

On the association level, we were able to identify two associations (*Festuco-Poetum xerophilae* and *Festuco-Caricetum supinae*). According to Braun-Blanquet (1936, 1961), the *Festuco-Poetum xerophilae* holds an intermediate position between the *Koelerio-Poetum xerophilae* from the Engadin (Switzerland), which has less xerophytes, and the *Festuco-Caricetum supinae*. In our investigation, we have a very small database for the *Festuco-Poetum xerophilae* with only five relevés. Nevertheless, the community is clearly separated by the character species *Achillea nobilis* and *Thesium linophyllon* from the *Festuco-Caricetum supinae*. Braun-Blanquet (1961) described two subassociations for the *Festuco-Poetum xerophilae*: *Erysimum rhaeticum*-subassociation and *Carex humilis*-subassociation. In addition, in the *Carex humilis*-subassociation two variants were mentioned by Braun-Blanquet (1961): one with *Pulsatilla montana* and one with *Bromus erectus*. Both species were recorded also in the 2019 relevés. However, discrimination of variants is by no means justifiable with only five relevés. Due to the unique occurrence of *Astragalus onobrychis*, the absence of *Achillea tomentosa* and *Carex supina*, the relevés are negatively separated from the *Festuco-Caricetum supinae* (cf. Schwabe and Kratochwil 2004). However, for a precise validation of this association more relevés are needed.

The *Festuco-Caricetum supinae* was well represented (87 relevés). The association is well justified by the character species. This holds also for the subassociations, based on the dominance of *Bothriochloa ischaemum*, *Stipa capillata* and *Stipa pennata* agg. Nevertheless, as our investigation points out, the three subassociations were floristically closely related and showed transitions. A mosaic distribution of different dry grassland "fragments" and fluent transitions of dry grassland communities in Vinschgau were already mentioned by Strimmer (1968, 1974) so that the subassociations in this study should not be considered as "strictly" delimited units. Furthermore, it has to be mentioned that Braun-Blanquet (1961) did not describe a plant community with *Stipa pennata* for the Vinschgau (cf. Schwabe and Kratochwil 2004). Finally, there were still remaining doubts about the affiliation of some relevés (Table 1, col. 8; Suppl. material 1, relevé numbers 87–92) to the association *Festuco-Caricetum supinae*. In these relevés character species of this association had a very low frequency (AC2, Table 1). To some extent, these relevés are related to the *Stipo capillatae-Seselietum variae* (cf. Schwabe and Kratochwil 2004) via *Scorzonera austriaca*, *Ephedra helvetica*, *Telephium imperati* and *Seseli pallasii* (= *S. varium* var. *levigatum*) (D7, Table 1). Most of these relevés come from Staben, at the eastern end of the investigated dry grassland transect. The border between the *Festuco-Caricetum supinae* and *Stipo capillatae-Seselietum variae* was set by Braun-Blanquet (1961) near Schlanders (cf. Schwabe and Kratochwil 2004). Further investigations have to prove whether the *Stipo capillatae-Seselietum variae* still occurs in Vinschgau.

On the whole, a more precise determination of some species on the subspecies level could perhaps lead to a more exact delimitation of the associations, subassociations and variants. A comprehensive phytosociological study of the entire inner-alpine steppe vegetation is definitely needed to gain a better syntaxonomical overview and classification in the context of western and eastern dry grassland communities (cf. Mucina et al. 2016).

Changes of species composition after 40–50 years

Over the last 40–50 years, considerable changes in species composition were recognized. The abundance and constancy of *Stipa capillata* and – to a weaker extent – of *Stipa pennata* agg. increased, while that of *Bothriochloa ischaemum* slightly decreased. The most impressive increase was shown by *Festuca rupicola*. These changes of the character species have to be interpreted with caution. Especially for *Festuca rupicola*, determination problems in the past cannot be excluded. According to our own observation, *F. rupicola* inhabits more mesophilic and deeper soils, while *F. valesiaca* grows dominantly on shallower and drier soils. The different requirements of the two species were already mentioned by Hroudová-Pučelíková (1972) and Florineth (1980). Braun-Blanquet (1961) found *F. ovina* subsp. *sulcata* (= *F. rupicola*) in the Vinschgau only a few times with a low frequency and mainly in the *Festuco-Poetum xerophilae* (Braun-Blanquet 1961; Kiem 1987).

Besides these uncertain changes, ruderalisation trends, mentioned already by Schwabe and Kratochwil (2004) seem to continue. An increase of annuals (e.g. *Arenaria serpyllifolia*, *Veronica verna*) and ruderal species (e.g. *Artemisia absinthium*, *Convolvulus arvensis*, *Erigeron annuus*) was found in our study sites similar to studies in Switzerland (Dengler et al. 2019). Some relevés show a relationship to the ruderal fringe community of the *Artemisieto-Agropyretum*, so immigration of species from this community towards dry grasslands can be assumed. The *Artemisieto-Agropyretum* is also floristically very close to the *Festuco-Brometea* (Kielhauser 1954; Braun-Blanquet 1961; Mucina 1993; Mucina and Kolbek 1993a). The occurrence of some ruderal species (e.g. *Artemisia absinthium*) may thereby also be related to former land use. Thus, these species can also be considered as indicators of land use change over time.

We also recognized that species from the *Sedo-Scleranthetea* class (e.g. *Erodium cicutarium*, *Trifolium campestre*; D1, Table 2) have immigrated to dry grasslands or increased their abundance. In general, the *Festuco-Brometea* and *Sedo-Scleranthetea* classes are floristically strongly related to each other. Several species are common in associations of the order *Festucetalia valesiacae* as well as in the order *Sedo-Scleranthetalia* (cf. Braun-Blanquet 1955, 1961; Korneck 1975; Mucina and Kolbek 1993b) such as *Allium lusitanicum*, *Alyssum alyssoides*, *Sedum album*, *Sempervivum arachnoideum* and *S. tectorum*.

Ecological factors and anthropogenic influence

According to our investigation the three subassociations of the *Festuco-Caricetum supinae* generally inhabit different parts in the Vinschgau. The subassociation *stipetosum pennatae* occurs on rockier and usually steeper areas, while the *bothriochloetosum ischaemi* stocks on heavily grazed pastures and the *stipetosum capillatae* grows mainly on deeper soils (Figure 4). We only analyzed the correlation of altitude, aspect and slope inclination with the floristic variation among subassociations. Despite the significance of inclination and altitude, these two environmental parameters cannot entirely explain the occurrence of these subassociations. The DCA (Figure 5) clearly shows the correlation of inclination for the *stipetosum pennatae*, which confirms our observation. However, there are sufficient reasons to assume that there is some other causal relationship behind the significancy of altitude: the *bothriochloetosum ischaemi* subassociation essentially characterizes the heavily grazed areas. These occur coincidentally more often near Mals (Figure 2), situated in the higher-altitude Vinschgau; i.e. the parameter altitude is probably a "pseudo-link", the different species compositions of the subassociation being more explained by the grazing intensity than by altitude. Considering this and taking into account that Vinschgau dry grasslands are also an anthropo-zoogenic habitat, management and especially grazing intensity seem to be more important in this case (cf. Braun-Blanquet 1961; Florineth 1973; Strimmer 1974; Köllemann 1981).

It is known that, in addition to ecological factors, changes in management, i.e. over- or undergrazing respectively abandonment of use, strongly influence species composition and community changes in steppe vegetation (Walter and Breckle 1994; Dúbravková and Hajnalová 2012; Korotchenko and Peregrym 2012; Rachkovskaya and Bragina 2012) and inner-alpine dry grasslands (Strimmer 1968, 1974; Florineth 1973; Köllemann 1981; Schwabe and Kratochwil 2004; Boch et al. 2019; Nota et al. 2021). Schwabe and Kratochwil (2012) mentioned that the succession processes in the inner-alpine dry valleys (primarily bush encroachment) take place very slowly. According to our own observation, shrubs (i.e. *Berberis vulgaris*, *Juniperus communis*, *Ligustrum vulgare*) grow mainly in the fringe of pastures and in rocky parts. Especially on areas and slopes with a tall and dense vegetation layer, presumably due to less grazing, shrubs and sometimes even seedlings of tree species (e.g. *Fraxinus ornus*, *Quercus pubescens*) appear. Clonally growing species such as *Hippophae rhamnoides* or *Prunus spinosa*, which often occur at the edge of the grasslands, may easily invade the grasslands. This could be observed even at small scale (e.g. near fences) especially where grazing intensity was obviously reduced. In addition, the lack of litter removal and lower soil disturbance as a consequence of lower grazing intensity or abandonment affect the floristic composition of dry grasslands in the long term (Ruprecht 2012). There is also evidence that *Stipa capillata* increased as a consequence of lower grazing intensity in dry grasslands and steppes (Strimmer 1968, 1974; Florineth 1973; Walter and Breckle 1994). According to our own observations and former investigations (Braun-Blanquet 1961; Strimmer 1968) *Festuca valesiaca* is very grazing tolerant. We found *F. valesiaca* more dominant in intensively grazed sites than *F. rupicola*, so that the latter seems to be slightly less tolerant against grazing. To what extent the three subassociations could be seen as different stages of succession, needs to be investigated. Additionally, the influence of other environmental factors such as temperature, precipitation, nutrient availability, etc. on the floristic composition needs to be studied in future. Furthermore, natural variations in cover values between years (Strimmer 1968, 1974; Gigon 1997), can be relatively high in dry grasslands, and, in contrast, vegetation changes in the long term should be analysed to disentangle the processes of land use change and climate change.

Conclusion

Our investigation shows that current dry grassland communities in the Vinschgau can be identified mainly as the *Festuco-Caricetum supinae* (order *Festucetalia valesiacae*). We suggest to include the investigated dry grasslands to the alliance *Festucion valesiacae*. Although the presented classification is sufficiently justified, the delimitation of the associations and subassociations still needs further discussion. Likewise, the rank of the character species at association, alliance and order level should be re-analysed. A comprehensive study is definitely needed not only to gain a better syntaxonomical overview of western and eastern alpine dry grassland communities but also to evaluate their relation to Eastern European dry grasslands. Especially, relevés from different years and over the whole season of one year are necessary for a more precise classification of the inner-alpine steppe vegetation, to be able to estimate the fluctuations in abundance between years. In addition, a more precise identification of some (sub)species could lead to a more exact delimitation on association-, subassociation- and variant level. The current classification and delimitation of dry grassland communities of the class *Festuco-Brometea* is neither uniform nor free of contradictions (cf. Mahn 1986; Mucina and Kolbek 1993a; Oberdorfer and Korneck 1993; Dierschke 1997; Ellenberg and Leuschner 2010; Willner et al. 2017, 2019) and needs a revision. Many questions also remain regarding the vegetation dynamics. Our data indicate that Vinschgau dry grasslands have changed floristically over time. In particular, the more mesophilous *Festuca rupicola* has increased its frequency and abundance. *Stipa capillata* also shows a positive trend over time. This floristic shift seems to be related to a lower grazing intensity. However, further studies are necessary to obtain a more detailed picture of dry grasslands in Vinschgau and their dynamics. In view of environmental and climate change, interdisciplinary approaches seem promising to obtain more comprehensive knowledge about dry grassland communities and their dynamics in general.

Author contributions

M.L. performed the fieldwork, did the statistical analysis, and wrote the first draft of the manuscript. B.E. supervised the work and improved the drafts of the manuscript.

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Supplementary material

Supplementary material 1
Sorted relevé table of dry grassland communities in the Vinschgau (South Tyrol, Italy) from 2019 (*.xlsx)
Link: https://doi.org/10.3897/VCS/2021/65217.suppl1

Supplementary material 2
Raw table of the relevés of dry grassland communities in the Vinschgau (South Tyrol, Italy) from 2019 (*csv)
Link: https://doi.org/10.3897/VCS/2021/65217.suppl2

Supplementary material 3
Raw table of the relevés of dry grassland communities in the Vinschgau (South Tyrol, Italy) from 2019 (*pdf)
Link: https://doi.org/10.3897/VCS/2021/65217.suppl3

VEGETATION CLASSIFICATION
AND SURVEY

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RESEARCH PAPER

CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC

Xeric grasslands of the inner-alpine dry valleys of Austria – new insights into syntaxonomy, diversity and ecology

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Abstract

Aims: We studied the syntaxonomic position, biodiversity, ecological features, nature conservation value and current status of dry grasslands investigated by Josias Braun-Blanquet more than 60 years ago. **Study area**: Inner-alpine valleys of Austria. **Methods**: We sampled 67 plots of 10 m^2, following the standardized EDGG methodology. We subjected our plots to an unsupervised classification with the modified TWINSPAN algorithm and interpreted the branches of the dendrogram syntaxonomically. Biodiversity, structural and ecological characteristics of the resulting vegetation units at association and order level were compared by ANOVAs. **Results**: All the examined grasslands belong to the class *Festuco-Brometea*. From ten distinguished clusters, we could assign four clusters to validly published associations, while the remaining six clusters were named tentatively. We classified them into three orders: *Stipo-Festucetalia pallentis* (*Armerio elongatae-Potentilletum arenariae*, *Phleo phleoidis-Pulsatilletum nigricantis*, *Medicago minima-Melica ciliata* community, *Koelerio pyramidatae-Teucrietum montani*), *Festucetalia valesiacae* (*Sempervivum tectorum-Festuca valesiaca* community); *Brachypodietalia pinnati* (*Astragalo onobrychidis-Brometum erecti*, *Agrostis capillaris-Avenula adsurgens* community, *Anthericum ramosum-Brachypodium pinnatum* community, *Ranunculus bulbosus-Festuca rubra* community, *Carduus defloratus-Brachypodium pinnatum* community). **Conclusions**: The ten distinguished dry grassland communities of the Austrian inner-alpine valleys differ in their ecological affinities as well as their vascular plant, bryophyte and lichen diversity. We point out their high nature conservation importance, as each of them presents a unique habitat of high value.

Taxonomic reference: Names of vascular plants, bryophytes and lichens follow Fischer et al. (2008), Frahm and Frey (2004) and Nimis et al. (2018), respectively.

Syntaxonomic reference: Names of orders and classes follow Mucina et al. (2016), references for associations and alliances are given in the text.

Abbreviations: ANOVA = analysis of variance; DCA: detrended correspondence analyses; EDGG: Eurasian Dry Grassland Group; EIV: ecological indicator value; FL: Fließ; GR: Griffen; GU: Gulsen; KA: Kaunerberg; LA: Laudegg castle in Ladis; MA: Marin; NM: Neumarkt in der Steiermark; OM: Obermauern; PÖ: Pöls; PU: Puxer Loch; TWINSPAN = Two-way indicator species analysis; ZS: Zinizachspitze.

Keywords

Austria, biodiversity, *Brachypodietalia pinnati*, *Festucetalia valesiacae*, *Festuco-Brometea*, inner-alpine dry valley, semi-natural grassland, soil parameter, resurvey, *Stipo-Festucetalia pallentis*, syntaxonomy, vegetation classification

Introduction

The European Alps ("Alps") form a nearly 1,200 km long arc from Nice in the southwest to Vienna in the northeast, with the widest sector in the centre of the Eastern Alps, stretching approximately 240 km from north to south (Ozenda 1988). The Alps represent a biodiversity hotspot in Central Europe, with 4,491 observed vascular plant species (Aeschimann et al. 2004; Barthlott et al. 2005). The inner-alpine valleys are the central parts of the great longitudinal valleys between the highest ridges of the Alps and represent islands of continentality within the relatively oceanic climate of the mountain ranges. One important aspect of continentality is the low precipitation, caused by the high altitudes of the mountains that cast rain shadows towards the south and southeast, leeward of the prevailing rain-bringing northwestern winds. While even the driest parts of the Alps are more humid than true steppes (Ozenda 1988), these valleys provide refugial habitats to many species with a distribution centred in the steppe biome of Eastern Europe (Kirschner et al. 2020). Similar intra-montane valleys with continental climate and *Festuco-Brometea* grasslands are known from other high mountain ranges, like the Caucasus (Belonovskaya et al. 2016).

The inner valleys of the Alps have been inhabited by humans since the Bronze Age (Sydow 1995; Bätzing 2005) or even earlier (Patzelt 1996), up to elevations exceeding 2,000 m (Braun-Blanquet 1961; Schwabe and Kratochwil 2012). Therefore, the contemporary landscape has been influenced by millennia of land use, mainly as pastures and meadows. It is evident that the traditional agro-pastoral practice exerted a positive feedback on the *Festuco-Brometea* grasslands, as already noticed by Braun-Blanquet (1961), who described the succession from the *Astragalo-Brometum* to *Larix decidua* or *Pinus sylvestris* forests after the cessation of management. Both the isolated relic character of these steppe elements and the requirement of adequate management underline the need of skilled nature protection measures in these unique habitats. Phytosociological studies are well suited for evidence-based decisions in nature conservation. However, most studies of the inner-alpine dry valleys (Buschardt 1979; Wagner 1979; Schwabe and Kratochwil 2004, 2012; Wiesner et al. 2015; Dengler et al. 2019) focused on the more (south)western parts of the Alps with a severe summer drought, and merely touched the Eastern Alps, which have only a moderately continental climate that is influenced by cyclones from the Adriatic Sea.

Our study is part of a long-term project of the Eurasian Dry Grassland Group (EDGG) that will cover the inner-alpine dry grasslands in the whole Alps (Dengler et al. 2020a; Magnes et al. 2020). In the present paper, we focus on the dry grassland vegetation of the inner-alpine valleys of the Austrian Alps, revisiting sites that were already described by Braun-Blanquet (1961). More specifically, we provide a preliminary syntaxonomic classification using modern multivariate methods, describe the biodiversity and ecology of these grasslands and discuss their conservation management.

Study area

We mainly sampled in three regions of Austria: the Upper Inn valley in North Tyrol, the Virgen valley in East Tyrol and the central Mur valley in Styria. Additionally, one site in the Carinthian Basin was visited (Figure 1). Aridity is most pronounced in the Upper Inn valley (Magnes et al. 2018), and although Landeck is located highest among the three weather stations presented (Figure 2), the annual mean temperature is higher and annual precipitation is lower than at stations in the other two.

Upper Inn valley

Sampling localities: Fließ (FL), Kaunerberg (KA), Laudegg castle in Ladis (LA) (Figure 1).

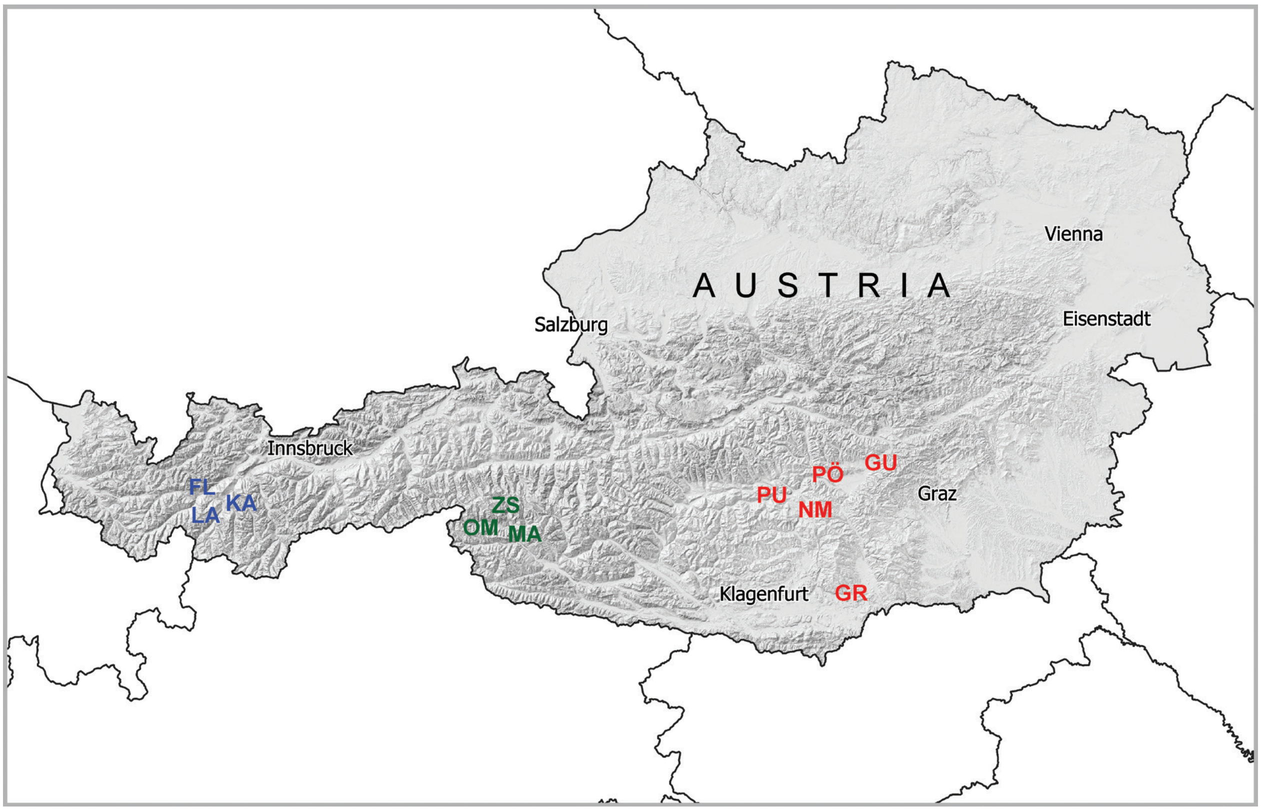

Figure 1. Location of the study sites: blue: Upper Inn valley (FL: Fließ, LA: Laudegg castle in Ladis, KA: Kaunerberg); green: Virgen valley (OM: Obermauern, ZS: Zinizachspitze, MA: Marin), red: Mur valley and Carinthian Basin (PU: Puxer Loch, NM: Neumarkt in der Steiermark, PÖ: Pöls, GR: Griffen, GU: Gulsen).

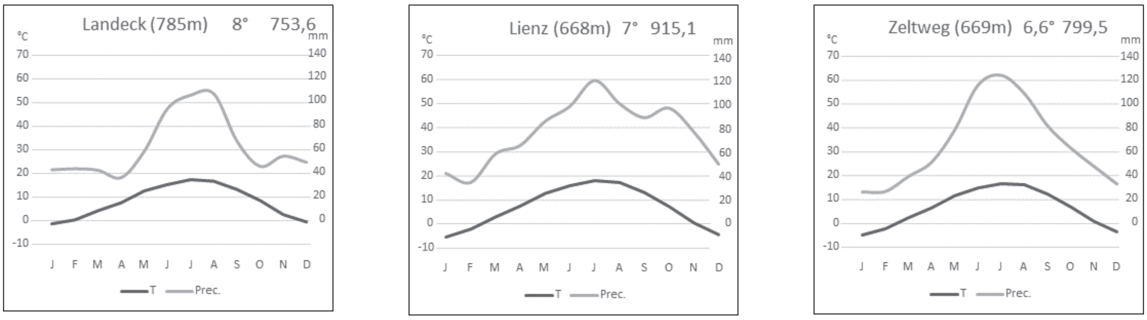

Figure 2. Climate diagrams from weather stations adjacent to the study sites (from west to east): The Upper Inn valley (Landeck), East Tyrol (Lienz, the closest ZAMG climate station to the Virgen valley), and the Mur valley (Zeltweg), based on data period 1971–2000 (ZAMG 2020). T: mean monthly temperature, Prec.: mean monthly precipitation.

The sampling was performed in the Nature Park Kaunergrat, southwest of Landeck, in one of the driest regions of the Austrian Alps. Our study area is close to the Engadin in Switzerland and the most continental area of the Eastern Alps, the Vinschgau in South Tyrol (Italy). Braun-Blanquet (1961) described the dry grasslands of the Austrian Upper Inn Valley in conjunction with those of the Lower Engadin because of the proximity and the similarity in geology, climate and species composition.

Geologically, the Kaunerberg (KA) and the study sites below the castle Laudegg (LA) belong to the easternmost part of the Engadin window. Kauns-Kaunerberg is located above Bündner schist, a metamorphic marine sediment from the Cretaceous period that is rich in calcium carbonate (Gruber et al. 2010). In contrast, the study sites below the Laudegg castle are situated above a much older, Triassic bedrock of metamorphic quartzite sandstone (Gruber et al. 2010). However, both rock materials favoured the formation of shallow soils at these localities. Another process that had a large influence on the composition of the soils at the studied sites was the deposition of drift and moraine material by the Inn glacier during the Würm Glacial. In course of this, rocks from a wider glacial catchment (e.g. Bündner schists, but also dolomites) were distributed and deposited along the valley slopes. This propagated the formation of calcareous soils at the study sites below Fließ (FL), although the bedrock below is exclusively made up of acidic mica schists of the Variscan Silvretta crystalline (Gruber et al. 2010).

The studied dry grassland sites bear witness of an old cultural landscape. Traditionally, these sites were communal pastures ("Allmende") for small livestock (mainly sheep, to a lesser amount goats) in spring and autumn, before and after summering on alpine pastures at higher elevations. This kind of management is documented back to the medieval ages, but likely is much older. Until the 1940s and early 1950s, several hundred animals were herded in the slopes below Fließ. However, this practice was abandoned alongside the economic upturn of the post-war era, leading to a reforestation of the sites. This negative trend lasted until 2002, when, following the long-lasting pressure of regional conservationists, the sites at Fließ were finally put under protection and integrated into the Natura 2000 network. The sites at Kauns-Kaunerberg followed shortly after and are protected under Tyrolean law since 2006. Since then, both sites have been managed by the Kaunergrat Nature Park. Management measures include the initial re-establishment of abandoned areas by removal of bushes and trees, and subsequent, targeted grazing by cattle, goats and sheep. Since their implementation, these activities have been regularly evaluated via monitoring studies on vegetation and selected insect taxa (butterflies, ants). The area is the best example of inner-alpine dry valleys in Austria concerning size and extent of dry and semi-dry grassland vegetation.

Virgen valley

Sampling localities: Obermauern (OM), Marin (MA), Zinizachspitze (ZS) (Figure 1).

The Virgen valley runs in a west-east direction south of the main ridge of the Alps. It is quite remote from modern traffic routes and accessible only from the east, following the Isel river upstream. Due to its position south of the giant mountain massif Großvenediger (3,662 m), the climate is rather dry with an average annual precipitation of about 900 mm. The nearest climate station (Lienz, 30 km to the southeast) shows sub-Mediterranean characteristics with a relatively low precipitation in late summer (Figure 2), while the precipitation in Virgen is probably significantly lower (Wagner 1979). The main settlements are found from 1,200 to 1,300 m. North of the valley the geological bedrock is dominated by the schist shell of the Upper Tauern Penninicum.

The valley has been populated since prehistoric times. *Triticum aestivum* was cultivated until the 1980s and up to an elevation of approximately 1,400 m. Cattle breeding is another important land use. Traditionally, the animals were brought across mountain passes to markets on the northern side of the main ridge (Oberwalder 1999). Since the 19th century, markets that are more distant have become relevant. The settlement structure in the valley is characterised by small villages surrounded by a structurally rich cultural landscape called "Virger Feldflur" (Michor 1999). Part of it are hedges with *Berberis vulgaris*, *Rosa* spp. and *Sorbus aucuparia*. The former arable fields were gradually transformed into grasslands, resulting in a saying in local dialect: "Virgn isch grin woagn" ("Virgen has become green") (Oberwalder 1999).

The montane and subalpine zones reach from the valley bottom up to more than 2,000 m. On the northern slopes, *Picea abies* forests are dominant. On the sunny southern slopes, the forests were replaced by grasslands centuries ago. The forest remnants are usually dominated by *Larix decidua* with low cover and are still used as reserve pastures for dry years. The often very steep slopes were not only grazed by cattle, sheep and goats, but also used as mountain hay meadows as farmers could not produce enough hay in the lower parts of the valley. Hay was used as forage in winter in addition to harvested leaves and straw. The mountain meadows, sometimes even above the timberline, were traditionally mown only every second year. They are situated in the neighbourhood of the mountain pastures, which are mainly used for young cattle (Oberwalder 1999).

The bedrock of the sampling localities is mainly calcareous slate, partly covered with moraine material, and only on the southern border of OM there is also some dark phyllite together with the calcareous slate (Frank et al. 1987).

Mur valley and Carinthian Basin

Sampling localities: Puxer Loch (PU), Neumarkt in der Steiermark (NM), Pöls (PÖ), Griffen (GR), Gulsen (GU) (Figure 1).

The studied part of the Mur valley is situated along the upper reaches of the river, approximately 80 to 120 km east of its source. Braun-Blanquet (1961) identified this area as the easternmost extension of the inner-alpine dry valleys. In comparison to the climate of Lienz (Figure 2), the precipitation is lower without a depression in late summer (Figure 2, climate station of Zeltweg). Additional to the two sites within the Mur valley itself (GU, PU), we include here plots in the area of an adjacent pass traversal (NM), one site in the Carinthian Basin (GR) and one site in a tributary valley of the Mur with the last population of the endemic *Stipa styriaca* (PÖ). The latter locality was not investigated by Braun-Blanquet (1961), because this species, probably a remnant of the glacial steppe-tundra, was discovered and described from this place only later (Melzer 1962; Martinovský 1970).

Although all sites are situated in the Austrian Central Alps, the geological bedrock is very diverse (Flügel and Neubauer 1984). While the westernmost site (PU) is located on a steep slope of Palaeozoic limestone (Murauer Palaeozoikum), the bedrock in NM consists of moraine material with quartzite. The habitat of *Stipa styriaca* in PÖ is a steep southern slope on black mica schist, and GU is part of the greatest connected serpentinite outcrop of Central Europe (Brooks 1987), its steep southern slopes being one of the most peculiar habitats in Austria (Magnes 2018). The castle hill of Griffen (GR), a landmark visible for miles around, is an isolated block of marble (Gleirscher and Pacher 2005).

Methods

Vegetation and environmental data

In total, we sampled 67 plots of 10 m^2 (15 nested-plot series with two 10-m^2 subplots each and additional 37 normal plots, Suppl. materials 1, 2) with the EDGG methodology (Dengler et al. 2016) between the 6th and 13th July 2018. Each nested-plot series ("EDGG Biodiversity Plots") consists of a 100-m^2 plot, with nested series of 0.0001, 0.001, 0.01, 0.1, 1 and 10 m^2 in two opposite corners. All terricolous vascular plants, bryophytes and lichens were recorded with the shoot presence method (Dengler 2008) for all plot sizes, and their cover value in percent was estimated in the 10-m^2 plots.

Soil of the uppermost 10 cm was collected in each plot by mixing five random samples. The following soil parameters were measured (all measured environmental variables as header data are provided in Suppl. material 1): skeleton content (mass fraction of particles > 2 mm), percentages of sand, clay and silt, texture class estimated with Robinson pipette method after removing organic matter with 6% H_2O_2, field capacity (%), drainage rate (cm/h), available water (%), saturation (%), permanent wilting point (%), pH (in a suspension of 10 g dry soil in 25 ml aqua dest.), electrical conductivity (EC) (in a suspension of 10 g dry soil in 50 ml aqua dest., dS/m), organic matter (as loss at ignition at 430°C, %), organic carbon (%), N content estimated with the Kjeldahl method (%), C/N, available P (estimated with the Mehlich 3 method (PM3), mg/kg).

Other recorded environmental and structural parameters were (for methodological details, see Dengler et al. 2016): geographical position (with precision of 1 m), elevation (m), aspect (°), inclination (°), maximum microrelief (cm), soil depth (cm, mean of five measurements per plot), total vegetation cover (%), cover shrub layer (%), cover herb layer (%), cover bryophyte/lichen layer (%), cover litter (%), cover stones and rocks (%), cover gravel (%), cover fine soil (%), maximum height of shrubs (m), maximum height of herbs (cm), height of herb layer (mean of five measurements per plot), relief (topographic) position, and land use, with indication of grazing, mowing, burning or abandonment. For each relevé, mean ecological indicator values for temperature, continentality, light, moisture, nutrients and soil reaction were calculated in the JUICE 7.1 software (Tichý 2002), based on the values published by Ellenberg et al. (1991).

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 AT_E. The 10-m^2 plots are also provided in Suppl. material 1 (header data) and Suppl. material 2 (sorted relevé table).

Data analysis

The compositional data, along with the header data, were entered into TURBOVEG (Hennekens and Schamineé 2001) and then imported into the program JUICE (Tichý 2002). Prior to the numerical analysis, occurrences of species in the shrub and herb layer were combined, using the formula of Fischer (2015). We conducted a TWINSPAN (Two-Way Indicator Species Analysis; Hill 1979) in the modified version proposed by Roleček et al. (2009), with the following settings: three pseudospecies cut levels (0%, 5% and 25%); total inertia as measure of heterogeneity; minimum group size: 2.

We tried cluster numbers up to 15 and finally selected the solution with 11 clusters as the basis for our classification, as it corresponded most closely to what we consider the association level. One cluster containing a single relevé was joined with another cluster, so finally ten relevé groups were distinguished. Moreover, three clusters were subdivided into regional variants. These variants partly corresponded to TWINSPAN clusters of finer resolution, but the assignment of relevés to regional variants was based on their geographical distribution.

Fidelity of species to relevé groups was calculated using the phi coefficient of association (Chytrý et al. 2002), assuming equal cluster size (Tichý and Chytrý 2006). To provide diagnostic species both at order and association level, the calculations were done in Excel, which precluded the application of Fisher's exact test. However, we set phi-value thresholds so high that essentially no non-significant species were chosen at the association level. Species were considered as diagnostic with phi ≥ 0.25 at order level and phi ≥ 0.45 at association level. Additionally, we required in both cases that the drop in phi-value to the syntaxon with the next highest phi-value was at least 0.25; otherwise, the species was also considered diagnostic in the latter syntaxon. If such a drop of 0.25 did not occur anywhere in the sequence of syntaxa ordered by decreasing phi-values, a species was considered not diagnostic. If a species was diagnostic at both order and association level, it was assigned to the level where the phi-value was higher, provided all other conditions were fulfilled. The term "diagnostic species" is used here in a data-set specific context and should not be understood as equivalent to character species (see Willner et al. 2009).

We tried to assign our relevé groups to phytosociological associations, alliances and orders described in the literature by comparing the species composition. If such an assignment was ambiguous, we used informal community names. We refrained from formally describing new syntaxa, as this will be the task of a future, more comprehensive revision of all dry grasslands of the Eastern Alps. To facilitate the syntaxonomic interpretation, we

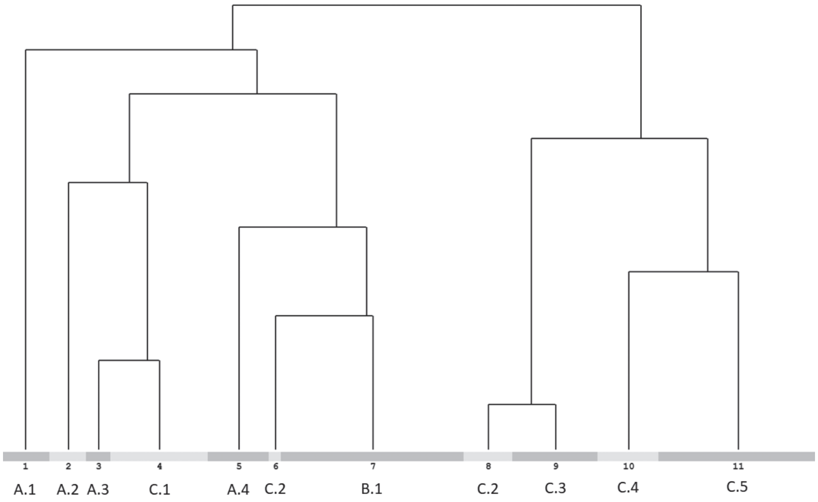

Figure 3. Dendrogram of the 11-cluster resolution from modified TWINSPAN analysis. Below the cluster numbers, the corresponding association/community is indicated (A.1–A.4: *Stipo-Festucetalia pallentis*, B.1: *Festucetalia valesiacae*, C.1–C.5: *Brachypodietalia pinnati*). For the meaning of the community codes, see text.

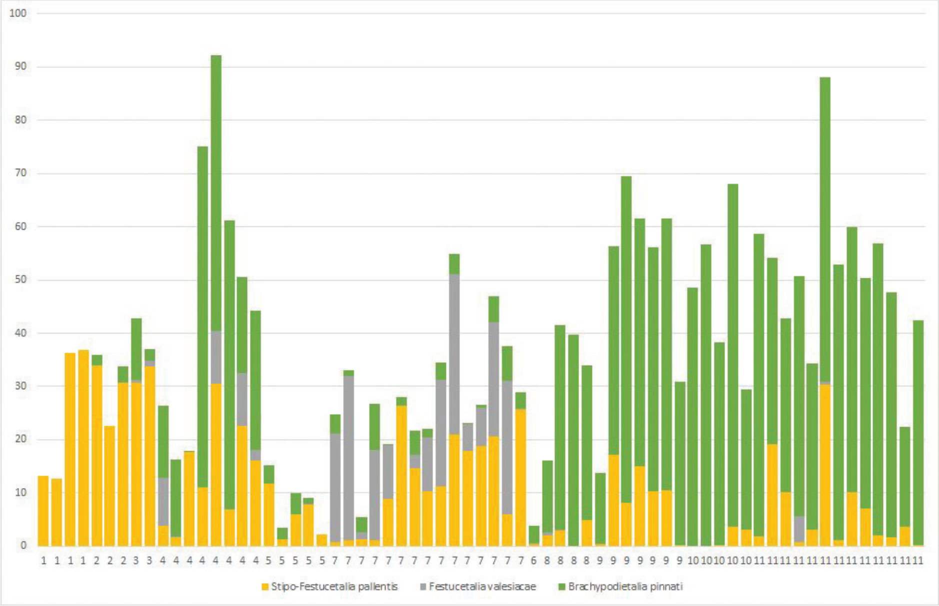

Figure 4. Stacked total percentage covers of the diagnostic species of the orders *Stipo-Festucetalia pallentis* (A), *Festucetalia valesiacae* (B) and *Brachypodietalia pinnati* (C) in each relevé. The numbers below the diagram are the TWINSPAN clusters. The sequence of the relevés is the same as in Figure 3 but differs from Table 1 in the position of cluster 4. Note that the percentage cover of non-diagnostic species is not shown.

calculated for each relevé the total percentage cover of the diagnostic species of orders according to Willner et al. (2019) using the function "total cover of <colour> species" in JUICE.

To visualize the relation of the species composition of the relevé groups (and relevés) to measured or calculated factors we performed a DCA using Canoco 5 (ter Braak and Šmilauer 2012) with downweighting of rare species and log-transformation of cover values.

The number and cover of red list species were calculated in JUICE based on Niklfeld and Schratt-Ehrendorfer (1999) for vascular plants, Grims and Köckinger (1999) and Saukel and Köckinger (1999) for bryophytes and Türk and Hafellner (1999) for lichens.

Results

Numerical classification

The first TWINSPAN division resulted in two groups roughly corresponding to the orders *Stipo-Festucetalia pallentis* (clusters 1–7) and *Brachypodietalia pinnati* (clusters 8–11) of the class *Festuco-Brometea* (Figure 3). Cluster 4 was transitional between the two orders, with most of its relevés having a higher total cover of *Brachypodietalia* species (Figure 4). Cluster 7 was transitional between the *Stipo-Festucetalia pallentis* and *Festucetalia valesiacae* with several relevés clearly belonging to the latter order (Figure 4). Cluster

6, containing a single relevé, showed a clear prevalence of *Brachypodietalia* species (Figure 4). As it shared several otherwise rare species with cluster 8 (e.g., *Allium carinatum*, *Avenula adsurgens*, *Jasione montana*, *Potentilla argentea*), and the relevés of both clusters were from the same location, we joined these two clusters into a single community. Otherwise, we refrained from moving single relevés between clusters based on their affinity to phytosociological orders, but potentially misclassified relevés are mentioned in the description of the individual communities.

Therefore, we classified our relevés into ten vegetation units at association level, which in turn were grouped in the three orders (A) *Stipo-Festucetalia pallentis*, (B) *Festucetalia valesiacae* and (C) *Brachypodietalia pinnati* (Table 1, Suppl. material 2). The alliance level remained unresolved (see Discussion).

Table 1. Abridged synoptic table of the associations, based on the 10-m² plots. For each syntaxon, the 10 species with the highest phi-values are shown plus all species with 10% or higher constancy across all plots. The number of presented vs. total species in each group is given in brackets. Values are percentage constancies. Species are sorted by decreasing fidelity within the respective syntaxon and by decreasing overall constancy in case of accompanying species. The complete synoptic and relevé table is provided in Suppl. material 2. B: bryophyte, L: lichen, V: vascular plant.

Syntaxon		**All**	**A**	**B**	**C**	**A.1**	**A.2**	**A.3**	**A.4**	**B.1**	**C.1**	**C.2**	**C.3**	**C.4**	**C.5**
Number of plots		**67**	**14**	**15**	**38**	**4**	**3**	**2**	**5**	**15**	**8**	**5**	**7**	**5**	**13**
Diagnostic species order A (3)															
Hypnum cupressiforme	B	16	43	7	11	50	.	50	60	7	.	20	14	20	8
Geranium columbinum	V	7	21	.	5	.	33	50	20	.	13	20	.	.	.
Echium vulgare	V	4	14	.	3	.	33	50	.	.	.	.	14	.	.
Diagnostic species association A.1 (11 of 15)															
Alyssum montanum	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Asplenium cuneifolium	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Dorycnium germanicum	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Koeleria pyramidata var. *pubiculmis*	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Potentilla incana	V	6	29	.	.	100	.	.	.	.	.	.	.	.	.
Festuca pallens	V	7	29	.	3	100	.	.	.	.	.	.	14	.	.
Lepraria lobificans	L	4	21	.	.	75	.	.	.	.	.	.	.	.	.
Erysimum sylvestre	V	15	50	13	3	100	.	.	60	13	13	.	.	.	.
Jovibarba globifera subsp. *hirta*	V	6	21	.	3	75	.	.	.	.	.	20	.	.	.
Notholaena marantae	V	3	14	.	.	50	.	.	.	.	.	.	.	.	.
Weissia brachycarpa	B	12	21	7	11	75	.	.	.	7	25	.	.	.	15
Diagnostic species association A.2 (10 of 13)															
Alliaria petiolata	V	3	14	.	.	.	67	.	.	.	.	.	.	.	.
Myosotis ramosissima	V	3	14	.	.	.	67	.	.	.	.	.	.	.	.
Origanum vulgare	V	10	21	.	11	.	100	.	.	.	.	.	57	.	.
Fallopia convolvulus	V	10	21	.	11	.	100	.	.	.	.	60	14	.	.
Stachys recta	V	12	29	.	11	.	100	50	.	.	13	.	43	.	.
Scabiosa ochroleuca	V	6	14	.	5	.	67	.	.	.	.	.	29	.	.
Teucrium chamaedrys	V	19	21	13	21	.	100	.	.	13	38	20	57	.	.
Aster amellus	V	12	14	27	5	.	67	.	.	27	25	.	.	.	.
Bromus inermis	V	1	7	.	.	.	33	.	.	.	.	.	.	.	.
Galeopsis pubescens	V	1	7	.	.	.	33	.	.	.	.	.	.	.	.
Diagnostic species association A.3 (10 of 15)															
Medicago minima	V	10	14	20	5	.	.	100	.	20	25	.	.	.	.
Agrimonia eupatoria	V	12	14	.	16	.	.	100	.	.	25	.	57	.	.
Amblystegium serpens	B	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Clinopodium nepeta agg.	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Erigeron acris	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Lapsana communis	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Silene latifolia	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Torilis arvensis	V	1	7	.	.	.	.	50	.	.	.	.	.	.	.
Melica ciliata	V	18	21	40	8	.	33	100	.	40	38	.	.	.	.
Artemisia absinthium	V	3	7	7	.	.	.	50	.	7	.	.	.	.	.
Galium lucidum	V	24	36	33	16	.	33	100	40	33	50	.	14	.	8
Diagnostic species association A.4 (12 of 19)															
Poa badensis agg.	V	9	36	7	.	.	.	.	100	7	.	.	.	.	.
- Poa molinieri		*4*	*14*	*7*	.	.	.	.	*40*	*7*	.	.	.	.	.
Toninia sedifolia	L	6	29	.	.	.	.	.	80	.	.	.	.	.	.
Tortella inclinata	B	6	29	.	.	.	.	.	80	.	.	.	.	.	.
Ditrichum flexicaule	B	7	29	.	3	.	.	.	80	.	.	.	.	20	.
Peltigera rufescens	L	7	29	.	3	.	.	.	80	.	.	.	.	20	.
Saxifraga paniculata	V	4	21	.	.	.	.	.	60	.	.	.	.	.	.
Psora decipiens	L	6	21	7	.	.	.	.	60	7	.	.	.	.	.
Cladonia symphycarpa	L	15	29	40	.	.	.	.	80	40	.	.	.	.	.
Physconia muscigena	L	7	21	13	.	.	.	.	60	13	.	.	.	.	.
Cladonia macrophyllodes	L	3	14	.	.	.	.	.	40	.	.	.	.	.	.
Endocarpon pusillum	B	10	21	27	.	.	.	.	60	27	.	.	.	.	.
Tortella tortuosa	B	22	29	40	13	.	.	.	80	40	.	.	.	20	31
Diagnostic species order B (21 of 35)															
Festuca valesiaca	V	33	14	93	16	.	.	50	20	93	38	.	.	20	15
Sempervivum tectorum	V	16	.	67	3	.	.	.	.	67	13	.	.	.	.

Syntaxon		**All**	**A**	**B**	**C**	**A.1**	**A.2**	**A.3**	**A.4**	**B.1**	**C.1**	**C.2**	**C.3**	**C.4**	**C.5**
Number of plots		**67**	**14**	**15**	**38**	**4**	**3**	**2**	**5**	**15**	**8**	**5**	**7**	**5**	**13**
Veronica spicata	V	19	.	67	8	.	.	.	.	67	25	.	.	20	.
Artemisia campestris	V	39	50	100	11	.	67	.	100	100	50	.	.	.	.
Koeleria macrantha	V	22	14	73	5	25	33	.	.	73	25	.	.	.	.
Dianthus sylvestris	V	33	36	87	11	.	.	.	100	87	25	.	.	40	.
Galium verum	V	31	7	73	24	.	.	50	.	73	75	.	.	60	.
Bromus erectus	V	39	7	80	34	.	.	50	.	80	100	.	14	40	15
Parmelia somloensis	L	13	.	47	5	.	.	.	.	47	.	40	.	.	.
Phleum phleoides	V	31	14	73	21	.	.	50	20	73	63	40	.	20	.
Tortula ruralis	B	19	14	60	5	.	.	.	40	60	13	20	.	.	.
Potentilla pusilla	V	48	43	93	32	.	.	50	100	93	63	.	.	60	31
Petrorhagia saxifraga	V	24	21	67	8	.	.	.	60	67	38	.	.	.	.
Sempervivum arachnoideum	V	19	21	60	3	.	.	.	60	60	.	.	.	20	.
Vincetoxicum hirundinaria	V	45	14	80	42	.	67	.	.	80	100	20	86	20	.
Sedum album	V	28	43	73	5	.	33	.	100	73	25	.	.	.	.
Festuca guestfalica	V	15	.	40	11	.	.	.	.	40	38	.	.	20	.
Sedum sexangulare	V	21	21	53	8	.	.	.	60	53	13	.	.	40	.
Hedwigia ciliata	L	16	7	40	11	.	.	50	.	40	.	60	.	20	.
Cladonia pyxidata	L	18	29	47	3	.	.	.	80	47	.	.	.	20	.
Scabiosa columbaria agg.	V	28	36	53	16	.	.	50	80	53	25	20	14	.	15
- *Scabiosa columbaria*		*13*	*29*	*13*	*8*	.	.	.	*80*	*13*	.	*20*	*14*	.	*8*
- *Scabiosa lucida*		*1*	.	.	*3*	.	.	.	.	.	.	.	.	.	*8*
- *Scabiosa triandra*		*13*	*7*	*40*	*5*	.	.	*50*	.	*40*	*25*	.	.	.	.
Diagnostic species order C (22 of 28)															
Leontodon hispidus	V	30	.	.	53	.	.	.	.	.	13	.	29	80	100
Achillea millefolium agg.	V	42	14	.	68	25	.	50	.	.	.	60	100	100	85
Lotus corniculatus	V	42	.	20	66	.	.	.	.	20	63	.	43	80	100
Dactylis glomerata	V	33	.	13	53	.	.	.	.	13	50	20	86	40	54
Veronica chamaedrys	V	18	.	.	32	.	.	.	.	.	.	60	43	80	15
Pimpinella saxifraga	V	30	14	.	47	.	.	50	20	.	.	20	71	60	69
- *Pimpinella saxifraga subsp. nigra*		6	.	.	*11*	.	.	.	.	.	.	.	*43*	.	*8*
Anthoxanthum odoratum agg.	V	16	.	.	29	.	.	.	.	.	.	20	14	60	46
Campanula glomerata	V	15	.	.	26	.	.	.	.	.	13	.	43	.	46
Cerastium holosteoides	V	12	.	.	21	.	.	.	.	.	.	.	14	40	38
Trifolium repens	V	12	.	.	21	.	.	.	.	.	13	20	14	40	23
Carex ornithopoda	V	10	.	.	18	.	.	.	.	.	.	.	.	40	38
Centaurea jacea	V	10	.	.	18	.	.	.	.	.	.	.	14	20	38
Galium pumilum	V	10	.	.	18	.	.	.	.	.	.	20	29	20	23
Larix decidua	V	10	.	.	18	.	.	.	.	.	.	.	.	40	38
Brachypodium pinnatum agg.	V	54	21	47	68	.	67	50	.	47	75	.	86	60	85
- *Brachypodium pinnatum*		*31*	*14*	.	*50*	.	*67*	.	.	.	.	.	*71*	*60*	*85*
- *Brachypodium rupestre*		*21*	*7*	*47*	*16*	.	.	*50*	.	*47*	*75*	.	.	.	.
Polygonatum odoratum	V	15	.	7	24	.	.	.	.	7	13	40	.	.	46
Fragaria vesca	V	15	7	.	24	.	.	50	.	.	13	20	57	60	.
Galium album	V	25	21	.	37	.	67	50	.	.	.	100	71	40	15
Koeleria pyramidata var. *pyramidata*	V	48	36	27	61	.	.	.	100	27	13	100	71	60	69
Seseli libanotis	V	18	7	7	26	.	.	50	.	7	38	.	43	.	31
Brachythecium rutabulum	B	12	7	.	18	.	.	50	.	.	13	20	14	20	23
Poa pratensis agg.	V	34	21	20	45	.	33	100	.	20	75	40	57	40	23
Diagnostic species association C.1 (2)															
Fragaria viridis	V	3	.	.	5	.	.	.	.	.	25	.	.	.	.
Astragalus onobrychis	V	9	.	20	8	.	.	.	.	20	38	.	.	.	.
Diagnostic species association C.2 (12 of 16)															
Potentilla argentea	V	10	.	13	13	.	.	.	.	13	.	100	.	.	.
Allium carinatum	V	10	.	7	16	.	.	.	.	7	.	100	14	.	.
Genista tinctoria	V	4	.	.	8	.	.	.	.	.	.	60	.	.	.
Jasione montana	V	4	.	.	8	.	.	.	.	.	.	60	.	.	.
Populus tremula	V	4	.	.	8	.	.	.	.	.	.	60	.	.	.
Potentilla rupestris	V	4	.	.	8	.	.	.	.	.	.	60	.	.	.
Avenula adsurgens subsp. *adsurgens*	V	15	7	.	24	.	33	.	.	.	.	100	43	.	8
Campanula rotundifolia	V	10	.	7	16	.	.	.	.	7	.	80	14	20	.
Viola arvensis	V	6	.	.	11	.	.	.	.	.	.	60	14	.	.
Ceratodon purpureus	B	7	.	7	11	.	.	.	.	7	13	60	.	.	.
Silene nutans	V	15	.	.	26	.	.	.	.	.	.	80	14	20	31
Cladonia fimbriata	B	12	7	13	13	25	.	.	.	13	.	60	.	20	8
Diagnostic species association C.3 (10 of 18)															
Anthericum ramosum	V	7	.	.	13	.	.	.	.	.	.	.	71	.	.
Campanula trachelium	V	7	.	.	13	.	.	.	.	.	.	.	71	.	.
Centaurea scabiosa	V	7	.	.	13	.	.	.	.	.	.	.	71	.	.
Tragopogon orientalis	V	7	.	.	13	.	.	.	.	.	.	.	71	.	.
Peucedanum oreoselinum	V	13	.	20	16	.	.	.	.	20	13	.	71	.	.
Astragalus glycyphyllos	V	9	7	.	13	.	33	.	.	.	.	.	71	.	.
Polygala comosa	V	4	.	.	8	.	.	.	.	.	.	.	43	.	.
Clinopodium vulgare	V	13	7	.	21	.	.	50	.	.	13	20	86	.	.
Viola hirta	V	16	7	.	26	.	.	50	.	.	38	.	86	.	8
Vicia cracca agg.	V	10	.	.	18	.	.	.	.	.	.	.	57	20	15
Diagnostic species association C.4 (11 of 19)															
Ranunculus bulbosus	V	9	.	.	16	.	.	.	.	.	.	.	14	100	.
Festuca rubra agg.	V	12	.	.	21	.	.	.	.	.	.	.	.	100	23

Syntaxon		**All**	**A**	**B**	**C**	**A.1**	**A.2**	**A.3**	**A.4**	**B.1**	**C.1**	**C.2**	**C.3**	**C.4**	**C.5**
Number of plots		**67**	**14**	**15**	**38**	**4**	**3**	**2**	**5**	**15**	**8**	**5**	**7**	**5**	**13**
- Festuca rubra		6	.	.	*11*	.	.	.	.	.	.	.	.	*60*	*8*
Knautia arvensis	V	4	.	.	8	.	.	.	.	.	.	.	.	60	.
Lolium perenne	V	4	.	.	8	.	.	.	.	.	.	.	.	60	.
Veronica officinalis	V	4	.	.	8	.	.	.	.	.	.	.	.	60	.
Calliergonella cuspidata	B	7	.	.	13	.	.	.	.	.	.	.	.	60	15
Ranunculus acris	V	7	.	.	13	.	.	.	.	.	.	.	.	60	15
Thuidium philibertii	B	7	.	.	13	.	.	.	.	.	.	.	.	60	15
Hieracium pilosella	V	25	.	27	34	.	.	.	.	27	.	40	.	100	46
Avenula pratensis	V	3	.	.	5	.	.	.	.	.	.	.	.	40	.
Plantago lanceolata	V	25	7	20	34	.	.	50	.	20	38	.	43	100	15
Diagnostic species association C.5 (21 of 55)															
Persicaria vivipara	V	13	.	.	24	.	.	.	.	.	.	.	.	.	69
Potentilla erecta	V	24	.	.	42	.	.	.	.	.	.	.	.	60	100
Phyteuma orbiculare	V	10	.	.	18	.	.	.	.	.	.	.	.	.	54
Plantago atrata	V	10	.	.	18	.	.	.	.	.	.	.	.	.	54
Ranunculus nemorosus	V	10	.	.	18	.	.	.	.	.	.	.	.	.	54
Thesium alpinum	V	15	.	.	26	.	.	.	.	.	.	.	.	20	69
Centaurea pseudophrygia	V	9	.	.	16	.	.	.	.	.	.	.	.	.	46
Gymnadenia conopsea	V	9	.	.	16	.	.	.	.	.	.	.	.	.	46
Laserpitium latifolium	V	9	.	.	16	.	.	.	.	.	.	.	.	.	46
Molinia caerulea	V	9	.	.	16	.	.	.	.	.	.	.	.	.	46
Pimpinella major	V	13	.	.	24	.	.	.	.	.	.	.	.	20	62
Polygala chamaebuxus	V	13	.	.	24	.	.	.	.	.	.	.	.	20	62
Carlina acaulis	V	27	.	7	45	.	.	.	.	7	.	.	29	60	92
Euphrasia officinalis	V	16	.	.	29	.	.	.	.	.	.	.	.	40	69
Galium anisophyllon	V	16	.	.	29	.	.	.	.	.	.	.	.	40	69
Carduus defloratus	V	19	7	.	32	25	.	.	.	.	13	.	.	20	77
Trifolium montanum	V	33	.	13	53	.	.	.	.	13	13	.	43	60	100
Campanula scheuchzeri	V	12	.	.	21	.	.	.	.	.	.	.	.	20	54
Sesleria caerulea	V	12	.	.	21	.	.	.	.	.	.	.	.	20	54
Anthyllis vulneraria	V	19	14	.	29	.	.	.	40	.	.	.	14	20	69
Hippocrepis comosa	V	12	.	.	21	.	.	.	.	.	13	.	.	20	46
Diagnostic species for more than one order (3)															
Carex caryophyllea	V	52	7	60	66	.	.	.	20	60	63	100	29	80	69
Allium lusitanicum	V	42	71	73	18	50	100	.	100	73	13	.	14	.	38
Thymus praecox	V	33	50	67	13	100	.	50	40	67	50	.	14	.	.
Diagnostic species for more than one association (18 of 25)															
Thymus pulegioides	V	37	29	20	47	.	.	.	80	20	25	.	.	80	92
Briza media	V	33	.	13	53	.	.	.	.	13	.	.	71	60	92
Salvia pratensis	V	31	7	60	29	.	.	50	.	60	63	.	86	.	.
Plantago media	V	25	.	7	42	.	.	.	.	7	38	.	.	60	77
Teucrium montanum	V	24	29	33	18	.	.	.	80	33	88	.	.	.	.
Agrostis capillaris	V	22	.	.	39	.	.	.	.	.	.	100	.	80	46
Trifolium pratense	V	22	7	.	37	.	.	50	.	.	.	.	14	100	62
Leucanthemum vulgare agg.	V	21	.	.	37	.	.	.	.	.	.	.	.	80	77
Linum catharticum	V	21	.	.	37	.	.	.	.	.	.	.	.	80	77
Verbascum chaixii subsp. *austriacum*	V	21	36	.	24	50	100	.	.	.	.	80	57	.	8
Arrhenatherum elatius	V	18	.	7	29	.	.	.	.	7	.	60	71	20	15
Taraxacum sect. *Ruderalia*	V	16	.	.	29	.	.	.	.	.	.	.	71	60	23
Primula veris	V	15	.	.	26	.	.	.	.	.	.	.	57	.	46
Hylotelephium maximum	V	13	29	.	13	75	33	.	.	.	.	100	.	.	.
Genista sagittalis	V	12	.	.	21	.	.	.	.	.	.	80	57	.	.
Homalotrichon (Avenula) pubescens	V	12	.	.	21	.	.	.	.	.	.	60	43	.	15
Prunella vulgaris	V	12	.	.	21	.	.	.	.	.	.	.	.	60	38
Trifolium arvense	V	12	7	27	8	.	.	50	.	27	.	60	.	.	.
Other species (22 of 209)															
Abietinella abietina	B	57	43	53	63	.	33	.	100	53	63	100	.	80	77
Euphorbia cyparissias	V	57	36	60	63	50	.	50	40	60	63	100	71	60	46
Carex humilis	V	55	57	73	47	75	100	100	.	73	88	20	29	.	62
Helianthemum nummularium subsp. *obscurum*	V	52	36	47	61	.	33	.	80	47	63	20	71	60	69
Festuca rupicola	V	48	50	27	55	.	100	.	80	27	38	100	86	60	31
Rhytidium rugosum	B	46	43	53	45	50	.	.	80	53	25	80	.	40	69
Medicago falcata	V	28	21	33	29	.	33	50	20	33	88	.	57	.	.
Bryum argenteum	B	18	21	27	13	.	.	.	60	27	13	60	.	20	.
Hypericum perforatum	V	16	14	.	24	25	33	.	.	.	.	40	71	40	.
Sanguisorba minor	V	16	7	13	21	.	33	.	.	13	38	.	43	40	.
Cuscuta epithymum	V	15	14	7	18	.	67	.	.	7	38	20	43	.	.
Arenaria serpyllifolia agg.	V	13	29	20	5	50	33	.	20	20	.	.	14	20	.
Asperula cynanchica	V	13	14	7	16	50	.	.	.	7	38	.	29	20	.
Medicago lupulina	V	13	14	.	18	.	33	.	20	.	13	.	29	20	23
Rosa canina agg.	V	12	14	7	13	.	33	50	.	7	25	20	29	.	.
Securigera varia	V	12	14	13	11	.	33	50	.	13	50	.	.	.	.
Cladonia furcata	L	10	.	13	13	.	.	.	.	13	.	20	.	.	31
Clinopodium alpinum	V	10	7	.	16	.	.	.	20	.	.	.	.	40	31
Didymodon rigidulus	B	10	14	27	3	.	.	.	40	27	.	.	.	20	.
Leucodon sciuroides	B	10	14	27	3	.	.	50	20	27	13	.	.	.	.
Prunus spinosa	V	10	7	.	16	.	.	50	.	.	25	40	29	.	.
Sedum acre	V	10	21	20	3	25	.	.	40	20	13	.	.	.	.

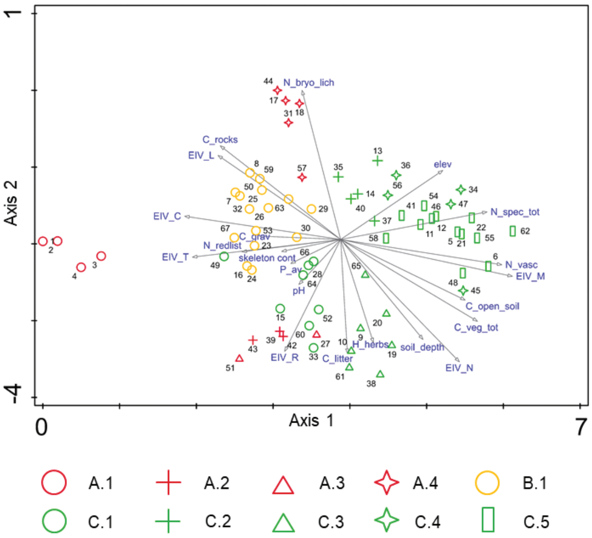

Figure 5. DCA of the 10-m² plots sampled during the 11th EDGG Field Workshop (gradient length/eigenvalue/cumulative explained variation of Axis 1: 6.12/0.646/8.56, Axis 2: 3.70/0.4086/13,97). A.1–C.5: clusters according to the order/association code in Table 1, Suppl. material 2: **red**: *Stipo-Festucetalia pallentis* (A), **yellow**: *Festucetalia valesiacae* (B), **green**: *Brachypodietalia pinnati* (C); **vectors**: **C_grav**: cover of gravel; **C_litter**: cover of litter; **C_open_soil**: cover open soil; **C_rocks**: cover of rocks and stones; **C_veg_ot**: total vegetation cover; **elev**: elevation; EIV_C: Ellenberg indicator value for continentality; EIV_L: Ellenberg indicator value for light; EIV_M: Ellenberg indicator value for moisture; EIV_N: Ellenberg indicator value for nutrients; EIV_R: Ellenberg indicator values for soil reaction; EIV_T: Ellenberg indicator values for temperature; **H_herbs**: maximum height of herbs; **N_bryo_lich**: species number of bryophytes and lichens; **N_redlist**: number of red-list species; **N_vasc**: number of vascular plant species; **N_grass**: number of grass species; **N_spec_tot**: total species number; **P_av**: available Phosphor; skeleton con: skeleton content. The numbers show the position of the plots (For TURBOVEG numbers, see Suppl. material 1).

Ordination

The first axis of the DCA graph (Figure 5) corresponds to a gradient of skeleton content and partly soil depth, supporting the division between the *Stipo-Festucetalia pallentis* (clusters A.1–A.4) on the left (high skeleton content, low soil depth) and the *Brachypodietalia pinnati* (clusters C.1–C.5) on the right, with cluster B.1 (*Festucetalia valesiacae*) in an intermediate position. Axis 2 depicts mainly litter cover, a good proxy for abandonment of management in the lower parts of the graph. The neatly grazed grassland of cluster A.4 (OM) in the upper part of the graph, having a high number of bryophytes and lichens, contrasts with the abandoned sites of PU and PÖ of clusters A.2 and A.3 having high litter cover and higher indicator values for nutrients.

Biodiversity and vegetation cover

Maximum species richness for all taxa increased from 9 in 0.0001 m² to 103 in 100 m² (Table 2). Across grain

Table 2. Scale-dependent species richness of the studied nested-plot series. We provide maximum values across all 15 nested-plot series and means ± standard deviation for each of the three distinguished orders. Number of samples is given in brackets (first number for grain sizes up to 10 m², second number for 100 m²).

Area [m²]	All Max.	Order A (n = 7/3)	 B (n = 9/4)	 C (n = 14/6)
All taxa				
0.0001	9	2.0 ± 2.0	2.1 ± 1.1	4.0 ± 1.9
0.001	11	3.0 ± 2.2	3.2 ± 1.6	6.6 ± 2.6
0.01	19	4.9 ± 2.4	5.6 ± 2.6	11.2 ± 3.9
0.1	36	11.6 ± 3.0	12.7 ± 3.2	22.3 ± 8.7
1	54	19.6 ± 7.4	25.3 ± 6.2	33.6 ± 11.5
10	71	29.9 ± 7.7	36.1 ± 5.4	51.2 ± 13.4
100	103	46.0 ± 13.9	60.8 ± 12.4	84.5 ± 14.3
Vascular plants				
0.0001	8	1.3 ± 1.1	1.2 ± 0.8	3.8 ± 1.7
0.001	11	1.6 ± 1.5	2.1 ± 1.1	6.2 ± 2.3
0.01	18	2.4 ± 2.4	3.9 ± 2.0	10.6 ± 3.7
0.1	33	7.0 ± 1.9	9.2 ± 2.9	21.6 ± 8.2
1	49	14.7 ± 7.2	18.6 ± 3.8	31.3 ± 11.4
10	66	20.0 ± 4.6	26.9 ± 4.0	46.6 ± 14.8
100	94	30.0 ± 3.6	43.0 ± 8.6	75.7 ± 17.9
Bryophytes				
0.0001	3	0.6 ± 1.1	0.8 ± 1.1	0.2 ± 0.6
0.001	3	1.1 ± 1.3	0.9 ± 1.3	0.3 ± 0.6
0.01	5	1.9 ± 2.0	1.3 ± 1.9	0.5 ± 0.7
0.1	7	3.7 ± 2.5	2.3 ± 2.3	1.1 ± 1.0
1	8	4.0 ± 2.7	3.8 ± 1.9	2.1 ± 1.5
10	14	6.6 ± 3.9	5.6 ± 2.1	3.5 ± 1.9
100	17	10.3 ± 5.9	9.0 ± 2.2	6.2 ± 1.7
Lichens				
0.0001	1	0.1 ± 0.4	0.1 ± 0.3	0.0 ± 0.0
0.001	2	0.3 ± 0.8	0.2 ± 0.4	0.1 ± 0.3
0.01	2	0.6 ± 1.0	0.3 ± 0.5	0.1 ± 0.3
0.1	3	0.9 ± 1.2	1.1 ± 1.3	0.1 ± 0.3
1	9	1.9 ± 2.7	3.0 ± 2.4	0.1 ± 0.4
10	9	3.3 ± 3.7	3.7 ± 2.1	0.6 ± 1.2
100	17	5.7 ± 4.7	8.8 ± 5.6	2.7 ± 5.6

Table 3. Biodiversity, structural and ecological characteristics of all 10 m^2 plots across the three orders. The *p*-values and significance levels refer to ANOVAs.

Parameter	All (*n* = 67)			Order A (*n* = 14)	Order B (*n* = 15)	Order C (*n* = 38)	*p*-value	Significance
	Mean	Min.	Max.	Mean ± SD	Mean ± SD	Mean ± SD		
Species richness								
Species richness (all taxa)	40.4	18	87	28.8 ± 6.9	34.4 ± 5.6	47.0 ± 15.8	<0.001	***
Species richness (vascular plants)	34.2	16	71	20.9 ± 4.2	26.1 ± 3.7	42.4 ± 14.6	<0.001	***
Species richness (bryophytes + lichens)	6.1	0	23	7.9 ± 7.9	8.3 ± 3.4	4.6 ± 4.1	0.021	*
Species richness (red-listed species)	2.5	0	9	2.9 ± 2.5	3.1 ± 1.5	2.1 ± 1.6	0.109	
Vegetation structure								
Cover vegetation [%]	78	30	100	64 ± 15	58 ± 18	90 ± 15	<0.001	***
Cover herb layer [%]	72	20	100	58 ± 22	47 ± 16	87 ± 18	<0.001	***
Cover bryophyte + lichen layer [%]	13	0	60	14 ± 20	18 ± 20	11 ± 15	0.423	
Cover litter [%]	29	0	95	22 ± 23	21 ± 16	35 ± 28	0.091	
Herb layer height mean [cm]	14.1	1.4	62.6	11.5 ± 9.5	8.4 ± 5.6	17.3 ± 12.5	0.018	*
Herb layer height SD [cm]	6.8	0.8	33.4	8.3 ± 9.0	5.6 ± 6.0	6.7 ± 6.4	0.564	
Ecological indicator values (not weighted by cover)								
EIV light	7.5	6.8	8.1	7.7 ± 0.3	7.8 ± 0.1	7.3 ± 0.2	<0.001	***
EIV temperature	5.4	3.2	6.2	5.8 ± 0.3	5.9 ± 0.1	5.1 ± 0.9	<0.001	***
EIV continentality	4.2	3.5	5.0	4.4 ± 0.3	4.5 ± 0.2	4.1 ± 0.3	<0.001	***
EIV moisture	3.4	2.6	4.9	3.0 ± 0.3	2.8 ± 0.1	3.9 ± 0.6	<0.001	***
EIV reaction	6.9	5.4	8.1	7.3 ± 0.4	6.8 ± 0.4	6.9 ± 0.7	0.031	*
EIV nutrients	2.7	1.6	4.6	2.3 ± 0.7	2.2 ± 0.2	3.1 ± 0.6	<0.001	***
Topography								
Elevation [m]	1180	549	1945	1078 ± 274	1114 ± 120	1243 ± 390	0.191	
Inclination [°]	36	8	59	40 ± 5	38 ± 7	33 ± 10	0.017	*
Southing	0.76	-0.97	1.00	0.79 ± 0.48	0.86 ± 0.31	0.71 ± 0.46	0.518	
Heat index	0.36	-0.98	1.19	0.36 ± 0.48	0.42 ± 0.38	0.34 ± 0.38	0.820	
Maximum microrelief [cm]	15	2	105	20 ± 12	23 ± 25	11 ± 7	0.011	*
Soil parameters [general]								
Cover rocks and stones [%]	18	0	85	37 ± 25	34 ± 28	5 ± 11	<0.001	***
Cover gravel [%]	7	0	50	16 ± 14	8 ± 11	3 ± 10	0.002	**
Cover fine soil [%]	73	1	100	41 ± 34	62 ± 29	89 ± 23	<0.001	***
Soil depth mean [cm]	17	1	56	11 ± 6	9 ± 5	22 ± 15	<0.001	***
Soil depth CV	58	12	225	73 ± 41	89 ± 66	40 ± 21	<0.001	***
Soil parameters [physical]								
Skeleton content [%]	31	0	77	44 ± 18	26 ± 8	28 ± 12	<0.001	***
Sand content [%]	70	48	81	70 ± 7	74 ± 3	68 ± 9	0.036	*
Silt content [%]	14	6	31	14 ± 5	12 ± 3	15 ± 6	0.170	
Clay content [%]	16	11	29	16 ± 4	14 ± 1	17 ± 4	0.060	
Water at saturation [%]	42.7	4.7	48.3	43.3 ± 1.5	42.4 ± 0.6	42.6 ± 6.6	0.863	
Water at field capacity [%]	20.5	17.9	27.7	20.5 ± 1.9	19.3 ± 0.7	21.1 ± 2.5	0.028	*
Water at permanent wilting point [%]	11.3	9.4	16.7	11.3 ± 1.5	10.5 ± 0.5	11.6 ± 1.8	0.063	
Plant-available water [%]	9.2	8.1	12.2	9.2 ± 0.7	8.8 ± 0.4	9.4 ± 1.0	0.080	
Drainage rate [cm/h]	1.3	0.3	2.2	1.3 ± 0.5	1.6 ± 0.3	1.2 ± 0.5	0.053	
Soil parameters [chemical]								
pH [in aqua dest.]	6.87	4.34	8.34	7.37 ± 0.56	6.87 ± 0.55	6.67 ± 1.02	0.040	*
Electrical conductivity [μS/cm]	148	25	511	214 ± 138	90 ± 53	147 ± 110	0.011	*
Organic matter [%]	14.2	6.0	32.3	16.4 ± 7.5	11.8 ± 5.1	14.4 ± 7.2	0.209	
Organic carbon [%]	8.2	3.5	18.8	9.5 ± 4.3	6.8 ± 3.0	8.3 ± 4.2	0.212	
N content [%]	1.4	0.1	4.6	2.0 ± 0.9	1.0 ± 0.6	1.4 ± 0.8	0.004	**
C/N ratio	7.9	2.8	61.8	4.8 ± 1.7	9.0 ± 6.8	8.6 ± 10.6	0.326	
P available [ppm]	18.5	8.8	47.3	23.1 ± 12.6	17.5 ± 5.0	17.2 ± 8.9	0.120	

sizes, maximum species richness was much higher for vascular plants (e.g. 94 species in 100 m^2) compared to bryophytes and lichens (e.g. 17 species each in 100 m^2) (Table 2). When comparing the mean species richness of vascular plants across the three orders, for all taxa as well as for vascular plants alone, order C was by far the richest, while order B was intermediate and order A poorest (Tables 2 and 3). For example, mean total richness in 10 m^2 decreased from 51.2 in order C via 36.1 in order B to 29.9 in order A. By contrast, bryophytes and lichens across all grain sizes were always richer in orders A and B than in order C, with little difference between the former (Tables 2 and 3). At the association level, the richness patterns were more diverse (Table 4, Figure 6): While species richness of vascular plants in all associations of orders A (rocky) and B (xeric) were equally low (around 20 in 10 m^2), in order C (meso-xeric) they ranged from 27 in C.1 to 54 in C.5. Mean richness of non-vascular taxa in 10 m^2 varied strongly within the orders, ranging from 0.3 to 16.6 in order A and from 1.3 to 9.6 in order C. Herb layer cover was generally higher in the meso-xeric communities (order C) compared to the xeric and rocky ones (orders A and B) (Tables 3 and 4, Figure 6), while cover values of non-vascular taxa varied independently of the order and were largely consistent with the respective richness patterns (Figure 6).

While we found the highest mean species richness of vascular plants in the mountain meadows of C.5

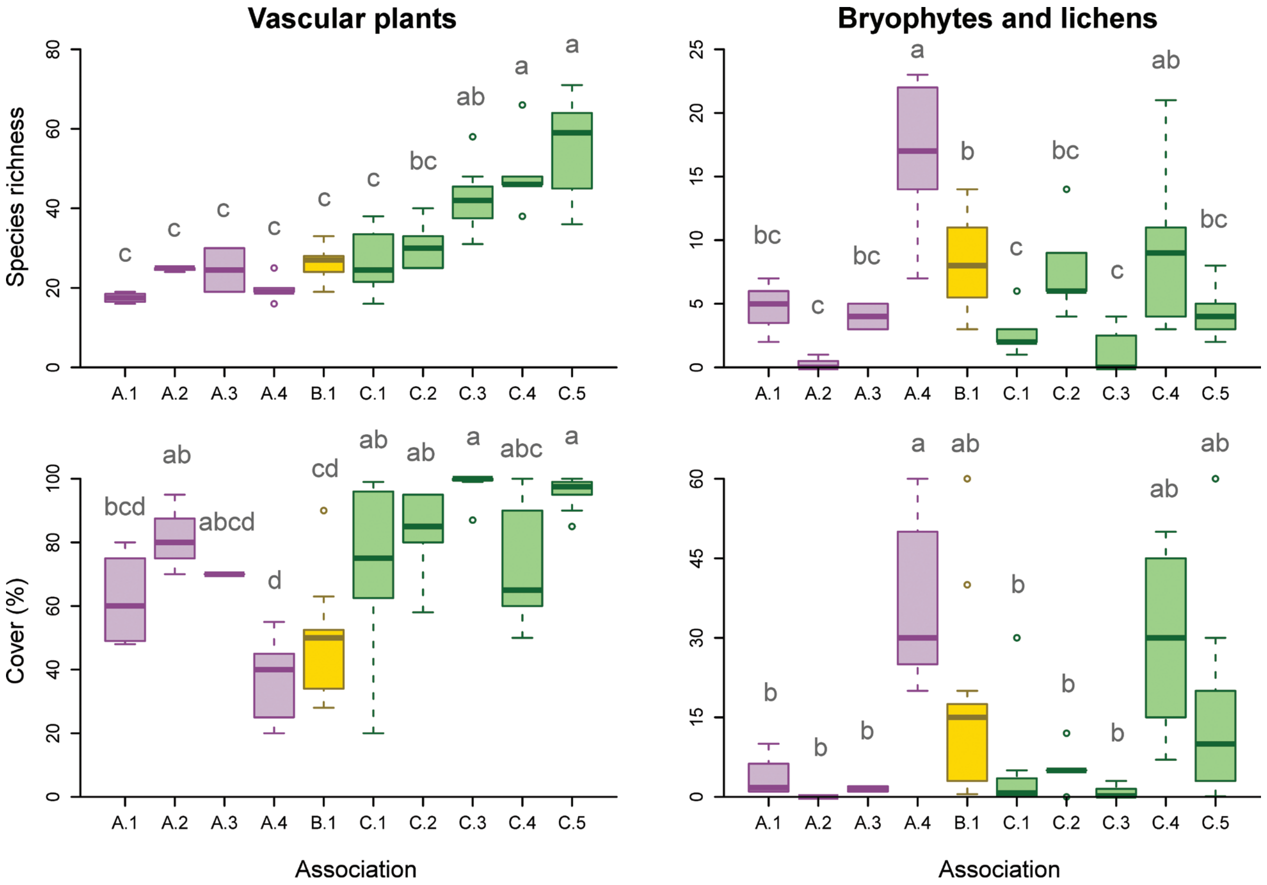

Figure 6. Comparison of species richness and cover of the two taxonomic-functional groups among the plots of the 10 communities at association rank. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

(58.5 species in 10 m^2), the record (87 species on 10 m^2) occurred in a plot of C.4 with shallow, acidic soil, grazed by cattle, sheep and goats in Fließ (Suppl. material 1). The highest cryptogam species richness was in a stand of A.4, a historically and recently grazed hill on calcareous slate in the Virgen valley in East Tyrol (Suppl. material 1). Concerning red list species, the non-managed steep grasslands on serpentinite (cluster A.1) had the highest values (Suppl. material 1), as many of the species are edaphic specialists with a restricted distribution.

Site conditions

According to all ecological indicator values except soil reaction, orders A and B were indistinguishable, but different from the meso-xeric order C, whose species composition stands for less light, lower temperature, lower continentality, more moisture and more nutrients (Table 3, Figure 7). By contrast, EIVs for soil reaction were high in order A, low in order B and intermediate in order C (Table 3, Figure 7). In general, measured topographic and soil variables showed only weak or no systematic difference between the orders, except skeleton content, which was clearly higher in the rocky grassland order A (Table 3).

At the association level, there were also strong differences for most of the measured variables (Table 4), with the most prominent ones shown in Figure 8: Within both the rocky and the meso-xeric order, the associations were segregated along an elevation gradient, with A.1 and C.3 occurring at the lowest and A.4 and C.5 at the highest elevations. Rock and stone cover generally was higher and more variable in the associations of the rocky and xeric orders (except A.3) compared to the meso-xeric associations. Soil depth in most communities was low (around 10–15 cm), but much higher in C.3 and C.5 (around 30 cm). Soil pH was high in most of the associations (6.9–7.4), but lower in C.4 (6.3) and much lower in C.2 (4.7). Nutrient concentrations (N and P) were generally low, with the noticeable exception of association A.2 with approximately two times higher values than all other associations.

Description of the associations and communities

In the following paragraphs, the ten accepted vegetation units at association level are described, and their syntaxonomic position is discussed. Four units could be unambiguously assigned to described associations, while the six remaining ones are labelled with informal community names.

Table 4. Biodiversity, structural and ecological characteristics across the 10 association-level communities. The *p*-values and significance levels refer to ANOVAs.

Parameter	A.1 (*n* = 4)	A.2 (*n* = 3)	A.3 (*n* = 2)	A.4 (*n* = 5)	B.1 (*n* = 15)	C.1 (*n* = 8)	C.2 (*n* = 5)	C.3 (*n* = 7)	C.4 (*n* = 5)	C.5 (*n* = 13)	*p*-value	
Species richness												
Species richness (all taxa)	22.3	25.0	28.5	36.4	34.4	29.3	38.4	43.7	58.4	58.5	<0.001	***
Species richness (vascular plants)	17.5	24.7	24.5	19.8	26.1	26.6	30.6	42.4	48.8	54.1	<0.001	***
Species richness (bryophytes + lichens)	4.8	0.3	4.0	16.6	8.3	2.6	7.8	1.3	9.6	4.5	<0.001	***
Species richness (red-listed species)	6.0	2.7	2.0	1.0	3.1	3.1	3.2	2.1	1.2	1.2	<0.001	***
Vegetation structure												
Cover vegetation [%]	63	82	70	53	58	76	86	98	88	98	<0.001	***
Cover herb layer [%]	62	82	70	37	47	73	83	98	73	96	<0.001	***
Cover bryophyte + lichen layer [%]	4	0	2	37	18	5	5	1	29	15	0.001	***
Cover litter [%]	8	43	55	8	21	48	40	56	19	20	<0.001	***
Herb layer height mean [cm]	13.9	16.7	10.3	7.0	8.4	10.4	22.8	32.6	11.9	13.4	<0.001	***
Herb layer height SD [cm]	12.0	7.2	6.1	7.0	5.6	3.3	17.4	9.5	4.0	4.1	0.008	**
Ecological indicator values												
EIV light	7.7	7.5	7.5	8.0	7.8	7.5	7.3	7.1	7.1	7.3	<0.001	***
EIV temperature	6.0	6.0	6.0	5.5	5.9	5.8	5.7	5.6	5.2	4.0	<0.001	***
EIV continentality	4.6	4.6	4.2	4.2	4.5	4.5	4.0	4.2	3.6	3.9	<0.001	***
EIV moisture	2.9	3.2	3.4	2.8	2.8	3.1	3.6	3.8	4.2	4.3	<0.001	***
EIV reaction	7.3	7.6	7.7	7.1	6.8	7.6	5.8	7.4	6.3	6.8	<0.001	***
EIV nutrients	2.0	3.1	3.3	1.8	2.2	2.6	2.9	3.7	3.4	3.0	<0.001	***
Topography												
Elevation [m]	810	899	1055	1410	1114	1112	905	854	1212	1675	<0.001	***
Inclination [°]	45	41	35	38	38	36	22	38	30	33	0.010	**
Southing	0.49	0.94	0.98	0.87	0.86	0.95	0.89	0.92	0.16	0.62	0.031	*
Heat index	0.32	0.40	0.40	0.35	0.42	0.45	0.20	0.71	0.16	0.21	0.322	
Maximum microrelief [cm]	30	11	26	15	23	11	15	8	17	7	0.083	
Soil parameters [general]												
Cover rocks and stones [%]	41	22	8	54	34	9	11	1	9	0	<0.001	***
Cover gravel [%]	18	10	25	15	8	3	1	7	8	0	0.047	*
Cover fine soil [%]	24	68	68	29	62	77	88	92	83	99	<0.001	***
Soil depth mean [cm]	9	18	13	6	9	14	8	33	11	31	<0.001	***
Soil depth CV	79	46	95	77	89	37	54	29	45	40	0.019	*
Soil parameters [physical]												
Skeleton content [%]	53	52	37	36	26	26	30	26	22	31	0.002	**
Sand content [%]	67	70	74	71	74	75	62	67	61	70	0.004	**
Silt content [%]	14	15	10	15	12	10	22	16	20	14	0.002	**
Clay content [%]	18	16	16	14	14	15	16	18	20	16	0.182	
Water at saturation [%]	44.3	43.3	43.2	42.6	42.4	42.8	44.0	44.0	45.0	39.9	0.739	
Water at field capacity [%]	21.6	20.4	20.1	19.8	19.3	19.7	21.7	21.5	23.0	20.7	0.037	*
Water at permanent wilting point [%]	12.3	11.2	11.4	10.5	10.5	11.1	11.3	12.0	12.8	11.5	0.178	
Plant-available water [%]	9.4	9.3	8.7	9.3	8.8	8.6	10.4	9.5	10.2	9.2	0.002	**
Drainage rate [cm/h]	1.0	1.3	1.3	1.6	1.6	1.4	1.3	1.1	1.0	1.3	0.192	
Soil parameters [chemical]												
pH [in aqua dest.]	7.12	7.27	7.35	7.64	6.87	7.22	4.73	7.15	6.28	7.00	<0.001	***
Electrical conductivity [µS/cm]	275	263	112	175	90	84	77	203	193	167	0.010	**
Organic matter [%]	19.9	25.7	11.3	10.0	11.8	12.7	25.8	13.6	15.0	11.0	<0.001	***
Organic carbon [%]	11.5	14.8	6.5	5.8	6.8	7.3	14.9	7.9	8.6	6.3	<0.001	***
N content [%]	1.7	3.3	1.6	1.7	1.0	0.9	2.1	1.4	2.1	1.2	<0.001	***
C/N ratio	7.0	4.4	4.1	3.6	9.0	14.1	8.2	5.7	4.6	8.4	0.589	
P available [ppm]	17.1	38.5	29.8	16.0	17.5	14.6	28.2	21.6	15.5	12.7	<0.001	***

A.1 *Armerio elongatae-Potentilletum arenariae*

(relevés 1–4 in Suppl. material 2, Table 1, Figure 9a)

Characterisation: Rocky grasslands on serpentine bedrock with low vegetation cover (48–80%). They are dominated by *Festuca pallens* and *Potentilla incana* with *Carex humilis*, *Dorycnium germanicum* and *Thymus praecox* as occasional subdominants. Among the species diagnostic or constant for this association, *Asplenium cuneifolium*, *Erysimum sylvestre*, *Koeleria pyramidata* var. *pubiculmis*, *Notholaena marantae* and *Silene otites* were recorded in our relevés. The cryptogam layer covered 1% to 10% of the surface and was dominated by *Rhytidium rugosum* and *Weissia brachycarpa*. The latter species, together with *Fissidens dubius* and *Mannia fragrans*, belongs to the diagnostic species of the association in our data set.

Ecology and distribution: Our relevés were recorded on very steep slopes with predominantly southern aspect and elevation between 785 and 830 m. The rugged terrain had a high cover of rocks and gravel on the surface and very shallow soils rich in skeleton. The high soil pH is typical for serpentinite (in this case it corresponds quite well with mean EIV-R of 7.2). N and P are rather low, but organic matter is high, even if there is a strikingly low litter cover (Table 4). Most of these species are adapted to the high magnesium soil content of the serpentine habitats. There is no management on these steep and dry southern slopes, although there is some moderate grazing by

Rupicapra. Nevertheless, there is no litter accumulation, and the low productivity seems in balance with the humification, as shown by the high organic matter content. In this cluster, we found the highest number and cover of red-list species, although the total species number was low. The special weathering of the serpentinite, which leads to very steep slopes, the dark soil surface caused by the high organic content, the low soil depth, the high soil magnesium content, and the position at a narrow section of the valley that increases wind velocity, interact to a very dry and specific habitat type. The history of this habitat might date back to the Neogene, as indicated by the occurrence of the palaeoendemic *Sempervivum pittonii* (Magnes et al. 2020), which has its closest relative in Bulgaria (Lippert 1995). The association is probably endemic to Styria, besides Gulsen occurring also near Kirchdorf und Traföß ("Tragöß") about 30 km downstream the Mur river where the serpentine layer reaches the surface again (Mucina and Kolbek 1993).

Syntaxonomy: Our relevés are from the locus classicus of this association, which was described by Braun-Blanquet (1961) and included in the alliance *Stipo-Poion xerophilae* and in the order *Festucetalia valesiacae*. Mucina and Kolbek (1993) described a new alliance *Avenulo adsurgentis-Festucion pallentis* within the *Stipo-Festucetalia pallentis*, based on the *Armerio-Potentilletum* as holotype. This alliance was intended to include all dry grasslands on serpentine in Austria. However, the alliance name is invalidly published as the name-giving *Avenula adsurgens* is not present in the original diagnosis (Art. 3f ICPN, Theurillat et al. 2021).

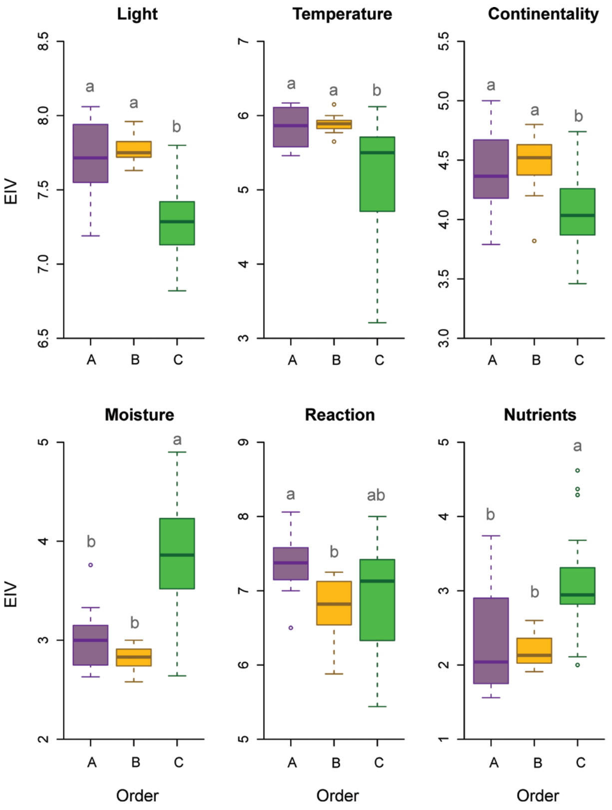

Figure 7. Comparison of six mean ecological indicator values among the plots of the three orders A (*Stipo-Festucetalia pallentis*), B (*Festucetalia valesiacae*) and C (*Brachypodietalia pinnati*). Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

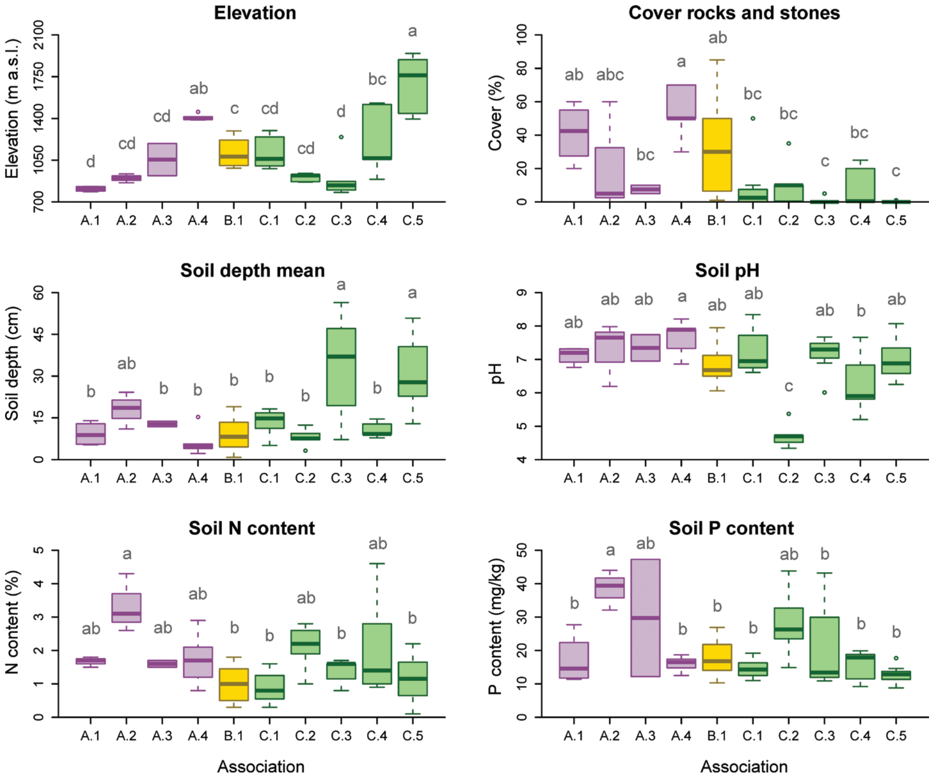

Figure 8. Comparison of six measured ecological variables among the plots of the 10 communities at association rank. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

A.2 *Phleo phleoidis-Pulsatilletum nigricantis*

(relevés 5–7 in Suppl. material 2, Table 1, Figure 9b–d)

Characterisation: Rocky grasslands on steep, south-facing slopes at elevations between 861 and 935 m. The vegetation is almost closed with bryophyte and lichen layers nearly absent (Table 4). The community is dominated by *Carex humilis* and *Festuca rupicola* with a constant occurrence of *Allium lusitanicum*, *Fallopia convolvulus*, *Origanum vulgare*, *Stachys recta*, *Teucrium chamaedrys*, and *Verbascum chaixii* subsp. *austriacum*. The endangered *Stipa styriaca* reached its highest cover in this association.

Ecology and distribution: The sampled stands were not managed. They have deep soils, the second highest organic matter content among all clusters and also relatively high litter cover, P and N (Table 4). The plots show clear indication of grassland abandonment. Apart from Pöls (PÖ) we recorded this vegetation around the Puxer Loch (PU), a medieval cave castle in a Paleozoic lime cliff, where *Galium mollugo* agg. was dominant.

Syntaxonomy: This unit perfectly matches the association *Phleo-Pulsatilletum nigricantis* described by Braun-Blanquet (1961) from various locations in Carinthia and one location in Styria. As in the previous unit, Braun-Blanquet included this association in the alliance *Stipo-Poion xerophilae*. Following a proposal by Franz (1988), Mucina and Kolbek (1993) merged the *Phleo-Pulsatilletum nigricantis* with the *Potentillo puberulae-Festucetum sulcatae* Br.-Bl. 1961 and transferred it to the alliance *Festucion valesiacae*. However, while the *Potentillo puberulae-Festucetum sulcatae* has indeed a strong affinity to the *Festucion valesiacae*, the *Phleo-Pulsatilletum nigricantis* clearly belongs to the *Stipo-Festucetalia pallentis*. We therefore suggest maintaining the *Phleo-Pulsatilletum nigricantis* as a separate association, which probably includes all rocky grasslands on relatively well-developed soils in the Styrian and Carinthian part of the Austrian central Alps. As in other regions of Central Europe, these moderate rocky grasslands have a more or less closed herb layer and are dominated by *Carex humilis* and *Festuca rupicola* (Janišová and Dúbravková 2010; Willner et al. 2013). The exact delimitation towards the *Seselietum austriacae* Br.-Bl. 1961, which comprises the more extreme, open rocky grasslands with *Festuca pallens* in the same region, requires further studies.

A.3 *Medicago minima-Melica ciliata* community

(relevés 8–9 in Suppl. material 2, Table 1, Figure 9e)

Characterisation: Cluster A.3 only includes two relevés from the Upper Inn valley, dominated by *Melica ciliata*. The vegetation cover is 70% while the cryptogam layer is poorly developed, covering only below 2%. Along with *Melica ciliata*, some other species have a high cover, such as *Artemisia absinthium*, *Brachypodium pinnatum*, *Bromus erectus*, *Galium lucidum* and *Thymus praecox*. Less abundant are *Agrimonia eupatoria*, *Carex humilis* and *Medicago minima*.

Ecology and distribution: The shallow soils on the steep south-facing upper slopes show a high skeleton content, high pH and P, but low N and organic matter, although the litter cover is very high (Table 4). Both sites were not managed. One is overgrown by shrubs (*Berberis vulgaris*, *Euonymus europaeus*, *Prunus spinosa*), and the other one has a strongly developed litter layer covering 80% of the soil surface. The number of species is low in all categories. We recorded this community in the Upper Inn valley, in FL and LA.

Syntaxonomy: This unit does not match any described association from the Eastern Alps. The closest syntaxon from the literature is the *Astragalo-Brometum stipetosum capillatae* of Kielhauser (1954), which was raised to association rank by Mucina and Kolbek (1993) under the name *Achnathero-Stipetum capillatae*.

A.4 *Koelerio pyramidatae-Teucrietum montani*

(relevés 10–14 in Suppl. material 2, Table 1, Figure 9f)

Characterisation: Rocky grasslands on extremely shallow soils on calcareous slate (Table 4). The most constant and abundant species in the herb layer are *Festuca rupicola*, *Koeleria pyramidata* and *Potentilla pusilla*. Further, *Allium lusitanicum*, *Artemisia campestris*, *Dianthus sylvestris*, *Juniperus sabina*, *Sedum album*, *Sempervivum wulfenii* and *Teucrium montanum* were constantly present. The most important diagnostic species are *Poa badensis* agg., *Saxifraga paniculata*, the lichens *Peltigera rufescens* and *Toninia sedifolia* as well as the bryophytes *Tortella inclinata* and *T. tortuosa*. Numerous further lichen species show high constancy and fidelity to this plant community, e.g. *Buellia elegans*, *Cladonia symphycarpa*, *C. pyxidata*, *Endocarpon pusillum*, *Physconia muscigena* and *Psora decipiens*. The most frequent bryophytes are *Abietinella abietina*, *Ditrichum flexicaule* and *Tortella inclinata*.

Ecology and distribution: Most of the surface (30–90%) is covered by rocks or gravel. Litter cover and organic content are low, like N and P content, with a high pH (Table 4). The plant layer is open, covering between 40 and 60%, and it is quite species poor, containing only 16 to 19 vascular plant species in 10 m^2. The cryptogam layer is well-developed, covering between 40 and 60% of the soil surface, and rich in species (median species number is 17, maximum 23 including both bryophytes and lichens), being the highest values of all clusters. In the past (until several decades ago) most of these grasslands were grazed by sheep. The lichen *Thamnolia vermicularis* subsp. *subuliformis*, which has its preferred habitat on alpine wind-heathland on stony open soil (Wirth et al. 2013; Nimis et al. 2018), is a witness for transport of thallus fragments by sheep because this wormlike fruticose chalk-white lichen never develops vegetative propagules such as isidia or soredia. Recently, all of these grasslands have been moderately grazed by cattle. We recorded the association in Obermauern (OM) in the Virgen valley (East Tyrol) on the top and southern and southeastern slopes of a hill called "Burg", at elevations of about 1,400 m.

Syntaxomy: This unit corresponds to the association *Koelerio pyramidatae-Teucrietum montani*, first proposed by Franz (1988) and validly described in Mucina and

Figure 9. Photos of associations and communities I. **a.** A.1 *Armerio elongatae-Potentilletum arenariae*, site GU; **b.** A.2 *Phleo-Pulsatilletum nigricantis*, PÖ; **c.** A.2 *Phleo-Pulsatilletum nigricantis*, PÖ; **d.** A.2 *Phleo-Pulsatilletum nigricantis*, PU; **e.** A.3 *Medicago minima-Melica ciliata* community, LA; **f.** A.4 *Koelerio pyramidatae-Teucrietum montani*, OM. Photos: J. Dengler (**a, b, e, f**) and M. Magnes (**c, d**).

Kolbek (1993). While Franz (l.c.) originally placed the association in the *Festucion valesiacae*, the latter authors classified it in the alliance "*Diantho lumnitzeri-Seslerion albicantis*". The community has some similarity with the *Teucrio-Caricetum humilis* Br.-Bl. 1961, which is traditionally classified in the *Stipo-Poion xerophilae* and includes rocky grasslands in the Upper Inn valley (Braun-Blanquet 1961; Mucina and Kolbek 1993). However, according to the species list in Franz (1988) and our own relevés, *Carex humilis* seems to be absent in this association. The floristic relationship between *Teucrio-Caricetum humilis* and *Koelerio-Teucrietum montani* should be further addressed in future studies.

B.1 *Sempervivum tectorum-Festuca valesiaca* community

(relevés 15–29 in Suppl. material 2, Table 1, Figure 10a)

Characterisation: This unit was documented from the Upper Inn valley, between 983–1,295 m on steep slopes. The rather low litter cover is connected with a high number and cover of cryptogams, indicated by the saxicole species *Grimmia ovalis*, *G. laevigata* and *Hedwigia ciliata* occurring on the rocks and *Crossidium squamiferum* and *Tortula ruralis* as bryophytes from open dry soil, interwoven by the common pleurocarpous dry grassland species *Abietinella abietina* and *Rhytidium rugosum*. Among grasses, *Festuca valesiaca* has a high constancy and cover. A fairly high number of annual species, typical of *Sedo-Scleranthetea*, form the largest bulk of diagnostic species.

Ecology and distribution: Shallow soils with rather low litter cover and organic content, and low N and P (Table 4). The community was recorded only in the Upper Inn valley (KA, FL and LA).

Syntaxonomy: This cluster is transitional between the orders *Stipo-Festucetalia pallentis* and *Festucetalia valesiacae*. In five relevés, the diagnostic species of the first order are more abundant, in seven relevés those of the second order, while in three relevés both species groups have more or less the same total cover (Figure 4). Diagnostic species of the order *Festucetalia valesiacae* that are present in this unit are *Bothriochloa ischaemum*, *Festuca valesiaca*, *Medicago minima*, *Stipa capillata* and *Trifolium arvense*. Kielhauser (1954) included similar grasslands of the same region in the *Astragalo-Brometum*. However, since the *Astragalo-Brometum* is a *Brachypodietalia* community (see below), this association name cannot be applied to unit B.1. Here, we provisionally include this unit in the alliance *Festucion valesiacae*. Without a comprehensive revision of all inner-alpine dry grasslands it is impossible to say if it might be assigned to one of the numerous associations described by Braun-Blanquet (1961) from South Tyrol and Switzerland, or if it must be described as a new association.

C.1 *Astragalo onobrychidis-Brometum erecti*

(relevés 30–37 in Suppl. material 2, Figure 10b)

Characterisation: Grasslands in the Upper Inn valley dominated by *Bromus erectus* and/or *Brachypodium rupestre*, *Carex humilis* and *Festuca rupicola*. This unit is similar to the previous one, but it has a much lower cover of stones and deeper soils. *Festuca valesiaca*, *Sempervivum tectorum* and other diagnostic species of unit B.1 are rare or absent.

Ecology and distribution: Our plots have open and shallow soils, which are poor in skeleton, organic matter, N and P, with a rather high litter cover (Table 4). Braun-Blanquet (1961) considered the association as typical for the calcareous Bündner schist of the geological unit "Lower Engadine Window", from Ardez in Switzerland to Landeck in Austria.

Syntaxonomy: This cluster can be assigned to the *Astragalo-Brometum*, described from the Lower Engadine (Switzerland) by Braun-Blanquet (1949) and originally included in the *Stipo-Poion xerophilae*. Braun-Blanquet's alliance assignment was followed by Mucina and Kolbek (1993). However, the type relevé of the association (selected by Terzi et al. 2017) clearly belongs to the *Brachypodietalia pinnati*. Likewise, the *Brachypodietalia* species prevail in most relevés of this cluster, although the *Stipo-Festucetalia pallentis* species also have a high proportion (Figure 4). We therefore follow the interpretation of Willner et al. (2019) who included the *Astragalo-Brometum* in the *Cirsio-Brachypodion*. Relevé 49, which contains almost no *Brachypodietalia* species, is probably misclassified. Kielhauser (1954), who studied the dry grasslands in the Tyrolian Upper Inn Valley, distinguished two subassociations within the *Astragalo-Brometum*: the *A.-B. stipetosum capillatae* on steep, rocky slopes (see unit A.3), and the *A.-B. festucetosum valesiacae* on less rocky or even deep soils. However, the latter subassociation is a heterogeneous unit, including both xeric grasslands of the *Festucetalia valesiacae* (corresponding to our unit B.1) and meso-xeric (semi-dry) grasslands of the *Brachypodietalia* (corresponding to the *Astragalo-Brometum* s.str. and our unit C.1).

C.2 *Agrostis capillaris-Avenula adsurgens* community

(relevés 38–42 in Suppl. material 2, Table 1, Figure 10c)

Characterisation: This is a semi-dry grassland with dominant *Agrostis capillaris* and *Koeleria pyramidata* and the presence of several acidophytes like *Avenella flexuosa*, *Potentilla argentea* or *Trifolium arvense*. Remarkable is the occurrence of some very rare lichens like *Rinodina cana* and *R. vezdae* (= *R. moziana*, new for Styria!).

Ecology and distribution: This unit occurs on siliceous soils (significantly lowest pH of all clusters, Table 4) over quartzite bedrock north of Neumarkt in der Steiermark (NM). Litter cover and organic matter are high (the latter is the highest of all clusters, Table 4), a consequence of abandonment as the grassland management was re-adopted just the year previous to our sampling, and also the high P and N contents are indicative for accumulation processes. The bryophytes *Bryum argenteum* and *Ceratodon purpureus* indicate high nutrient levels.

Syntaxonomy: This community has some similarity with the associations *Chamaecytiso hirsuti-Koelerietum* and *Genisto sagittalis-Festucetum rupicolae*, both (invalidly) described from southern Styria – near to the Slovenian border – by Steinbuch (1995). In the revision of the semi-dry grasslands of Central and Eastern Europe by Willner et al. (2019), the *Chamaecytiso hirsuti-Koelerietum* was partly assigned to the *Festuco rupicolae-Brometum* Zielonkowski 1973, and partly to the *Colchico-Festucetum rupicolae* Lengyel et al. 2016 while the *Genisto-Festucetum rupicolae* remained unclassified, indicating that there are still some unresolved problems in the classification of semi-dry grasslands in Austria. There is also a slight similarity to the *Brachypodio-Avenuletum adsurgentis* that was (also invalidly) described from the Kőszeg Mts. in western

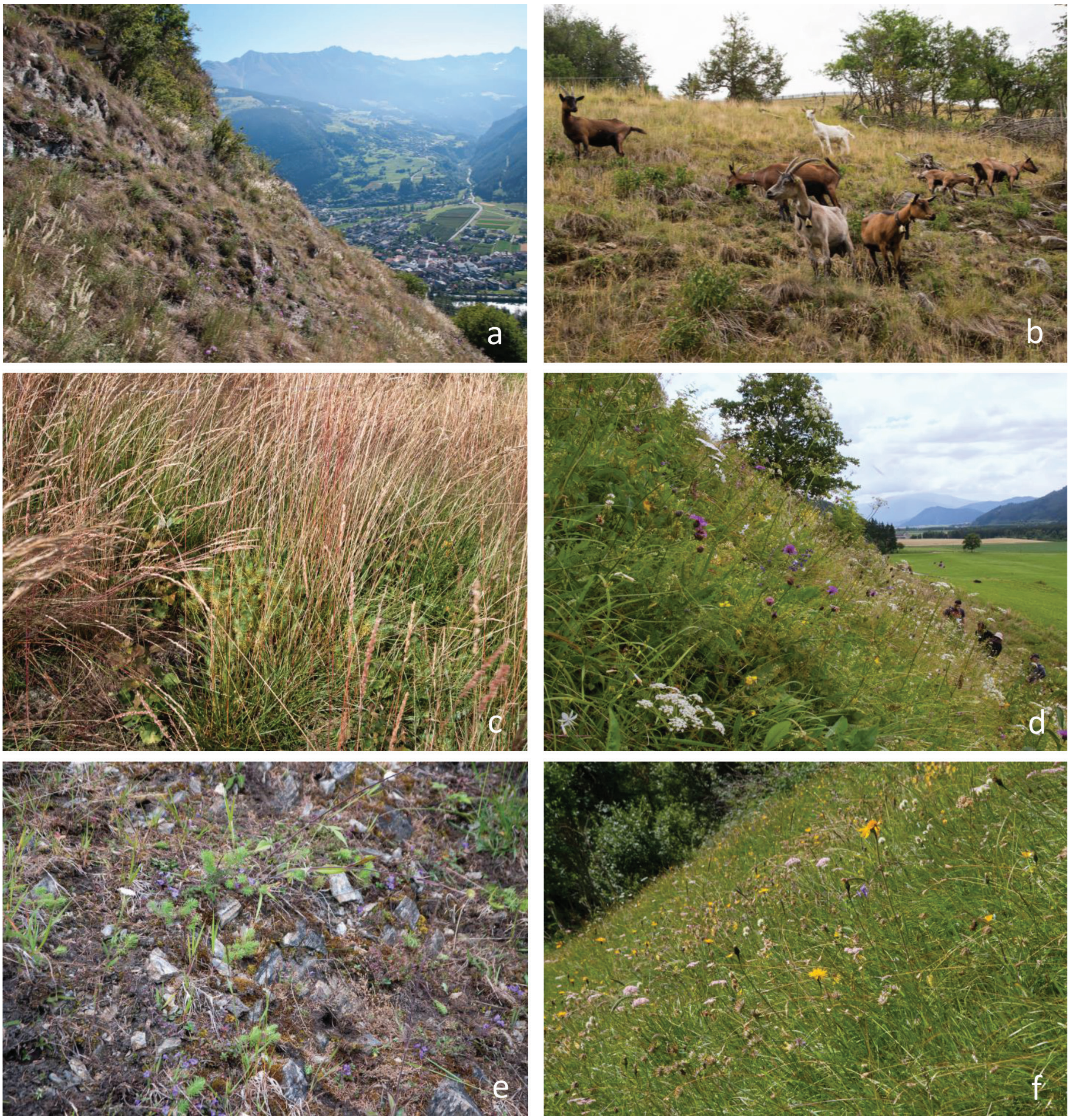

Figure 10. Photos of associations and communities II. **a.** B.1 *Sempervivum tectorum-Festuca valesiaca* community, site FL; **b.** C.1 *Astragalo onobrychidis-Brometum erecti*, KA; **c.** C.2 *Agrostis capillaris-Avenula adsurgens* community, NM; **d.** C.3 *Anthericum ramosum-Brachypodium pinnatum* community, PÖ; **e.** C.4 *Ranunculus bulbosus-Festuca rubra* community, MA; **f.** C.5 *Carduus defloratus-Brachypodium pinnatum* community, ZS. Photos: J. Dengler.

Hungary (Kovács 1994). Here, we prefer to use an informal community name for this cluster, leaving the clarification of its syntaxonomic status to a future revision.

C.3 *Anthericum ramosum-Brachypodium pinnatum* community

(relevés 43–49 in Suppl. material 2, Table 1, Figure 10d)

Characterisation: These semi-dry grasslands on calcareous soils are dominated by *Brachypodium pinnatum* and *Festuca rupicola*. *Clinopodium vulgare*, *Salvia pratensis*, *Vincetoxicum hirundinaria*, *Viola hirta*, and together with *Molinio-Arrhenatheretea* taxa such as *Achillea millefolium* agg., *Arrhenatherum elatius*, *Dactylis glomerata*, *Taraxacum* sect. *Ruderalia* and *Tragopogon orientalis* are also common.

Ecology and distribution: This cluster mainly includes the semi-dry grasslands on base rich, very deep and fine soils near Pöls (PÖ) that had been abandoned for years before grassland management was started again by clearing shrubs only a few years ago. Because of the occurrence of *Stipa styriaca*, the site was declared as a Natura 2000 protected area. With the reintroduction of grazing by sheep in 2020, there is a good chance that *Stipa* will be able to spread again from the rocky areas (see unit A.2) to the parts with deep soils. In this community, there is nearly no rock and gravel cover and also skeleton soil content, P and N are low (Table 4). The high litter cover does not lead to high organic matter, but suppresses the development of a bryophyte layer as well as the germination of most vascular plant species. The one relevé from Griffen (variant a) represents a grassland parcel within the bounding walls of the castle that was cleared from trees a few years ago, and the grassland management was started only after that. One relevé from Tyrol (KA) is included in this cluster as well.

Syntaxonomy: Three geographical variants can be distinguished in this cluster: The relevé from Griffen (variant a) is a strongly disturbed, ruderalized grassland of doubtful phytosociological position. The relevé from Kaunerberg (variant c) might represent a more mesic variant of the *Astragalo-Brometum* (see unit C.1). The remaining relevés (variant b) could be assigned to the *Scabioso ochroleucae-Brachypodietum* Klika 1933, which was described in Bohemia (Klika 1933). This association has not been reported from Austria before, but its presence in the Eastern Alps was predicted by the expert system developed by Willner et al. (2019). Against its Pannonian vicariant *Polygalo majoris-Brachypodietum* Wagner 1941, the *Scabioso ochroleucae-Brachypodietum* is only negatively differentiated.

C.4 *Ranunculus bulbosus-Festuca rubra* community

(relevés 50–54 in Suppl. material 2, Table 1, Figure 10e)

Characterisation: This unit lacks dominant species, but some *Molinio-Arrhenatheretea* species show high constancy, like *Achillea millefolium* agg., *Festuca rubra* agg., *Plantago lanceolata* and *Trifolium pratense*. Species number is very high, especially in variant (b) from FL, as well as cryptogam species number and cover.

Ecology and distribution: The soils are shallow and pH is remarkably low (with the exception of variant c) and both litter cover and organic soil matter are low (Table 4). P is low, while N has high values, especially in variant (b). The bryophyte layer with *Calliergonella cuspidata*, *Plagiomnium undulatum* and *Thuidium philibertii* shows a good water supply. The cluster includes relevés from three locations from each of the investigated main valley systems (NM, MA, FL).

Syntaxonomy: This is a rather heterogeneous cluster consisting of three geographical variants. Variant (a) includes a single relevé from Neumarkt in der Steiermark (NM), which is dominated by *Arrhenatherum elatius* and might belong to the alliance *Arrhenatherion* (class *Molinio-Arrhenatheretea*). Variant (b) contains two relevés from the Upper Inn Valley (FL), which have a high portion of acidophilous species (e.g. *Calluna vulgaris*, *Danthonia decumbens*, *Viola canina*). These relevés have some similarity with the *Agrostio-Dianthetum deltoidis*, which was described by Braun-Blanquet (1976) in the Lower Engadin and the Val Müstair (Switzerland). Variant (c) comprises two relevés from Virgen (MA) that share some species with the next unit.

C.5 *Carduus defloratus-Brachypodium pinnatum* community

(relevés 55–67 in Suppl. material 2, Table 1, Figure 10f)

Characterisation: Semi-dry grasslands in the montane and subalpine belt on steep southern slopes dominated by *Brachypodium pinnatum* agg. and *Laserpitium latifolium* and with (sub)alpine species such as *Astragalus penduliflorus*, *Campanula scheuchzeri*, *Carex sempervirens*, *Festuca norica*, *Plantago atrata*, *Rhinanthus glacialis* and *Soldanella alpina*.

Ecology and distribution: Grasslands on deep soils with low organic matter and low P and N (Table 4), mainly found in the Virgen valley. The subalpine plots from ZS and FL represent subalpine hay-meadows. The montane grassland in MA was managed similarly, mown only once and late in the year (August) without any fertilization. Although the subalpine grassland from ZS, an avalanche corridor, is not mown anymore, litter cover is low in all plots. Together with cluster 10b (part of C.4) we found here the highest vascular species number.

Syntaxonomy: This community is characterised by the presence of several subalpine and alpine species and therefore is transitional towards the class *Elyno-Seslerietea*. In this respect, it is similar to the *Carlino-Caricetum sempervirentis* Lutz et Paul 1947 of the northern Alps. According to the alliance concept of Willner et al. (2019), the *Carlino-Caricetum sempervirentis* belongs to the *Mesobromion*, while the grasslands in East Tyrol probably belong to the *Cirsio-Brachypodion*. However, the diagnostic species of the latter alliance are not very abundant in this cluster, and in some relevés they are even completely absent. Thus, the alliance assignment remains provisional. Another association that has similarity with this cluster is the *Centaureo-Gentianetum cruciatae*, described by Braun-Blanquet (1976) from the Upper and Lower Engadine (Switzerland). Some relevés from the highest elevations might already belong to the *Campanulo scheuchzeri-Festucetum noricae* Isda 1986 (alliance *Caricion ferruginei*, see Grabherr et al. 1993), that was mentioned from other alpine hay meadows in the Virgen valley (Isda 1986).

Discussion

Alliances and orders

While the assignment of the TWINSPAN clusters to phytosociological orders was relatively straightforward, the identification of the alliances remains doubtful for the most part.

The rocky grasslands of the Eastern Alps were included in three alliances by Mucina and Kolbek (1993): *Avenulo adsurgentis-Festucion pallentis* (comprising the *Armerio elongatae-Potentilletum arenariae* as the only association), *Diantho-Seslerion* (comprising the rocky grasslands on calcareous soils from East Tyrol and Salzburg eastwards) and *Stipo-Poion xerophilae* (comprising all dry grassland of the Inn valley). However, none of these names is acceptable because (1) the *Avenulo adsurgentis-Festucion pallentis* is not validly published (see description of unit A.1), (2) the *Diantho-Seslerion* is based on associations of the Bükk mountains in Hungary that are very different from the rocky grasslands of the Alps (see remark in the syntaxonomic scheme below), and (3) the *Stipo-Poion xerophilae* has been typified with a *Festucetalia valesiacae* community of the Vinschgau (Terzi et al. 2017). Thus, it seems that the rocky grasslands of the Eastern Alps are lacking a valid alliance name, unless they are included in a broadly conceived *Seslerio-Festucion pallentis* Klika 1931. However, it is impossible to decide from our dataset whether all rocky grasslands belong to the same alliance, or if they can be included in one of the alliances described from the Pannonian Basin. Therefore, we refrain from assigning our *Stipo-Festucetalia pallentis* communities to an alliance and leave this question to a broad-scale syntaxonomic revision of the order.

Grass steppes of the *Festucetalia valesiacae* are represented by a single community in our data set (*Sempervivum tectorum-Festuca valesiaca* community), which probably can be assigned to the *Festucion valesiacae*. It must be noted, however, that the current concept of the order *Festucetalia valesiacae* is much narrower than that of Braun-Blanquet (1961) who included all dry and semi-dry grasslands of the study area in this order. Whether the *Stipo-Poion xerophilae* can be maintained as an inner-alpine geographical vicariant of the *Festucion valesiacae*, remains to be further investigated.

Among the semi-dry grasslands of the *Brachypodietalia pinnati*, the communities of Styria (*Agrostis capillaris-Avenula adsurgens* community, *Anthericum ramosum-Brachypodium pinnatum* community) clearly belong to the *Cirsio-Brachypodion*, which includes the meadow steppes of eastern Central Europe (Willner et al. 2019). The most important differential species against the western *Bromion erecti* (= *Mesobromion* nom. cons. propos.) is *Festuca rupicola*, which was present with high cover in all relevés. The position of the *Ranunculus bulbosus-Festuca rubra* community and the *Carduus defloratus-Brachypodium pinnatum* community, both observed in the Virgen valley, is less clear. While they do not contain any diagnostic species of the *Mesobromion* (except for a single, probably misclassified relevé from the Inn valley where *Festuca guestfalica* was present), the *Cirsio-Brachypodion* species are also absent in half of the relevés. In fact, the *Carduus defloratus-Brachypodium pinnatum* community is transitional towards alpine grasslands of the *Caricion ferrugineae* (*Elyno-Seslerietea*), and so it even has a marginal position within the class. Finally, the *Astragalo-Brometum* of the Upper Inn valley, originally included in the heterogeneous *Stipo-Poion xerophilae* by Braun-Blanquet (1961), might belong to a hitherto undescribed meso-xeric alliance having its main distribution in the inner-alpine valleys of the Western Alps (and the dealpine gravel plains north and south of the Alps), differentiated against both *Cirsio-Brachypodion* and *Mesobromion* by the high constancy of *Brachypodium rupestre* and *Potentilla pusilla* (see Table 1), which are completely absent from typical stands of either alliance (Dengler et al., in prep.; see Dengler et al. 2020a).

Associations

Perhaps surprisingly, only four clusters could be unambiguously assigned to described associations. The main reason is that a comprehensive syntaxonomic revision of the dry and semi-dry grasslands of the inner Eastern Alps is still lacking. Instead of adopting names of associations that might or might not correspond to our units, we preferred to use informal community names, thus making the insufficient knowledge clearly visible. The relationship between these communities and described associations such as the *Achnathero-Stipetum capillatae* and *Teucrio-Caricetum humilis* (Mucina and Kolbek 1993) could only be clarified in a revision based on all available plot data from the Eastern Alps. For the *Brachypodietalia pinnati* communities, it will be particularly important to include data from Italy and Switzerland, which both were not covered by the revision of Willner et al. (2019). For the syntaxonomic interpretation of the *Festucetalia valesiacae*, a comparison with data from the most continental part of the Eastern Alps, the Vinschgau in South Tyrol (Italy), will be crucial.

Beside the lack of comprehensive studies another reason for the lacking match with associations from the literature might be the unstable management of most of the sites during the last thirty years. Even at sites that have recently become protected under the Natura 2000 regime (like the grasslands of FL and KA in the Upper Inn valley or PÖ in the Mur valley), the current management is very different from the historical, much more intensive use, and it will take quite some time for the vegetation to get in balance with the new type of management.

Our results do not support a closer relationship of the dry and semi-dry grasslands of the Austrian inner-alpine dry valleys with the Pannonian steppes (see Willner et al. 2013), a finding that is also supported by genetic analyses of plant and animal species known from both regions (Kirschner et al. 2020, see paragraph nature conservation below).

Proposed syntaxonomic scheme

Class: *Festuco-Brometea* Br.-Bl. et Tx. ex Klika et Hadač 1944

A. Order: *Stipo pulcherrimae-Festucetalia pallentis* Pop 1968

Alliance: ??? [*Avenulo adsurgentis-Festucion pallentis* Mucina in Mucina et Kolbek 1993 nom. inval. (Art. 3f), "*Diantho lumnitzeri-Seslerion albicantis*" sensu Mucina et Kolbek 1993 p.p.]

Nomenclatural remark: The name *Diantho-Seslerion* (Soó 1971) Chytrý et Mucina 1993 is often used with wrong species epithets and/or in a way that excludes its type. Neither *Dianthus lumnitzeri* s.str. nor *Sesleria albicans* (= *S. caerulea*) occur in the original diagnosis of the alliance. Soó (1971) described this syntaxon as a suballiance of the *Seslerio-Festucion pallentis* Klika 1931 and listed three associations for it: (1) "*Asplenio rutae-murariae-Melicetum ciliatae*", (2) "*Diantho-Seslerietum heuflerianae-hungaricae*" [≡ *Seslerietum heuflerianae* Zólyomi 1936] and (3) "*Seslerio-Festucetum pallentis*" [≡ *Campanulo divergentiformis-Festucetum pallentis* Zólyomi 1966]. We could not verify if the first association name is valid. However, Borhidi (Borhidi et al. 2012) classifies the *Asplenio rutae-murariae-Melicetum ciliatae* in the alliance *Alysso alyssoidis-Sedion* Oberd. et Müller 1961, so it could hardly be a suitable lectotype. The two other associations, which were both described from the Bükk mountains in Hungary, are often classified in the *Bromo pannonici-Festucion pallentis* Zólyomi 1966 (e.g. Janišová and Dúbravková 2010; Škodová et al. 2015). We are not aware of a published choice of a lectotype for the *Diantho-Seslerion*. It could be argued, that Art. 20 (automatic type) is applicable it this case, but this interpretation needs further confirmation.

A.1 *Armerio elongatae-Potentilletum arenariae* Br.-Bl. 1961
A.2 *Phleo phleoidis-Pulsatilletum nigricantis* Br.-Bl. 1961
A.3 *Medicago minima-Melica ciliata* community
A.4 *Koelerio pyramidatae-Teucrietum montani* Franz in Mucina et al. 1993

B. Order: *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 nom. cons. propos. [= *Festucetalia* Soó 1940 ≡ *Festucetalia valesiacae* (Soó 1940) 1947 nom. illeg.]

Nomenclatural remark: For the nomenclatural problems surrounding the name *Festucetalia valesiacae* and a formal proposal for a *nomen conservandum*, see Terzi et al. (2017).

Alliance: *Festucion valesiacae* Klika 1931 nom. cons. propos. (= *Festucion sulcatae* Soó 1930; incl. *Stipo-Festucion xerophilae* Br.-Bl. et Richard 1950)

Nomenclatural remark: Kuzemko et al. (2014) proposed to conserve the name *Festucion valesiacae* Klika 1931 against the earlier *Festucion sulcatae* Soó 1930, and this proposal was also adopted by Mucina et al. (2016). However, no formal proposal has been submitted so far.

B.1 *Sempervivum tectorum-Festuca valesiaca* community

C. Order: *Brachypodietalia pinnati* Korneck 1974 nom. cons. propos. (= *Brometalia erecti* Koch 1926)

Nomenclatural remark: Dengler et al. (2003) proposed to reject the name *Brometalia erecti* Koch 1926 as nomen ambiguum, and Kuzemko et al. (2014) proposed to conserve the name *Brachypodietalia pinnati* Korneck 1974. This proposal was also adopted by Mucina et al. (2016), but no formal proposal has been submitted so far.

Alliance: *Cirsio-Brachypodion pinnati* Hadač et Klika in Klika et Hadač 1944

C.1 *Astragalo onobrychidis-Brometum erecti* Br.-Bl. 1950
C.2 *Agrostis capillaris-Avenula adsurgens* community
C.3 *Anthericum ramosum-Brachypodium pinnatum* community
C.4 *Ranunculus bulbosus-Festuca rubra* community
C.5 *Carduus defloratus-Brachypodium pinnatum* community

Biodiversity

For vascular plants, our findings that meso-xeric stands were substantially richer in species than either rocky or xeric grasslands across all grain sizes, is consistent with results from various other regional studies (Dengler et al. 2012, 2019; Pedashenko et al. 2013) as well as a synthesis across the Palaearctic (Dengler et al. 2020b). Our scale-dependent richness values were similar to mean richness from nested-plot sampling in meso-xeric grasslands across the Palaearctic, but about 25% lower in the xeric grasslands and about 40% lower in the rocky grasslands (GrassPlot Diversity Explorer v.2.10; https://edgg.org/databases/GrasslandDiversityExplorer; Biurrun et al. 2021). By contrast, our values for the first two orders (20.0 species for rocky grasslands, 26.9 species for xeric grasslands in 10 m^2) were rather similar to richness data found for such types in the inner-alpine valleys of Italy (Wiesner et al. 2015: 25 species in 10 m^2) and Switzerland (Dengler et al. 2019: 26.3 species for rocky and 24.3 species for xeric grasslands in 10 m^2). Actually, if we exclude the high-elevation associations (transitional to *Elyno-Seslerietea*) of the meso-xeric grasslands also there the richness values were below average and similar to those found in Aosta Valley and Valais (Wiesner et al. 2015; Dengler et al. 2019). While for the Austrian stands one might be tempted to explain the low plot-scale richness with the small size of the majority of remaining patches, this is not the case for the two other regions where there are still large and well-managed dry grasslands persisting. Therefore, we assume that it is rather due to an impoverished species pool in consequence of the glaciations and the isolated position compared to other dry grassland types, but this definitely requires further studies in a broader geographic context, for which the GrassPlot database provides excellent opportunities (Dengler et al. 2018). By contrast, the strong increase of the plot-scale vascular plant species richness with elevation in the meso-xeric order (Table 4, Figure 6: from 27 to 54 species in 10 m^2) is a well-known phenomenon for grasslands of the Alps. Data from the Swiss Biodiversity Monitoring, for example, also show that mean vascular plant species richness across all grassland types increases from 28 via 33 to 44 species in 10 m^2, in the colline, montane and subalpine belts, respectively (Koordinationsstelle Biodiversitäts-Monitoring Schweiz 2009). Specifically, the high species richness in subalpine hay meadows is a well-known phenomenon (Isda 1986; Matouch et al. 2000; Mayer and Grabner 2004).

For bryophytes and lichens, the situation was reversed in comparison to mean values from nested-plot sampling throughout the Palaearctic (GrassPlot Diversity Explorer v.2.10; https://edgg.org/databases/GrasslandDiversityExplorer; Biurrun et al. 2021). Here, the Austrian stands of the rocky and xeric order were on average nearly twice as rich in species than the Palaearctic average, while in the meso-xeric order we had fewer bryophyte species normally with unclear pattern for lichens in the meso-xeric order. One possible explanation is the large species pool of terricolous cryptogams of open stands from the nearby alpine habitats in case of the first two orders.

Nature conservation

Based on the similar floristic composition of their vegetation, traditional vegetation ecology has anticipated close ties between the inner-alpine dry valleys and the Eastern European steppes (Braun-Blanquet 1961). Such scenarios assume that the biota of inner-alpine steppes are relatively young remnants of the cold-stage steppe belt. In other words, the inner-alpine steppe vegetation was often seen as a young and species poor derivative of the steppe vegetation of Eastern Europe. Genetic data from multiple steppe plants and insects challenged this scenario: The biota of the inner-alpine dry valleys were shown to consist of genetic lineages that have evolved in long-term isolation, and are not closely related to European steppe biota from Central and Eastern Europe (Kirschner et al. 2020). It was also shown that the genetic separation between the biota of inner-alpine and Eastern European steppes did not occur postglacial, i.e. at the beginning of the Holocene, but dates back as early as the mid-Pleistocene epoch (Kirschner et al. 2020). Accordingly, these extrazonal lineages must have survived climate driven range contractions throughout the Pleistocene climate fluctuations, such as during the LGM and the mid-Holocene forest optimum, in isolation, that is in refugia apart from the Pannonian and Eastern European steppes. The palaeoendemic *Sempervivum pittonii* from Gulsen can support these findings. Practically, the isolated nature of Alpine steppe outposts and their previously disregarded genetic uniqueness in respect to the Eastern European steppes raises their conservation value significantly. Adequate management and skilled nature protection activities are key to preserve the inner-alpine steppes and their rich genetic diversity for the future. In this respect, the importance of even small remnants of species-rich grasslands should be pointed out: they are often the last resources for propagules of autochthonous species for restoration projects (Kiehl et al. 2010; Bischoff et al. 2018).

Conclusions and outlook

Our study provides the first phytosociological overview of dry and semi-dry grasslands of the Austrian inner-alpine valleys using new plot data since the seminal work of Braun-Blanquet (1961). While a comprehensive syntaxonomic revision remains a task for future studies, the investigated plots are important references of the current situation. It is obvious that in regions with a still predominantly traditional type of farming, like in the Virgen valley, or in larger continuous areas with a proper management, like in the Nature Park Kaunergrat (Upper Inn valley), biodiversity of grassland-specialists is higher than on smaller grassland parcels within a matrix of high-input agriculture. Regarding the number and cover of red list species, the big serpentinite outcrop Gulsen in the Styrian Mur valley is the leader – without any management, but with very special habitat conditions. With the exceptions of the serpentinite grasslands and former hay meadows on avalanche corridors, all the studied grasslands are depending on a proper management, otherwise they would undergo mostly a natural succession to forests. Many of the grasslands are not only hotspots of biodiversity but also a cultural heritage, some of them maybe for millennia, and therefore have an extraordinarily high conservation value. The results of this study support the importance of grazing animals for achieving conservation targets in species-rich grasslands, as most of the detected biodiversity records are located in grazed habitats.

Data availability

The plot data presented in this paper were recorded on the occasion of the 11th EDGG Field Workshop 2018 in Austria. They are included in the Suppl. material of this paper and are stored in and available from the GrassPlot database (https://edgg.org/databases/GrassPlot; Dengler et al. 2018).

Author contributions

M.M. organized the 11th EDGG Field Workshop and guided it together with H.M. and P.K. As former and current EDGG Field Workshop Coordinators, J.D. and I.D. ensured consistent application of the EDGG methodology. M.M identified critical vascular plant species and led the writing of the manuscript. H.M. identified the lichens and provided information about rare or stenoecious lichens. E.A.K. analysed the soil samples, C.B. identified the bryophytes and added ecological aspects. W.W. prepared the syntaxonomic table and framework, wrote most of the syntaxonomic discussions and revised several other parts of the manuscript, M.J. contributed the descriptions of the *Stipo-Festucetalia pallentis*, J.D. prepared the vegetation tables. P.K. wrote the description of the Upper Inn valley and contributed to the discussion of the nature conservation value. R.G. supported the description of the *Brachypodietalia pinnati* and revised the Introduction. H.R. wrote the description of the Virgen valley. I.D. prepared the map and conducted the inferential statistical analyses, while J.D. wrote the Results and Discussion on biodiversity aspects. All authors revised and approved the whole text.

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Supplementary material

Supplementary material 1
Geographic, environmental and structural data of the analysed plots (pdf)
Link: https://doi.org/10.3897/VCS/2021/68594.suppl1

Supplementary material 2
Complete, sorted relevé and synoptic table (pdf)
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REVIEW AND SYNTHESIS INTERNATIONAL VEGETATION CLASSIFICATION

A novel biome concept and classification system based on bioclimate and vegetation – a Neotropical assay

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Abstract

The knowledge of biomes as large-scale ecosystem units has benefited from advances in the ecological and evolutionary sciences. Despite this, a universal biome classification system that also allows a standardized nomenclature has not yet been achieved. We propose a comprehensive and hierarchical classification method and nomenclature to define biomes based on a set of bioclimatic variables and their corresponding vegetation structure and ecological functionality. This method uses three hierarchical biome levels: Zonal biome (Macrobiome), Biome and Regional biome. Biome nomenclature incorporates both bioclimatic and vegetation characterization (i.e. formation). Bioclimate characterization basically includes precipitation rate and thermicity. The description of plant formations encompasses vegetation structure, physiognomy and foliage phenology. Since the available systems tend to underestimate the complexity and diversity of tropical ecosystems, we have tested our approach in the biogeographical area of the Neotropics. Our proposal includes a bioclimatic characterization of the main 16 Neotropical plant formations identified. This method provides a framework that (1) enables biome distribution and changes to be projected from bioclimatic data; (2) allows all biomes to be named according to a globally standardized scheme; and (3) integrates various ecological biome approaches with the contributions of the European and North American vegetation classification systems.

Taxonomic reference: Jørgensen et al. (2014).

Dedication: This work is dedicated to the memory of and in homage to Prof. Dr. Salvador Rivas-Martínez.

Keywords

bioclimatic belts, biogeography, formations, geocatena, Neotropics

Biome: a concept with a universal scope

From the earliest definitions of biome as a climax biotic community over a large geographic area (Clements 1917; Shelford and Olson 1935; Clements and Shelford 1939), to the present day, where recent definitions incorporate ecological, functional and evolutionary advances, the biome remains a key concept in ecology and biogeography (Mucina 2018; Hunter et al. 2021). However, these scientific streams have so far not produced a universal biome classification system that allows a standardized nomenclature based on a set of criteria or quantifiable variables that can explain and causally predict the distribution and global characteristics of biomes (Holdridge 1947, 1967; Box 1981a, 1981b; Bailey 1989a, 2005). This can be explained not only by the polysemic use of the biome concept but also by the considerable overlap between concepts relating to biomes, such as ecoregion, ecosystem, ecological system, biogeoclimatic ecosystem, ecological division, ecozone, formation, and bioregion, among others (Ellenberg and Mueller-Dombois 1967; Holdridge 1967; Whittaker 1970; Bailey 1989a; Dinnerstein et al. 1995; Olson et al. 2001; Josse et al. 2003; Ibisch et al. 2003; Rutherford et al. 2006; Sayre et al. 2008; MacKenzie and Meidinger 2018; Keith et al. 2020).

Assuming ecosystems can be defined as a biotic assemblage of species with an associated abiotic environment, the interactions within and between these complexes, and the physical space in which they operate (Faber-Langendoen et al. 2020), biomes can be considered as large-scale ecosystems. Biome schemes based on ecological concepts have been defined using either vegetation-climate relationships (Holdridge 1947; Olson et al. 2001) or in functional terms (Paruelo et al. 2001; Scheiter et al. 2013; Higgins et al. 2016; Conradi et al. 2020). Other works implicitly link climate to vegetation physiognomy (Whittaker 1970; Walter 1973; Larcher 1975; Bailey 1989a; Box 2016) or vegetation activity to climate restrictions (Larcher 1975; Higgins et al. 2016). All these approaches make little use of comparable ecological factors or fail to use a similar and replicable nomenclatural sequence of criteria. To overcome these limitations, it is necessary that a biome classification contributes to and facilitates the creation of an interpretative and predictive system (Walter 1973; Bailey 1989a; Mucina 2018; Hunter et al. 2021). In our proposal, the biome classification is built on the relationships between both bioclimate and vegetation classifications, understanding bioclimate as a range of climate variables explaining the distribution of a set of biotas and growth forms.

A bioclimate-based approach is eco-functional in nature since the limiting climate variables condition and determine the appearance and structural adaptations of the vegetation, as well as the soil complexes on which it develops; thus, bioclimates behave as ecosystem drivers. The bioclimatic indices enable the objective extrapolation and prediction of existing biomes in different geographically separated locations. Building on our expert knowledge of most Neotropical ecosystems in the field, the aim of this work was to establish a parsimonious and comprehensive biome classification and nomenclature system based on consistent objective and hierarchical criteria. We accomplish this by specifically demonstrating the applicability and representativity of our proposal for tropical biomes (see Tables 1, 2 and Figures 1–5). This proposal is based on hierarchical classifiers for defining biomes, and to some extent follows the vegetation classification of EcoVeg (Faber-Langendoen et al. 2014, 2016, 2018), which is widely used in America, and the Worldwide Bioclimatic Classification System (Rivas-Martínez et al. 2011a) developed in Europe.

Prior assumptions

Our biome approach is founded on six assumptions:

(a) Macrobioclimate is the major factor driving the zonation of biomes, whereby biomes are distributed by global climate zonation into what are known as zonobiomes (Walter 1985). We favour the term macrobioclimate in preference to macroclimate since the bioclimatic approach – linking biota and climate – emphasizes the limiting climate factors that explain the structural and functional differentiation of ecosystems. The role of climate factors (determining zonal biomes) versus other abiotic factors (determining pedobiomes, lithobiomes, hydrobiomes) has been widely discussed (Mucina 2018; Hunter et al. 2021).

(b) Bioclimate is an essential feature in biome definition (Troll 1961; Bailey 1989a, 1989b; Rivas-Martínez et al. 2011a). We consider bioclimate to define the differentiation and zonation of the biomes within each macrobioclimate (Table 1 and Figure 1) by including information on (i) the magnitude and rhythm of rainfall and temperature, (ii) the intensity and duration of the dry season, and (iii) the annual thermicity. Current world bioclimatic maps show a high degree of agreement with biome and ecosystem maps (Rivas-Martínez et al. 2011; Metzger et al. 2012).

(c) The easiest and most intuitive way to identify, describe and classify biomes is through vegetation (Figure 1). The type of vegetation involved in biome definition must be the potential natural vegetation or climax, since it is in balance with the prevailing climate and soil conditions (Tüxen 1956; Loidi et al. 2010; Mucina 2010; Loidi and Fernández-González 2012; Zhao et al. 2019). It should be noted that the potential natural vegetation is sometimes difficult to identify, since it may have been removed by human activities or only be represented by remnants in a matrix of different substitution stages (Figure 2C). Vegetation-based biome maps are currently available, both globally (Bailey 1989b; Olson et al. 2011; Keith et al. 2020) and regionally for several countries (e.g., Neotropical vegetation maps). For reasons of scale, these maps mostly interpret and map the potential natural vegetation and have been taken into account for this proposal. Derived successional stages should be considered as being subsumed in the potential natural vegetation, which is the concept of sigmetum or vegetation series (Tüxen 1979; Géhu and Rivas-Martínez 1981; Rivas-Martínez 2005). The vegetation series or sigmetum expresses the whole set of plant communities or stages that can be found in related geographic spaces as a result of the succession process, which includes both the representative association of the climax stage, and the initial or subserial associations that can replace it (e.g. Figure 2C). It also comprises the disclimax cases created by vegetation dominated by exotics that cannot evolve towards the potential natural vegetation (e.g. Figure 3A).

(d) We assumed that the biome refers to the landscape matrix, that is to say, the dominant and more continuous or connected ecosystem (Forman and

Godron 1986) in a landscape mosaic. Thus, each type of dominant or zonal vegetation – potential natural vegetation or climax vegetation – also includes the azonal vegetation with which it is repeatedly associated in the landscape, such as xeric vegetation on rocky outcrops or sandy soils, or wetland vegetation on flooded soils. Therefore, the biome is not restricted to a single structural type of vegetation, but encompasses different structural types that are functionally and geomorphologically associated and connected in the landscape in a repetitive way. Following the concept of the association geocomplex, geocatena or vegetation geoseries (geosigmetum concept: Schmithusen 1959; Tüxen 1979; Rivas-Martínez 2005; Rivas-Martínez et al. 2011b; Choisnet et al. 2019), each biome consists of a specific geoseries that occupies a regional area with the same bioclimate and biogeography, or of a group of homologous geoseries (macrogeoseries) whose zonal (climatophilous) series share analogous physiognomic-structural characteristics. We thus consider macrogeoseries as an accessory spatial qualifier for biomes, and geoseries for regional biomes (Table 1).

(e) Other abiotic factors such as lithology and hydrology are important, but usually play a role at finer scales within biomes, e.g. as regional biomes (Tables 1 and 2). However, when azonal vegetation is the dominant landscape matrix, we consider it as a biome in its own right (e.g. extensive wetlands – Figure 2D – or vast special substrates such as rocks, serpentine or sands). Such landscapes are considered as azonal biomes (Walter 1973; Navarro et al. 2010) since they are not directly determined by the macroclimate but by the hydrology.

(f) The physiognomy and structure of the potential natural vegetation are adequate descriptors of biomes (Loidi et al. 2010; Mucina 2010) since they represent a global biological response to past and present climate conditions. Biomes based primarily on floristic composition should not be considered at the global level, mainly due to the scale of application of the concept. Similarly, fauna is not directly addressed, as it is regarded as dependent and adapted to the vegetation-climate complex: in general, we assume that each type of vegetation contains characteristic fauna ensembles.

(g) Anthropogenic cultural systems (or anthromes) are considered here a secondary biome because, although these biomes are human-altered, they currently occupy large areas (Faber-Langendoen et al. 2014; Ellis 2015, 2020) and are also influenced by the bioclimate and altitudinal zonation (Table 2; Figure 3A–D).

Hierarchical classifiers for defining biomes

We propose that biome classification should be based on the typology of a hierarchical system in which, as a first step, the macrobiome (zonobiome) is defined through the macrobioclimate and plant formation characteristics, and in a second step, the biome is defined through the altitudinal belt and characterization of the bioclimate.

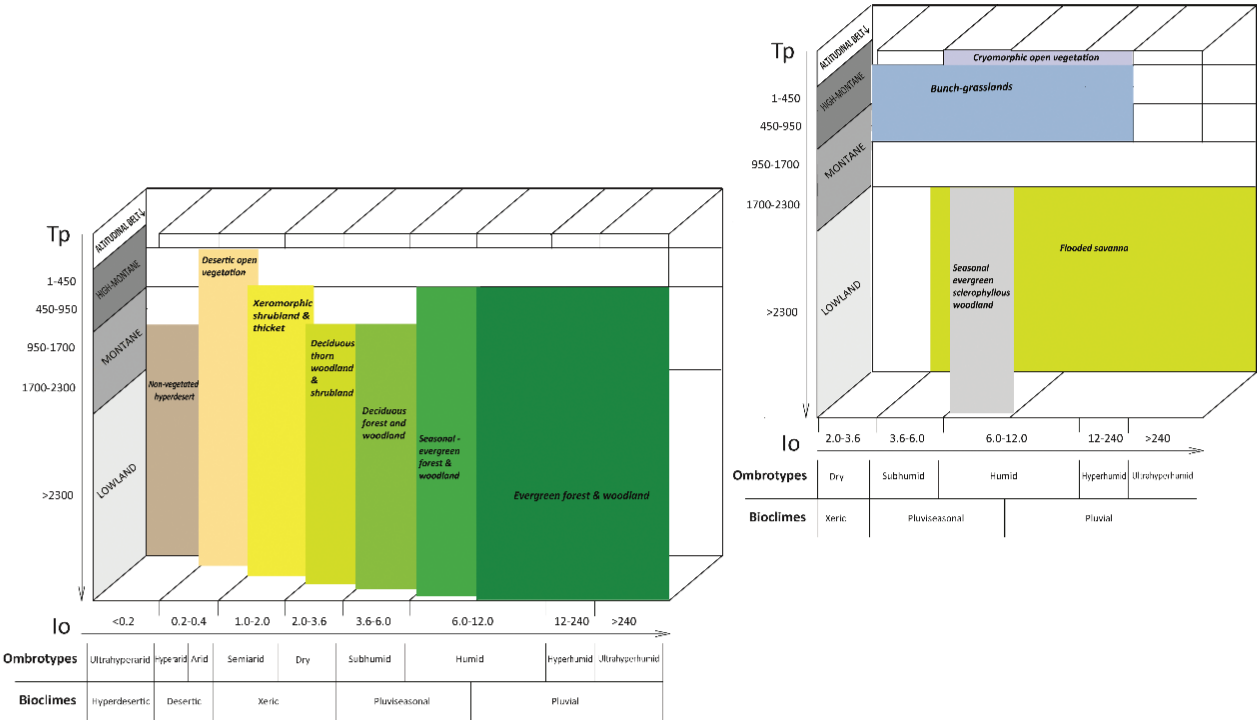

Figure 1. Whittaker-style diagram showing neotropical biomes distribution in relation to Rivas-Martínez values of positive temperature (Tp) and ombrothermic index (Io).

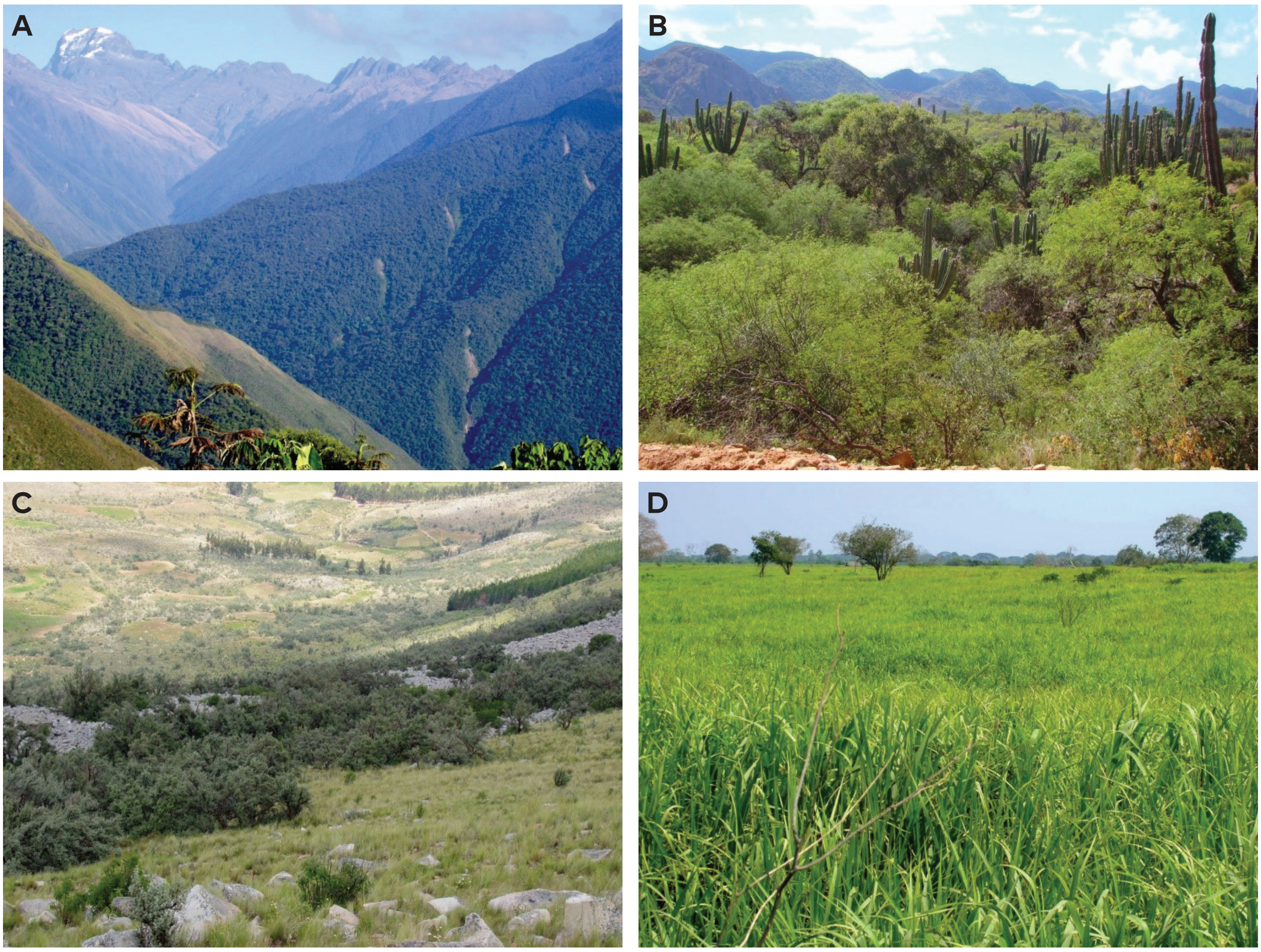

Figure 2. Representative examples of biomes from South America, showing their classification and nomenclature according to the proposal of this work. **A.** Belt zonation in the north-eastern Bolivian Andes showing two main altitudinal belts, montane, and high-montane (Cordillera Real, La Paz, 1900 m to 5100 m); **B.** Tropical montane deciduous thorn woodland and shrubland, *Neocardenasia herzogiana-Schinopsis haenkeana* community (Interandean dry valleys, Cochabamba, 1890 m); **C.** Remnants of Tropical montane evergreen seasonal sclerophyllous woodland of *Polylepis subtusalbida* community in a matrix of seral stages, mainly bunch-grasslands (pajonal) of *Festuca dolichophylla*, and scattered plantations of *Eucalyptus* (Cordillera Tiraque, Cochabamba, 3670 m); **D.** Tropical lowland flooded savanna, *Paspalum fasciculatum* community (Llanos del Beni, 148 m). (Photos: Gonzalo Navarro).

Here we follow the Rivas-Martínez bioclimatic system (Rivas-Martínez et al. 2011a), which hierarchically differentiates the macrobioclimate at higher scales, and within this, several bioclimates differentiated by specific ranges of bioclimatic indices. A biome regionalization, with consideration of floristic composition, can also be defined when a biogeographic typology is included, as biogeographic sectorization is mainly based on the regional distribution of plant species and communities. Our procedure also emphasises the importance of using the same nomenclatural sequence to define biomes, and implicitly or explicitly includes bioclimatic characteristics. It is also important to note that our approach is actualistic, in the sense that it seeks to explain the current adaptive occurrence of biomes, which may vary depending on the diverse and complex incidence of climate change around the world. This is the case of various relict vegetation types that do not correspond directly to the current climate, which implies a degree of uncertainty in the causal relationships between climate and vegetation. A good illustration of this phenomenon are vegetation types that are currently in separate or disjunct zones with respect to their main continuous areas of distribution. For example, in South America, climatic fluctuations during the Quaternary (drier climates oscillating along the north-south direction) can explain the isolated and disjunct areas of Gran Chaco vegetation currently located much further north, within the Beni, Chiquitanía or Pantanal (Navarro and Maldonado 2002; Navarro 2011).

We therefore adopt, for regional biome characterization, both the classical biogeographical approach largely based on climate and vegetation alone (De Candolle 1855; Engler 1879–1882; Drude 1890; Schimper 1898; Schmithüsen 1959), and other integrated proposals (Cabrera and Willink 1973; Rivas-Martínez et al. 2011b), one of whose main bases is phytochorionomy (Takhtajan 1986), which recognizes different scales

Figure 3. Representative examples of biomes from South America, showing their classification and nomenclature according to the proposal of this work. **A.** Tropical lowland permanent livestock anthrome (Bolivia, Santa Cruz, 440 m); **B.** Tropical lowland pluvial exotic cultural anthrome, oil palm crops of *Elaeis guineensis* (Ecuador, Esmeraldas, 60 m); **C.** Tropical montane pluviseasonal subhumid traditional cultural anthrome (Bolivian Andes, Cochabamba, 3600 m); **D.** Tropical montane urban anthrome (Bolivian Andes, Cochabamba, 2600 m); **E.** Tropical high-montane Andean mining anthrome (Bolivia, Potosí, Cerro Rico, 4300 m); **F.** Tropical high-montane pluviseasonal subhumid traditional cultural anthrome (Bolivian Andes, Cochabamba, 3800 m). (Photos: Gonzalo Navarro).

of biogeographic units, namely: region, province and sector (Good 1974). Additionally, biogeophysical and landscape qualifiers are considered when specifying biomes at regional scales.

Defining macrobiomes and biomes

In our proposal, the macrobiome (= zonobiome) is defined by the macrobioclimate and the potential vegetation structure (plant formation), as shown in Table 1 for the Neotropics (columns 1 and 2). Most of the current biome terminology initially refers to some type of macroclimate and ecosystem aspect, whether physiognomic or structural, that can be related to plant formation. This is unsurprising, since macroclimate plays a fundamental role in the structure and functioning of ecosystems and thus in the evolutionary-adaptive groups of associated flora and fauna. In this context, "evolutionary" refers to biotic assemblages that have evolved adaptively and differentially in each biome, depending on the different climatic conditions. Major macrobioclimates can be summarized in a few types such as Tropical, Mediterranean (included by certain authors in Temperate), Temperate, Boreal and Polar (Rivas-Martinez et al. 2011a). We do not consider the desert bioclimate (according with Rivas-Martínez et al. 2011) to be a single bioclimate since it is present in areas with differing macrobioclimates and consequent different floristic assemblages (e.g., deserts occur under different Mediterranean, Tropical and Temperate macrobioclimates). Ecosystem aspects such as vegetation structure and foliage phenology – including the morphology and persistence of plant leaves – photosynthetic rates, the formation and dynamics of humus types, rates of biogeochemical cycles and others, are primarily conditioned by the macrobioclimate (Troll 1961; Holdridge 1967; Whittaker 1970; Larcher 1975; Walter and Box 1976; Box 1981a,b; Bailey 2004; Mucina 2018). Major natural formations worldwide can also be summarized in a few broad types, namely forest, woodland, savanna, shrubland, tundra, grassland, and steppe (Ellenberg and Mueller-Dombois 1967). We propose a detailed characterization and definition of Neotropic plant formations in Table 2.

Biome relates ecosystems to climate through bioclimate. Different bioclimate zones can be defined within each macrobioclimate when biome zonation is related to ranges in thermicity (bioclimatic belts) and rainfall/temperature ratios (ombrotypes) along both altitudinal and latitudinal gradients (Table 1; Figure 1). In addition, the numerical calculation of bioclimatic indices (e.g. Rivas-Martínez et al. 2011a) from extensive and updated global climate data (e.g. Fick and Hijmans 2017) confers a robust possibility of prediction and extrapolation. Thus, bioclimate classifies aspects of vegetation structure and phenology more precisely than macrobioclimate. In our proposal, the biome is primarily defined by the bioclimate, the altitudinal belt and the plant formation.

Likewise, the regional biome incorporates additional qualifiers referring to the biogeographic distribution (centres of origin and evolution of the flora) and landscape qualifier (geoseries). Our proposal to some extent overlaps with the International Vegetation Classification (IVC; Faber-Langendoen et al. 2020). Thus, macrobiome, biome and regional biome, as defined here, are roughly equivalent to the formation, division and macrogroup levels of the IVC.

Table 1. Successive application of the five main criteria proposed (macrobioclimate, formation, altitudinal belt, bioclimate, biogeography) and additional qualifiers to identify and name the three levels of scale proposed for the Neotropics biomes.

Zonobiome		**Biome** **Landscape additional qualifier: macrogeoseries**		**Regional Biome** **Landscape additional qualifier: geoseries**
1. Macrobioclimate	2. Formation	3. Altitudinal belt (thermicity)	4. Bioclimate (ombric rhytms)	5. Biogeography (Biogeographic region)
Tropical	1. Cryomorphic open vegetation 2. Bunch-Grassland 3. Evergreen forest 4. Evergreen seasonal forest & woodland 5. Evergreen seasonal sclerophyllous woodland 6. Deciduous forest and woodland 7. Deciduous thorn woodland and shrubland 8. Xeromorphic shrubland & thicket (semidesert) 9. Desert open vegetation 10. Non vegetated hyperdesert 11. Foggy coastal hyperdesert 12. Flooded forest and woodland 13. Mangroves 14. Flooded savanna 15. Non flooded savanna 16. Anthropic and cultural vegetation	High-montane (3,900–5,200 m)	Pluvial	NEOGRANADIAN (Colombian-Venezolan) TROPICAL SOUTH ANDEAN
			Pluviseasonal	NEOGRANADIAN (Colombian-Venezolan) TROPICAL SOUTH ANDEAN
		Montane (1,000–3,900 m)	Pluvial	NEOGRANADIAN (Colombian-Venezolan) GUYANAN-ORINOQUIAN TROPICAL SOUTH ANDEAN AMAZONIAN BRAZILIAN-PARANEAN
			Pluviseasonal	NEOGRANADIAN (Colombian-Venezolan) TROPICAL SOUTH ANDEAN AMAZONIAN BRAZILIAN-PARANEAN
			Xeric	NEOGRANADIAN (Colombian-Venezolan) TROPICAL SOUTH ANDEAN
			Desertic	TROPICAL SOUTH ANDEAN
			Hyperdesertic	HYPERDESERTIC TROPICAL PACIFIC
		Lowland (< 1,000 m)	Pluvial	NEOGRANADIAN (Colombian-Venezolan) GUYANAN-ORINOQUIAN AMAZONIAN BRAZILIAN-PARANEAN
			Pluviseasonal	NEOGRANADIAN (Colombian-Venezolan) GUYANAN-ORINOQUIAN AMAZONIAN BRAZILIAN-PARANEAN
			Xeric	NEOGRANADIAN (Colombian-Venezolan) BRAZILIAN-PARANEAN CHACOAN
			Desertic	HYPERDESERTIC TROPICAL PACIFIC
			Hyperdesertic	HYPERDESERTIC TROPICAL PACIFIC

Biome nomenclature

Some examples are provided to aid the understanding of the nomenclatural procedure in our approach (see also Figures 1–5). The first step defines the macrobiome or zonobiome (Table 1). For instance, the name of the Tropical evergreen forest macrobiome (Table 2, formation type 3, columns 1 and 2) – also broadly known as the Tropical evergreen rainforest biome – refers to both the macrobioclimate (Tropical) and the formation (evergreen forest).

The second step defines the biome, which takes into account the altitudinal belt and the bioclimate. An example is the Tropical lowland pluvial evergreen forest biome (Table 1, formation type, column 1, 2, 3, 4). In this definition "lowland" corresponds to the altitudinal belt and pluvial to bioclimate. It is worth noting that in most biome classifications, the formation name is often linked to an adjective denoting the dominant leaf morphology or phenology, e.g., "sclerophyllous woodland and shrubland", or "evergreen broadleaf forest", whereas other times it is related to the growth form, e.g., "prostrate dwarf-shrub tundra". In our proposal each plant formation (Table 2) is defined by their physiognomy (e.g., forest, woodland, shrubland) and the phenology of the foliage of the dominant stratum (e.g., evergreen, semi-deciduous), since these are the elements most closely related with both the bioclimate and the key soil factors and adaptive history of each biogeographic region. In some cases, we consider it properly justified to introduce complementary specific qualifiers in the formation's name. This additional nomenclature is related to key geobiophysical variables such as hydrological factors (e.g., flooded forest).

Biogeographical qualifiers (at the biogeographic region or province level) can more accurately specify the regional biome (Table 1) and can be entered in brackets after the main biome name: e.g., Tropical lowland evergreen forest biome [Amazonian]. We do not consider it useful or practical to formally use local or regional names to denominate the biomes, such as the "South American Cerrado", or the "South African Fynbos". Nevertheless, due to the long tradition of their use in certain biomes, it may be useful to point out equivalences between regional names and plant formations (see Table 2).

Table 2. Physiognomic-structural characterization of the 16 plant formations recognized for the Neotropics and their correspondence with bioclimates, altitudinal belts and dominant major soil groups. This correspondence emphasizes the simultaneous use of structural and eco-functional criteria in the proposed methodology for the classification of biomes. Soil types follow Gardi et al. (2015).

Formation	Structure and foliage phenology	Bioclimate	Altitudinal belt/ Geographical distribution	Soils
1. Cryomorphic open vegetation	Dwarf caespitose grasslands and open or sparse low perennial subfruticose herbs on cryoturbed high montane Andean soils	Humid Pluviseasonal and Pluvial	Subnival > 4600 m	**Cryosols,** Leptosols, Regosols
2. Bunch-Grassland	Mountain tropical tall to medium-high graminoid grasslands that grow forming somewhat separate tillers or tufts with dense rooting (*Puna*, *Páramo*, *Pajonal*). Including swamp-grasslands and peat-bogs.	Humid Pluvial and Pluviseasonal	Upper Montane and High Montane belts / Tropical Andean, High Guyanas	**Umbrisols,** **Regosols,** **Histosols,** **Gleysols,** Leptosols
3. Evergreen forest	Tall or medium-high forests and woodlands with perennial foliage (*Rainforest*, *Selva*). It presents a complex and very diverse vertical structure: emergent strata, canopy, sub-canopy, shrub layers, herbaceous layers, lianas and epiphytes	Humid to Hyperhumid Pluvial and Humid Pluviseasonal	Lowland, Montane and Upper Montane belts / Amazonian, Tropical Andean (N. & C.), Atlantic Brazil, Guyanean	**Ferralsols,** **Acrisols,** **Ultisols,** Umbrisols
4. Evergreen seasonal forest and woodland	Tall to medium or low-high forests and woodlands with foliage which is partially lost continuously, although with a maximum loss in dry season, but simultaneously regenerates it in moderately short time so the foliage looks green all year. (*Seasonal rainforest*, *Seasonal Andean Polylepis woodland*)	Humid to subhumid Pluviseasonal	Lowland, Montane and Upper Montane belts / Amazonian, Tropical Andean, Venezuelan, Atlantic and central Brazil, Guyanean	**Ferralsols,** Acrisols, Umbrisols
5. Evergreen seasonal sclerophyllous-woodland	Dense to open low woodlands with notoriously sclerophyllous or chartaceous perennial to semi-persistent foliage (*Cerrado* –on poor and acidic soils developed on laterite substrates–, Amazonian *Campinarana* –on white quartzitic sands–). The Cerrado is a successional complex (vegetation series) whose climax vegetation is sclerophyllous woodland. It includes: *Cerradão* (dense woodland), *Cerrado* (open woodland), *Campo Cerrado* (bush savanna) and *Campo limpo* (herbaceous savanna)	Humid to subhumid Pluviseasonal	Lowland belt / Central Brazil, E Bolivia, NE Paraguay (*Cerrado*); and Central-Southern Amazonia (*Amazonian Campinarana*)	**Ferralsols,** **Plinthosols,** Planosols, Tropical Podzols
6. Deciduous forest and woodland	Medium-high forests and woodlands with foliage which is fully or almost fully lost (deciduous to semideciduous) during the dry season (*Seasonally dry forests & woodlands*). Generally, with abundant vines and climbers	Subhumid Pluviseasonal and Dry Xeric	Lowland and Montane belts / Venezuelan, Tropical Andean, Central and NE Brazil, Northern Chaco	**Ferralsols,** **Cambisols,** Luvisols
7. Deciduous thorn woodland and shrubland	Dense intricate to open low woodlands and shrublands with wholly or almost *deciduous*, predominantly microfoliate leaves and/or many thorns on branches and stems, as well as cacti (*Guajira*, Brazilian *Caatinga*, *Chaco*)	Dry Xeric	Lowland and Montane belts / Venezuelan, N. Colombian, NE Brazil, Tropical Andean, Gran Chaco (Bolivia, Argentina, Paraguay)	**Luvisols,** **Cambisols** Solonetzs, Vertisols
8. Xeromorphic shrubland and thicket (semidesert)	Semi-dense to open and sparse, low xeromorphic shrublands and thickets with predominantly microfoliate and/or resinous leaves and often with many cacti and other succulent plants (*Guajira*, *Caatinga*, *Chaco*, Central-Southern Dry *Puna*: Andean *Altiplano*)	Semiarid Xeric (semidesertic)	Lowland, Montane and Upper Montane belts / Venezuelan, N. Colombian, NE Brazil, Central-Southern Tropical Andean, Gran Chaco (Bolivia, Argentina, Paraguay)	**Regosols,** Leptosols, Luvisols

Formation	Structure and foliage phenology	Bioclimate	Altitudinal belt/ Geographical distribution	Soils
9. Desert open vegetation	Low and sparse extremely xeromorphic thickets with therophytes and several succulents. In ecological situations such as temporary streams, the desert may include linear dense to sparse formations of woody phreatophytes. (*Atacama Puna*, *Argentina Monte*, *Central Chilean Desert*, *Peruvian montane desert*)	Arid Desertic	Lowland, Montane, Upper Montane and High montane belts. Southern Tropical Andean	**Regosols,** Leptosols
10. Non vegetated hyperdesert	Mountainous reliefs and plains devoid of superior vegetation, except for some populations of extreme xeromorphic or phreatophytic plants that can grow dispersedly in beds of ravines or occasional streams. In ecological situations such as seasonal streams and rivers, the desert may include linear dense to sparse formations of riparian shrubby or arboreal vegetation. (Atacama Desert, Peruvian Desert)	Hyperarid Desertic	Lowland and Montane. Pacific coastal and hilly deserts in extreme south-western Ecuador, western Perú and north-central western Chile	**Regosols, Leptosols**
11. Foggy coastal hyperdesert	Succulent xeromorphic vegetation foggy-dependent on coastal areas of the Pacific Chilean-Peruvian Hyperdesert, locally named as "Lomas": *Tillandsia* Lomas and Succulent *Eulychnia* Lomas. (Atacama Desert, Peruvian Desert)	Hyperarid Desertic	Lowland. Coastal Pacific areas from northern Perú to central Chile	**Arenosols, Leptosols**
12. Flooded forest and woodland	Tall or medium-high dense and diverse forests and woodlands with perennial or semi-perennial foliage, that are flooded seasonally or permanently due to rainfall or river overflow (*Várzea*, *Igapó*, *Bañados chaqueños*)	Pluvial, Pluviseasonal and Xeric	Lowland and Montane belts / Widely distributed	**Gleysols, Fluvisols,** Stagnosols, Vertisols
13. Mangroves	Low or medium high forest & woodland with coastal distribution and affected by both, tidal sea water and fresh water from the mouth of rivers. Typically, on substrates with acidic iron sulfates (jarosite and natrojarosite)	Pluvial, Pluviseasonal and Xeric	Coastal lowlands	**Fluvisols tidalic thionic,** Planosols thionic
14. Flooded savanna	Tropical tall-grasslands (graminoid and cyperoid) with or without open coverage of palms, shrubs and trees patches, that are flooded seasonally (for 4 to 7 months on average), or permanently, due to rainfall and/or river overflow (*Venezuelan-Colombian Llanos*, *Beni –Llanos de Moxos–*, *Gran Pantanal*)	Pluvial and Pluviseasonal	Lowland belt / S. Venezuela, E. Colombia, E. Bolivia, SW Brazil	**Planosols,** Stagnosols, Gelysols
15. Non flooded savanna	Tropical grasslands on well-drained soils. With or without open coverage of palms, shrubs and trees patches. Often as secondary formation. Only represents the potential natural vegetation on unfavorable substrates and soils	Pluviseasonal	Widely distributed in the Neotropical lowlands and montane belts	Ferralsols, Acrisols, Cambisols, Luvisols, Fluvisols, Regosols, Leptosols
16. Anthropic and Cultural Vegetation (Anthromes)	Landscapes largely dominated by vegetation types cultivated or strongly conditioned by man, including agricultural biomes (woody and or herbaceous crops, cultivated pastures, as well as irrigated or rain-fed agriculture). Livestock extensive areas, and the natural seral vegetation that colonizes substrates of anthropogenic origin in urban-industrial ecosystems, such as streets, roadsides, parks and gardens, urban wastelands, mining and industrial waste, dumps and abandoned or fallow crops	Pluvial, Pluviseasonal, Xeric, Desertic, Hyperdesertic	Widely distributed in the Neotropical lowlands, montane, upper montane and high- montane belts	Anthrosols, Technosols, Regosols, Fluvisols, Vertisols, Chernozems

Application to the Neotropics

We used the Neotropical region for the initial development and testing of our proposal. This application is primarily based on the vegetation classification work and maps of Navarro and Maldonado (2002), Navarro and Ferreira (2007), and Navarro (2011). The Neotropics extends southward from southern North America to Central America and north-central South America. We follow the criteria of Rivas-Martínez (1997) and Rivas-Martínez et al. (1999, 2011b), who recognize the Neotropical-Austro-American kingdom, and within it, the Neotropical sub-kingdom whose northern limit is located towards 33°N latitude in southwestern USA (California, Texas, Arizona) and towards 27°S in southeast Texas and Florida. Tropical (warm) deserts are included in this concept. In South America, the border with the Austro-American sub-kingdom runs approximately along the 30°S latitude line in northern Uruguay, southern Paraguay, northern Argentina and northern Chile.

All this area, from the lowlands to the high mountains, has a Tropical macrobioclimate (Rivas-Martínez et al. 2011a) and is possibly one of the most biodiverse areas in the world. The Americas, with over 125,000 species, represent 33% of the estimated number of vascular plants worldwide. Specifically, South America is home to 6% more vascular plants than the whole of Africa, which has an area twice its size (Antonelli and Sanmartín 2011; Ulloa et al. 2017). It is worth noting that the main feature of the Tropical macrobioclimate is that, if there is a seasonal difference in rainfall throughout the year, then the wettest and warmest periods coincide (Troll 1961; Bailey 1989). This phenomenon is constant in both the lowlands and the mountains. It is also important to highlight that in the tropical mountains the value of the daily thermal range exceeds the value of the annual thermal range (Troll 1961). These two main factors together condition the structure, composition, differentiation and functioning of tropical biomes and set them apart (Rivas-Martínez et al. 2011a) from other biomes in adjacent extratropical macrobioclimates with opposing annual rainfall and temperature rhythms (Mediterranean macrobioclimate with summer hot dryness), or which do not follow differentiated or pronounced annual rainfall patterns (Temperate oceanic bioclimate). As noted above, in our proposal and based on Rivas-Martínez et al. (2011a), the desert bioclimate is not a single bioclimate since it is present in areas with differing macrobioclimates and consequent different floristic assemblages.

All the possible tropical ecological altitudinal levels (= bioclimatic belts or thermotypes) occur in the Neotropics. Bioclimatic belts are nomenclaturally and numerically delimited by thermicity values (Rivas-Martínez et al. 2011a). These altitudinal levels use terms widely adopted in Latin America (Josse et al. 2009) for the tropical Andes (Venezuela south to Northern Argentina and Chile), and include, in an operative, parsimonious and simplified way, three main altitudinal belts: Lowland, Montane, and High-montane (High Andean). The lowland belt (0–1,000 m) occupies the lowland plains, foothills and lower areas of the neotropical mountain ranges, and corresponds to infratropical and thermotropical Rivas-Martínez thermotypes. The montane belt (1,000–3,900 m) is widely distributed in zones with intermediate to medium high altitudes in the Andes, and in the mountain ranges of southern Venezuela, Tepuís and north and south-eastern Brazil, and corresponds to mesotropical and supratropical Rivas-Martínez thermotypes. The high-montane belt (>3,900 m) occurs mainly in the Andes, and corresponds to Rivas-Martínez's orotropical, cryorotropical and gelid thermotypes.

All the tropical bioclimates are recognized in the Neotropics (Rivas-Martínez et al. 2011a, 2011b). They include the following bioclimates: Pluvial, Pluviseasonal, Xeric, Desertic and Hyperdesertic (Table 2). The great climate diversity of the Neotropics also comprises the whole variation of ombrotypes, from the ultra-hyper-arid to the ultra-hyper-humid. Both the bioclimate and ombrotype show a close correlation with the structure of the Neotropical plant formations, and a close relationship can also be seen between most formations and the large groups of zonal soils recognized in the FAO world classification system (Chesworth et al. 2008; Gardi et al. 2015; see Table 2).

Sixteen plant formations are identified in the Neotropics (Table 2), and serve as the cornerstone of the biomes we recognize in this biogeographical region. Four of these formations correspond exclusively to the lowland belt, four to the lowland and montane belts, one to the high-montane belt, while the others are distributed in more than two ecological belts. The tropical cryomorphic open-vegetation occurs in a humid climate in the high-montane belt (Figure 4A). Andean mountains are also characterized by a tropical bunch-grassland which consists of graminoid grasslands growing in pluviseasonal-pluvial bioclimates in the high-montane belt (Figure 4B).

The tropical pluvial and/or pluviseasonal evergreen forest extends from the lowland to the high-montane belt under a humid to hyperhumid climate (Figure 4C). The tropical evergreen seasonal forest corresponds to the distinctive forests and woodlands whose foliage is partially and continuously lost and regenerating. It occurs in humid to subhumid climates from the lowland to high-montane belt (Figure 4D). The tropical lowland seasonal-evergreen sclerophyllous-woodland consists of woodland with perennial or semi-persistent foliage developing under a subhumid to humid climate in the lowland belt (Figure 4E, F). The tropical pluviseasonal and xeric dry-deciduous forest and woodland occur in a subhumid to dry climate from the Lowland to the Montane belt.

In the Neotropics, drier biomes are found from the lowland to the high-montane belt under an ultra-hyperarid to dry climate. Specifically, the tropical xeric dry-deciduous thorn woodland and shrubland extends under a dry climate in the lowland and montane belts (Figure 5A). The tropical xeric shrubland and thicket occurs under a semiarid climate (semidesert) from the lowland to the high-montane belt (Figure 5B; Table 1, 2). Tropical desertic open vegetation consists mainly of xeromorphic thickets occurring under an arid climate from the lowland to the high-montane belt (Figure 5C). The tropical hyperdesertic non-vegetated is found under a hyperarid to ultra-hyperarid climate from the lowland to the montane belt (Figure 5D). The tropical foggy coastal hyperdesert, characterized by fog-dependent succulent xeromorphic vegetation, is found on coastal areas of the Pacific. Biomes on wet soils are typically restricted to azonal conditions. Specifically, the tropical flooded forest and woodland is widely distributed on seasonally or permanently flooded soils (Figure 5E). The mangroves formation is restricted to tropical coastal tidal and deltaic environments. The tropical flooded savanna is widely distributed (Figure 2D), whereas the tropical non-flooded savanna extends throughout the neotropical lowland and montane belts. Azonal tropical anthropic and cultural vegetation is widely distributed in the Neotropics (Figure 3). This anthrome is found in rural and urban industrial ecosystems characterized by the anthropic influence. They include such diverse systems as crops, groves, pastures, cities, mines, quarries and dumps.

Discussion

In general, publications referring to biomes or related concepts can be grouped into biogeographic, ecoregional, ecological and functional approaches (Table 3). Biogeographic classifications and maps are diverse and mainly based on the distribution patterns of plants and/or animal species (Cabrera and Willink 1973; Udvardy 1975; Takhtajan 1986; Morrone 2001); and on integrated criteria that include the bioclimate, plant communities and geophysical factors (Rivas-Martínez et al. 2011b). The nomenclature of these biogeographic units is heterogeneous and their cartographic delimitation is difficult to replicate as it is mainly based on expert knowledge. Our proposal considers the higher scale biogeographic levels such as region and province as complementary criteria in the delimitation of biomes and regional biomes. EcoVeg (Faber-Langendoen et al. 2014) implicitly uses biogeographic region and biogeographic province at the division and macrogroup levels of their classification respectively. NatureServe (Josse et al. 2003) also includes the biogeographic province level in the characterization of ecological systems.

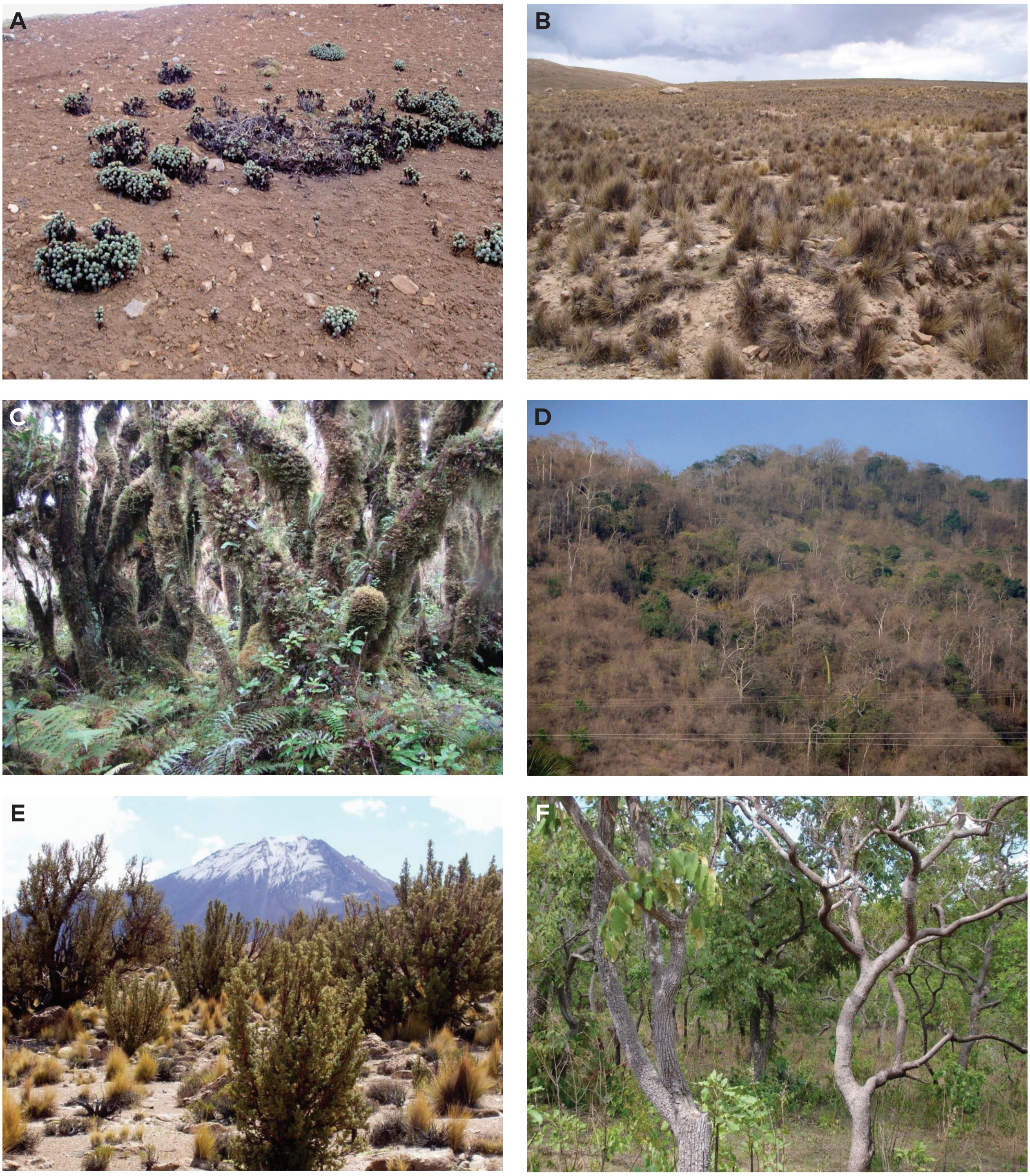

Figure 4. Representative examples of biomes from South America, showing their classification and nomenclature according to the proposal of this work. **A.** Tropical high-montane cryomorphic open vegetation with *Xenophyllum dactilophyllum* (Bolivia, La Paz, Cordillera Real, 4900 m); **B.** Tropical high-montane seasonal bunch-grassland of *Festuca orthophylla* (Cordillera de Morococala, 4100 m); **C.** Tropical montane and high-montane evergreen woodland, *Weinmannia fagaroides* community (Andean Yungas, Bolivia, Cochabamba, 3000 m); **D.** Tropical lowland deciduous forest and woodland (Coastal central Ecuador, 220 m); **E.** Tropical high montane evergreen seasonal sclerophyllous-woodland of *Polylepis tarapacana* (Bolivian Andes, western Oruro, 4400 m); **F.** Tropical lowland evergreen seasonal sclerophyllous-woodland (Bolivian Cerrado, Santa Cruz, Chiquitanía, 460 m). (Photos: Gonzalo Navarro).

Ecoregional approaches (Bailey 1996a, 1996b; Olson et al. 2001; Dinnerstein et al. 2005, 2017) have produced world maps that are widely used; however, the cartographic delimitation of ecoregions is also fundamentally based on expert knowledge and is difficult to replicate (Table 3). Furthermore, the ecoregion concept and its nomenclature are not yet consistently defined and there are several overlaps between criteria such as vegetation, biogeography,

Figure 5. Representative examples of biomes from South America, showing their classification and nomenclature according to the proposal of this work. **A.** Tropical lowland deciduous thorn-woodland and shrubland (central coastal Ecuador, 120 m); **B.** Tropical high montane xeromorphic shrubland and thicket, *Trichocereus atacamensis-Fabiana densa* community (Oruro, Bolivia 3700 m); **C.** Tropical high-montane desert with *Acantholippia punensis-Atriplex imbricata* community (northern piedmont of Ollagüe Volcano, Atacama Puna, Potosí, Bolivia, 3820 m); **D.** Tropical low montane hyperdesert (Lima, Perú, 760 m); **E.** Tropical lowland evergreen flooded forest (Amazonian Várzea, Río Beni, Pando, Bolivia, 120 m). (Photos: Gonzalo Navarro).

climate and environmental factors. The recent IUCN global proposal (Keith et al. 2020) is cartographically based on Olson et al. (2001), and its approach is explicitly functional, with a focus on the traits and ecological drivers of biomes. Many of these traits and ecological drivers can be derived directly or indirectly from the interactions between climate and vegetation. The IUCN biomes are roughly equivalent to our zonal biomes; the typology of this IUCN system is discussed in detail by the authors, but so far there is a lack of explicit standard nomenclatural protocol to systematically name the ecosystem functional group (EFG), which may be equivalent to our biomes, although the difference in delimitation and nomenclatural criteria makes this comparison uncertain.

Ecological Systems of NatureServe (Josse et al. 2003) differs from our proposal in terms of bioclimatic criteria and the dynamic-successional concept of ecosystem, and in the scale of application. In general, ecological systems are partially equivalent to our regional biomes, and related ecological systems ensembles are roughly equivalent to our biomes. Ecological land units (Sayre et al. 2014, 2015) are conceptually related to ecological systems, and their cartographic expression produces units with a finer level of detail than what is often accepted for biomes. These units are based on the geospatial superposition of several objective physical and ecological criteria (elevation, landforms, geology, bioclimate, land cover), thus conferring the advantage of repeatability. The results are a global map with a detailed map of terrestrial ecological units (ELUs) for South America and the world (Sayre et al. 2014, 2015); however, unlike ecoregional approaches, cartographic units have a much finer scale that goes beyond the required and generally accepted scale for biomes. Our work largely agrees with Sayre et al. (2014) in the general hierarchy of land units.

Functional approaches use geospatial variables, methodologies and models (whose main inputs are spatial vegetation layers or the distributions of several species attributes) to address the cartographic delimitation of biomes. The correspondence between the resulting functional units and known biogeographic or biome units, which are based on more structural characters, has in many cases failed. Paruelo et al. (2001) modelled the ecosystem functional types (EFT) for Temperate South America based on the seasonal dynamics of the normalized difference vegetation index (NDVI) from NOAA/AVHRR satellites, which reflect similar seasonal patterns of biomass or productivity, and they did not find a clear correspondence between EFT and phytogeographical provinces. Conradi et al. (2020) used range modelling of plant species to reveal spatial attractors for different growth-form assemblages that define biomes but contain no ecological hypothesis of why these growth forms co-occur and how they interact with one another. Echeverría-Londoño et al. (2019) examined distributions of functional diversity of plant species across the biomes of North and South America, finding that widespread species in any biome tend to be functionally similar whereas the most functionally distinctive species are restricted in their distribution. These authors proposed a functional diversity biome classification for the Americas and their equivalence with the biome classification of Olson et al. (2001).

Table 3. A comparison between the key criteria in our approach and some other related proposals. The weaknesses and strengths of each proposal can be derived from this comparison.

	The present integrated approach	**Ecoregional approaches** Bailey (1996a, 1996b), Olson et al. (2011), [Keith et al. (2020) – maps based on ecoregions]	**Eco-vegetational approaches** IVC-EcoVeg (Faber-Langendoen et al. 2014, 2017, 2020)	**Ecosystem based approaches**: ELUs (Sayre et al. 2015), Ecological Systems (Josse et al. 2003)
Tentative equivalences between several types of units	Zonobiome (macrobiome) Biome Regional biome	Biome Ecoregion Ecosystem functional type (EFT)	Formation Division Macrogroup or group	Uncertain equivalences with the former, as ecological land units (ELUs) have a finer scale and are not comparable with biomes. However, several ecological systems defined for Latin America may correspond to regional or subregional biomes, and groups of related ecological systems may correspond to our biome concept.
Standardized nomenclatural protocol for naming units	Systematic use of the same sequence of naming criteria and in this order: macrobioclimate, plant formation, bioclimatic level, biogeography, which apply according to the macrobiome-biome-regional biome levels. E.g.: Step 1. Macrobiome (zonal biome): *Tropical evergreen forest* Step 2. Biome: *Tropical montane evergreen forest* Step 3. Regional biome: *Tropical montane Andean Yungas evergreen forest*.	Heterogeneous nomenclature with no consistency or homogeneity in the GFS names assigned. Detailed principles designed for a global ecosystem typology, but lacking an objective, consistent and explicit protocol or keys to properly name the units. As the authors say: "Names of functional groups are vernacular — we adopt names and descriptors frequently applied in the literature that reflect key functional features. A vernacular (rather than systematic) approach" (Keith et al 2020). e.g. T4.3 Hummock savannas T2.1 Boreal and temperate montane forests and woodlands T5.3 Sclerophyllous deserts and semi-deserts T6.5 Tropical alpine meadows and shrublands	Use of a similar and consistent sequence of criteria to name the units: Formation criteria: macrobioclimate-plant formation-bioclimatic level (not always applied) Division criteria: biogeography (ca. region level) Macrogroup-group criteria: Biogeography (ca. province level), Floristic composition However, biogeographical names are not standardized or somewhat ambiguous: biogeographical names mixed with purely geographic or plant names at the same hierarchical level. e.g. D227 1. A.2.Ek Brazilian-Parana lowland humid forest: M597 Cerrado humid forest M595 Brazilian Atlantic forest D006 1. B.1.Na Southeastern North American forest & woodland: M007 Longleaf pine woodland US M885 South-eastern coastal plain Evergreen oak – mixed hardwood	Ecological Systems use somewhat inconsistent nomenclature without a standardized protocol. ELUs cartographic unit labels follow the same more or less consistent descriptors: bioclimate, land form, lithology, Coberture. E.g.: "Cool moist mountains on metamorphic rock with mostly deciduous forest" "Cold wet mountains on acidic volcanic rocks with mostly needleleaf/evergreen forest"

	The present integrated approach	**Ecoregional approaches** Bailey (1996a, 1996b), Olson et al. (2011), [Keith et al. (2020) – maps based on ecoregions]	**Eco-vegetational approaches** IVC-EcoVeg (Faber-Langendoen et al. 2014, 2017, 2020)	**Ecosystem based approaches**: ELUs (Sayre et al. 2015), Ecological Systems (Josse et al. 2003)
Predictive capacity and repeatability	Viable: based on numerical bioclimatic indexes and bioclimatic world maps	Difficult to standardize and repeat, as the units and their mapping are based on expert opinion. However, the IUCN approach includes detailed descriptive definition criteria.	Viable: based on explicit criteria to define the proposed units. However, there is some overlap and repetition of the defining criteria. Some difficulties for extrapolating outside the Americas	Viable: based on explicit definition criteria applied with an accurate geospatial methodology for mapping detailed units.
Consistency and propriety in the use of clear descriptors and classifiers	Consistent use of the same sequence of criteria and in the same order: *macrobioclimate*, *plant formation*, *bioclimatic belt*, *biogeography*, which apply according to the macrobiome-biome-regional biome levels. Structural consideration of biomes	Ecofunctional explicit approach Key assembly gradients: *water deficit*, *seasonality*, *temperature*, *nutrient deficiency*, *fire activity and herbivory*. (Keith et al. 2020) Mixing and overlapping of the descriptors and classifiers used: some overlaps between the vegetation structure and the bioclimate: e.g., is “humid” a vegetation term or a climate term? Do the terms “desert” and “semi-desert” refer to the physiognomy of the vegetation? or the climate? or both?	Use of a similar and consistent sequence of criteria: Formation: *macrobioclimate-plant formation-bioclimatic level (not always applied)* Division: *biogeography* (*ca. region level*) Macrogroup-group: *Biogeography (ca. province level), Floristic composition* Somewhat inconsistently applied names for descriptors and nomenclature. e.g. Mixed forest Hardwood forest & woodland	ELUs use the same criteria applied to design mapping units. Input layers: *elevation*, *landforms*, *geology*, *bioclimate*, *land cover*. Structural consideration of ecosystems: “Ecosystems can therefore be spatially delineated by mapping and integrating these structural components in geographic space” (Sayre et al. 2015).
Proper definition of the concepts used related to plant formation names	Clear and consistently applied plant formation concepts, based on the same sequence of *growth forms* and *phenological leaf persistency*. Repeatable terminology for growth forms and foliage persistency, largely based on Ellenberg & Mueller-Dombois (1967), Rivas-Martínez (2005) and EcoVeg (2014). The criterion of leaf phenology is easier to apply consistently than the commonly applied terms of humidity, which alternate or superimpose “climate humidity” with “vegetation humidity”: the denomination “evergreen” is preferable to “humid” and “rainforest”, as evergreen implies a pluvial bioclimate.	Glossary definition of several terms used in the EFG descriptions. The terminology of plant formations is not standardized or well-defined and delimited. Some examples: - What is the difference and clear delimitation between *steppes, grasslands and savannas*? - Some relevant Neotropical formations are not represented, e.g., the extensive woodlands and wooded or arboreal savannas of the Cerrado biome in South America (Brazil, Bolivia, Paraguay). - There is no climatic qualifier for savannas, but the proper concept of savanna is only tropical. - Inappropriate use of the term “alpine” for tropical high-montane grasslands.	Based on dominant plant growth forms. Detailed descriptions of plant growth forms, however, plant formation names remain non-standardized. e.g. Overlap between the vegetation structure and the bioclimate: Is “humid” a vegetation or a climatic term?	Global ELUs use the following land cover classes and class mosaics: *bare areas, artificial surfaces and urban areas, shrubland, closed to open, broadleaved or needle-leaved, evergreen or deciduous, herbaceous vegetation, closed to open, grassland, savannas or lichens/mosses* *mosaic forest or shrubland with grassland mosaic grassland with forest or shrubland mosaic vegetation (grassland/shrubland/forest) with cropland* South American ELUs are based on LAC NatureServe denominations of ecological systems with somewhat poorly defined and delimited or inconsistently applied plant formation names.
Proper definition of the concepts used related to bioclimates	Based on the World Bioclimatic System (Rivas-Martínez et al. 2011) that defines with numerical indexes: *thermotype, ombrotype, bioclimate, bioclimatic levels*.	*Tropical, Subtropical, Temperate, Cool temperate, Boreal, Polar, Lowland, Montane, High-montane*: there is no clear delimitation and conceptual definition for these terms, and they do not explicitly follow any bioclimatic system. Terms are not consistently applied in all EFGs: e.g. only “cool” deserts? The Mediterranean bioclimate is subsumed or immersed in the Temperate bioclimate which introduces uncertainty in several EFGs	Somewhat poorly defined and delimited or confusingly applied climatic categories e.g. Dry/Seasonal dry Temperate/Mediterranean Semi-desert/Hyperdesert Cool/warm desert	Ecological System partially uses the World Bioclimatic System of Rivas-Martínez (only ombrotypes). Global ELUs use simplified climate categories: *Arctic* *Very Cold Very Wet* *Very Cold Wet* *Very Cold Moist* *Very Cold Semi-Dry* *Very Cold Dry* *Very Cold Very Dry* South American ELUs use global meteorological raster data and formulas developed by the Rivas-Martinez bioclimatic system to delineate isobioclimate regions
Dynamic-successional character of the vegetation	Successional approach: we postulate that biome is defined by the natural potential vegetation, and that the successional states are considered (at these scales) to be included in the potential natural vegetation.	Actualistic approaches: successional states are not considered to be immersed in the potential vegetation, but rather constitute different units: e.g. (EcoVeg and Ecological Systems: “M515 Caribbean-Mesoamerican Lowland Ruderal Grassland & Shrubland”; “M123 Eastern North American Ruderal Grassland & Shrubland”; “M310 Southeastern North American Ruderal Flooded & Swamp Forest”. IUCN (Keith et al. 2020) “T7: Intensive Land Use Biome” are roughly equivalent to anthromes.		

	The present integrated approach	**Ecoregional approaches** Bailey (1996a, 1996b), Olson et al. (2011), [Keith et al. (2020) – maps based on ecoregions]	**Eco-vegetational approaches** IVC-EcoVeg (Faber-Langendoen et al. 2014, 2017, 2020)	**Ecosystem based approaches**: ELUs (Sayre et al. 2015), Ecological Systems (Josse et al. 2003)
Dynamic-successional character of the vegetation	However, in highly transformed landscapes, when the dominant landscape matrix is extensively disturbed ecosystems, we still consider them as anthromes (anthro-biomes) (Ellis 2020).	Not explicit		
Ecological landscape framework to address biomes or units	We introduce a geographic-ecological framework to qualify biomes, through the concept of geoseries (geocatena, geosigmetum) that is applicable to regional biomes and biomes.	Not explicit	Not explicit	Not explicit Ecological Systems: "spatially co-occurring assemblages of vegetation types sharing a common underlying substrate, ecological process or gradient" (Josse et al. 2003)
Ecological or bioclimatic levels	We consider the altitudinal zonation as a characteristic of each biome, and one that serves to delimit it. Altitudinal levels are in accordance with the thermicity index values of Rivas-Martínez et al. (2011). We performed an operational simplification of the detailed Rivas-Martínez bioclimatic levels, based on Josse et al. (2009), in order to make them easier to apply at the biome scale.	Altitudinal belts are underrepresented (only lowland/montane), and their delimitation criteria are not explicit.	There is no standardized use of the nomenclature of the elevation; the delimitation criteria are not explicit. Altitudinal levels are more detailed in South American units (lowland, low-montane, montane, upper montane, high-montane) than in North American units (lowland, lower montane, montane, high montane, subalpine). The criteria delimiting altitudinal levels are not explicit.	They accept elevation classes based on published literature for South American ecosystems: 0–500 m, 500–1000 m, 1000–2000 m, 2000–3300 m, and > 3300 m
Eco-functional approach	We stated that a bioclimate-based structural approach is ecofunctional in nature since the limiting climate variables condition and determine the appearance and structural adaptations of the vegetation, and the soil complexes on which it develops, thus behaving as ecosystem drivers.	Ecofunctional explicit approach. However, several IUCN ecofunctional drivers, key assembly gradients or properties described in the EFGs can be derived consistently from the respective bioclimates, in a more parsimonious way: at least water deficit, temperature and thermal seasonality in a direct way, and indirectly, nutrient deficiency, fire activity and herbivory.	Not explicit	

Conclusions

We propose a hierarchical biome classification and nomenclature in three steps. In the first step, macrobiomes or zonobiomes are defined by macrobioclimate and plant formation. In the second step, biomes are defined by bioclimatic belt and bioclimate. Finally, in a third step, regional biomes incorporate the biogeographic typology at the region level, following Rivas-Martínez et al. (2011b). Additionally, we include landscape qualifiers to define biomes and regional biomes. The overall combination of these traits enables a comprehensive and hierarchical nomenclature that offers a predictive system of global value that can be widely understood and applied. These three biome classification levels are also roughly and preliminarily equivalents to the formation, division and macrogroup levels of the International Vegetation Classification (IVC, Faber-Langendoen et al. 2014).

The main novelties or contributions of our proposal can be summarized as follows:

1. Importance of using the same nomenclatural sequence criteria to define and name biomes, namely macrobioclimate-altitudinal belt-plant formation -[biogeography]-[biogeophysical: FAO GSR (soils), hydrological variables].
2. Clear and consistently applied concepts of plant formation, based on the same sequence order of growth forms and phenological leaf or foliage persistency, largely based on Ellenberg and Mueller-Dombois (1967), Rivas-Martínez (2005) and EcoVeg (2014).
3. Standardized use of bioclimate variables and concepts based on the World Bioclimatic System (Rivas-Martínez et al. 2011a): thermotype, ombrotype, bioclimate, as well as an operational use of bioclimatic belts based on Josse et al. (2009).
4. Possibility of mapping and extrapolation of biomes based on both climate data and bioclimatic indexes.
5. Consideration of a dynamic-successional character of the vegetation in the definition of the biome.
6. An ecological landscape framework, that treats the biome as a macrogeosigmetum (macrogeoseries) which occupies a territory with a homogeneous bioclimate and biogeography.
7. A bioclimate-based proposal that serves as an eco-functional approach since the limiting climate variables condition and determines the appearance and structural adaptations of the vegetation, its biomass, and the soil complexes on which it develops, thus behaving as ecosystem drivers.

Author contributions

G.N. designed the survey and provided the core data information. J.A.M. contributed substantially to the writing and took part in shaping the proposal.

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RESEARCH PAPER

The vegetation of rich fens (*Sphagno warnstorfii-Tomentypnion nitentis*) at the southeastern margins of their European range

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Abstract

Question: Rich fens of the *Sphagno warnstorfii-Tomentypnion nitentis* alliance require a specific combination of base richness and climate to occur. Their rarity at the southeastern margins of their European range has previously prevented rigorous vegetation classification. We asked how many associations may be delimited here and whether some of them are restricted to the high Balkan Mountains showing high endemicity. **Study area:** Entire territories of Bulgaria and Romania. **Methods:** We compiled all available vegetation-plot records, including some hitherto unprocessed data. We classified them by both divisive (modified TWINSPAN) and agglomerative (beta-flexible clustering) numerical classification method, with OPTIMCLASS1 applied to set the number of clusters. A semi-supervised approach (k-means) was additionally applied to confirm the classification of Southern-Carpathian (Romania) rich fens, where some Balkan taxa occur. Differences in base richness and elevation were tested by one-way ANOVA with Tukey's pairwise test. **Results:** Three associations were delimited and all three occur in Bulgaria, from where only one association had been previously reported. Two associations characterised by *Sphagnum contortum* and Balkan and Southern-European species occur in Bulgaria, but not in Romania, one at lower elevations around 1,200 m, and one at higher elevations around 2,000 m where pH is lower. One lower-elevation (around 1,300 m) association with *S. warnstorfii* and *S. teres* is shared between Romania, Bulgaria and Central Europe. **Conclusions:** We have described a new high-mountain association, with two subassociations that differ by successional stage and dominant peat moss species (*S. contortum* and *S. warnstorfii*, respectively). These subassociations could be reconsidered when more data from other Balkan countries are available. Rich fens in southeastern Europe are rare, have a diverse vegetation, and are deserving of the further attention of nature conservation authorities and vegetation scientists.

Taxonomic reference: The nomenclature was harmonized following The Euro+Med PlantBase (Euro+Med 2021) for vascular plants and Hill et al. (2006) for bryophytes, except of *Angelica pancicii* that is accepted as a separate taxon in Bulgaria (Andreev et al. 1992; Delipavlov et al. 2003). Critical taxa, not always reliably differentiated in the field and in literary sources, were merged to aggregates: *Alchemilla vulgaris* agg. (all *Alchemilla* species), *Anthoxanthum odoratum* agg. (*A. alpinum*, *A. odoratum*), *Molinia caerulea* agg. (*M. arundinacea* subsp. *arundinacea*, *M. arundinacea* subsp. *freyi*, *M. caerulea*), *Palustriella commutata* agg. (*P. commutata*, *P. falcata*), *Plagiomnium affine* agg. (*P. affine*, *P. elatum*, *P. ellipticum*), *Sphagnum palustre* agg. (*S. centrale*, *S. palustre*).

Syntaxonomic reference: Peterka et al. (2017) for alliances.

Keywords

Balkans, Bulgaria, endemic and relict species, mires, rich fens, Romania, Sphagno warnstorfii-Tomentypnion nitentis, vegetation survey

Introduction

Rich fens, a habitat in which acidicole and calcicole species both occur, are one of the most important wetland habitats in terms of biodiversity conservation, being increasingly endangered across Europe (Janssen et al. 2016; Chytrý et al. 2019; Singh et al. 2019). They are usually formed by calcium-tolerant peat moss species, non-sphagnaceous brown mosses and both calcicole and acidicole vascular plants (Du Rietz 1925; Rydin et al. 2013; Peterka et al. 2014; Singh et al. 2019), unlike other mire types where either peat mosses with acidicole vascular plants or brown mosses with calcicole vascular plants dominate. The coexistence of different species groups is caused not only by the intermediate pH and calcium levels, but also low nutrient availability and specific climate conditions such as total precipitation and the number of hot days (Hájek et al. 2021a). Calcium-tolerant peat mosses found in fens fed by moderately calcium-rich water, require either a stable water level of a narrow pH and calcium range (semi-aquatic species such as *Sphagnum contortum*), or the ability to escape from calcium-rich groundwater by forming hummocks (*S. warnstorfii*). To survive on calcium-rich groundwater any *Sphagnum* requires a constantly humid climate that facilitates a downward transport of toxic calcium from photosynthesizing capitula (Vicherová et al. 2017). If a summer dry period occurs, calcium moves upwards due to evapotranspiration and its high concentration in capitula can be lethal (Hájek et al. 2014). This mechanism explains why calcium-tolerant peat mosses barely colonise calcium-rich fens in areas experiencing dry summers, such as the submediterranean-subcontinental regions of the Balkan Peninsula (Hájek et al. 2008a, 2014). In extremely seasonal climates, calcium-tolerant peat mosses do not occur at all (Naqinezhad et al. 2021). A balance between the two major functional groups of mire mosses, peat mosses and brown mosses, may be disrupted not only by a change in climate, but also by increasing nutrient availability that supports the expansion of some calcium-tolerant species of peat moss such as *Sphagnum teres* (Hájek et al. 2015; Vicherová et al. 2015), or declines in water table that allow calcifuge peat mosses to avoid carbonate-rich groundwater and spread over the fen surface (van Diggelen et al. 2006; Granath et al. 2010; Kooijman 2012). The spread of calcifuge peat mosses can be associated with the loss of some endangered vascular plants, whose seedlings or offsets cannot compete with fast-growing acidicole peat mosses (Singh et al. 2019). The high level of endangerment and a sensitivity to environmental and climatic changes focuses the attention of plant ecologists and vegetation scientists on rich fens, especially at the margin of their range. Assessments of rich fens are, however, complicated by insufficient attention on their classification. The vegetation of rich fens, combining different functional groups of mire plants, have previously been neglected in traditional phytosociology, and descriptions of such vegetation are missing from several countries. In the current European-scale overviews, the rich fens have been clearly delimited at the levels of the vegetation alliance *Sphagno warnstorfii-Tomentypnion nitentis* (Mucina et al. 2016; Peterka et al. 2017) and the EUNIS habitats (https://eunis.eea.europa.eu/habitats.jsp; Chytrý et al. 2020). According to the synthesis of Peterka et al. (2017), they widely occur in northern Europe, the Baltic region, and Central-European mountains and highlands (the Alps, the Western Carpathians, Bohemian Massif). South and southeast of these mountains, rich fens are extremely rare, with the edge of the range in the Eastern and Southern Carpathians in Romania (see also Hájek et al. 2021b) and isolated islands in the Eastern Balkans, specifically in south-west Bulgaria (Hájek et al. 2008a; Peterka et al. 2017). Due to their rarity, the alliance *Sphagno warnstorfii-Tomentypnion nitentis* has not been distinguished in vegetation surveys from the Bulgarian high mountains (Roussakova 2000; Hájek et al. 2005; Hájková et al. 2006) and only one association has been reported from lower elevations (Hájek et al. 2008a). This low-elevation association, *Geo coccinei-Sphagnetum contorti* Hájek et al. 2008, is characterised by the semi-aquatic calcium-tolerant peat moss *Sphagnum contortum* and lawn-forming *S. teres*, coexisting with some endangered brown mosses (*Hamatocaulis vernicosus*), calcicole vascular plants (*Eriophorum latifolium*) and several species of wet grasslands. Although hummock-forming *S. warnstorfii* does occur in Bulgaria (Natcheva and Ganeva 2005; Hájková and Hájek 2013), its rarity at low elevations has prevented distinguishing a separate association. In high elevations, fens with *S. warnstorfii* contain some Balkan endemics which has resulted in their classification within the *Cirsio heterotrichi-Caricetum nigrae* (Soó 1957) Hájek et al. 2005 and *Primulo exiguae-Caricetum echinatae* Roussakova 2000 associations, previously classified to the *Caricion fuscae* alliance (Roussakova 2000; Hájková et al. 2006), later re-arranged to *Narthecion scardici* (Peterka et al. 2017). The synthesis of Peterka et al. (2017), however, showed that some high-mountain plots with *S. warnstorfii* from Bulgaria are closer to *Sphagno warnstorfii-Tomentypnion nitentis* than to *Narthecion scardici*.

In Romania, a neighbouring country also at the edge of the range for calcium-tolerant peat mosses and fen specialists (Horsáková et al. 2018), the *Sphagno warnstorfii-Tomentypnion nitentis* communities have also been rarely recorded (Hájek et al. 2021b). Most of them have been classified to the *Sphagno warnstorfii-Eriophoretum latifolii*

Rybníček 1974 association, described from the Czech Republic (Rybníček 1974), while a single relevé has been classified as the *Menyantho trifoliatae-Sphagnetum teretis* Warén 1926 association characterised by tall sedges of boreal distribution. The high-mountain communities in the Southern Carpathians have been classified within the *Sphagno warnstorfii-Eriophoretum latifolii*, although they contain some Balkan species (*Gymnadenia frivaldii*, *Dactylorhiza cordigera*, *Plantago gentianoides*) and may show some similarities with Bulgarian high mountain species.

In this study we ask whether some associations with *S. warnstorfii* can be distinguished from Bulgaria, along with the previously reported *Geo coccinei-Sphagnetum contorti*, and whether Southern Carpathian rich fens may belong to the same association as Bulgarian ones. The output from our study is a classification of Bulgarian and Romanian rich fens at the association level.

Material and methods

Data set

To answer our two questions, we merged the existing limited datasets from previous studies (Romanian, Bulgarian high-mountain and Bulgarian low-elevation) into one, and added new original data from the Vitosha Mts (Bulgaria) sampled in 2006, after the Hájková et al. (2006) paper was published. We followed a habitat classification system for fens in which rich fens are delimited from extremely rich fens and calcareous fens by the presence of *Sphagnum* species (Malmer 1986; Hájek et al. 2006; Chytrý et al. 2020). We therefore only kept records with at least a 1% (Braun-Blanquet cover code 1) cover of *Sphagnum* species. The resulting dataset (70 relevés; Figure 1) is quite small considering that the geographical survey area covers two countries, but the dataset includes nearly all the rich fens known to occur in Bulgaria and the majority of rich fens that occur in Romania. An advantage of our data set is a unified sampling protocol and unified effort to identify bryophytes. Two co-authors (M.H., P.H.) participated in the sampling of all relevés, and two other co-authors (I.A., D.S.) participated in sampling a number of relevés in both countries and I.G. and D.D. in Romania. Sampling took place between 2001 and 2018, with most plots sampled in July or the beginning of August, and the majority of the plots have a standard plot size of 16 m^2. We recorded all vascular plants and bryophytes using the nine-grade Braun-Blanquet scale (Westhoff and van der Maarel 1978) for cover and abundance estimation (r = few individuals covering < 1% of the area; + = more individuals covering < 1%; 1 = cover 1–5%; 2m = many tiny individuals or ramets covering < 5%; 2a = cover 5–15%; 2b = cover 15–25%; 3 = cover 25–50%; 4 = cover 50–75%; 5 = cover 75–100%). The total percentage cover for all bryophytes and all vascular plants was also recorded.

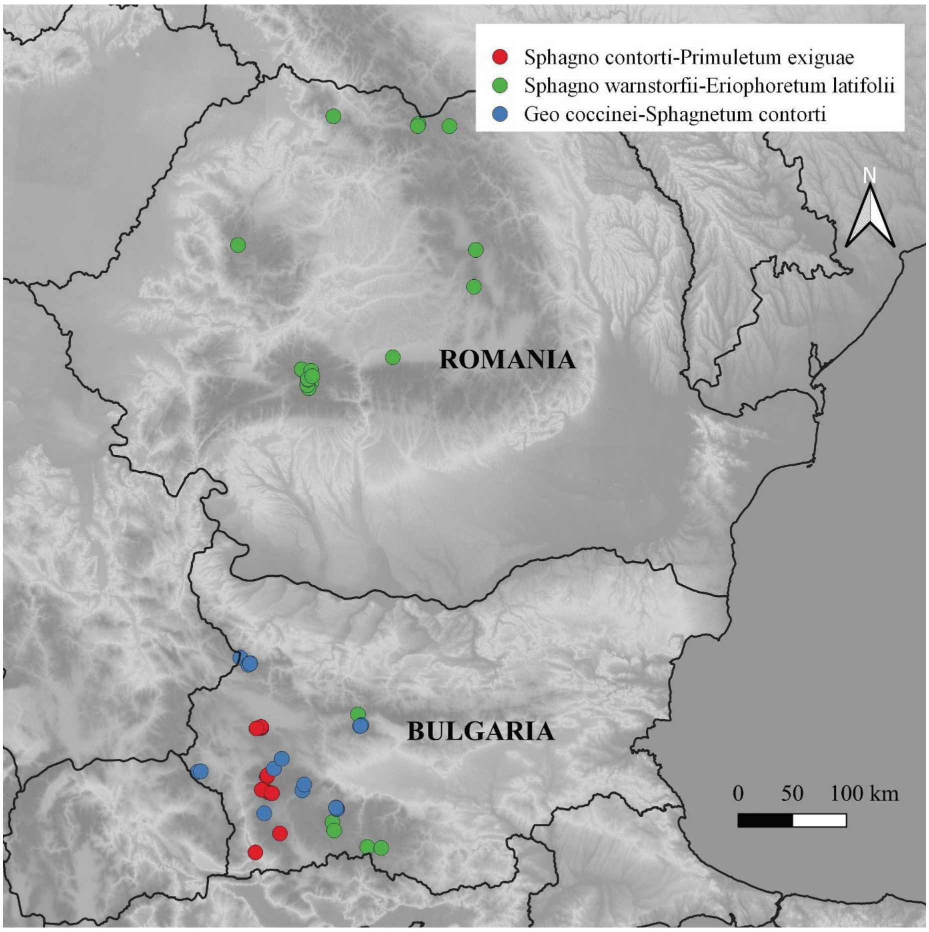

Figure 1. Distribution of study sites and delimited associations.

Water pH, conductivity and adjusted pH

We measured water pH and conductivity from the centre of the patch of fen being studied using portable instruments (mostly HACH HQ40d or CM 101 and PH 119, Snail Instruments). A shallow hole was dug before each measurement was taken to allow a pool of water to form. For testing the differences between associations, we further combined these two variables into a single variable called *adjusted pH* (Plesková et al. 2016) that expresses the joint physiological effect of pH and calcium richness on dominant moss species. For this calculation, we first estimated calcium concentration from water conductivity, using the imputation model of Hájek et al. (2021a). Secondly, we calculated adjusted pH by adding the decadal logarithm of the millimolar Ca^{2+} concentration to the actual pH value (Plesková et al. 2016).

Classification of vegetation

As a first step, we ran unsupervised hierarchical classifications, using two different approaches. One was based on partitioning the major gradients (modified TWINSPAN, Roleček et al. 2009; with total inertia as a measure of cluster heterogeneity), and one was based on agglomerative clustering (the Beta-Flexible Clustering Method with the beta value -0.25 and the Bray-Curtis distance). The pseudospecies cut-off levels of 0, 5 and 25% were used in both cluster analyses in order to take into account the estimated percentage covers of individual species (Tichý et al. 2020). The number of interpreted clusters (four and five, respectively) corresponded to the number where the OPTIMCLASS 1 algorithm (Tichý et al. 2010), with Fisher exact test threshold for diagnostic species being set to $P < 10^{-4}$, started to flatten or decrease. For each group we present the most diagnostic species (with the highest phi-coefficient; simultaneously with Fisher Exact test significance of $p < 0.05$).

As a second step, we tested whether Southern Carpathian rich fens (Romania) belong to the same association as Bulgarian high-mountain rich fens, and whether some low-elevation fens of Bulgaria belong to the same association as Romanian *S. warnstorfii* rich fens. The goal was to clarify the national-level syntaxonomical synopses. For this purpose, we constructed three species groups (named *Pinguicula balcanica* group, *Sphagnum warnstorfii* group and *Geum coccineum* group; cf. Table 1) using the COCKTAIL method (Bruelheide and Chytrý 2000) and utilised them in simple formal definitions for the three major vegetation types appearing in the unsupervised hierarchical classifications (Table 1). According to formal definitions we classified 49 vegetation-plot records, and 21 remaining records were classified by the semi-supervised k-means classification with three pseudospecies cut-off levels to take account of species covers (0, 5, 25%), 10 starts and two vegetation-plot records forming a centroid. We allowed one additional cluster to appear (i.e, the final number of clusters was four), because four groups has resulted from the initial beta-flexible clustering.

In the synoptic table, we consider a species as diagnostic if it has a statistically significant association with a cluster ($P < 0.05$; Fisher exact test). We also present the species occurring in at least 20% of vegetation-plot records.

Table 1. Species groups used in the formal definitions for the three associations before the run of semi-supervised k-means classification. The *Sphagno contorti-Primuletum exiguae* association (10 relevés from Bulgaria) had been defined by the presence of the *Pinguicula balcanica* group (at least two species had to be present), the *Sphagno warnstorfii-Eriophoretum latifolii* association (17 relevés, out of which two are from Bulgaria) is based on the presence of the *Spagnum warnstorfii* group (at least two species had to be present) and the *Geo coccinei-Sphagnetum contorti* association (27 relevés from Bulgaria) is based on the presence of the *Geum coccineum group* (at least two species had to be present) and the absence of the *Pinguicula balcanica* group.

Name of species group	Taxa involved
Pinguicula balcanica	Primula frondosa subsp. exigua, Pinguicula balcanica, Carex bulgarica, Plantago gentianoides
Sphagnum warnstorfii	Sphagnum warnstorfii, S. angustifolium, Valeriana simplicifolia, Calliergon giganteum
Geum coccineum	Sphagnum contortum, Geum coccineum, Juncus thomasii, Veratrum lobelianum

Differences among vegetation types

Differences among associations in edaphic and climatic variables were visualised by box-and-whisker plots showing medians, interquartile ranges, extremes and outliers, and tested by one-way ANOVA with Tukey's pairwise test with Copenhaver-Holland correction. Water conductivity was log-transformed prior to testing to achieve normal distribution. Normality of the data was tested using the Anderson-Darling normality test. All analyses were conducted using the Past 4 software (Hammer et al. 2001).

Results

Unsupervised classifications

Based on the OPTIMCLASS 1 algorithm, modified TWINSPAN resulted in five clusters, while beta-flexible clustering resulted in four clusters. However, their interpretation is the same (Figures 2, 3). The group of Bulgarian relevés characterised by Balkan species (especially by *Primula frondosa* subsp. *exigua* and *Pinguicula balcanica*), the small group of Romanian relevés characterised by *Ligularia sibirica* and *Epipactis palustris*, and the group of Romanian and Bulgarian *S. warnstorfii* fens characterised by *Calliergon giganteum* and *Valeriana simplicifolia* appeared in both classifications, largely with the same diagnostic species. The group of Bulgarian *S. contortum* fens with SE-European species (the *Geo coccinei-Sphagnetum contorti* association) also appeared in

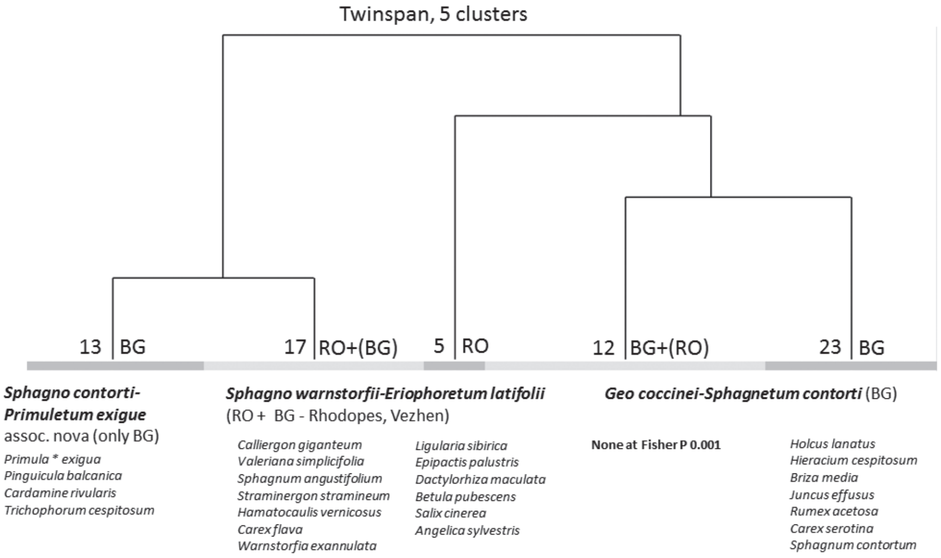

Figure 2. The results of unsupervised divisive classification (modified Twinspan) at the level of five clusters (the number set according to the results of the Optimclass method): dendrogram, species showing the highest fidelity to a cluster, number of relevés in a cluster, involved countries or regions (with minor country in brackets), and expert syntaxonomical interpretation of a cluster.

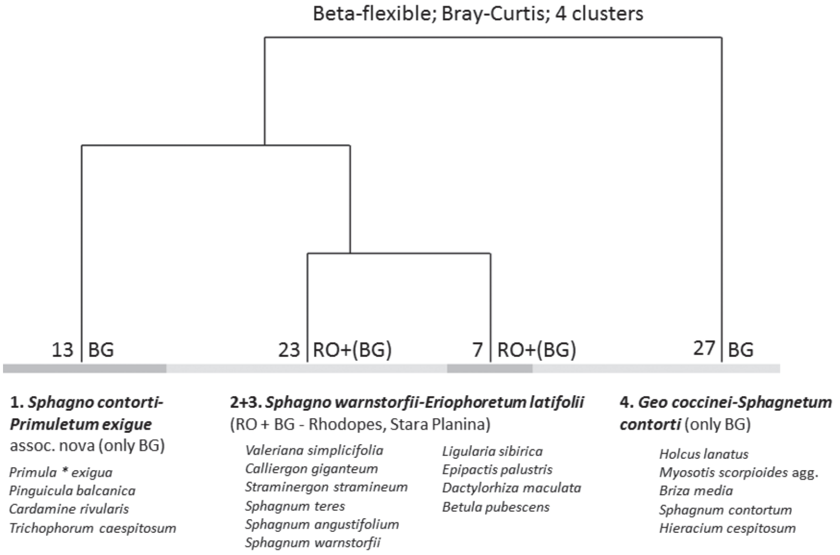

Figure 3. The results of unsupervised agglomerative classification (beta -0.25; Bray-Curtis distance) at the level of four clusters (the number set according to the results of the Optimclass method): dendrogram, species showing the highest fidelity to a cluster, number of relevés in a cluster, involved countries or regions (with minor country in brackets), and expert syntaxonomical interpretation of a cluster.

both classifications, but in TWINSPAN it was further divided into the two clusters based on different grassland species.

Semi-supervised k-means

When we set three formally defined vegetation types (Bulgarian high-mountain rich fens, low-elevation *S. warnstorfii* rich fens, and Bulgarian *S. contortum* rich fens) as predefined groups and ran semi-supervised k-means, the small Romanian cluster with *Ligularia sibirica* also appeared, but this group included only three relevés with *Ligularia sibirica* and *S. warnstorfii*. No Romanian relevé was assigned to the cluster of Balkan high-mountain rich fens. A single Romanian relevé was assigned to the cluster of Bulgarian *S. contortum* rich fens, but it lacks SE-European species and is transitional to poor fens, making its assignment to the *Geo coccinei-Sphagnetum contorti* association inappropriate.

Syntaxonomical conclusions

We interpret the cluster of Bulgarian high-mountain rich fens as a new plant association, with a distribution range restricted to the Balkans, and we describe it formally in this paper with the name *Sphagno contorti-Primuletum exiguae*. In approximately half of the relevés, *Sphagnum warnstorfii* dominates, with certain changes in species composition suggesting advanced succession; we suggest treating these as the *sphagnetosum warnstorfii* subassociation.

We further interpret the cluster of low-elevation *S. warnstorfii* rich fens as the *Sphagno warnstorfii-Eriophoretum latifolii* association and report it as a new association for Bulgaria. Finally, we discovered that the *Geo coccinei-Sphagnetum contorti* association (cluster of Bulgarian *S. contortum* rich fens) does not occur in Romania and is restricted to the Balkans. A small cluster of Romanian rich fens characterised by *L. sibirica* and *Epipactis palustris* were not definitively interpreted syntaxonomically. However, as these relevés were dominated by peat moss species and high-mountain species were absent, we merged it with the *Sphagno warnstorfii-Eriophoretum latifolii* association, where it may be considered as a separate subassociation.

The synoptic table shows the three delimited associations resulted from the beta-flexible classification at the level of four clusters, with the two clusters we interpreted as the same association *Sphagno warnstorfii-Eriophoretum latifolii* merged (Table 2). The full records for the associations new to Bulgaria are presented in Table 3.

The new association

Sphagno contorti-Primuletum exiguae ass. nov.

Nomenclatural type: Table 3, Relevé 1 (holotypus).

Name giving taxa: *Sphagnum contortum*, *Primula frondosa* subsp. *exigua* (Syn.: *P. farinosa* subsp. *exigua*).

Diagnostic species (with respect to other associations within the order): *Primula frondosa* subsp. *exigua*, *Pinguicula balcanica*, *Taraxacum* sect. *Alpina*, *Cardamine rivularis*, *Sesleria comosa*, *Gentianella bulgarica*, *Trichophorum cespitosum*, *Carex bulgarica*, *Cirsium heterotrichum*, *Soldanella pindicola*, *Plantago gentianoides*, *Vaccinium uliginosum*, *Crocus veluchensis*, *Carex nigra*.

Table 2. Synoptic table in percentage frequency. Species are sorted according to decreasing fidelity (unstandardized phi-coefficient) to an association. Species with a statistically significant fidelity to a cluster (Fisher exact test < 0.05) are considered diagnostic and highlighted by grey shading.

Associations	1	2	3
number of relevés	13	30	27
from Bulgaria	13	5	27
from Romania	0	25	0
Alliance species (Peterka et al. 2017)			
Sphagnum contortum	77	30	**96**
Sphagnum warnstorfii	46	**67**	4
Sphagnum teres	46	63	19
Paludella squarrosa	0	7	0
Aulacomnium palustre	38	73	67
Tomentypnum nitens	8	27	11
Diagnostic species of individual associations			
1. *Sphagno contorti-Primuletum exiguae*			
Primula frondosa subsp. *exigua*	**77**	0	0
Pinguicula balcanica	**77**	3	4
Taraxacum sect. *Alpina*	**85**	3	0
Cardamine rivularis	**85**	30	0
Sesleria comosa	**38**	0	0
Gentianella bulgarica	**38**	0	0
Trichophorum cespitosum	**38**	0	0
Carex bulgarica	**38**	0	0
Cirsium heterotrichum	**38**	0	0
Soldanella pindicola	**46**	0	4
Plantago gentianoides	**46**	7	0
Vaccinium uliginosum	**31**	0	0
Crocus veluchensis	**31**	0	0
Carex nigra	**100**	60	33
2. *Sphagno warnstorfii-Eriophoretum latifoliae*			
Valeriana dioica subsp. *simplicifolia*	0	**43**	0
Galium uliginosum	0	**40**	0
Sphagnum angustifolium	0	**33**	0
Agrostis stolonifera	0	**30**	0
Calliergon giganteum	0	**33**	4
Straminergon stramineum	31	**57**	11
3. *Geo coccinei-Sphagnetum contorti*			
Holcus lanatus	0	7	**74**
Myosotis scorpioides agg.	23	30	**100**
Briza media	0	10	**59**
Pilosella caespitosa	0	3	**44**
Juncus effusus	0	27	**70**
Plagiomnium affine agg.	8	20	**67**
Calliergonella cuspidata	0	67	**96**
Rumex acetosa	0	3	**41**
Cynosurus cristatus	0	3	**41**
Ranunculus acris	8	10	**48**
Prunella vulgaris	0	30	**63**
Oenanthe banatica	0	0	**26**
Ranunculus flammula	0	0	**26**
Mentha arvensis	0	0	**26**
Carex panicea	15	20	**59**
Galium palustre	0	57	**81**
Lysimachia vulgaris	0	10	**41**
Crepis paludosa	0	20	**52**
Species with frequency above 20% in the entire data set			
Carex echinata	85	87	100
Potentilla erecta	46	93	96
Eriophorum latifolium	100	67	89
Festuca rubra	77	83	67
Parnassia palustris	69	60	85
Luzula sudetica	92	63	70
Agrostis canina	62	70	70
Nardus stricta	100	57	56
Carex rostrata	8	70	52
Bryum pseudotriquetrum	54	50	52
Epilobium palustre	23	43	70
Warnstorfia exannulata	69	60	22
Climacium dendroides	31	40	63
Dactylorhiza cordigera	69	37	48
Geum coccineum	85	7	67
Carex flava	8	53	44
Anthoxanthum odoratum	46	23	56
Alchemilla vulgaris agg.	31	33	48
Aneura pinguis	54	40	26
Juncus articulatus	23	30	48
Deschampsia cespitosa	62	37	19
Campylium stellatum	46	37	26
Caltha palustris	15	27	48
Eriophorum angustifolium	31	27	41
Succisa pratensis	38	13	52
Sphagnum subsecundum	38	37	22
Hamatocaulis vernicosus	0	43	33
Philonotis fontana	15	17	52

Constant species (100–60%): *Eriophorum latifolium*, *Nardus stricta*, *Luzula sudetica*, *Carex echinata*, *Geum coccineum*, *Sphagnum contortum*, *Festuca rubra*, *Parnassia palustris*, *Dactylorhiza cordigera*, *Warnstorfia exannulata*, *Agrotis canina*, *Deschampsia cespitosa*.

Nomenclatural note: When the name of a syntaxon is formed from the names of two taxa of which only one belongs to the highest of the dominant strata determining the vertical structure, then the name of that taxon appears in the second place (the Code of Phytosociological Nomenclature; Theurillat et al. 2021). In rich fens with *Sphagnum contortum* and *S. warnstorfii*, the moss stratum is the dominant one in terms of cover and biomass, but the herb layer is the highest one that determines vertical structure. Therefore *P. frondosa* subsp. *exigua* must appear on the second place in the syntaxon name even if *S. contortum* usually dominates.

Internal variability:

a) subassociation *typicum*. Successionally initial phase, developing from spring vegetation. Differential species: *Sphagnum contortum* (dom.), *Bryum pseudotriquetrum*, *Campylium stellatum*, *Soldanella pindicola*, *Veratrum lobelianum*.

b) subassociation *sphagnetosum warnstorfii* subass. nov. Successionally advanced phase. Differential species: *Sphagnum warnstorfii* (dom.), *Trichophorum cespitosum*, *Eriophorum vaginatum*. Nomenclatural type: Table 3, relevé 8 (holotypus).

Environmental differences among the three associations

The high-mountain association *Sphagno contorti-Primuletum exiguae* occurred at significantly higher elevations, while the other two associations did not differ in elevation. The *Sphagno warnstorfii-Eriophoretum latifolii* association showed the highest water pH, with statistically significant differences compared with the other two associations, while the *Geo coccinei-Sphagnetum contorti* association exhibited the highest water conductivity (Figure 4). The *Sphagno contorti-Primuletum exiguae* showed the lowest pH. When pH and conductivity were joined into a single variable, *adjusted pH*, the difference between the *Sphagno warnstorfii-Eriophoretum latifolii* and the *Geo coccinei-Sphagnetum contorti* was no longer significant, suggesting ecologically equivalent conditions for the occurrence of calcium-tolerant peat moss species.

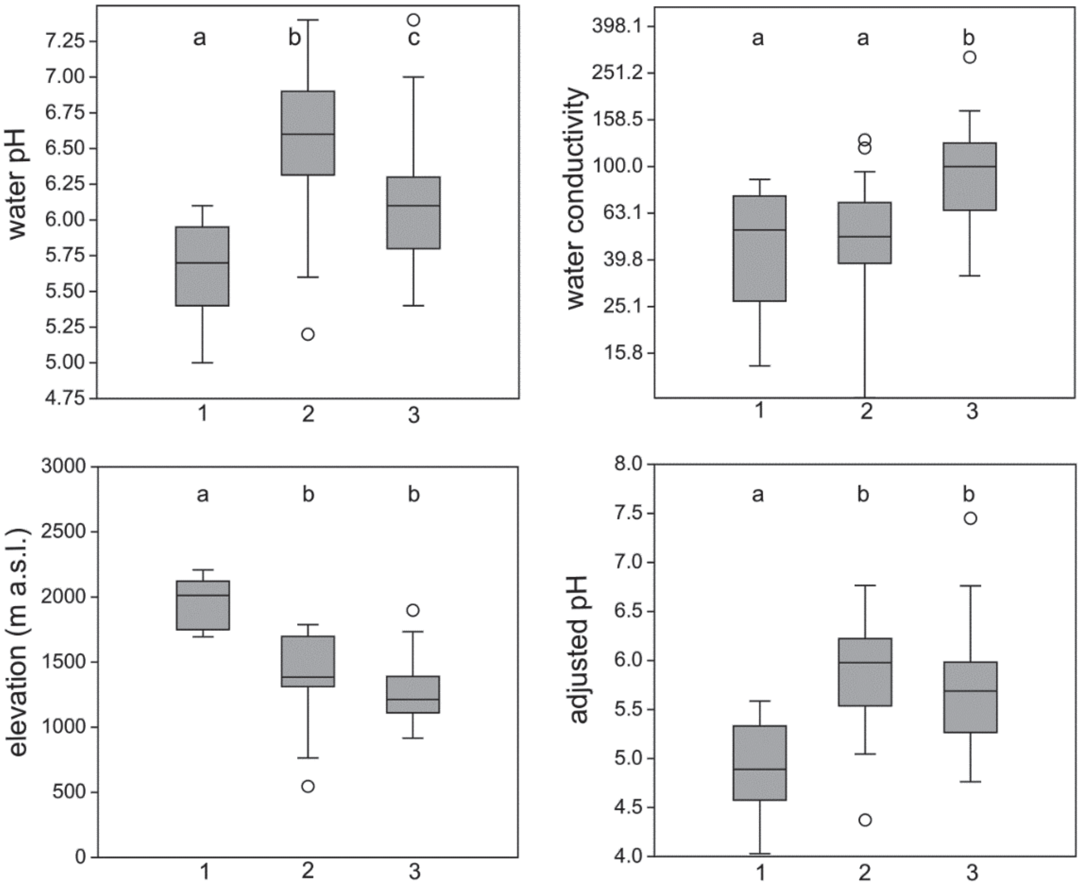

Figure 4. Box-and-whisker plots showing medians, interquartile ranges, extremes and outliers of elevation (m a. s. l.) and pH, adjusted pH and conductivity (μS.cm^{-1}) for the groundwater for the three associations. The different letters above boxes indicate significant differences. Explanations: 1 – *Sphagno contorti-Primuletum exiguae*, 2 – *Sphagno warnstorfii-Eriophoretum latifolii*, 3 – *Geo coccinei-Sphagnetum contorti*.

Table 3. Full table of phytosociological relevés for the two associations new to Bulgaria. Only relevés from Bulgaria are presented.

Relevé number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
Original turboveg number	1	585	359	360	352	79	362	582	586	627	182	10	67	510	504	50	520	131
Relevé area (m^2)	6	16	16	16	16	10	16	16	16	16	16	9	4	16	16	25	16	8
Herb cover (%)	85	65	80	85	75	80	75	65	70	60	80	50	70	70	75	85	50	60
Moss cover (%)	60	20	75	70	75	70	50	85	80	100	70	90	90	80	90	85	95	60
Water pH	.	6.1	5.9	5.7	5.9	5.7	5.5	6.1	5.4	5.0	5.4	.	.	6.0	5.8	6.9	5.6	5.2
Water conductivity (μS.cm^{-1})	.	73	60	47	22	5	44	80	65	28	14	.	.	55	80	50	73	39
Differential species of species of *Sphagno contorti-Primuletum exiguae*																		
Pinguicula balcanica	1	+	+	+	.	2a	2a	+	.	+	.	+	1	.	.	.	.	+
Cardamine rivularis	+	1	1	1	1	1	.	+	+	r	+	1	.	.	.	.	.	.
Taraxacum sect. *Alpina*	.	+	+	1	r	+	+	+	+	r	1	2a	.	.	.	.	.	.
Primula frondosa subsp. *exigua*	+	.	2a	15	2m	2m	2b	.	.	+	1	1	+	.	.	.	.	.
subass. ***typicum***																		
Bryum pseudotriquetrum	+	.	2a	2a	+	2a	+	+	.	.	.	.	.	.	.	.	.	.
Campylium stellatum	.	.	+	1	+	+	+	2a	.	.	.	.	.	.	.	.	.	.
Soldanella pindicola	.	.	1	2b	1	+	+	.	.	.	.	.	+	.	.	.	.	.
Veratrum lobelianum	+	+	r	+	r	.	.	+	.	.	.	.	.	.	.	.	.	.
subass. ***sphagnetosum warnstorfii***																		
Eriophorum vaginatum	.	.	.	.	.	.	.	+	+	.	.	1	.	.	.	.	.	.
Trichophorum cespitosum	2m	.	.	.	.	.	.	1	+	2a	.	.	2a	.	.	.	.	.
Differential species of *Sphagno warnstorfii-Eriophoretum latifolii*																		
Carex rostrata	.	.	.	.	.	.	.	.	+	.	.	.	.	2a	1	1	.	.
Juncus effusus	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	1
Galium palustre	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	2a	.
Carex canescens	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	2b	1	.
Alliance species																		
Sphagnum contortum	.	1	2b	2a	3	2a	2b	1	2a	1	+	.	.	.	.	.	.	.
Sphagnum teres	1	2a	.	.	.	.	.	2a	2b	2b	1	.	.	3	+	4	4	.
Sphagnum warnstorfii	.	.	.	.	.	.	.	4	1	4	4	4	4	2a	.	.	.	2a
Aulacomnium palustre	1	+	.	.	.	.	.	.	+	.	+	2a	.	2a	+	.	1	.
Tomentypnum nitens	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Other mire species																		
Eriophorum latifolium	+	2a	3	2b	2a	2a	2b	2a	2a	1	1	2a	2a	2a	2b	2b	1	1
Carex nigra	3	3	2a	2a	3	2a	2a	2b	2a	2a	2a	2a	+	+	1	.	.	1
Carex echinata	+	.	+	+	+	2a	1	1	.	2a	2a	+	1	1	+	2a	2a	2a
Agrostis canina	+	+	.	1	1	.	1	+	+	.	.	1	.	1	+	+	2m	+
Parnassia palustris	r	+	+	+	1	.	.	+	+	+	+	.	.	1	+	.	+	1
Dactylorhiza cordigera	1	1	1	1	r	.	.	+	+	+	1	.	.	.	1	2a	+	r
Warnstorfia exannulata	+	1	1	1	1	3	.	.	+	+	.	+	.	.	.	2b	+	.
Gymnadenia frivaldii	1	.	.	.	+	.	1	+	.	1	1	.	2m	.	1	.	.	1
Sphagnum subsecundum	3	.	.	.	.	.	.	.	2a	.	2a	1	+	2b	.	.	2b	3
Eriophorum angustifolium	2b	.	.	.	.	.	.	+	2a	2a	.	.	.	2a	1	.	.	.
Straminergon stramineum	.	+	.	.	.	.	.	.	.	.	1	1	+	+	.	2a	.	.
Philonotis seriata	.	.	3	2a	3	.	.	.	.	.	.	1	.	.	.	2a	.	.
Carex panicea	.	.	+	+	.	.	.	.	.	.	.	.	.	1	.	+	.	.
Vaccinium uliginosum	r	.	.	.	.	.	.	1	+	+	.	.	.	.	.	.	.	.
Allium schoenoprasum	+	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Warnstorfia sarmentosa	.	.	.	.	.	+	3	+	.	.	.	.	.	.	.	.	.	.
Drosera rotundifolia	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2a
Sphagnum flexuosum	.	.	.	.	.	.	.	.	.	2a	.	.	.	.	5	.	.	.
Philonotis fontana	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.
Sphagnum palustre s.l.	.	.	.	.	.	.	.	.	3	+	.	.	.	.	.	.	.	.
Comarum palustre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	.
Sphagnum auriculatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Juncus alpinoarticulatus	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Polytrichum commune	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum platyphyllum	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Carex flava	.	.	.	.	.	2a	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum capillifolium	.	.	.	.	.	.	.	.	.	.	.	.	2b	.	.	.	.	.
Other species (sorted by frequency)																		
Nardus stricta	1	+	1	2a	2a	+	2a	+	+	1	2b	2a	2a	1	2a	+	1	2b
Luzula sudetica	+	+	+	1	+	+	+	+	+	+	2a	+	.	+	+	+	.	.
Festuca rubra	1	+	2m	1	+	+	.	+	+	.	.	+	+	.	+	2m	1	+
Geum coccineum	+	+	+	2a	2a	1	+	+	.	r	1	+	.	.	.	+	.	+
Deschampsia cespitosa	+	+	.	.	+	.	.	+	+	.	+	+	1	+	.	1	+	.
Potentilla erecta	2a	+	.	.	.	.	.	1	2a	1	2a	.	.	2a	2b	2a	+	1
Ranunculus montanus agg.	+	+	1	1	1	.	.	r	.	.	.	.	+	+	2a	.	.	.
Aneura pinguis	.	.	.	+	+	+	+	.	+	+	.	+	.	+	.	.	.	.
Trifolium pratense	+	+	1	.	.	.	.	+	+	.	+	.	.	.	.	.	+	.
Climacium dendroides	+	+	.	.	.	.	.	1	1	.	.	.	.	+	.	1	+	.
Scapania irrigua	1	.	+	.	2a	.	.	2a	+	1	.	.	r	.	.	.	.	.
Plantago gentianoides	.	.	2a	2b	.	r	+	.	.	.	+	.	+	.	.	.	.	.

Relevé number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
Anthoxanthum odoratum	+	.	+	.	.	.	.	+	+	.	.	1	1	.	.	.	.	.
Succisa pratensis	+	1	.	.	.	.	.	1	2a	1	.	.	.	.	.	.	.	2a
Myosotis scorpioides agg.	.	.	+	.	.	1	.	.	.	.	+	.	.	+	.	2a	+	.
Juncus thomasii	.	.	.	+	.	.	.	+	.	.	+	.	.	.	.	1	.	+
Juncus articulatus	.	.	+	.	.	2m	+	.	.	.	.	.	.	+	.	.	.	1
Alchemilla vulgaris agg.	.	.	1	+	+	.	.	.	.	.	r	.	.	.	.	2a	.	.
Gentianella bulgarica	+	.	.	.	.	.	.	+	+	+	.	+	.	.	.	.	.	.
Carex bulgarica	.	.	+	+	.	1	1	.	.	.	.	.	+	.	.	.	.	.
Cirsium heterotrichum	1	1	.	.	.	.	.	2a	2a	r	.	.	.	.	.	.	.	.
Sesleria comosa	+	.	.	.	.	.	.	+	+	+	.	+	.	.	.	.	.	.
Equisetum palustre	.	1	.	.	.	.	.	+	+	.	.	.	.	.	.	1	.	.
Molinia caerulea agg.	1	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2a
Crocus veluchensis	+	+	.	.	.	.	.	1	.	.	.	+	.	.	.	.	.	.
Juncus filiformis	.	1	.	.	.	+	.	.	.	.	.	.	.	.	.	1	+	.
Epilobium palustre	.	+	.	.	.	+	.	.	.	+	.	.	.	+	.	.	.	.
Saxifraga stellaris	.	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Scapania undulata	.	+	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Homogyne alpina	.	.	.	.	.	r	.	.	.	.	.	+	+	.	.	.	.	.
Sanguisorba officinalis	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.
Salix lapponum	.	+	.	.	.	.	.	1	2a	.	.	.	.	.	.	.	.	.
Caltha palustris	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	1	.	.
Scorzoneroides autumnalis	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.
Luzula luzulina	.	.	.	.	r	.	+	+	.	.	.	.	.	.	.	.	.	.
Trifolium spadiceum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	1	.
Bruckenthalia spiculifolia	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	+
Ligusticum mutellina	.	.	+	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Vaccinium vitis-idaea	.	.	.	.	.	.	.	.	.	1	.	.	.	+	+	.	.	.
Equisetum fluviatile	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	.	2m	.
Chiloscyphus polyanthos	.	.	1	.	.	.	.	1	.	.	.	+	.	.	.	.	.	.
Oenanthe silaifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.
Palustriella decipiens	.	.	2a	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scapania paludicola	.	.	.	.	.	.	.	.	.	.	+	2a	.	.	.	.	.	.
Dichodontium palustre	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola rotundifolia	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.
Selaginella selaginoides	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Geum rhodopeum	.	.	.	.	.	.	.	.	.	.	.	.	.	2b	2a	.	.	.
Epilobium nutans	.	.	.	.	r	.	.	.	.	.	+	.	.	.	.	.	.	.
Riccardia multifida	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Angelica pancicii	.	.	.	.	.	+	.	r	.	.	.	.	.	.	.	.	.	.
Calliergonella cuspidata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+
Holcus lanatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Ranunculus acris	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Trifolium repens	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.
Bistorta officinalis	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Cardamine acris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	+	.
Carex pallescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Veronica beccabunga	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Atrichum undulatum	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Danthonia decumbens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Bistorta vivipara	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Euphrasia hirtella	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Leontodon hispidus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Gentiana pyrenaica	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	.	.	.	.
Dicranum bonjeanii	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Euphrasia officinalis agg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Carex leporina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Juncus conglomeratus	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Lathyrus pratensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Carex viridula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a
Chaerophyllum hirsutum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Blindia acuta	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Plagiomnium undulatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	.
Trifolium hybridum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Bartsia alpina	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Vicia cracca	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Euphrasia liburnica	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scirpus sylvaticus	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Primula deorum	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	.	.	.	.
Ceratodon purpureus	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Pinus peuce	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Prunella vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Pilosella caespitosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Viola palustris	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Plagiomnium affine agg.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Relevé number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
Palustriella falcata	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Salix waldsteiniana	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex umbrosa	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica scutellata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Calliergonella lindbergii	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula alpinopilosa	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Picea abies	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium fontanum subsp. *vulgare*	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Poa annua	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Jacobaea pancicii	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Localities: 1. Vitosha Mt., western edge of the Torfeno Branishte Nature Reserve, 2 km N from Cherni Vrah peak, June 2001, altitude 1950 m, coordinates: 42°35'09"N, 23°15'29"E, field number BG1/2001; **2.** Vitosha Mt., Platoto locality, between the Aleko chalet and Ushite peak, 26 June 2006, altitude 1695 m, coordinates 42°35'48"N, 23°16'56"E, field number BG14/2006; **3.** SW Rila Mts, S slopes of Markov Kamak peak, 9 August 2004, altitude 2208 m, coordinates 42°03'22"N, 23°23'33"E, field number BG15/2004b; **4.** SW Rila Mts, S slopes of Golyam Mechi Vrah peak, 9 August 2004, altitude 2100 m, coordinates 42°02'55"N, 23°25'30"E, field number BG16/2004b; **5.** SW Rila Mts, Dobro Pole saddle below the Tsarev Vrah peak, 8 August 2004, altitude 2065 m, coordinates 42°04'22"N, 23°19'11"E, field number BG8/2004b; **6.** Rila Mts, Malyovitsa river valley, 2.8 km NNE from the peak Malyovitsa, by the path to the chalet, 25 June 2002, coordinates 42°11'40"N, 23°22'39"E, field number BG20/2002; **7.** SW Rila Mts, below Makedonia chalet, W slopes of Mechi Prohod saddle, 9 August 2004, altitude 2120 m, coordinates 42°02'50"N, 23°26'13"E, field number BG18/2004b; **8.** Vitosha Mt., between the Aleko chalet and Platoto locality, close to the yellow-marked path, 26 June 2006, altitude 1745 m, coordinates 42°35'17"N, 23°17'14"E, field number BG11/2006; **9**. Vitosha Mt., Kapaklivets locality, 26 June 2006, altitude 1730 m, coordinates 42°35'29"N, 23°17'11"E, field number BG15/2006; **10.** Vitosha Mt., above the Zvezditsa chalet, above the timberline, 1 July 2006, altitude 1754 m, coordinates 42°34'53"N, 23°13'47"E, field number BG56/2006; **11.** Pirin Mts, Izvorite locality (blue-marked path from Ribni lakes towards N slopes of the Choveko peak), 30 June 2003, 2012 m, coordinates 41°42'53"N, 23°32'35"E, field number BG50/2003; **12.** Vitosha Mt., 1 km S from Cherni Vrah peak, June 2001, altitude 2150 m, coordinates 42°32'57"N, 23°16'46"E, field number BG10/2001; **13.** Rila Mts, 1.1 km NNE from the peak Malyovitsa (2729), 24 June 2002, altitude 2123 m, coordinates 42°10'59"N, 23°22'16"E, field number BG8/2002; **14.** Central Rhodopes Mts, close to the Beglika reservoir, 30 June 2005, altitude 1530 m, coordinates 41°49'29"N, 24°07'23"E, field number BG28/2005; **15.** Central Rhodopes Mts, Shiroka Polyana village, ca 1 km S from the village, 30 June 2005, altitude 1547 m, coordinates 41°45'23"N, 24°08'44"E, field number BG22/2005; **16.** Central Rhodopes Mts, 2.5 km N from the Mugla village, close to fountain by the path to Lednitsata chalet, 5 July 2001, altitude 1732 m, coordinates 41°37'40"N, 24°31'11"E, field number BG50/2001; **17.** Central Rhodopes Mts, Smolyanski lakes, close to the bus end-station, 2 July 2005, altitude 1548 m, coordinates 41°37'21"N, 24°40'34"E, field number 38/2005; **18.** Stara Planina (Balkan) Mts, Vezhen-Teteven part, 3.6 km SW from the peak Vezhen, brook valley Vartopa, 5 July 2002, altitude 1339 m, coordinates 42°43'50"N, 24°22'14"E, field number BG72/2002.

Discussion

At the margin of their southeastern range in the Balkan Peninsula, rich fens may be robustly classified into three associations, one high-mountain association occurring above the treeline in the Balkans, and two occurring at lower elevations. The high-mountain association is characterised by Balkan species that otherwise occur in the Balkan high-mountain fens of the *Narthecion scardici* alliance (Peterka et al. 2017; referred to as *Caricion fuscae* in Roussakova 2000 and Hájková et al. 2006) from which the *Sphagno contorti-Primuletum exiguae* may develop in the course of autogenic succession or succession after a drop in the water table. Such a succession from brown-moss dominated fen communities towards rich fens with calcium-tolerant peat mosses is well known (Rybníček 1974; Kooijman 2012; Vicherová et al. 2017; Singh et al. 2021), and the combination of Balkan fen species with calcium-tolerant peat mosses in Bulgaria was to be expected. Yet, it had not been reported in previous studies from the Balkans (Roussakova 2000; Hájková et al. 2006; Hájek et al. 2008a; Tzonev et al. 2009) and in our study it was represented by only 13 records, while the *Narthecion scardici* fens that lack diagnostic species of rich fens, especially calcium-tolerant peat mosses, are much more common. Obviously not all *Narthecion scardici* fens develop into rich fens with calcium-tolerant peat mosses. The reason is that calcium and pH content is quite low in most *Narthecion scardici* fens (Hájková et al. 2006) and succession tends to move towards acidicole hummock-forming peat mosses (*Sphagnum capillifolium*, *S. russowii*) with dwarf shrubs such as *Bruckenthalia spiculifolia* (Hájek et al. 2005; Hájková et al. 2006). Enhanced pH and calcium concentrations may be the reason why *Sphagno contorti-Primuletum exiguae*, especially its subassociation with *S. warnstorfii*, may develop from the *Narthecion scardici* fens, but the values measured in the Bulgarian vegetation plots (Figure 4) are quite low, lower than optimum values for calcium-tolerant peat mosses (*S. warnstorfii*, *S. teres*, *S. contortum*) in other regions (Mikulášková et al. 2015; Plesková et al. 2016). Mikulášková et al. (2015, 2017) studied Bulgarian populations of *S. warnstorfii* genetically, along with other populations worldwide, and found slight yet apparent pH- and magnesium-related genetic variation within *S. warnstorfii*, with Bulgarian populations at the acidic and magnesium-poor end of the cline. Another calcium-tolerant peat moss species, *S. contortum*, is more frequent in Bulgarian rich fens including the high-mountain ones. Vascular plants occurring in the *Sphagno contorti-Primuletum exiguae* (e.g., *Eriophorum latifolium*) also seem to be adapted to lower levels of calcium and pH as compared to other regions (Hájková et al. 2008). An occurrence of calcicole species in quite acidic and calcium-poor conditions has also been reported from other cold and nutrient-poor areas such as Scandinavia (Peterka et al. 2020) and also from Central Europe in the recent past, before the period of current eutrophication and warming (Rybníček 1974; Hájek et al. 2015). The species combination that characterises *Sphagno contorti-Primuletum exiguae* may hence mirror specific refugial conditions, such as cold climate and low nutrient availability. In warmer and nutrient-richer conditions, acidicole peat mosses are expected to outcompete calcium-tolerant moss species (Kooijman 2012; Kolari et al. 2021) and the seedlings or offsets of calcicole vascular plants such as *Eriophorum latifolium*, *Parnassia palustris*, *Pinguicula* sp. or *Primula farinosa* agg. (Singh et al. 2019) that characterise the *Sphagno contorti-Primuletum exiguae*. The *Sphagno contorti-Primuletum exiguae*, especially its subassociation with *S. warnstorfii*, should therefore be viewed as a sensitive, relict vegetation, deserving of the attention of nature conservation authorities and of phytosociologists working in the Balkans. Further research in the high mountains of the Balkans, where Balkan endemics frequently occur in fens (Northern Macedonia, Montenegro, Kosovo, Albania), may discover further areas of the *Sphagno contorti-Primuletum exiguae* that could eventually act as a basis for segregating the sucessionally advanced subassociation *sphagnetosum warnstorfii* as a separate association, analogous to fens below the timberline.

At lower elevations where high-mountain Balkan fen species do not occur, rich fens with *S. warnstorfii* (*Sphagno warnstorfii-Eriophoretum latifolii*) develop from calcareous brown-moss fens, or from *S. contortum* rich fens. Because such development requires high climate humidity throughout the entire year (Vicherová et al. 2017), they are quite rare in the submediterranean-subcontinental climate of Bulgaria and they were not delimited in the previous study of Hájek et al. (2008a). When analysed together with Romanian rich fens, the *Sphagno warnstorfii-Eriophoretum latifolii* clearly occurs in Bulgaria, but only in a few specific areas of the Rhodope and Stara Planina Mts, at elevations of 1,530–1,550 m a. s. l. Although we call them low-elevation fens to distinguish them from high-mountain (subalpine to alpine) fens, such elevations are higher than those at which the association occurs in the Czech Republic in Central Europe (Chytrý 2011, interquartile range 500–700 m a. s. l.). The elevational shift in climate conditions between Central and Southeastern Europe is mirrored in the distribution of other groundwater-dependent habitats such as wet grasslands (Hájek et al. 2008b). The association *Sphagno warnstorfii-Eriophoretum latifolii* is a very rare vegetation type in Bulgaria, occurring at the very margin of its distribution. The reason for its rarity in Bulgaria may be that it requires a high precipitation: temperature ratio, especially during the summer (Vicherová et al. 2017) and generally it requires a cold and wet climate. In the Carpathians, most occurrences of this association are in areas where the annual precipitation is at least 800 mm, mean annual temperatures are below 6°C and there are only zero to one hot days with maximum temperature above 30°C (Hájek et al. 2021a).

The *Geo coccinei-Sphagnetum contorti* association, from which the *Sphagno warnstorfii-Eriophoretum latifolii* may develop if the abovementioned climate conditions are met, is much more widespread in Bulgaria because it only depends on particular groundwater chemistry and does not require such a specific climate (Hájek et al. 2008a). It may therefore occupy the lowest elevations and warmest areas of the three rich fen vegetation types known from SE Europe, but as such it is quite poor in specialised and relict fen plants that are generally rare in SE Europe (Horsáková et al. 2018) and may contain many wet-grassland and reed-bed species (Table 2). Despite this, a couple of disjunctly occurring and hypothetically relict species such as *Hamatocaulis vernicosus*, *Eriophorum gracile* or *Carex lasiocarpa* have been found (Hájek et al. 2009), making these fens important biodiversity hotspot and refugia for boreal species in South-Eastern Europe. Our analysis has demonstrated that this association is strongly associated with the Balkans, not reaching the Southern and Eastern Carpathians. Although this association shows higher water conductivity than the previous one, water pH is lower. When pH and conductivity are combined to capture their joint physiological effect on peat mosses (Vicherová et al. 2015; Plesková et al. 2016), there is no difference between the two low-elevation associations.

Rich fens with *Ligularia sibirica*

This delimited cluster was quite small and comprised predominantly vegetation plots with *S. warnstorfii*. We interpreted it as a specific vegetation type within the *Sphagno warnstorfii-Eriophoretum latifolii*, but further research on the continental scale is needed. The relevés of this cluster come from the area of the Eastern Carpathians where phosphorus-enriched, nitrogen-limited fens of the *Saxifrago-Tomentypnion* occur (the Harghita and Covasna regions; Peterka et al. 2017; Hájek et al. 2021b). *Ligularia sibirica* links this cluster with the *Saxifrago-Tomentypnion* fens. It seems the cluster represents rich fens that have developed from these nitrogen-limited fens (the *Drepanoclado adunci-Ligularietum sibiricae* Hájek et al. 2021 association). In the whole-Carpathian analysis of calcium-rich fens (Hájek et al. 2021b), however, this vegetation type was not delimited by the analyses, and individual records were classified as *Sphagno warnstorfii-Eriophoretum latifolii* or, in a single case, as the *Menyantho trifoliatae-Sphagnetum teretis* association.

We cannot exclude the possibility that rich fens that have developed from N-limited extremely-rich fens of the *Saxifrago-Tomentypnion*, but mostly without *Ligularia sibirica*, may occur in other European areas such as Latvia, Estonia, Finnland, Russia or Swiss Jura Mts (compare distribution of *Saxifrago-Tomentypnion* in Peterka et al. 2017), but it seems premature to describe a new association based on so few vegetation-plot records. We have therefore classified the plots forming this cluster within the *Sphagno warnstorfii-Eriophoretum latifolii* association.

To conclude, we have presented evidence for distinguishing three well-supported associations of rich fens in Bulgaria, the *Geo coccinnei-Sphagnetum contorti*, the *Sphagno warnstorfii-Eriophoretum latifolii* and the *Sphagno contorti-Primuletum exiguae* ass. nov., with the latter two being reported for Bulgaria for the first time. All these rich-fen associations are rare in SE Europe, occurring here at the margin of their range and acting as irreplaceable refugia of fen biota in this part of the world.

Data availability

The working data sheets are in Electronic Suppl. material 1 and Suppl. material 2. Full records for the associations new to Bulgaria are further presented in Table 3. The full records for the other Bulgarian records are taken from Hájek et al. (2008a).

Author contributions

M.H. and P.H. planned the research and led sampling, data processing and writing. M.H., P.H. I.A., D.S., I.G. and D.D. conducted the field sampling; the last two authors only in Romania. All authors critically revised the manuscript.

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Supplementary material

Supplementary material 1
Working species-by-sample matrix (csv file)
Link: https://doi.org/10.3897/VCS/2021/69118.suppl1

Supplementary material 2
Working sample-by-variables matrix and geographical coordinates (csv file)
Link: https://doi.org/10.3897/VCS/2021/69118.suppl2

VEGETATION CLASSIFICATION AND SURVEY
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SHORT COMMUNICATION PHYTOSOCIOLOGICAL NOMENCLATURE

New syntaxa of tall-forb vegetation in the Pamir-Alai and western Tian Shan Mts. (Tajikistan and Kyrgyzstan, Middle Asia) – an addendum to Nowak et al. 2020

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Abstract

We validate eleven syntaxa (eight associations and three alliances) of tall-forb vegetation that were published earlier as *nomina provisoria* according to the International Code of Phytosociological Nomenclature. The validation concerns syntaxa of tall-forb vegetation of the class *Prangetea ulopterae* Klein 1987 reported from Pamir-Alai and western Tian Shan Mountains (Tajikistan and Kyrgyzstan).

Taxonomic reference: Cherepanov (1995).

Abbreviations: ICPN = International Code of Phytosociological Nomenclature.

Keywords

International Code of Phytosociological Nomenclature (ICPN), Middle Asia, phytosociological nomenclature, *Prangetea ulopterae*, syntaxonomy, tall forb, validation

Introduction

According to the older version of the International Code of Phytosociological Nomenclature (ICPN, Weber et al. 2000), an effectively published syntaxon should be distributed as a printed matter to the general public or at least to libraries accessible to botanists (Article 1 ICPN). This is related also to the date of the valid publication and to the rule of priority (Articles 2, 6, 23 ICPN). In the last few years, many publishers decided to broadcast parts of papers (e.g. tables, large data sets, pictures, figures) or whole journals online only, without printed versions. This causes some difficulties, particularly with effective publication of names of newly established syntaxa that had to be regarded as *nomina inedita* if the paper was entirely published on-line, or as *nomen nudum*, if the typus relevés were distributed only as on-line appendix (nevertheless it has a digital identifier). This is why the latest version of the code already provides the possibility of valid publishing of the syntaxon name in an electronic version of the paper, which does not appear as a printed copy. An electronic publication is accepted as effective on or after 1 January 2021 only in the form of Portable Document Format (PDF) that would bear either an International Standard Book Number (ISBN) or an International Standard Serial Number (ISSN) or a Digital Object Identifier (DOI) (Theurillat et al. 2021).

As a result of the phytosociological survey in alpine and subalpine belts of Pamir Alai and Tian Shan Mts. in Middle Asia, eleven new syntaxa of tall-forb vegetation were described with the provisional names (Nowak et al. 2020). We originally assumed that the paper will be published in 2021. However, due to the fast reviewing and editing process, the article was already published in 2020. Therefore, in agreement with the Editors of VCS, we decided that we will publish the new syntaxa as *nomina provisoria* and validate them in 2021 in accordance with the regulations of the ICPN.

The aim of this paper is to validate the provisional names of tall-forb syntaxa according to the current ICPN and to present the overview of the vegetation types that were described in the first paper devoted to tall-forbs of Middle Asia (Nowak et al. 2020).

Validation of syntaxa

The numbers of syntaxa refer to the synopsis at the end of the paper. Diagnostic taxa are provided in Nowak et al. (2020).

Forb rich mesophilous tall-forbs of the western Pamir-Alai Mts.

2.1. Alliance: *Ligulario thomsonii-Geranion regelii* Nowak et al. all. nov. hoc loco

Holotypus: *Eremuretum kaufmannii* Nowak et al. ass. nov. hoc loco (see below)

2.1.3. *Heracleetum lehmannianii* Nowak et al. ass. nov. hoc loco

Holotypus: 02 July 2017; 40.24556°N, 73.34028°E; 2157 m a.s.l.; aspect N; slope 3°; plot area 10 m^2; cover herb layer 90%; cover moss layer 3%; species richness: 28.

Herb layer: *Geranium regelii* 3, *Euphorbia lamprocarpa* 3, *Achillea millefolium* 2, *Carum carvi* 2, *Dactylis glomerata* 2, *Poa pratensis* 2, *Ranunculus brevirostris* 2, *Heracleum lehmannianum* 2, *Amoria repens* 1, *Convolvulus arvensis* 1, *Cousinia pseudarctium* 1, *Festuca rubra* 1, *Galium turkestanicum* 1, *Glycyrrhiza glabra* 1, *Hordeum turkestanicum* 1, *Ligularia thomsonii* 1, *Mentha asiatica* 1, *Nepeta cataria* 1, *Plantago lanceolata* 1, *Codonopsis clematidea* +, *Cynoglossum viridiflorum* +, *Erigeron allochrous* +, *Lithospermum officinale* +, *Polygonum coriarium* +, *Potentilla pedata* +, *Trifolium pratense* +, *Vicia tenuifolia* +. Moss layer: *Ceratodon purpureus* 1. [relevé number in Nowak et al. (2020): supplementary material 1: 40]

2.1.4. *Eremuretum kaufmannii* Nowak et al. ass. nov. hoc loco

Holotypus: 23 June 2014; 39.25722°N, 68.17833°E; 2836 m a.s.l.; aspect N; slope 25°; plot area 10 m^2; cover herb layer 95%; species richness: 17; species composition:

Herb layer: *Geranium regelii* 3, *Myosotis alpestris* 3, *Ligularia thomsonii* 2, *Poa urssulensis* 2, *Artemisia dracunculus* 1, *Astragalus saratagius* 1, *Carex turkestanica* 1, *Eremurus kaufmannii* 1, *Pedicularis grigorjevii* 1, *Tulipa ingens* 1, *Veronica rubrifolia* 1, *Alopecurus pratensis* +, *Astragalus nuciferus* +, *Myosotis micrantha* +, *Nepeta podostachys* +, *Oxytropis capusii* +, *Ziziphora pamiroalaica* +. [relevé number in Nowak et al. (2020): supplementary material 1: 127]

2.1.5. *Anthriscidetum glacialis* Nowak et al. ass. nov. hoc loco

Holotypus: 16 June 2019; 38.65522°N, 70.73306°E; 2762 m a.s.l.; aspect W; slope 10°; plot area 10 m^2; cover herb layer 100%; species richness: 33.

Herb layer: *Anthriscus glacialis* 3, *Geranium regelii* 2, *Ligularia thomsonii* 2, *Paeonia intermedia* 2, *Polygonum hissaricum* 2, *Astragalus aksuensis* 1, *Carex dimorphotheca* 1, *Crepis darvazica* 1, *Dactylis glomerata* 1, *Euphorbia glomerulans* 1, *Fritillaria regelii* 1, *Leonurus turkestanicus* 1, *Myosotis alpestris* 1, *Phleum pratense* 1, *Poa pratensis* 1, *Polygonum coriarium* 1, *Amoria repens* +, *Astragalus adpressipilosus* +, *Astragalus tecti-mundi* +, *Calamagrostis pseudophragmites* +, *Crocus korolkowii* +, *Euphorbia sarawschanica* +, *Galium aparine* +, *Ligularia alpigena* +, *Lolium cuneatum* +, *Medicago romanica* +, *Oberna wallichiana* +, *Pedicularis olgae* +, *Picris nuristanica* +, *Potentilla sericea* +, *Rumex nepalensis* +, *Scilla puschkinioides* +, *Taraxacum* sp. +. [relevé number in Nowak et al. (2020): supplementary material 1: 75]

Scree-like tall-forb communities of the eastern Irano-Turanian region

2.2. Alliance: *Rheion maximoviczii* Nowak et al. all. nov. hoc loco

Holotypus: *Eremuretum stenophyllido-comosi* Nowak et al. ass. nov. hoc loco (see below)

2.2.2. *Phlomoidetum kaufmannianae* Nowak et al. ass. nov. hoc loco

Holotypus: 29 May 2015; 39.20556°N, 67.81694°E; 1715 m a.s.l.; aspect W; slope 15°; plot area 10 m^2; cover herb layer 80%; cover moss layer 10%; species richness: 25.

Herb layer: *Phlomoides kaufmanniana* 3, *Papaver pavoninum* 2, *Anisantha tectorum* 1, *Artemisia rutifolia* 1, *Crambe kotschyana* 1, *Crepis pulchra* 1, *Ferula kokanica* 1, *Ferula ovina* 1, *Piptatherum kokanicum* 1, *Scandix stellata* 1, *Taeniatherum crinitum* 1, *Alcea nudiflora* +, *Alyssum calycinum* +, *Arabis recta* +, *Arenaria serpyllifolia* +, *Cerastium inflatum* +, *Erodium cicutarium* +, *Galium aparine*

+, *Galium spurium* +, *Geranium divaricatum* +, *Lappula consanguinea* +, *Perovskia virgata* +. Moss layer: *Bryum caespiticium* 1, *Pohlia nutans* 1, *Encalypta vulgaris* +. [relevé number in Nowak et al. (2020): supplementary material 1: 136]

2.2.5. *Eremuretum stenophyllido-comosi* Nowak et al. ass. nov. hoc loco

Holotypus: 22 May 2019; 38.70359°N, 70.46913°E; 1667 m a.s.l.; aspect SW; slope 40°; plot area 10 m2; cover shrub layer 15%; cover herb layer 70%; species richness 40.

Shrub layer: *Cerasus verrucosa* 2, *Rosa popovii* 2. Herb layer: *Eremurus comosus* 2, *Ferula kuhistanica* 2, *Prangos pabularia* 2, *Phlomoides lehmanniana* 1, *Vinca erecta* +, *Achillea biebersteinii* r, *Alcea nudiflora* r, *Anisantha sterilis* r, *Antonina debilis* r, *Asparagus neglectus* r, *Asperula setosa* r, *Astragalus macronyx* r, *Bromus lanceolatus* r, *Bunium persicum* r, *Callipeltis cucullaris* r, *Centaurea squarrosa* r, *Convolvulus arvensis* r, *Dianthus darvazicus* r, *Diarthron vesiculosum* r, *Dichasianthus subtilissimus* r, *Eremurus stenophyllus* r, *Euphorbia franchetii* r, *Euphorbia sarawschanica* r, *Galium spurium* r, *Hordeum bulbosum* r, *Lactuca tatarica* r, *Lallemantia royleana* r, *Lappula consanguinea* r, *Papaver litwinowii* r, *Poterium polygamum* r, *Rheum maximowiczii* r, *Rhinopetalum bucharicum* r, *Salvia sclarea* r, *Serratula chartacea* r, *Strigosella trichocarpa* r, *Tanacetum pseudachillea* r, *Taraxacum nuratavicum* r, *Veronica rubrifolia* r. [relevé number in Nowak et al. (2020): supplementary material 1: 186]

Dry tall-forb communities of the subhumid zone of the eastern Irano-Turanian region

2.3. Alliance: *Scabioso songaricae-Phlomoidion lehmannianae* Nowak et al. all. nov. hoc loco

Holotypus: *Phlomoido lehmannianae-Onobrychidetum grandis* Nowak et al. ass. nov. hoc loco (see below)

2.3.3. *Lathyretum mulkaki* Nowak et al. ass. nov. hoc loco

Holotypus: 17 June 2019; 38.58247°N, 70.76009°E; 2640 m a.s.l.; aspect SW; slope 25°; plot area 10 m^2; cover shrub layer 2%; cover herb layer 75%; species richness: 31.

Shrub layer: *Rosa ovczinnikovii* 1. Herb layer: *Ferula kokanica* 3, *Dictamnus angustifolius* 2, *Lathyrus mulkak* 2, *Senecio franchetii* 2, *Bunium persicum* 1, *Centaurea ruthenica* 1, *Delphinium batalinii* 1, *Nepeta ucranica* 1, *Poa bulbosa* 1, *Scabiosa songarica* 1, *Thalictrum kuhistanicum* 1, *Ziziphora pamiroalaica* 1, *Allium hissaricum* +, *Asperula setosa* +, *Colchicum luteum* +, *Cousinia pseudarctium* +, *Dianthus darvazicus* +, *Galium spurium* +, *Hypericum scabrum* +, *Iris darwasica* +, *Lappula occultata* +, *Lophanthus elegans* +, *Nepeta podostachys* +, *Origanum tyttanthum* +, *Phlomoides arctifolia* +, *Poa zaprjagajevii* +, *Pseudoclausia turkestanica* +, *Rhinopetalum bucharicum* +, *Thymus seravschanicus* +, *Vinca erecta* +. [relevé number in Nowak et al. (2020): supplementary material 1: 90]

2.3.7. *Eremuretum robusti* Nowak et al. ass. nov. hoc loco

Holotypus: 05 June 2015; 38.82000°N, 70.20778°E; 1436 m a.s.l.; plot area 10 m^2; cover herb layer 100%; species richness: 23.

Herb layer: *Phlomoides arctifolia* 3, *Vicia tenuifolia* 3, *Galium pamiroalaicum* 2, *Phlomoides lehmanniana* 2, *Eremurus comosus* 1, *Eremurus robustus* 1, *Eremurus stenophyllus* 1, *Hordeum bulbosum* 1, *Pimpinella peregrina* 1, *Poa bulbosa* 1, *Poa pratensis* 1, *Potentilla transcaspia* 1, *Poterium lasiocarpum* 1, *Prangos pabularia* 1, *Arenaria serpyllifolia* +, *Arum korolkowii* +, *Cousinia pseudarctium* +, *Galium aparine* +, *Orobanche sulphurea* +, *Plantago lanceolata* +, *Salvia sclarea* +, *Taraxacum* sp. +, *Torilis arvensis* +. [relevé number in Nowak et al. (2020): supplementary material 1: 179]

2.3.8. Phlomoido lehmannianae-Onobrychidetum grandis Nowak et al. ass. nov. hoc loco

Holotypus: 14 June 2019; 38.84710°N, 71.30857°E; 2519 m a.s.l.; aspect S; slope 30°; plot area 10 m^2; cover shrub layer 5%; cover herb layer 100%; species richness: 26.

Shrub layer: *Rosa ovczinnikovii* 2. Herb layer: *Ferula kuhistanica* 3, *Phlomoides lehmanniana* 3, *Prangos pabularia* 3, *Onobrychis grandis* 2, *Scabiosa songarica* 2, *Carex turkestanica* +, *Poa bulbosa* +, *Alyssum calycinum* r, *Arenaria serpyllifolia* r, *Asperula setosa* r, *Drepanocaryum sewerzowii* r, *Elaeosticta allioides* r, *Gentiana olivieri* r, *Handelia trichophylla* r, *Hypericum scabrum* r, *Lappula patula* r, *Neurotropis kotschyana* r, *Poa zaprjagajevii* r, *Polygonum paronychioides* r, *Polygonum polycnemoides* r, *Rochelia cardiosepala* r, *Serratula chartacea* r, *Stellaria alsinoides* r, *Taraxacum* sp. r, *Veronica cardiocarpa* r. [relevé number in Nowak et al. (2020): supplementary material 1: 242]

Synopsis of the tall-forb communities of the Pamir-Alai and western Tian Shan Mountains

This overview follows the classification scheme of Nowak et al. (2020).

Mesic mown and grazed subalpine meadows and pastures on fertile soils

Class: Molinio-Arrhenatheretea Tx. 1937

1. Order: *Poo alpinae-Trisetetalia* Ellmauer et Mucina 1993
    1.1. Alliance: *Poion alpinae* Gams ex Oberd. 1950
        1.1.1. Community of *Phlomoides oreophila*

Irano-Turanian thermophilous, mesic tall-forb communities of the western Pamir-Alai and Tian Shan Mountains

Class: *Prangetea ulopterae* Klein 1987.

Forb rich mesophilious tall-forb communities of the western Pamir-Alai Mountains

    2.1. Alliance: *Ligulario thomsonii-Geranion regelii* Nowak et al. 2021 all. nov.

- 2.1.1. Community of *Allium hymenorhizum*
- 2.1.2. *Feruletum sumbuli* Nowak et al. 2015
- 2.1.3. *Heracleetum lehmannianii* Nowak et al. 2021 ass. nov.
- 2.1.4. *Eremuretum kaufmannii* Nowak et al. ass. 2021 ass. nov.
- 2.1.5. *Anthriscidetum glacialis* Nowak et al. 2021 ass. nov.

Scree-like tall-forb communities of the eastern Irano-Turanian region

- 2.2. Alliance: *Rheion maximoviczii* Nowak et al. all. 2021 all. nov.
  - 2.2.1. Community of *Cousinia batalinii* and *Euphorbia pamirica*
  - 2.2.2. *Phlomoidetum kaufmannianae* Nowak et al. 2021 ass. nov.
  - 2.2.3. *Phlomoidetum tadshikistanicae* Nowak et al. 2016 nom. corr. (= *Eremostachyetum tadschikistanicae* Nowak et al. 2016)
  - 2.2.4. Community of *Senecio saposhnikovii*
  - 2.2.5. *Eremuretum stenophyllido-comosi* Nowak et al. 2021 ass. nov.

Dry tall-forb communities of the subhumid zone of the eastern Irano-Turanian region

- 2.3. Alliance: *Scabioso songaricae-Phlomoidion lehmannianae* Nowak et al. 2021 all. nov.
  - 2.3.1. Community of *Inula macrophylla*
  - 2.3.2. *Stipetum margelanicae* Nowak et al. 2016
  - 2.3.3. *Lathyretum mulkaki* Nowak et al. 2021 ass. nov.
  - 2.3.4. *Potentillo orientalis-Eremuretum fusci* Świerszcz et al. 2020
  - 2.3.5. *Hordeo bulbosi-Astragaletum retamocarpi* Świerszcz et al. 2020
  - 2.3.6. Community of *Ferula kuhistanica*
  - 2.3.7. *Eremuretum robusti* Nowak et al. 2021 ass. nov.
  - 2.3.8. *Phlomoido lehmannianae-Onobrychidetum grandis* Nowak et al. 2021 ass. nov.

Author contributions

A.N. led the writing, while all authors critically revised the final manuscript.

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VEGETATION CLASSIFICATION AND SURVEY

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RESEARCH PAPER

CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC

Grasslands of Navarre (Spain), focusing on the *Festuco-Brometea*: classification, hierarchical expert system and characterisation

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Abstract

Aims: To clarify the syntaxonomic position of the grasslands in Navarre, with special focus on the dry grasslands, and to characterise the resulting syntaxonomic units in terms of diagnostic species and ecological conditions. **Study area:** Navarre (northern Spain). **Methods:** We sampled 119 plots of 10 m^2 following the standardised EDGG methodology and analysed them together with 839 plots of similar size recorded in the 1990. For the classification, we used the modified TWINSPAN algorithm, complemented by the determination of diagnostic species with phi coefficients of association, which led to the creation of an expert system. We conducted these steps in a hierarchical manner for each syntaxonomic rank. We visualised the position of the syntaxa along environmental gradients by means of NMDS. Species richness, and structural and ecological characteristics of the syntaxa were compared by ANOVAs. **Results:** We could clearly identify five phytosociological classes: *Lygeo-Stipetea, Festuco-Brometea, Molinio-Arrhenatheretea, Nardetea strictae,* and *Elyno-Seslerietea*. Within the *Festuco-Brometea* a xeric and a meso-xeric order could be distinguished, with two alliances each, and eight associations in total: *Thymelaeo-Aphyllanthetum, Jurineo-Festucetum, Helianthemo-Koelerietum, Prunello-Plantaginetum, Carduncello-Brachypodietum, Helictotricho-Seslerietum, Calamintho-Seselietum* and *Carici-Teucrietum.* **Conclusions:** The combination of numerical methods allowed a consistent and more objective classification of grassland types in Navarre than previous approaches. At the association level, we could largely reproduce the units previously described with traditional phytosociological methods. By contrast, at higher syntaxonomic level, our analyses suggest significant modifications. Most importantly, a major part of the units traditionally included in the *Festuco-Ononidetea* seem to fall within the *Festuco-Brometea*. We could show that bryophytes and lichens are core elements of these grasslands and particularly the Mediterranean ones of *Lygeo-Stipetea*, both in terms of biodiversity and of diagnostic species. We conclude that the combination of our different numerical methods is promising for deriving more objective and reproducible delimitations of syntaxa in a hierarchical manner.

Taxonomic references: Euro+Med (2006–2021) for vascular plants, Hodges et al. (2020) for bryophytes and The British Lichen Society (2021) for lichens, except for *Endocarpon loscosii, Heppia lutosa, Psora saviczii* and *P. vallesiaca*, which follow Nimis and Martellos (2021), and *Buellia zoharyi, Fulgensia poeltii, Lichenochora clauzadei* and *Toninia massata*, which follow Llimona et al. (2001).

Syntaxonomic reference: Mucina et al. (2016), except for those syntaxa specifically treated here and given with authorities.

Abbreviations: ANOVA = analysis of variance; EDGG = Eurasian Dry Grassland Group; NMDS: non-metric multidimensional scaling; TWINSPAN = Two-Way Indicator Species Analysis.

Keywords

diagnostic species, electronic expert system, *Elyno-Seslerietea*, *Festuco-Brometea*, *Festuco-Ononidetea*, grassland, *Lygeo-Stipetea*, modified TWINSPAN, *Molinio-Arrhenatheretea*, *Nardetea strictae*, Navarre, vegetation classification

Introduction

Grasslands represent one of the most extensive and diverse formations of the world, yet undervalued and under-researched. Grasslands are spontaneously occurring herbaceous vegetation types that are mostly dominated by grasses (*Poaceae*) or other graminoids (*Cyperaceae, Juncaceae*) and have a relatively high herb-layer cover (usually > 10%), while woody species (dwarf shrubs, shrubs and trees), if present at all, have a significantly lower cover than the herbs (Dengler et al. 2020a). Extending in all continents except Antarctica, grasslands host thousands of habitat specialist species, support agricultural production, people's livelihoods based on traditional and indigenous lifestyles, and several other ecosystem services such as pollination for crops and water regulation (Bengtsson et al. 2019). Palaearctic grasslands represent the richest habitats for vascular plants at small spatial scales (Dengler et al. 2020a). Temperate grasslands are, however, among the most threatened biomes of the world with the highest proportion of habitat conversion but lowest protection (Hoekstra et al. 2005).

Since the second half of the 20th century, European grasslands have experienced two extremes of the land-use gradient, and both resulted in the loss of grassland biodiversity (Török and Dengler 2018), which is specifically important in Western Europe, were grasslands are mostly secondary, originating from human land use (Boch et al. 2020): (i) intensification of land use or conversion to croplands in productive areas, and (ii) abandonment of marginal lands resulted in the regeneration of forest and shrublands, both processes leading to the loss of grassland-specific biodiversity (Dengler and Tischew 2018). It is necessary to understand biodiversity patterns of grasslands and how they relate to land use to be able to design conservation and management actions. This understanding requires the harmonisation and standardisation of grassland classification that leads to a consistent syntaxonomy at the European level and therefore, then will increase the usefulness of vegetation typologies for conservation and management (Willner et al. 2017).

During the last decades, a great effort on grassland classification has been made, based on large vegetation-plot databases and numerical analysis in several countries or regions across Europe to delimit and define the different syntaxonomic units. Several studies have been developed at a regional, up to continental scale on dry-grasslands (Illyés et al. 2007; Vassilev et al. 2012; Aćić et al. 2015) or mesic and wet grasslands (Kuzemko 2016; Rodríguez-Rojo et al. 2017; Škvorc et al. 2020). The broadest studies regarding syntaxonomic scope and geographic extent are focused on dry and semi-dry grasslands (Willner et al. 2017, 2019). As a result, great advances to define the classes *Festuco-Brometea, Molinio-Arrhenatheretea, Nardetea strictae* and *Koelerio-Corynephoretea* in temperate Europe have been made. However, grasslands of Southern Europe are still not well-known and the distinction of the Mediterranean grasslands from those of temperate Europe is not clear, especially along the submediterranean areas that, although broadly classified as temperate, still exhibit the "Mediterranean" sharp drop in summer precipitation levels (Apostolova et al. 2014; Aćić et al. 2015).

Phytosociological studies in the Iberian Peninsula have been broadly developed in the last century and were synthesized in the syntaxonomic checklist of Spain (Rivas-Martínez 2011). More recently, some reviews based on large vegetation databases aimed to obtain a consistent grassland classification (Rodríguez-Rojo and Fernández-González 2014; Rodríguez-Rojo et al. 2014; García-Madrid et al. 2016; Gavilán et al. 2017). Nevertheless, there is a lack of studies on the typical Mediterranean grassland and low scrub classes *Festuco hystricis-Ononidetea striatae, Ononido-Rosmarinetea* and *Lygeo sparti-Stipetea tenacissimae* (but see Marcenò et al. 2019). Moreover, in the submediterranean areas, these Mediterranean grasslands are in touch (across elevational or edaphic gradients) with temperate grasslands placed in the class *Festuco-Brometea*, but their boundaries are not clearly defined (Cancellieri et al. 2020). Studies of such transitional areas are necessary to discriminate between different grassland types and define the diagnostic species that differentiate these classes.

Navarre region, located in northern Iberian Peninsula, is a bioclimatically diverse region where Alpine, Atlantic and Mediterranean biogeographical areas converge. The long history of grazing and management throughout the area has resulted in the broad spread of grasslands. The region has an important elevational and precipitation gradient that allows the coexistence of dry and mesic grasslands as well as alpine and Mediterranean semi-arid communities (Berastegi 2013). This makes this region very suitable for studying the diversity of grassland communities that are driven by ecological and management gradients. Navarre is also an interesting area for the challenge of drawing the boundaries between the temperate and Mediterranean grasslands and establishing their valid classification. Many phytosociological studies have been carried out in Navarran grasslands (Darquistade et al. 2004; Berastegi et al. 2005; Berastegi et al. 2010; Berastegi 2013). Nevertheless, only a few of these studies have applied numerical methods (Peralta and Olano 2001), and none of them included bryophytes and lichens, although these taxonomic groups may become an important component of several grassland types (Biurrun et al. 2021).

According to Berastegi (2013), 69 grassland associations or communities can be recognised in Navarre, grouped in 32 alliances and 11 phytosociological classes. In the high-elevation areas of Pyrenees, communities of *Carici rupestris-Kobresietea bellardii, Juncetea trifidi,* and *Elyno-Seslerietea* coexist; in the temperate zone, grasslands of *Nardetea strictae, Sedo-Scleranthetea, Molinio-Arrhenetheretea* and *Festuco-Brometea,* and in Mediterranean areas communities of *Festuco-Ononidetea, Lygeo-Stipetea, Poetea bulbosae* and *Stipo-Trachynietea* (Berastegi 2013). Although some of these classes are well defined floristically and biogeographically, those occurring in submediterranean areas need clarification as many species of different floristic origin coexist in the same area. In these cases, the occurrence of temperate or Mediterranean grasslands is driven by edaphic and microclimatic conditions. There are also some interpretation issues, such as the inclusion of some Mediterranean communities in *Festuco-Ononidetea* or *Ononido-Rosmarinetea* (Berastegi et al. 2005; Berastegi 2013). All this led to the organisation of the 7th Field Workshop (Biurrun et al. 2014) to sample by means of biodiversity plots (Dengler et al. 2016a) all types of grasslands along latitudinal and elevational gradients. The expedition ran from subalpine areas in Pyrenees to semi-arid Mediterranean ones where information on bryophytes and lichens as well as vascular plants was recorded.

The high grassland diversity in Navarre reflects the richness of grassland habitats of interest for European Community (European Commission 2013). Regarding the habitat types included in the Annex I of the Habitat Directive, nine of those belonging to natural and semi-natural grassland formations are present in Navarre (Peralta et al. 2018). Phytosociological classifications of formally defined syntaxa were also used to interpret the types in the Habitats Directive, so determining diagnostic species for different types of grassland is necessary to interpret the habitats and to assess their conservation status (Tsiripidis et al. 2018). However, the definition of these habitats is sometimes ambiguous and there are still some inconsistent interpretations between countries and regions, which impede effective conservation of grasslands habitats (Evans 2013). Rodriguez-Rojo et al. (2020) aimed to develop an expert system for semi-natural grassland habitat identification through the analysis of their characteristic species, but Mediterranean grasslands were not included in the analysis. The delimitation and definition of diagnostic species of the Mediterranean grassland classes would help to properly interpret the habitat types that would lead to their adequate management and protection.

The large amount of data available related to grassland in the region of Navarre and its strategic geographical position where different climatic conditions converge provide a unique opportunity to clarify grassland syntaxonomy, especially those from submediterranean areas. More specifically, we aim to 1) Identify the main grassland types in Navarre using numerical and reproducible methods, 2) Compare our results with existing traditional classifications at the level of alliance or association 3) Define the diagnostic species of syntaxa including bryophytes and lichens. 4) Characterise and differentiate associations with regard to topographic, edaphic and climatic variables.

Study area

Navarre is a territory of 10,391 km^2 located in the north-central part of the Iberian Peninsula. There is a wide elevational range in the region, from 25 m a.s.l. in Endarlatsa, 15 km from the Cantabrian Sea in the north, to 2,466 m a.s.l. in the Mesa de los Tres Reyes in the western Pyrenees. The bioclimate is temperate in the northern part of the region, and Mediterranean in the south, with large submediterranean areas in the central part (Loidi and Báscones 2006; Peralta et al. 2018). As regards the thermic and humidity types proposed in the bioclimatic classification of Rivas-Martínez (Rivas-Martínez 1996), mesotemperate (colline), supratemperate (montane), orotemperate (subalpine) and cryorotemperate (alpine) thermotypes can be distinguished in the temperate zone, while in the Mediterranean areas only the mesomediterranean and the supramediterranean occur. There is a high ombrotype diversity, from the semiarid in the Ebro valley to the ultrahyperhumid in the northern mountains (Peralta et al. 2018). The temperate-climate area is included in the Atlantic and Alpine regions. The western part has a stronger Atlantic influence (Atlantic region) while the eastern area is more influenced by the Pyrenees (Alpine region). The Mediterrranean-climate area is included in the Mediterranean region.

Several types of deciduous forests prevail in the temperate zone, where secondary grasslands, mainly mesic and meso-xeric grasslands, are an important component of the landscape. Sclerophyllous woodlands dominate in the Mediterranean areas of southern Navarre, with Mediterranean grasslands and garrigues as secondary vegetation. In the Pyrenees, alpine grasslands and scrubs occur above 1,700 m a.s.l., in the subalpine belt mostly as secondary vegetation replacing *Pinus uncinata* woodlands, and as potential natural vegetation in the alpine belt, above ca. 2,100 m a.s.l. (Loidi and Báscones 2006).

Geological diversity also has a great influence on the vegetation. Shales, quartzites or granites from the Palaeozoic are common in the northern area of Navarre, mostly in the Atlantic region. Red sandstones and conglomerates from the Triassic surround these Palaeozoic rocks. Limestones, marls and dolomites from the Jurassic and Cretaceous period, and also limestones, marls, flysch substrates, but also calcarenites from the continental Tertiary are dominant in all of the central area of Navarre. From the continental Tertiary, sandstones, clays, slimes, but also limestones and gypsum are dominant in the south of Navarre, mostly in the Mediterranean region (Del Valle Lersundi et al. 1997).

Methods

Vegetation data

We took 119 10-m² plots sampled following the standard EDGG methodology (Dengler et al. 2016a) during the EDGG Field Workshop in Navarre, between 16th and 23rd of June 2014 (Biurrun et al. 2014). The sampling focused on dry and semi-dry grasslands but covered the full climatic/elevation gradient in the region. All vascular plants as well and terricolous bryophytes and lichens, and their percentage cover were recorded. Additionally, an extensive set of structural and site variables were recorded (for all available variables and the underlying methodology, see Suppl. material 1).

Furthermore, we included those 839 vegetation plots from Berastegi (2013), recorded between 1996 and 1999, that had a plot size between 5 and 25 m². We excluded smaller and larger plots because otherwise serious distortion of species constancies and fidelities would be expected (Dengler et al. 2009). In these plots, only vascular plants were recorded, with a 7-step variant of the Braun-Blanquet scale (Braun-Blanquet 1932). Apart from coordinates and elevation, no other structural or site variables are available for these data.

Although these plots from the additional dataset were evenly distributed across the region and all grassland types, we wish to highlight that four of the 11 classes represented in Berastegi (2013) were only documented by fewer than 10 relevés. Two of them normally occur as small patches in mosaics with grasslands of other classes (*Stipo-Trachynietea* and *Poetea bulbosae)* and the other two are very rare in Navarre (*Carici-Kobresietea* and *Caricetea curvulae)*. Another important aspect of this dataset is that the classes *Festuco-Ononidetea* and *Ononido-Rosmarinetea* have been only partially included. The former one encompasses oro- and supramediterranean grasslands and shrublands (Mucina et al. 2016), but Berastegi (2013) only considered the dry grasslands of the associations *Carici-Teucrietum pyrenaici*, *Helianthemo-Koelerietum vallesianae* and *Helictotricho-Seslerietum hispanicae* from the order *Ononidetalia striatae* (and thus excluded dwarf-shrub communities), and those belonging to the order *Festuco-Poetalia*. The *Ononido-Rosmarinetea*, and specifically the order *Rosmarinetalia*, are defined as Mediterranean scrub (tomillar, espleguer, romeral, garrigue) on base-rich substrates (Mucina et al. 2016). In this study we only considered the association *Thymelaeo-Aphyllanthetum monspeliensis,* described from the central part of Navarre (Braun-Blanquet 1966) and characterised by dwarf chamaephytes of the genera *Thymus*, *Helianthemum, Fumana* and *Teucrium* among others. Berastegi (2013) only sampled stands of the subassociation *brachypodietosum retusi,* dominated by hard-leaved grasses (*Brachypodium retusum, Helictochloa bromoides*) and other hemicryptophytes such as *Bromopsis erecta* subsp. *erecta, Carex humilis, Helictochloa pratensis* subsp. *iberica, Sanguisorba minor* aggr. and *Carex flacca* subsp. *flacca*.

The combination of both datasets resulted in a total of 958 vegetation plots. The data from EDGG expedition are stored in and available from the GrassPlot database (Dengler et al. 2018a; Biurrun et al. 2019; https://edgg.org/databases/GrassPlot) as dataset ES_A. The data from Berastegi (2013) are stored in the Vegetation-Plot Database of the University of the Basque Country (BIOVEG) (Biurrun et al. 2012), which is available in the European Vegetation Archive (Chytrý et al. 2016) and the Global Vegetation Database sPlot (Bruelheide et al. 2019) as dataset EU-00-011. All plots are provided in Suppl. materials 1 (header data) and 2 (composition data).

Soil analyses

Soil samples were collected in each EDGG plot. Samples were taken with a hand shovel from the uppermost 5–10 cm at five random points within the plot, merged in a mixed sample and air-dried. The coarse fragment of the samples was determined by dry screening (Ø > 2 mm) and soil texture was determined by the Bouyoucos hydrometer method (Gee and Bauder 1986). The acidity and electrical conductivity (EC) were determined in air-dried soil samples dissolved in pure water using pH meter and EC meter (Thomas 1996). Lime content was determined by a Scheibler calcimeter. Soil organic matter content was determined by Walkley-Black wet combustion.

Climatic data

We retrieved climatic data from CHELSA dataset version 1.2 (Karger et al. 2017) at 30 arc sec resolution. As climatic parameters, we selected mean annual temperature, annual precipitation and Mediterranity Index: Med = Eva / Prec, where Eva is mean potential evapotranspiration during summer months, and Prec is sum of precipitation during the summer months (Rivas-Martínez 1996).

Data preparation for classification analyses

Before numerical analysis, we unified species taxonomy and nomenclature. Vascular plants were named according to Euro+Med PlantBase (Euro+Med 2006–2021), bryophytes according to Hodges et al. (2020) and lichens according to The British Lichen Society (2021), with the exception of those taxa not included there: *Endocarpon loscosii*, *Heppia lutosa*, *Psora saviczii* and *P. vallesiaca* follow Nimis and Martellos (2021), while *Buellia zoharyi*, *Fulgensia poeltii*, *Lichenochora clauzadei* and *Toninia massata* follow Llimona et al. (2001). We merged several groups of closely related species that cannot always be determined to species level into aggregates (aggr.), whose definitions are provided in Suppl. material 3. Species recognised only at the genus level were deleted, and subspecies that were not always recognised by the authors were combined into species. Bryophytes and lichens were removed for the initial unsupervised classification, but re-integrated later (see below) since they were only recorded in a subset of relevés.

Numerical classification and expert system development

For the initial unsupervised classifications, we used the modified version of TWINSPAN (Roleček et al. 2009) implemented in JUICE (Tichý 2002) with the three pseudospecies cut levels at 0%, 5% and 15%, and average Sørensen dissimilarity as a measure of cluster heterogeneity. Species with only one occurrence were excluded. TWINSPAN analysis resulted in ten groups as the best solution that corresponded very closely to the phytosociological classes of grasslands represented in the study area according to a previous study (Berastegi 2013).

In the case of very large datasets, classification is highly dependent on the selection of attributes (species) used. The more attributes used, the data become more scattered (Visa et al. 2011). In this context, the selection of diagnostic species that can be used in the classification of vegetation is one of the challenges to be addressed. Here we used confusion matrices to select relevés that matched both supervised and unsupervised classifications for subsequent selection of diagnostic species. These species were used for further classification (expert system) of the entire dataset, so that misclassified relevés were reorganised appropriately.

We created the confusion matrix comparing the original (expert-based) and new numerical (unsupervised) classifications (see Suppl. material 4). We selected those relevés that were consistently classified in both approaches as a sort of consensus core of the respective vegetation units. Based on these plots (n = 639), we determined the diagnostic species for the classes (see below). The list of diagnostic species was then translated into an expert system implemented in JUICE (Tichý 2002), with the principle that each plot is assigned to the class whose diagnostic species prevail, based on the sum of square root transformed cover values (as for example widely implemented in Chytrý et al. (2020)). This approach in its current implementation in JUICE leaves a few plots unassigned if they have exactly the same score of diagnostic species for two classes. After applying the so-developed expert system to the whole dataset, we then determined the diagnostic species of the resulting classes again.

In the case of the classes, we found that three of the traditional classes shared a significant number of frequent species and therefore, we decided to merge them and rerun the previous steps to achieve the final expert system and the final set of diagnostic species of classes. We continued then, with the same approach, with our main target class *Festuco-Brometea* to search for the most plausible division into orders. Criteria were based on how well the resulting units were floristically and ecologically characterised and how closely they matched the general syntaxonomic system of Europe. Next, we continued in each of the resulting orders to find an appropriate division into alliances and finally for each of the alliances we analysed the appropriate subdivision into associations separately. For each syntaxonomic level and cluster we therefore followed the procedure of: (1) running modified TWINSPAN, (2) identifying a reasonable number of syntaxa of the next lower level and (3) determining their diagnostic species. In the case of order and alliance we selected the relevés that matched both the expert and TWINSPAN classification, but for associations we used only the TWINSPAN results, (4) translating these into an expert system, (5) appling this expert system to the data including the type relevés of all associations included in *Festuco-Brometea* (details provided in Suppl. material 5) and (6) re-determining the diagnostic species based on the group assignment resulting from the expert system. Accordingly, we can then present a hierarchical expert system in JUICE syntax that allows the standardised reproduction of our classification and its application on new relevés (Suppl. material 6–12).

We followed the fourth edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021) for the nomenclature of plant communities.

We determined diagnostic species using the phi coefficient of association (Chytrý et al. 2002) standardised to equal plot number per cluster (Tichý and Chytrý 2006). We also determined the diagnostic species in a hierarchical fashion, corresponding to the hierarchical nature of syntaxonomy (Dengler et al. 2008; Theurillat et al. 2021) and to our hierarchical expert system. Since this approach is not implemented in JUICE (Tichý 2002) thus far, we carried out all calculations in Microsoft Excel, which also allowed the production of formatted tables. We acknowledge that this approach has the potential shortcoming of not being able to filter for statistical significance with Fisher's exact test as is possible in JUICE. However, given the relatively large number of plots per unit and the relatively high thresholds for phi that we applied, the number of non-significant diagnostic species should be negligible. We considered species as diagnostic when phi ≥ 0.25 and as highly diagnostic when phi ≥ 0.5. While phi-values refer to the concentration of a species in one syntaxon compared to the rest of the dataset as a whole, in fact the syntaxonomically relevant aspect is the comparison to the syntaxon of the same rank where the species reaches the next-higher constancy/fidelity (see Dengler 2003; Dengler et al. 2005, 2018b; Tsiripidis et al. 2009). Therefore, for species to be considered diagnostic, we also required that their phi-value was at least 0.25 higher than in the syntaxon of the same rank with the next-higher phi-value. If all syntaxa of a certain rank were ordered by decreasing phi-values of a certain species, the species was considered diagnostic for the first syntaxa prior to a decrease in phi-values ≥ 0.25. If no such decrease occurred or if the maximum phi-value was below 0.25, the species was not considered diagnostic anywhere. We applied these calculations for all four syntaxonomic levels and identified a species as diagnostic to the level where it reached its maximum phi-value, provided all aforementioned criteria were fulfilled. Last but not least, we also determined diagnostic species for the bryophytes and lichens, which had not been used in the set-up of the system, by adding their data again post-hoc. Importantly, here the constancy values were calculated based on the smaller sample of plots from the EDGG Field Workshop only, but otherwise in the same way.

NMDS ordination

To visualize the gradient of vascular plant species composition across the vegetation types, we used non-metric multidimensional scaling (NMDS; McCune and Grace 2002) calculated in the Canoco 5 software (ter Braak and Šmilauer 2012). Prior to the calculation, the Braun-Blanquet scale was transformed to mean percentage cover values. Bray-Curtis dissimilarity was calculated on the log-transformed cover of each vascular plant species in each plot. The sample configuration from non-metric multidimensional scaling (NMDS) was centred and rotated by principal component analysis. Elevation and three bioclimatic variables (mean annual temperature, annual precipitation and Mediterraneity Index) were used as supplementary variables. The whole data set (containing 958 samples) as well as the data subset of relevés included in the *Festuco-Brometea* (containing 339 samples) were analysed.

Analyses of differences between syntaxa

Differences among classes regarding structural, topographic, bioclimatic and soil variables, as well as regarding richness values, were analysed by means of analyses of variance (ANOVAs) in the R programming language (R Core Team 2021). The same was done with the *Festuco-Brometea* subset to compare associations and alliances. Tukey's post-hoc test was applied following a significant ANOVA ($p < 0.05$). We checked whether the assumptions of linear models (homoscedasticity and normality of residuals) were severely violated by visual inspection of the boxplots, and since this was not the case, we stuck to the linear model (ANOVA) (see Quinn and Keough 2002).

Results

Subdivision of all grasslands into classes

At the level of ten groups, the TWINSPAN analysis resulted in a division of the data where the classification into seven classes proposed by Berastegi (2013) can be recognised to a large extent (Figure 1). We then reduced the hierarchy of these groups into eight clusters. Clusters 1 and 2 were related to *Elyno-Seslerietea* and *Festuco-Ononidetea* classes, respectively. Cluster 3 grouped relevés from *Lygeo-Stipetea* and *Stipo-Trachynietea* classes. Cluster 4 was composed mostly of the relevés of the association *Elytrigio campestris-Brachypodietum phoenicoidis,* traditionally assigned to the order *Brachypodietalia phoenicoidis* in *Festuco-Brometea*. Clusters 5 and 6 were related to *Ononido-Rosmarinetea* and *Festuco-Brometea*, respectively. Groups 7, 8 and 9 corresponded to three orders of *Molinio-Arrhenatheretea* (*Holoschoenetalia, Molinietalia* and *Arrhenatheretalia*), so we grouped them in Cluster 7. Cluster 8 grouped relevés belonging to the classes *Nardetea strictae* and *Sedo-Scleranthetea*.

The synoptic table with the diagnostic species for each cluster of the modified TWINSPAN analysis is presented in Suppl. material 13 (cluster 4 was not considered as it was related only to one association). In this table, we can see that the relevés in clusters 2 and 5 related to the classes *Festuco-Ononidetea* and *Ononido-Rosmarinetea* presented many diagnostic species considered characteristic of *Festuco-Brometea* (*Bromopsis erecta* subsp. *erecta, Carex humilis, Carthamus mitissimus, Potentilla tabernaemontani*). Therefore, these two groups were joined to cluster 6, related to the *Festuco-Brometea,* for subsequent analyses. We finally recognised five groups corresponding to the following classes of grasslands in Navarre: LYG (*Lygeo-Stipetea*), FES (*Festuco-Brometea*), MOL (*Molinio-Arrhenatheretea*), NAR (*Nardetea strictae*) and SES (*Elyno-Seslerietea*).

The relationship between the previous expert-based classification (Berastegi 2013) and our classification of five classes based on the expert system analysis is displayed in

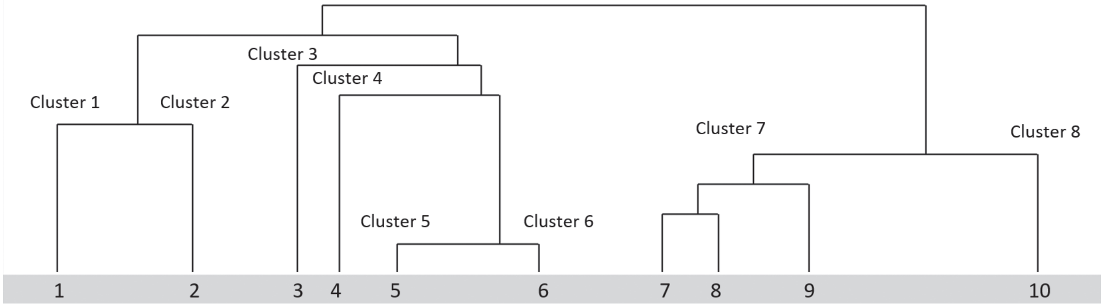

Figure 1. Dendogram of the modified TWINSPAN classification of the 958 grassland relevés from Navarre into ten groups gathered in eight clusters.

Table 1. Relationship between the original classification and the expert system classification. In each column the number of relevés and the proportion related to the total of relevés belonging to the original classification (in brackets) that match the expert system are shown.

Syntaxonomic classes (original classification)	**Expert System classification**						**Nº rel. per class**
	LYG (%)	**FES (%)**	**MOL (%)**	**NAR (%)**	**SES (%)**	**Non-classified**	
Lygeo–Stipetea	25 (96)	1 (4)					26
Stipo–Trachynietea	10 (100)						10
Ononido–Rosmarinetea	5 (13)	33 (87)					38
Festuco–Brometea	8 (4)	131 (61)	34 (16)	40 (19)		2	215
Festuco–Ononidetea		158 (75)	1 (< 1)	2 (1)	48 (23)	1	210
Molinio–Arrhenatheretea		13 (6)	185 (86)	17 (8)		1	216
Nardetea strictae				149 (96)	5 (3)	1	155
Sedo–Scleranthetea				11 (85)	1 (8)	1	13
Elyno–Seslerietea		1 (2)		3 (5)	58 (93)	2	64
Carici–Kobresietea					2		2
Caricetea curvulae				1			1
Poetea bulbosae	6	2					8
Nº relevés per group	54	339	220	223	114	8	958

Table 1. The proportion of relevés matching in both classifications (in brackets) ranged between 60 and 100%. In FES the expert system gathered most of the relevés previously classified in *Festuco-Brometea*, *Festuco-Ononidetea* and *Ononido-Rosmarineta*. However, 35% of relevés previously classified in *Festuco-Brometea* were distributed among MOL and NAR. From the class *Festuco-Ononidetea* 23% relevés were classified in SES and 13% relevés from *Ononido-Rosmarinetea* were included into LYG. Only eight relevés (0,8%) remained unclassified.

LYG – *Lygeo-Stipetea* (Figure 2D)

The expert system analysis included in this group LYG most relevés that were originally classified in the class *Lygeo-Stipetea*. Communities dominated by therophytes of *Stipo-Trachynietea* and those from *Poetea bulbosa*e were also classified in this group, as they shared many annual species: *Bombycilaena erecta*, *Catapodium rigidum, Linum strictum, Trachynia distachya,* etc. LYG also includes some relevés from the subassociation *Thymelaeo-Aphyllanthetum brachypodietosum retusi* of the class *Ononido-Rosmarinetea* and from the association *Elytrigio campestris-Brachypodietum phoenicoidis* of *Festuco-Brometea*.

These communities are characterised by the presence of hard-leaved grasses such as *Brachypodium retusum, Helictochloa bromoides, Lygeum spartum* and *Stipa parviflora* and dwarf chamaephytes as well as many therophytes (Table 2). They are distributed throughout the southern part of Navarre, with a typical Mediterranean climate, although they also occur in the lower elevations of the central area, always in the mesomediterranean thermotype (Figure 3).

FES – *Festuco-Brometea*

After applying the expert system most relevés of *Festuca-Brometea*, *Festuco-Ononidetea* and *Ononido-Rosmarinetea* were classified in the FES group (Table 1). The diagnostic species for this group with highest fidelity index were *Bromopsis erecta* subsp. *erecta, Carthamus mitissimus, Carex humilis, Potentilla tabernaemontani, Coronilla minima, Festuca rectifolia* and *Seseli montanum* subsp. *montanum* (Table 2).

This group (FES) occupies the transition areas between the Pyrenees and Cantabrian mountains and the Mediterranean region (Figure 3). These communities grow at moderate elevations, mostly in the upper colline and montane belts, and with average precipitation and temperatures of 1,230 mm and 10 °C, respectively (Table 3).

Table 2. Abridged constancy table of the five grassland classes considered in this study. Values are percentage constancies, and species are ordered by decreasing phi-values in the respective syntaxon, respectively by decreasing overall constancy for non-diagnostic species. In the upper part vascular plants are given, in the lower part bryophytes and lichens, whose constancies and fidelities have been calculated based only on the plots of the EDGG Field Workshop. In the table, the 15 vascular plant taxa and the eight non-vascular plant taxa with the highest fidelity in a class are shown, plus all taxa that are diagnostic for multiple classes and all taxa with at least 10% overall constancy. Diagnostic species (phi ≥ 0.25) are highlighted in grey, highly diagnostic species (phi ≥ 0.5) in dark grey. The complete constancy table combined with the table of the underlying 958 vegetation plots is given in Suppl. material 2.

Class	All	LYG	FES	MOL	NAR	SES
# plots	958	54	339	220	223	114
# plots with bryophyte/lichen treatment	119	19	64	8	11	17
Class LYG (47 taxa)						
Linum strictum	3.9	52	2	1	.	.
Brachypodium retusum	8.4	52	14	1	.	.
Catapodium rigidum	4.3	43	5	1	.	.
Lygeum spartum	2.0	33	<1	.	.	.
Asterolinon linum-stellatum	2.2	33	1	<1	.	.
Artemisia herba-alba	1.8	31	.	.	.	.
Thymus vulgaris subsp. *vulgaris*	9.9	50	20	.	.	.
Polygala monspeliaca	2.4	33	1	.	.	.
Trachynia distachya	3.0	35	2	<1	.	1
Teucrium capitatum subsp. *capitatum*	4.3	35	6	.	.	.
Bombycilaena erecta	2.8	31	3	.	.	.
Euphorbia exigua	3.9	33	5	<1	.	.
Plantago lagopus subsp. *lagopus*	1.5	26	.	.	.	.
Plantago albicans	1.5	26	.	.	.	.
Atractylis humilis	1.8	24	1	.	.	.
[...]						
Class FES (21 taxa)						
Bromopsis erecta subsp. *erecta*	27.1	2	65	6	5	11
Carthamus mitissimus	19.4	7	51	1	3	2
Carex humilis	14.5	4	40	.	.	1
Potentilla tabernaemontani	19.5	6	48	1	4	10
Coronilla minima	14.2	7	38	<1	.	1
Festuca rectifolia	17.7	4	42	.	2	15
Seseli montanum subsp. *montanum*	14.1	2	33	1	6	4
Helictochloa pratensis subsp. *iberica*	20.9	2	46	<1	4	30
Geum sylvaticum	6.8	.	18	.	1	1
Scabiosa columbaria subsp. *columbaria*	11.1	.	25	4	3	5
Medicago lupulina	20.1	6	39	18	3	8
Onobrychis conferta subsp. *hispanica*	6.3	2	17	1	.	.
Sanguisorba minor aggr.	16.0	17	34	6	6	1
Teucrium chamaedrys	6.8	4	18	.	.	2
Trifolium montanum subsp. *montanum*	6.2	.	15	2	1	.
[...]						
Class MOL (33 taxa)						
Holcus lanatus	11.6	.	3	44	1	.
Ranunculus acris subsp. *friesianus*	7.8	.	1	32	<1	.
Agrostis stolonifera subsp. *stolonifera*	9.1	2	3	34	<1	.
Trifolium fragiferum	6.6	.	.	28	1	.
Ranunculus repens	6.5	.	.	26	2	.
Poa trivialis subsp. *trivialis*	8.9	.	6	30	.	.
Lolium perenne	11.1	2	4	35	7	.
Schedonorus arundinaceus subsp. *arundinaceus*	6.4	.	2	25	.	.
Juncus articulatus	4.9	.	.	21	<1	.
Juncus inflexus	4.3	.	.	19	.	.
Centaurea debeauxii	6.8	.	4	23	1	.
Anthoxanthum odoratum	10.5	.	4	30	9	2
Rumex acetosa subsp. *acetosa*	4.8	.	<1	19	.	3
Potentilla reptans	6.7	6	2	24	1	.
Veronica chamaedrys subsp. *chamaedrys*	5.0	.	<1	18	3	.
[...]						
Class NAR (17 taxa)						
Potentilla erecta	16.7	.	1	5	63	4
Galium saxatile	11.5	.	<1	<1	48	1
Agrostis capillaris	35.4	.	18	27	86	23
Festuca microphylla	40.2	.	22	19	94	48
Polygala serpyllifolia	8.6	.	2	<1	33	.
Nardus stricta	8.5	.	.	.	34	5
Danthonia decumbens	17.1	.	10	9	47	4

Class	All	LYG	FES	MOL	NAR	SES
# plots	958	54	339	220	223	114
# plots with bryophyte/lichen treatment	119	19	64	8	11	17
Agrostis curtisii	5.7	.	.	.	25	.
Jasione laevis subsp. *laevis*	5.8	.	.	.	25	1
Carex pilulifera subsp. *pilulifera*	5.5	.	.	<1	23	.
Calluna vulgaris	7.4	.	.	.	27	8
Veronica officinalis	5.0	.	.	<1	21	1
Helictochloa marginata subsp. *marginata*	6.7	.	3	.	24	2
Trifolium alpinum	3.7	.	.	.	16	.
Vaccinium myrtillus	2.7	.	.	.	11	1
[...]						
Class SES (46 taxa)						
Helictotrichon sedenense subsp. *sedenense*	5.6	.	.	.	<1	46
Carex sempervirens subsp. *sempervirens*	5.4	.	1	.	<1	43
Alchemilla plicatula aggr.	13.5	.	4	.	19	61
Festuca gautieri subsp. *scoparia*	4.7	.	<1	.	<1	38
Poa alpina	10.4	.	5	.	12	50
Androsace villosa subsp. *villosa*	4.4	.	1	.	.	32
Paronychia kapela subsp. *serpyllifolia*	4.6	.	1	.	2	32
Agrostis schleicheri	3.9	.	1	.	.	29
Carex ornithopoda	4.8	.	2	.	2	32
Ranunculus carinthiacus	4.1	.	1	.	2	29
Sesleria caerulea subsp. *caerulea*	4.3	.	2	.	<1	29
Trifolium thalii	7.9	.	<1	.	13	38
Silene acaulis	3.4	.	.	.	1	26
Aster alpinus	3.5	.	1	.	<1	25
Saxifraga paniculata	2.9	.	<1	.	.	24
[...]						
Anthyllis vulneraria	13.6	4	22	1	1	43
Diagnostic for multiple classes (13 taxa)						
Eryngium campestre	16.1	37	32	9	1	.
Genista scorpius	7.0	30	15	.	.	.
Koeleria vallesiana	25.1	37	53	.	.	34
Dactylis glomerata	21.0	52	20	43	3	2
Carex flacca subsp. *flacca*	25.3	.	45	35	4	3
Pilosella officinarum	29.6	13	41	5	48	13
Thymus praecox	42.5	.	63	1	43	82
Carex caryophyllea	27.9	4	31	4	51	30
Helianthemum canum subsp. *canum*	14.6	2	27	.	1	39
Teucrium pyrenaicum	11.0	.	24	<1	<1	18
Trifolium repens	30.0	.	17	47	52	8
Campanula scheuchzeri	7.0	.	1	<1	15	25
Plantago alpina	6.5	.	1	.	20	13
Companion species						
Lotus corniculatus	44.3	4	53	32	54	43
Plantago lanceolata	37.5	7	50	47	29	11
Trifolium pratense	32.0	4	29	46	37	20
Bellis perennis	31.1	7	26	43	41	15
Achillea millefolium	25.6	2	24	24	41	12
Hypochaeris radicata	24.8	15	19	30	40	9
Plantago media	24.7	.	31	24	30	9
Galium pumilum	23.7	2	40	8	15	34
Briza media subsp. *media*	22.2	.	38	25	9	9
Brachypodium rupestre	21.5	.	32	19	18	10
Ranunculus bulbosus subsp. *bulbosus*	21.5	2	28	20	24	11
Cerastium fontanum subsp. *vulgare*	17.7	.	11	22	35	6
Daucus carota	16.1	19	22	32	.	.
Linum catharticum subsp. *catharticum*	15.7	.	28	3	13	18
Galium verum subsp. *verum*	14.3	13	20	12	15	2
Potentilla montana	13.6	.	17	1	26	10
Cynosurus cristatus	13.0	.	13	27	10	.
Prunella vulgaris	11.5	.	7	26	12	3
Helianthemum nummularium	11.3	.	21	<1	8	15
Blackstonia perfoliata	11.0	17	25	5	.	.
Hippocrepis comosa	10.9	2	20	<1	5	18
Leontodon saxatilis subsp. *saxatilis*	10.9	19	12	15	9	.
Colchicum montanum	10.8	.	20	1	11	5
Trifolium campestre	10.8	13	19	12	3	.
Phleum pratense	10.5	11	17	15	1	.
Erica vagans	10.4	.	17	.	17	4
[...]						

Class	All	LYG	FES	MOL	NAR	SES
# plots	958	54	339	220	223	114
# plots with bryophyte/lichen treatment	119	19	64	8	11	17
Bryophytes and lichens (based on plots from the Field Workshop)						
Class LYG (12 taxa)						
Seirophora lacunosa	5.9	37	.	.	.	.
Gyalolechia fulgens	5.9	37	.	.	.	.
Didymodon acutus	23.5	58	25	.	.	6
Squamarina cartilaginea	6.7	37	.	.	.	6
Weissia condensa	7.6	32	3	.	.	6
Fulgensia poeltii	4.2	21	2	.	.	.
Lathagrium cristatum	4.2	21	2	.	.	.
Enchylium tenax	10.1	32	8	.	.	6
[...]						
Class FES (5 taxa)						
Cladonia rangiformis	14.3	.	27	.	.	.
Cladonia convoluta	8.4	.	16	.	.	.
Eurhynchiastrum pulchellum	5.9	.	11	.	.	.
Campyliadelphus chrysophyllus	12.6	.	20	.	.	12
Cladonia foliacea	4.2	.	8	.	.	.
Class MOL (2 taxa)						
Brachythecium laetum	4.2	.	.	50	9	.
Rhytidiadelphus squarrosus	2.5	.	3	13	.	.
Class NAR (3 taxa)						
Tortula acaulon	1.7	.	.	.	18	.
Lophocolea minor	0.8	.	.	.	9	.
Tortula inermis	0.8	.	.	.	9	.
Class SES (20 taxa)						
Cladonia pocillum	5.9	.	3	.	.	29
Tortella tortuosa	20.2	.	23	.	9	47
Fissidens dubius	15.1	.	19	.	.	35
Mnium marginatum	2.5	.	.	.	.	18
Polytrichum juniperinum	2.5	.	.	.	.	18
Scapania calcicola	2.5	.	.	.	.	18
Tortella inclinata	10.9	5	8	.	9	35
Ptychostomum capillare aggr.	11.8	5	13	.	.	29
[...]						
Ditrichum pusillum	10.1	11	6	.	9	29
Diagnostic for multiple classes						
Tortella squarrosa	31.1	32	41	.	.	29
Abietinella abietina	10.9	.	19	13	.	.
Ctenidium molluscum	31.1	.	44	13	.	47
Flexitrichum gracile	21.0	.	33	.	.	24
Companion species						
Homalothecium lutescens	34.5	16	42	50	9	35
Weissia controversa	23.5	42	23	13	9	18
Hypnum cupressiforme	22.7	5	28	.	36	24
Pseudoscleropodium purum	13.4	.	20	13	9	6
Calliergonella cuspidata	12.6	.	20	13	9	.

MOL – *Molinio-Arrhenatheretea* (Figure 2C)

86% of the relevés previously assigned to the *Molinio-Arrhenetheretea* were included in the group MOL, together with 16% of the relevés of *Festuco-Brometea*. This group is characterized by several diagnostic species of the class *Molinio-Arrhenatheretea*, such as *Agrostis stolonifera* subsp. *stolonifera, Anthoxanthum odoratum*, *Holcus lanatus, Juncus articulatus, J. inflexus, Lolium perenne, Poa trivialis* subsp. *trivialis, Ranunculus acris* subsp. *friesianus, R. repens* and *Trifolium fragiferum* subsp. *fragiferum,* among other species (Table 2).

The relevés from *Festuco-Brometea* class classified in the group MOL had been originally assigned to the associations *Seseli-Brachypodietum* and *Elytrigio-Brachypodietum phoenicoidis* from *Festuco-Brometea*. The presence of *Agrimonia eupatoria, Agrostis stolonifera* subsp. *stolonifera, Bromus hordeaceus* subsp. *hordeaceus, Poa trivialis* subsp. *trivialis, Potentilla reptans, Ranunculus acris* subsp. *friesianus* and *Schedonorus arundinaceus* subsp. *arundinaceus* relates these relevés to this group (MOL).

This group is widely distributed throughout the study area (Figure 3), although it does not reach high elevations. In the temperate zone it can be found in the meso- and supratemperate, and in the Mediterranean zone it is restricted to wet soils, both in the meso- and the supramediterranean. These grasslands and pastures grow on flat areas with a proportion of 100% fine soil, which results in an almost total vegetation cover (Table 3).

NAR – *Nardetea strictae* (Figure 2B)

Table 1 shows that almost all the relevés originally classified in the class *Nardetea strictae* have been classified in group NAR by the expert system. Most relevés of the

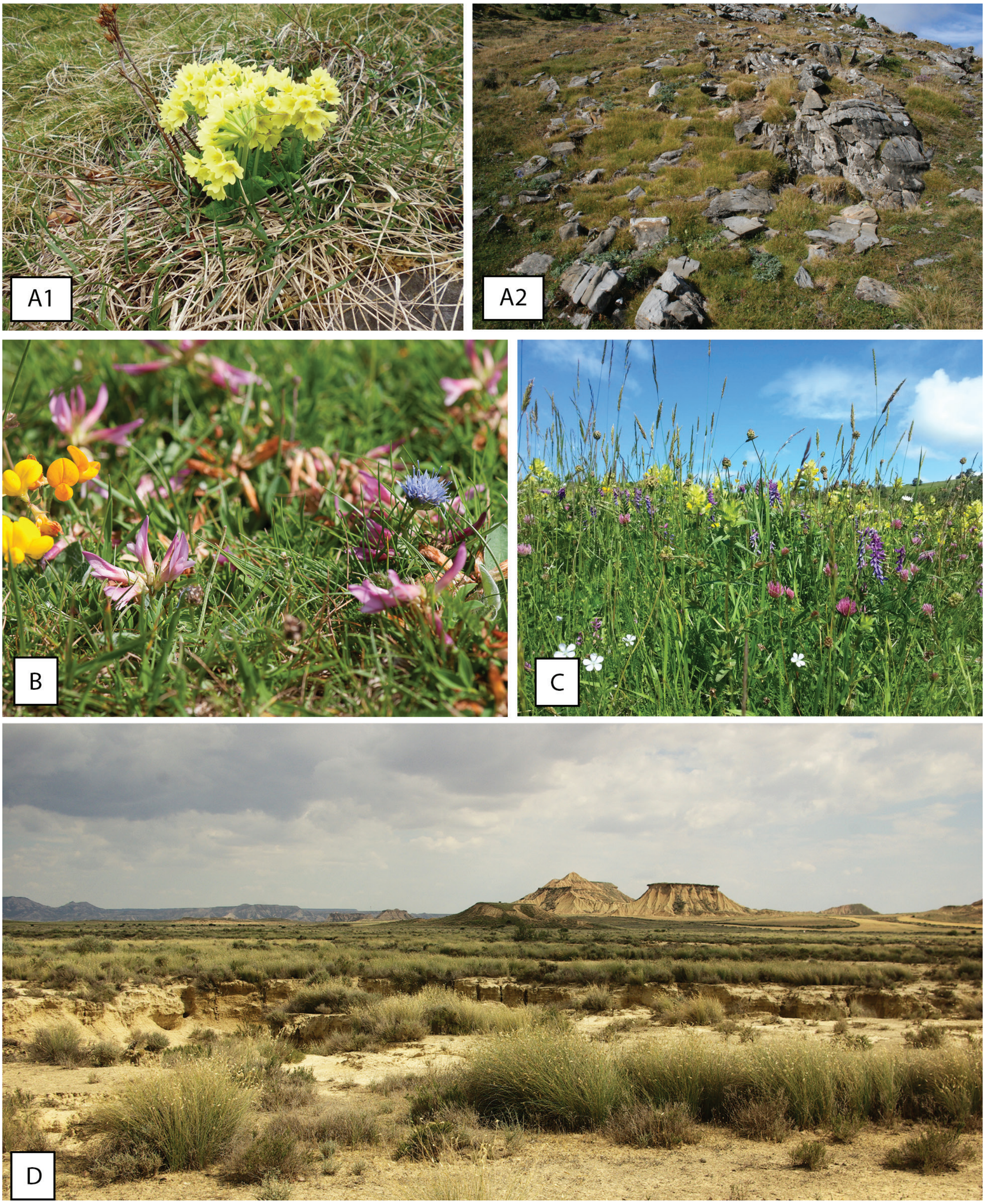

Figure 2. Photo plate showing typical stands of four of the five distinguished vegetation classes (for *Festuco-Brometea*, see Figures 13–14). A *Elyno-Seslerietea*, A1 *Primula intricata*, A2 *Festuca gautieri* subsp. *scoparia*; B *Nardetea strictae* (*Nardus stricta, Trifolium alpinum, Lotus alpinus, Jasione laevis* subsp. *laevis*); C *Molinio-Arrhenatheretea*; D *Lygeo-Stipetea* (*Lygeum spartum*). Photos: J. Dengler (A1, A2, B); A. Berastegi (C); Renaud Jaunatre (D).

class *Sedo-Scleranthetea* were also classified in this group, as well as some relevés of *Festuco-Brometea* (19%) and *Molinio-Arrhenateretea* (8%). The diagnostic species include acidophilous taxa such as *Agrostis capillaris, Carex pilulifera* subsp. *pilulifera, Danthonia decumbens, Galium saxatile, Jasione laevis* subsp. *laevis* or *Potentilla erecta* (Table 2).

Relevés from *Festuco-Brometea* included in this group correspond to communities of the association *Calamintho-Seselietum montani* that grow in places with a very humid ombroclimate, which causes acidification of the soil leading to the presence of acidophilous species diagnostic of *Nardetea*. As regards *Molinio-Arrhenatheretea*, relevés originally assigned to the association *Merendero-Cynosuretum* were classified in this group. In both cases, the species shared with *Nardetea* were *Agrostis capillaris, Carex pilulifera* subsp. *pilulifera, Danthonia decumbens, Festuca microphylla, Galium saxatile, Helictochloa marginata* subsp. *marginata, Luzula campestris, Jasione laevis* subsp. *laevis, Polygala serpyllifolia, Potentilla erecta,* among others.

The relevés of this group are widely distributed in the montane and subalpine belts of the Pyrenees and Basque-Cantabrian mountains under temperate climate (Figure 3).

SES – *Elyno-Seslerietea* (Figure 2A)

The expert system classification within the group SES included most of the relevés of the class *Elyno-Seslerietea* and 23% of relevés from *Festuco-Ononidetea*. *Agrostis schleicheri, Alchemilla plicatula* aggr., *Androsace villosa* subsp. *villosa, Carex ornithopoda* subsp. *ornithopoda, C. sempervirens* subsp. *sempervirens, Festuca gautieri* subsp. *scoparia, Helictotrichon sedenense* subsp. *sedenense, Paronychia kapela* subsp. *serpyllifolia, Poa alpina, Ranunculus carinthiacus, Sesleria caerulea* subsp. *caerulea, Silene acaulis* and *Trifolium thalii* are diagnostic species of this group (Table 2).

Relevés of *Festuco-Ononidetea* included in this group correspond to communities of the Pyrenean subalpine alliance *Festucion scopariae,* which share most of the diagnostic species of the group, such as *Aster alpinus, Minuartia verna* subsp. *verna,* and *Saxifraga paniculata,* in addition to those aforementioned.

This group SES includes the plots at highest elevations in calcareous mountains, in the upper montane and subalpine belts. In these cases, they share territories with the previous group NAR, but in rocky calcareous places (Figure 3). However, the concentration of calcium carbonate in the soil is very low due to the decarbonation effect caused by high precipitation and snow accumulation (Table 3).

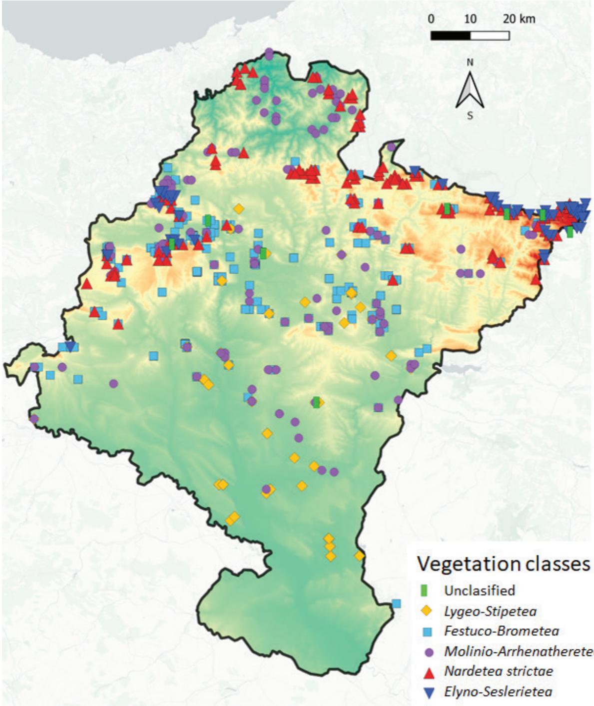

Figure 3. Study area (Navarre) and location of grassland relevés classified to classes according to expert system analysis.

Ordination

The NMDS ordination diagram clearly differentiated between the five groups defined by our class expert system (Figure 4). Axis 1 distributes *Lygeo-Stipetea, Festuco-Brometea, Molinio-Arrhenatheretea, Nardetea strictae* and *Elyno-Seslerietea* along a decreasing mediterraneity and increasing precipitation gradient. Axis 2 separates classes *Molinio-Arrhenatheretea* and *Nardetea*, in the upper part, from the others. This axis could be related to soil moisture.

Site conditions and biodiversity of different classes

The differences between classes regarding elevation and climatic conditions can be seen in Table 3 and Figure 5. The class *Lygeo-Stipetea* (LYG) shows the highest Mediterraneity index and the highest mean annual temperature and is generally present at lower elevations with the lowest annual precipitation. On the other hand, the classes *Nardetea* (NAR) and *Elyno-Seslerietea* (SES) develop at the highest elevations, linked to the highest annual precipitation and lowest mean annual temperature and Mediterraneity Index.

Regarding soil, topographic and structural variables (Table 3, Figure 5), the class *Nardetea* represents the highest soil depth and is also the most acidophilous communi-

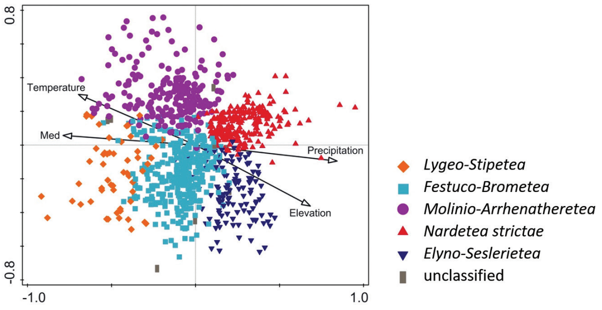

Figure 4. NMDS ordination of all grassland relevés. Eigenvalues: Axis 1 – 0.4434, Axis 2 – 0.4010, Axis 3 (not shown) – 0.1556. Med stands for Mediterraneity Index.

Table 3. Comparison of climatic, structural, ecological and diversity characteristics among the five classes. The *p*-values and significance levels refer to ANOVAs.

Parameter	LYG	FES	MOL	NAR	SES	*p*-value	Sig.
Total number of relevés	54	339	220	223	114		
Number of relevés from EDGG FW	19	64	8	11	17		
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD		
Parameters calculated for all relevés							
Geographical and climatic parameters							
Elevation [m a.s.l.]	439 ± 157	853 ± 286	577 ± 272	1265 ± 378	1752 ± 386	<0.001	***
Mediterranity index	1.36 ± 0.46	0.66 ± 0.19	0.77 ± 0.31	0.41 ± 0.1	0.36 ± 0.08	<0.001	***
Annual mean temperature [°C]	13.2 ± 1.3	10.5 ± 1.5	11.8 ± 1.6	8.0 ± 2.4	5.3 ± 2.7	<0.001	***
Mean annual precepitation [mm]	686 ± 260	1232 ± 283	1134 ± 331	1751 ± 271	1865 ± 232	<0.001	***
Parameters calculated for relevés from EDGG Field Workshop							
Vegetation structure							
Cover vegetation total [%]	67 ± 22	81 ± 19	98 ± 2	86 ± 9	55 ± 22	<0.001	***
Cover shrub layer [%]	1 ± 1	1 ± 3	0 ± 0	0 ± 0	0 ± 0	0.138	
Cover herb layer [%]	55 ± 25	76 ± 20	98 ± 2	77 ± 25	51 ± 22	<0.001	***
Cover cryptogam layer [%]	19 ± 21	16 ± 18	31 ± 32	1 ± 2	10 ± 10	0.005	**
Cover litter [%]	16 ± 17	9 ± 14	8 ± 12	6 ± 6	14 ± 25	0.365	n.s.
Herb layer maximum height [cm]	66 ± 26	65 ± 31	108 ± 32	31 ± 17	24 ± 19	<0.001	***
Species richness							
Species richness (total)	35.6 ± 6.8	55.3 ± 14.5	45.3 ± 14.7	40.5 ± 6.9	44.0 ± 11.7	<0.001	***
Species richness (vascular plants)	29.2 ± 7.5	48.0 ± 11.9	43.5 ± 14.0	37.5 ± 6.4	34.4 ± 7.7	<0.001	***
Species richness (cryptogams)	6.4 ± 4.2	7.3 ± 4.9	2.0 ± 1.7	2.9 ± 2.0	9.6 ± 6.2	<0.001	***
Species richness (bryophytes)	3.2 ± 2.0	6.3 ± 4.2	2.0 ± 1.7	2.5 ± 1.6	7.2 ± 5.6	<0.001	***
Species richness (lichens)	3.2 ± 3.2	1.0 ± 1.3	0.0 ± 0.0	0.4 ± 0.7	2.4 ± 2.3	<0.001	***
Topography							
Southing (cosine of aspect)	0.1 ± 0.6	-0.3 ± 0.68	-0.46 ± 0.65	0.24 ± 0.69	0.08 ± 0.89	0.019	*
Inclination [°]	8 ± 9	16 ± 13	6 ± 6	26 ± 9	32 ± 11	<0.001	***
Maximum microrelief [cm]	7 ± 7	9 ± 8	4 ± 3	9 ± 4	29 ± 26	<0.001	***
Soil parameters							
Soil depth mean [cm]	12 ± 6	16 ± 8	17 ± 5	36 ± 16	6 ± 5	<0.001	***
Soil depth CV	54 ± 32	50 ± 40	49 ± 34	30 ± 16	97 ± 51	0.001	***
Cover rocks and stones [%]	6 ± 13	7 ± 14	0 ± 0	2 ± 3	35 ± 23	<0.001	***
Cover gravel [%]	19 ± 29	6 ± 15	0 ± 0	1 ± 1	13 ± 16	0.011	*
Cover fine soil [%]	75 ± 35	88 ± 22	100 ± 0	97 ± 3	52 ± 32	<0.001	***
Coarse fragments [%]	16 ± 13	22 ± 17	15 ± 14	12 ± 8	24 ± 16	0.139	n.s.
Fine fragments < 2mm [%]	84 ± 13	78 ± 17	85 ± 14	88 ± 8	76 ± 16	0.139	n.s.
pH	7.69 ± 0.24	7.52 ± 0.42	7.66 ± 0.99	6.8 ± 0.29	7.46 ± 0.38	<0.001	***
Electrical conductivity [µS/cm]	283 ± 184	232 ± 86	168 ± 78	146 ± 80	310 ± 158	0.002	**
CaCO3 [%]	40.7 ± 10.5	26.7 ± 19.1	8.5 ± 8.5	4 ± 1.1	4.6 ± 1.8	<0.001	***
Organic matter [%]	0.6 ± 0.6	1.4 ± 0.8	1.2 ± 0.3	1.3 ± 0.2	2.2 ± 0.7	<0.001	***

ty. The class *Elyno-Seslerietea* is characterised by a higher cover of stones and rocks as well as higher soil organic matter content, and, together with *Nardetea* and *Molinio-Arrhenatheretea,* is the poorest in soil carbonate content. Conversely, *Lygeo-Stipetea* is signified by its high soil carbonate content and low soil organic matter. *Molinio-Arrhenatheretea* is distinghuished by its high cover of the herb layer and cryptogams.

The total species richness is highest in *Festuco-Brometea,* although differences with the second richer class *Molinio-Arrhenatheretea* are not significant (Figure 6). *Festuco-Brometea* is also rich in vascular plants and bryophytes, although for the former values do not significantly differ from those of *Molinio-Arrhenatheretea*, and for the latter from those of *Elyno-Seslerietea*. The latter class stands out because of its high cryptogam richness, both in bryophytes and lichens. On the other hand, *Molinio-Arrhenetheretea* and *Nardetea* are the poorest in cryptogams. Finally, *Lygeo-Stipetea* shares with *Elyno-Seslerietea* the high number of lichens, although its richness in bryophytes is lower.

Subdivision of the *Festuco-Brometea* into orders, alliances and associations

The TWISPAN analysis for the group FES related to the class *Festuco-Brometea* resulted in four main divisions that can be interpreted at order and alliance levels (Figure 7). Order 1 grouped relevés originally classified in the classes *Ononido-Rosmarinetea* (*Thymelaeo-Aphyllanthetum monspeliensis)* and *Festuco-Ononidetea* (*Ononidetalia striatae*: *Helianthemo-Koelerietum vallesianae*; *Festuco-Poetalia ligulatae*: *Jurineo-Festucetum hystricis*). The dry grasslands of the *Thymelaeo-Aphyllanthetum* association were included in alliance 1.1. The two associations from *Festuco-Ononidetea, Helianthemo-Koelerietum* and *Jurineo-Festucetum*, were merged in the alliance 1.2.

Diagnostic species for order 1 were *Carex humilis, Galium lucidum* subsp. *fruticescens, Helianthemum apenninum* subsp. *apenninum* and *Koeleria vallesiana* (Table 4). The alliance 1.1 was characterized by the presence of Mediterranean species such as *Aphyllanthes monspeliensis, Brachypodium retusum, Coris monspeliensis*, *Helictochloa*

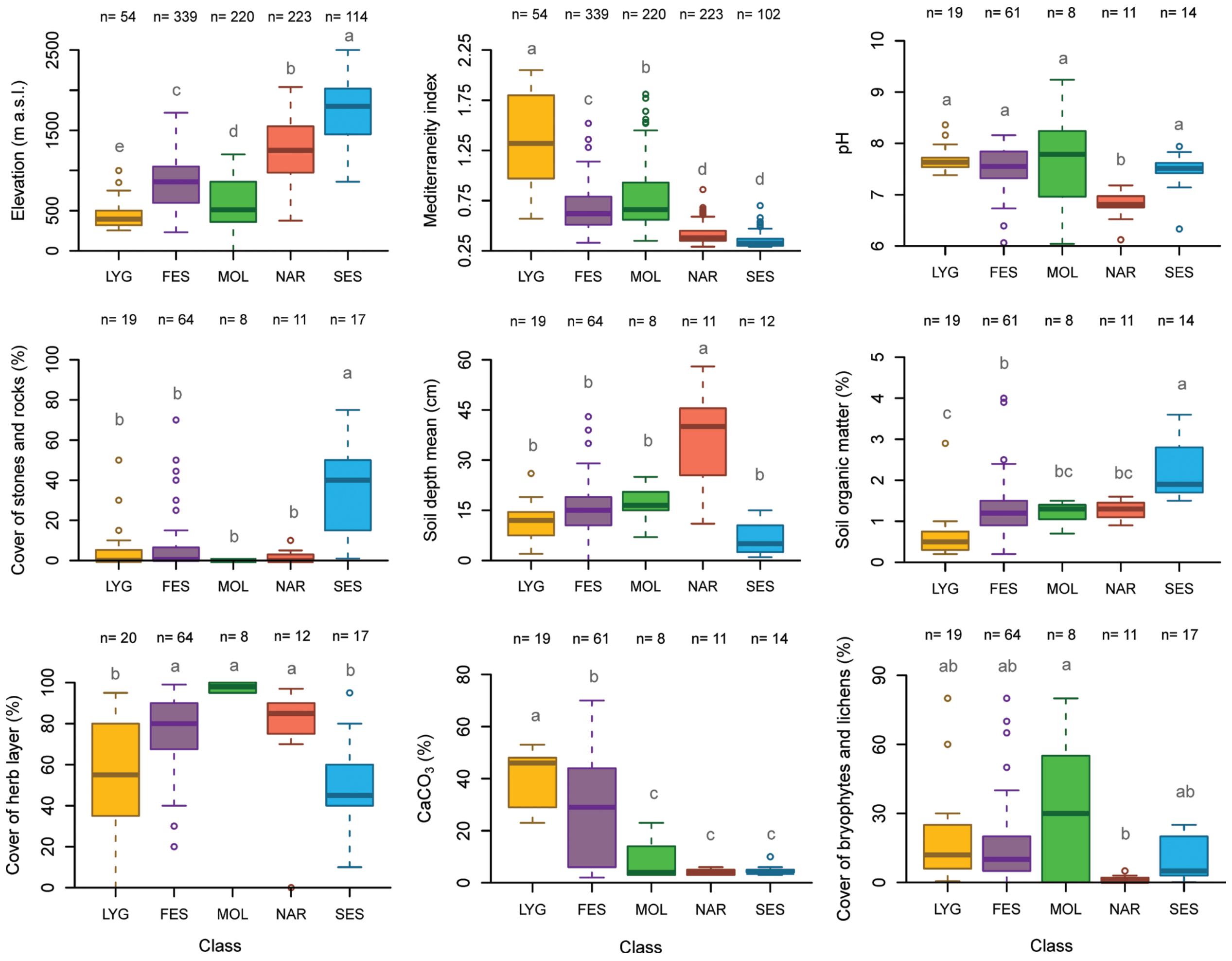

Figure 5. Comparison of nine ecological variables among the five classes. For elevation and Mediterraneity Index, all relevés were analysed, whereas for the rest of variables only relevés from EDGG Field Workshop were used. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

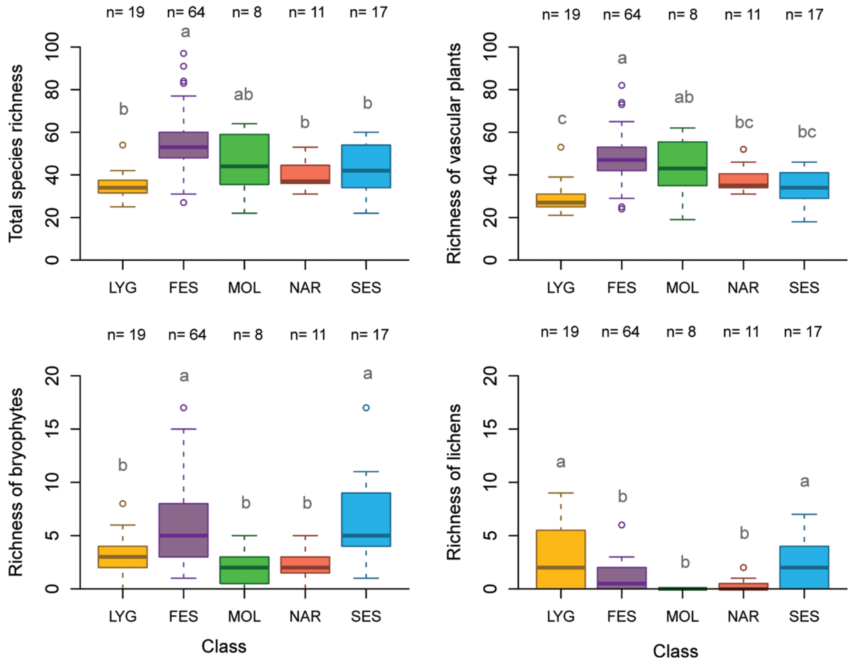

Figure 6. Comparison of species richness divided into four groups (total species, vascular plants, bryophytes and lichens) among the five classes using the relevés from EDGG Field Workshop. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

Table 4. Abridged constancy table of the class *Festuco-Brometea* and its subordinate syntaxa. Values are percentage constancies, and species are ordered by decreasing phi-values in the respective syntaxon, respectively by decreasing overall constancy for non-diagnostic species. In the upper part vascular plants are given, in the lower part bryophytes and lichens, whose constancies and fidelities have been calculated based on the plots of the EDGG Field Workshop only where they have been recorded (in italics if based on data from a single plot, with ? if no such data were available for any plot). In the table, the 15 vascular plant taxa and the eight non-vascular plant taxa with the highest fidelity in a syntaxon are shown, plus all taxa that are diagnostic for multiple syntaxa and all taxa with at least 10% overall constancy. Diagnostic species (phi ≥ 0.25) for higher syntaxa highlighted in light grey, diagnostic species for associations in dark grey, while differential species of associations within the respective alliance are given with a frame. The complete constancy table combined with the table of the underlying 339 vegetation plots is given in Suppl. material 14.

Class	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Ord. 1 (4 taxa)															
Koeleria vallesiana	53.1	92	26	85	97	15	29	85	100	95	36	4	<1	27	36
Carex humilis	40.1	66	22	65	67	8	26	65	96	56	14	4	42	28	19
Helianthemum apenninum subsp. *apenninum*	13.6	29	3	19	34	3	3	19	32	36	<1	4	<1	3	4
Galium lucidum subsp. *fruticescens*	9.7	21	2	15	24	3	2	15	24	25	<1	4	17	<1	1
All. 1.1 (38 taxa + 1 multiple diagnostic taxon)															
Brachypodium retusum	14.5	29	5	75	1	18	1	75	<1	2	43	4	8	1	<1
Thymus vulgaris subsp. *vulgaris*	20.1	45	3	81	24	8	1	81	44	16	7	8	<1	1	1
Lavandula latifolia	7.1	17	1	42	1	3	<1	42	4	<1	<1	4	<1	<1	<1
Aphyllanthes monspeliensis	14.7	24	9	58	3	10	8	58	4	3	14	8	<1	13	4
Coris monspeliensis	6.8	14	2	38	<1	8	<1	38	<1	<1	14	4	<1	<1	<1
Teucrium chamaedrys	18.0	35	7	60	20	10	6	60	16	21	14	8	42	3	3
Helictochloa bromoides	6.2	13	2	35	<1	8	<1	35	<1	<1	14	4	<1	<1	<1
Bupleurum rigidum subsp. *rigidum*	4.7	11	1	29	<1	3	<1	29	<1	<1	7	<1	<1	<1	<1
Linum appressum	9.7	17	5	40	2	8	4	40	4	2	21	<1	8	4	4
Genista scorpius	15.0	23	10	58	2	35	3	58	4	2	50	27	8	4	1
Dorycnium pentaphyllum subsp. *pentaphyllum*	16.5	24	12	58	3	33	6	58	4	3	64	15	33	5	3
Santolina villosa	3.8	9	1	23	<1	<1	1	23	<1	<1	<1	<1	8	<1	<1
Coronilla minima	38.3	60	23	79	49	25	23	79	72	41	36	19	8	29	17
Fumana ericifolia	3.5	8	1	21	<1	<1	1	21	<1	<1	<1	<1	<1	<1	1
Linum narbonense	6.2	12	3	29	1	5	2	29	<1	2	14	<1	8	3	<1
[...]															
Asperula cynanchica	17.7	22	15	44	9	8	16	44	4	11	14	4	17	18	14
Catananche caerulea	13.6	17	12	42	1	23	9	42	<1	2	21	23	<1	17	1
Festuca marginata subsp. *andres-molinae*	10.3	14	8	35	2	20	4	35	8	<1	29	15	<1	9	<1
Assoc. 1.1.1 (7 taxa)															
Rhamnus alaternus subsp. *alaternus*	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Odontites kaliformis	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Lithodora fruticosa	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Gladiolus illyricus	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Atractylis humilis	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Aster willkommii	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Helichrysum stoechas subsp. *stoechas*	1.8	4	<1	10	1	<1	<1	10	<1	2	<1	<1	<1	<1	<1
All. 1.2 (8 taxa + 1 multiple diagnostic)															
Sedum album	14.2	27	6	2	41	<1	7	2	48	39	<1	<1	8	<1	14

Class	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Ononis striata	4.7	12	<1	2	17	<1	<1	2	20	16	<1	<1	<1	<1	<1
Asperula pyrenaica	12.7	19	8	4	29	3	9	4	28	30	<1	4	<1	4	17
Plantago atrata subsp. *discolor*	5.6	12	2	2	17	<1	2	2	12	20	<1	<1	<1	3	1
Anthyllis vulneraria	22.1	29	18	8	41	15	18	8	40	43	14	15	<1	15	23
Thymus praecox	62.8	60	65	33	76	23	76	33	80	74	21	23	42	67	91
Oreochloa confusa	3.8	7	2	<1	11	<1	2	<1	16	8	<1	<1	<1	<1	4
Dianthus pungens subsp. *brachyanthus*	3.2	6	1	<1	10	<1	1	<1	16	8	<1	<1	<1	<1	3
Brimeura amethystina	3.2	6	1	<1	10	<1	1	<1	4	13	<1	<1	<1	1	1
Assoc. 1.2.1 (13 taxa)															
Arenaria grandiflora subsp. *grandiflora*	13.0	29	2	4	44	<1	3	4	88	25	<1	<1	<1	<1	6
Festuca hystrix	5.9	14	<1	4	21	<1	<1	4	56	7	<1	<1	<1	<1	<1
Helianthemum canum subsp. *canum*	26.8	49	12	12	71	<1	14	12	100	59	<1	<1	<1	12	20
Klasea nudicaulis	6.5	15	1	4	22	<1	1	4	48	11	<1	<1	<1	<1	1
Anthyllis montana	2.9	7	<1	<1	11	<1	<1	<1	32	3	<1	<1	<1	<1	<1
Jurinea humilis	3.5	8	1	<1	13	<1	1	<1	28	7	<1	<1	<1	<1	1
Erucastrum nasturtiifolium subsp. *sudrei*	1.8	4	<1	<1	7	<1	<1	<1	20	2	<1	<1	<1	<1	<1
Trinia glauca	7.7	17	1	10	22	<1	1	10	36	16	<1	<1	<1	3	<1
Festuca ovina aggr.	11.2	18	7	8	24	<1	8	8	44	16	<1	<1	8	8	9
Aster alpinus	1.2	3	<1	<1	5	<1	<1	<1	16	<1	<1	<1	<1	<1	<1
Paronychia kapela subsp. *kapela*	0.9	2	<1	<1	3	<1	<1	<1	12	<1	<1	<1	<1	<1	<1
Arenaria erinacea	0.9	2	<1	<1	3	<1	<1	<1	12	<1	<1	<1	<1	<1	<1
Scilla verna	6.8	10	5	4	14	3	5	4	28	8	<1	4	<1	5	4
Assoc. 1.2.2 (5 taxa + 1 multiple diagnostic taxon + 1 differential taxon)															
Conopodium arvense	4.4	9	2	<1	14	<1	2	<1	<1	20	<1	<1	<1	3	1
Sedum acre	2.9	6	1	<1	10	<1	1	<1	<1	15	<1	<1	<1	<1	1
Deschampsia media subsp. *hispanica*	3.2	7	1	<1	11	3	<1	<1	<1	16	<1	4	<1	<1	<1
Helianthemum salicifolium	1.5	4	<1	<1	6	<1	<1	<1	<1	8	<1	<1	<1	<1	<1
Erodium glandulosum	1.5	4	<1	<1	6	<1	<1	<1	<1	8	<1	<1	<1	<1	<1
Medicago lupulina	38.9	33	43	12	46	33	46	12	4	64	21	38	8	54	43
Ord. 2 (12 taxa)															
Lotus corniculatus	52.8	24	73	13	30	58	77	13	20	34	57	58	17	85	78
Trifolium pratense	28.6	4	46	2	6	45	46	2	<1	8	29	54	8	62	35
Briza media subsp. *media*	38.3	17	54	25	11	45	56	25	4	15	43	46	33	83	29
Trifolium ochroleucon	15.6	1	26	<1	2	20	27	<1	<1	3	7	27	<1	47	9
Trifolium repens	16.5	2	27	2	2	20	28	2	<1	3	<1	31	<1	27	35
Cynosurus cristatus	12.7	<1	22	<1	<1	28	20	<1	<1	<1	7	38	<1	35	7
Ranunculus bulbosus subsp. *bulbosus*	28.0	12	40	17	8	45	38	17	4	10	21	58	8	44	38
Plantago lanceolata	50.4	32	64	23	37	50	67	23	12	48	43	54	<1	73	72
Endressia castellana	9.4	<1	16	<1	<1	10	18	<1	<1	<1	<1	15	25	23	10
Ononis spinosa	13.0	2	21	2	2	28	19	2	<1	3	7	38	<1	35	4
Trisetum flavescens subsp. *flavescens*	11.8	2	19	4	1	20	18	4	<1	2	<1	31	<1	31	7
Festuca nigrescens	9.1	1	15	<1	1	13	16	<1	<1	2	<1	19	17	24	4
All. 2.1 (11 taxa + 1 multiple diagnostic taxon)															
Schedonorus arundinaceus subsp. *fenas*	5.9	<1	10	<1	<1	38	3	<1	<1	<1	36	38	<1	5	1

Class	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Centaurea jacea	17.1	6	25	13	2	55	17	13	<1	3	57	54	17	29	3
Arrhenatherum elatius	6.2	1	10	4	<1	33	4	4	<1	<1	29	35	33	3	<1
Convolvulus arvensis	4.4	1	7	2	<1	28	2	2	<1	<1	21	31	<1	3	1
Brachypodium phoenicoides	10.0	8	12	19	1	43	4	19	<1	2	43	42	<1	4	4
Blackstonia perfoliata	24.8	23	26	58	2	68	16	58	<1	3	79	62	<1	27	6
Daucus carota	21.8	10	30	17	6	53	24	17	<1	8	36	62	17	44	4
Carex flacca subsp. *flacca*	45.1	26	59	58	7	80	53	58	4	8	86	77	58	81	22
Agrimonia eupatoria	4.1	1	7	2	<1	20	3	2	<1	<1	14	23	<1	6	<1
Poa compressa	3.2	1	5	<1	1	18	2	<1	<1	2	7	23	<1	4	<1
Dactylis glomerata	19.8	15	23	27	8	48	17	27	4	10	29	58	58	21	6
Medicago sativa subsp. *sativa*	1.2	<1	2	<1	<1	10	<1	<1	<1	<1	7	12	<1	<1	<1
Assoc. 2.1.1 (7 taxa + 2 differential taxa)															
Plantago maritima subsp. *serpentina*	6.8	6	7	15	1	25	3	15	<1	2	57	8	<1	3	3
Festuca capillifolia	5.3	4	7	6	2	28	1	6	4	2	50	15	<1	3	<1
Jasonia tuberosa	6.2	9	4	21	2	15	1	21	<1	3	43	<1	<1	1	1
Prunella hyssopifolia	11.5	8	14	19	1	35	9	19	<1	2	57	23	<1	15	3
Agrostis stolonifera subsp. *stolonifera*	2.7	<1	5	<1	<1	18	1	<1	<1	<1	29	12	<1	3	<1
Lotus tenuis	0.6	<1	1	<1	<1	5	<1	<1	<1	<1	14	<1	<1	<1	<1
Lathyrus latifolius	0.6	<1	1	<1	<1	5	<1	<1	<1	<1	14	<1	<1	<1	<1
Assoc. 2.1.2 (28 taxa + 3 differential taxa)															
Phleum pratense	17.1	4	26	10	1	53	19	10	<1	2	14	73	<1	28	13
Poa trivialis subsp. *trivialis*	5.6	<1	10	<1	<1	28	5	<1	<1	<1	<1	42	<1	8	3
Vicia parviflora	3.2	<1	6	<1	<1	23	1	<1	<1	<1	<1	35	<1	1	1
Brachypodium phoenicoides x rupestre	9.4	2	15	6	<1	40	8	6	<1	<1	7	58	8	12	4
Xeranthemum cylindraceum	2.7	1	4	2	<1	18	1	2	<1	<1	<1	27	<1	<1	1
Trifolium campestre	18.6	7	27	6	8	40	23	6	8	8	<1	62	<1	24	26
Vicia sativa subsp. *nigra*	5.9	2	9	2	2	25	4	2	<1	3	<1	38	8	6	1
Iris spuria subsp. *maritima*	1.8	<1	3	<1	<1	13	1	<1	<1	<1	<1	19	<1	1	<1
Gaudinia fragilis	2.1	<1	4	<1	<1	13	1	<1	<1	<1	<1	19	<1	3	<1
Trifolium angustifolium	2.4	1	4	2	<1	13	1	2	<1	<1	<1	19	<1	<1	3
Lathyrus pratensis subsp. *pratensis*	1.5	<1	3	<1	<1	10	1	<1	<1	<1	<1	15	<1	1	<1
Jacobaea vulgaris	3.2	<1	6	<1	<1	18	3	<1	<1	<1	7	23	<1	5	<1
Allium oleraceum	1.8	<1	3	<1	<1	10	1	<1	<1	<1	<1	15	<1	1	1
Cerastium fontanum subsp. *vulgare*	10.6	4	15	<1	7	23	13	<1	4	7	<1	35	<1	14	14
Picris hieracioides	7.1	4	9	12	<1	23	6	12	<1	<1	7	31	<1	10	1
[...]															
Eryngium campestre	32.4	29	35	58	13	58	29	58	8	15	29	73	25	31	28
Galium verum subsp. *verum*	19.8	9	27	6	11	38	24	6	<1	16	14	50	17	22	29
Anacamptis pyramidalis	10.6	7	13	19	<1	28	9	19	<1	<1	14	35	<1	19	<1
All. 2.2 (10 taxa + 1 multiple diagnostic taxon)															
Brachypodium rupestre	32.4	12	47	12	11	3	58	12	4	15	7	<1	92	73	36
Festuca microphylla	22.4	4	35	2	6	3	43	2	<1	8	7	<1	25	46	43
Achillea millefolium	24.5	7	37	6	8	13	43	6	12	7	7	15	8	47	42
Agrostis capillaris	17.7	3	28	<1	5	5	34	<1	4	5	<1	8	8	37	35

Class	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Erica vagans	17.1	3	27	6	1	13	31	6	4	<1	<1	19	58	41	14
Potentilla montana	16.8	3	27	<1	5	8	31	<1	4	5	<1	12	25	24	39
Helianthemum nummularium	21.2	7	31	<1	11	<1	39	<1	<1	16	<1	<1	17	36	46
Danthonia decumbens	10.3	1	17	<1	1	3	21	<1	<1	2	<1	4	<1	29	14
Scabiosa columbaria subsp. *columbaria*	25.4	12	35	10	14	10	41	10	<1	20	7	12	42	56	23
Gentiana verna subsp. *verna*	5.6	1	9	<1	1	<1	11	<1	<1	2	<1	<1	<1	9	16
Assoc. 2.2.1 (21 taxa + 1 multiple diagnostic taxon + 2 differential taxa)															
Vincetoxicum hirundinaria subsp. *intermedium*	3.8	4	4	4	3	<1	5	4	4	3	<1	<1	58	1	<1
Sesleria autumnalis	2.7	1	4	<1	2	<1	4	<1	<1	3	<1	<1	50	1	<1
Tanacetum corymbosum subsp. *corymbosum*	2.9	1	4	2	1	<1	5	2	<1	2	<1	<1	33	5	<1
Genista hispanica subsp. *occidentalis*	15.9	7	22	10	6	10	25	10	8	5	7	12	67	32	9
Euphorbia characias	2.1	2	2	4	1	<1	3	4	<1	2	<1	<1	25	<1	1
Euphorbia amygdaloides	0.6	<1	1	<1	<1	<1	1	<1	<1	<1	<1	<1	17	<1	<1
Cruciata laevipes	0.6	<1	1	<1	<1	<1	1	<1	<1	<1	<1	<1	17	<1	<1
Teucrium pyrenaicum	23.9	22	25	10	30	3	31	10	28	30	7	<1	67	29	26
Pimpinella major subsp. *major*	1.2	<1	2	<1	<1	<1	3	<1	<1	<1	<1	<1	17	1	1
Helictotrichon cantabricum	6.8	6	8	12	2	13	6	12	4	2	21	8	42	5	1
Viola alba aggr.	3.5	4	3	12	<1	<1	4	12	<1	<1	<1	<1	25	4	<1
Dianthus hyssopifolius subsp. *hyssopifolius*	4.1	3	5	<1	5	<1	6	<1	<1	7	<1	<1	25	3	7
Helleborus foetidus	0.9	<1	2	<1	<1	3	1	<1	<1	<1	<1	4	17	<1	<1
Senecio lagascanus	1.8	3	1	4	2	<1	1	4	<1	3	<1	<1	17	<1	<1
Echium vulgare subsp. *vulgare*	2.1	1	3	2	1	<1	3	2	<1	2	<1	<1	17	3	1
Assoc. 2.2.2 (4 taxa + 1 multiple diagnostic taxon + 2 differential taxa)															
Leontodon hispidus	9.1	1	15	2	1	<1	18	2	<1	2	<1	<1	<1	32	6
Plantago media	31.3	9	47	8	9	25	53	8	8	10	14	31	8	72	39
Linum catharticum subsp. *catharticum*	27.7	12	39	19	7	25	43	19	<1	10	29	23	<1	63	28
Polygala vulgaris subsp. *vulgaris*	7.1	1	12	2	<1	5	13	2	<1	<1	<1	8	<1	24	1
Prunella vulgaris	6.8	1	11	2	1	5	12	2	<1	2	<1	8	<1	21	4
Holcus lanatus	2.9	<1	5	<1	<1	3	6	<1	<1	<1	<1	4	<1	12	<1
Assoc. 2.2.3 (10 taxa + 1 multiple diagnostic taxon)															
Carex caryophyllea	31.3	14	43	6	20	13	51	6	8	25	7	15	17	36	72
Festuca rectifolia	42.5	45	41	6	68	8	49	6	36	80	<1	12	17	26	81
Bellis perennis	25.7	12	35	6	16	18	39	6	<1	23	7	23	<1	31	57
Colchicum montanum	20.4	17	23	2	25	3	28	2	8	33	<1	4	<1	19	43
Alchemilla plicatula aggr.	3.5	1	6	<1	1	<1	7	<1	<1	2	<1	<1	<1	1	14
Aira caryophyllea subsp. *caryophyllea*	9.1	5	12	2	7	8	13	2	<1	10	<1	12	<1	4	26
Vicia pyrenaica	2.9	1	4	<1	2	<1	5	<1	<1	2	<1	<1	<1	<1	12
Poa alpina	4.7	3	6	<1	5	<1	8	<1	<1	7	<1	<1	<1	1	16
Cerastium arvense	8.3	9	8	<1	14	<1	10	<1	8	15	<1	<1	<1	<1	23
Erinus alpinus	3.8	3	5	<1	5	<1	6	<1	<1	5	<1	<1	<1	<1	13
Euphrasia salisburgensis	2.1	<1	4	<1	<1	<1	4	<1	<1	<1	<1	<1	<1	1	9
Other species (class character species and companion species)															
Bromopsis erecta subsp. *erecta*	65.2	60	69	69	55	53	73	69	32	66	29	65	75	82	61
Carthamus mitissimus	50.7	56	47	58	55	23	53	58	44	61	14	27	33	63	45

Class	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Potentilla tabernaemontani	48.1	56	43	52	59	20	48	52	36	69	21	19	8	36	68
Helictochloa pratensis subsp. *iberica*	45.7	48	44	52	46	18	51	52	36	51	7	23	42	51	51
Pilosella officinarum	41.3	31	49	40	25	23	55	40	8	33	29	19	<1	59	61
Galium pumilum	39.8	27	49	44	17	48	49	44	4	23	36	54	58	60	33
Sanguisorba minor aggr.	33.9	29	37	44	21	20	41	44	8	26	14	23	25	54	30
Seseli montanum subsp. *montanum*	32.7	32	34	23	37	35	33	23	32	39	21	42	8	32	38
Hippocrepis comosa	20.4	12	27	13	10	10	31	13	8	11	14	8	8	41	22
Hypochaeris radicata	18.9	10	25	15	7	25	25	15	<1	10	43	15	17	32	19
Geum sylvaticum	18.0	12	23	12	11	10	26	12	8	13	7	12	17	32	20
Onobrychis conferta subsp. *hispanica*	16.8	20	15	31	14	8	16	31	16	13	14	4	<1	28	6
Trifolium montanum subsp. *montanum*	15.3	6	22	2	9	15	23	2	8	10	7	19	<1	33	14
Clinopodium alpinum subsp. *pyrenaeum*	14.2	19	11	13	23	<1	13	13	8	30	<1	<1	<1	10	19
Leucanthemum pallens	13.6	9	17	19	3	23	15	19	<1	5	14	27	17	26	3
Filipendula vulgaris	12.7	6	17	<1	10	13	18	<1	12	10	7	15	33	13	20
Astragalus monspessulanus subsp. *monspessulanus*	12.4	19	8	15	21	5	9	15	28	18	7	4	<1	10	9
Leontodon saxatilis subsp. *saxatilis*	12.1	8	15	8	8	25	13	8	<1	11	21	27	8	12	14
Prunella laciniata	12.1	4	18	8	1	8	21	8	<1	2	<1	12	8	26	17
Thymelaea ruizii	11.5	12	12	21	6	10	12	21	4	7	14	8	8	17	7
Ononis pusilla	10.3	19	4	25	16	5	4	25	8	20	14	<1	<1	3	6
Bellis sylvestris	10.0	14	8	23	8	10	7	23	8	8	7	12	<1	10	4
[...]															
Bryophytes and lichens (based on plots from the Field Workshop)															
Ord. 1 (1 taxon)															
Tortella squarrosa	40.6	70	24	72	60	13	27	72	?	60	*<1*	14	*<1*	20	42
All. 1.1 (1 taxon)															
Flexitrichum gracile	32.8	48	24	61	<1	<1	30	61	?	<1	*<1*	<1	*<1*	30	33
All. 1.2 (8 taxa)															
Cladonia foliacea	7.8	13	5	<1	60	<1	6	<1	?	60	*<1*	<1	*<1*	<1	17
Didymodon acutus	25.0	30	22	22	60	<1	27	22	?	60	*<1*	<1	*<1*	40	8
Lathagrium cristatum	1.6	4	<1	<1	20	<1	<1	<1	?	20	*<1*	<1	*<1*	<1	<1
Pseudocrossidium hornschuchianum	1.6	4	<1	<1	20	<1	<1	<1	?	20	*<1*	<1	*<1*	<1	<1
Scytinium schraderi	1.6	4	<1	<1	20	<1	<1	<1	?	20	*<1*	<1	*<1*	<1	<1
Encalypta vulgaris	3.1	4	2	<1	20	<1	3	<1	?	20	*<1*	<1	*<1*	<1	8
Didymodon vinealis	4.7	9	2	6	20	<1	3	6	?	20	*<1*	<1	*<1*	5	<1
Ditrichum pusillum	6.3	9	5	6	20	<1	6	6	?	20	*<1*	<1	*<1*	5	8
Ord. 2 (4 taxa)															
Pseudoscleropodium purum	20.3	<1	32	<1	<1	25	33	<1	?	<1	*<1*	29	*<1*	40	25
Cladonia rangiformis	26.6	9	37	6	20	13	42	6	?	20	*100*	<1	*<1*	20	83
Eurhynchiastrum pulchellum	10.9	<1	17	<1	<1	25	15	<1	?	<1	*<1*	29	*<1*	20	8
Fissidens dubius	18.8	4	27	6	<1	13	30	6	?	<1	*100*	<1	*100*	25	33
All. 2.1 (2 taxa)															
Calliergonella cuspidata	20.3	<1	32	<1	<1	50	27	<1	?	<1	*100*	43	*<1*	35	17
Weissia controversa	23.4	17	27	17	20	50	21	17	?	20	*100*	43	*100*	25	8
Assoc. 2.1.2 (6 taxa)															

Class	**Class**	**Ord.**	**Ord.**	**All.**	**All.**	**All.**	**All.**	**Assoc.**	**Assoc.**	**Assoc.**	**Assoc.**	**Assoc.**	**Assoc.**	**Assoc.**	**Assoc.**
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Oxyrrhynchium hians	6.3	4	7	6	<1	38	<1	6	?	<1	<1	43	<1	<1	<1
Fissidens taxifolius	14.1	4	20	6	<1	38	15	6	?	<1	<1	43	<1	25	<1
Brachytheciastrum velutinum	1.6	<1	2	<1	<1	13	<1	<1	?	<1	<1	14	<1	<1	<1
Brachythecium rutabulum	1.6	<1	2	<1	<1	13	<1	<1	?	<1	<1	14	<1	<1	<1
Plagiomnium undulatum	1.6	<1	2	<1	<1	13	<1	<1	?	<1	<1	14	<1	<1	<1
Weissia condensa	3.1	4	2	6	<1	13	<1	6	?	<1	<1	14	<1	<1	<1
All. 2.2 (6 taxa)															
Entodon concinnus	12.5	<1	20	<1	<1	<1	24	<1	?	<1	<1	<1	<1	20	33
Abietinella abietina	18.8	9	24	11	<1	<1	30	11	?	<1	<1	<1	<1	30	33
Enchylium tenax	7.8	<1	12	<1	<1	<1	15	<1	?	<1	<1	<1	<1	20	8
Cladonia convoluta	15.6	9	20	11	<1	<1	24	11	?	<1	<1	<1	<1	20	33
Thuidium assimile	6.3	<1	10	<1	<1	<1	12	<1	?	<1	<1	<1	<1	10	17
Cladonia cariosa	4.7	<1	7	<1	<1	<1	9	<1	?	<1	<1	<1	<1	10	8
Assoc. 2.2.2 (4 taxa)															
Barbula unguiculata	6.3	<1	10	<1	<1	<1	12	<1	?	<1	<1	<1	<1	20	<1
Campyliadelphus chrysophyllus	20.3	13	24	17	<1	13	27	17	?	<1	<1	14	<1	40	8
Rhytidiadelphus squarrosus	3.1	<1	5	<1	<1	<1	6	<1	?	<1	<1	<1	<1	10	<1
Thuidium delicatulum	3.1	<1	5	<1	<1	<1	6	<1	?	<1	<1	<1	<1	10	<1
Assoc. 2.2.3 (23 taxa)															
Exsertotheca crispa	14.1	<1	22	<1	<1	<1	27	<1	?	<1	<1	<1	<1	15	50
Ptychostomum capillare aggr.	12.5	4	17	<1	20	<1	21	<1	?	20	<1	<1	<1	5	50
- Ptychostomum capillare	*7.8*	*4*	*10*	*<1*	*20*	*<1*	*12*	*<1*	*?*	*20*	*<1*	*<1*	*<1*	*5*	*25*
- Ptychostomum elegans	*6.3*	*<1*	*10*	*<1*	*<1*	*<1*	*12*	*<1*	*?*	*<1*	*<1*	*<1*	*<1*	*<1*	*33*
Tortella tortuosa	23.4	17	27	17	20	<1	33	17	?	20	<1	<1	<1	20	58
Hypnum cupressiforme	28.1	17	34	17	20	13	39	17	?	20	<1	14	<1	30	58
Cetraria islandica	3.1	<1	5	<1	<1	<1	6	<1	?	<1	<1	<1	<1	<1	17
Lophocolea heterophylla	3.1	<1	5	<1	<1	<1	6	<1	?	<1	<1	<1	<1	<1	17
Tortella inclinata	7.8	9	7	11	<1	<1	9	11	?	<1	<1	<1	<1	<1	25
Bryum argenteum	4.7	<1	7	<1	<1	<1	9	<1	?	<1	<1	<1	<1	5	17
[...]															
Other species (class character species and companion species)															
Ctenidium molluscum	43.8	35	49	44	<1	38	52	44	?	<1	*100*	29	<1	55	50
Homalothecium lutescens	42.2	35	46	44	<1	63	42	44	?	<1	*100*	57	<1	40	50
Syntrichia ruralis aggr.	12.5	13	12	11	20	<1	15	11	?	20	<1	<1	<1	5	33
[...]															

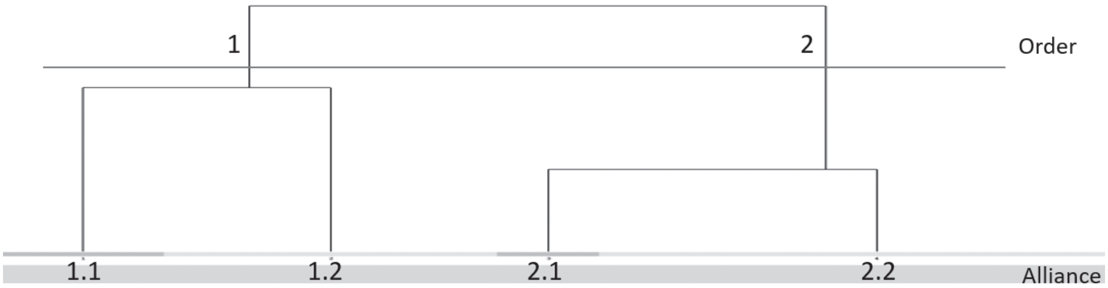

Figure 7. Dendogram of the modified TWINSPAN classification of the 339 relevés from *Festuco-Brometea* into two orders and four alliances.

bromoides and *Thymus vulgaris* subsp. *vulgaris* (Table 4). Only one association was recognised in this alliance and corresponded to *Thymelaeo-Aphyllanthetum monspeliensis,* as both the type relevé of the association (Braun-Blanquet 1966) and the type of the subassociation *brachypodietum retusi* (Berastegi et al. 2005) were placed in this group by the expert system. Inside the alliance 1.2 the relevés were split into two groups. The types of the associations *Jurineo-Festucetum hystricis* and *Helianthemo-Koelerietum vallesianae*, both described by Berastegi (2013), were classified to the groups 1.2.1 and 1.2.2. respectively. The diagnostic species for this alliance were *Asperula pyrenaica, Ononis striata, Plantago atrata* subsp. *discolor* and *Sedum album,* among others.

The NMDS analysis in Figure 8 shows a clear separation of this order 1 in the upper left part of the diagram. There is also a clear segregation of the alliances. Alliance 1.1 is associated with mediterraneity and high temperatures and alliance 1.2 with elevation and precipitation.

The order 2 was defined by *Briza media* subsp. *media, Cynosurus cristatus*, *Lotus corniculatus*, *Trifolium ochroleucon* and *T. pratense* subsp. *pratense,* as diagnostic species (Table 4). It was divided into two alliances. Alliance 2.1 grouped relevés that develop in more Mediterranean areas with lower mean annual precipitation and some of its diagnostic species were *Arrhenatherum elatius, Blackstonia perfoliata, Brachypodium phoenicoides, Centaurea jacea* and *Schedonorus arundinaceus* subsp. *fenax*. Relevés from more humid areas were classified in alliance 2.2, that presented *Achillea millefolium* subsp. *millefolium, Agrostis capillaris, Brachypodium rupestre* and *Festuca microphylla* among its diagnostic species. These two alliances are also clearly separated in the ordination diagram along the mediterraneity and precipitation gradients (Figure 8).

Inside the alliance 2.1 two groups were distinguished. Each one was related to one association previously described according to the analysis of their types: group 2.1.1 to the association *Prunello-Plantaginetum serpentinae* and group 2.1.2 to the association *Carduncello-Brachypodietum phoenicoidis.*

Finally, alliance 2.2 was split into three groups corresponding to the associations *Helictotricho-Seslerietum hispanicae, Calamintho-Seselietum montani* and *Carici-Teucrietum pyrenaici* according to the position of their type relevés. The latter is mainly distributed in the calcareous Cantabrian and Pyrenean mountains (Figure 9) and was correlated with the highest elevations and annual precipitation values (Figure 8).

Site conditions and biodiversity of the different vegetation units

The alliance 1.2 is distributed in the highest elevations but also shows by far the highest values of southing; alliance 2.2 is also found in high elevations, and both share lower mediterraneity values compared to alliances 1.1 and 2.1; the two latter alliances show similar values of high temperature and low precipitation but 2.1 occurs in the most thermic and less rainy areas (Table 5, Figure 10). Differences are not so clear in the case of soil carbonate content, although alliance 1.1 shows the highest mean. Regarding structural parameters, the biggest differences amongst alliances are in their shrub layer cover, with highest values for alliance 1.1 (Table 5). At association level, Figure 11 shows that 2.2.3 is found at higher elevations than the other two associations within the alliance, reaching similar elevations as the two associations in alliance 1.2, and shows the lowest mediterraneity values. Association 2.1.2 is found at the lowest elevations and shows the highest mediterraneity, although the lowest precipitation corresponds to its sister association 2.1.1 (Table 6).

The total species richness is similar among the different alliances, as well as richness of vascular plants and lichens (Figure 12). On the contrary, alliance 2.2 outstands by its high bryophyte richness (Figure 12).

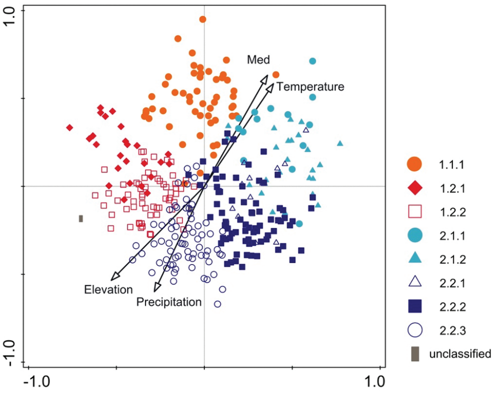

Figure 8. NMDS ordination of relevés from *Festuco-Brometea*. Eigenvalues: Axis 1 – 0.4308, Axis 2 – 0.3302, Axis 3 (not shown) – 0.2389. Med stands for Mediterraneity Index.

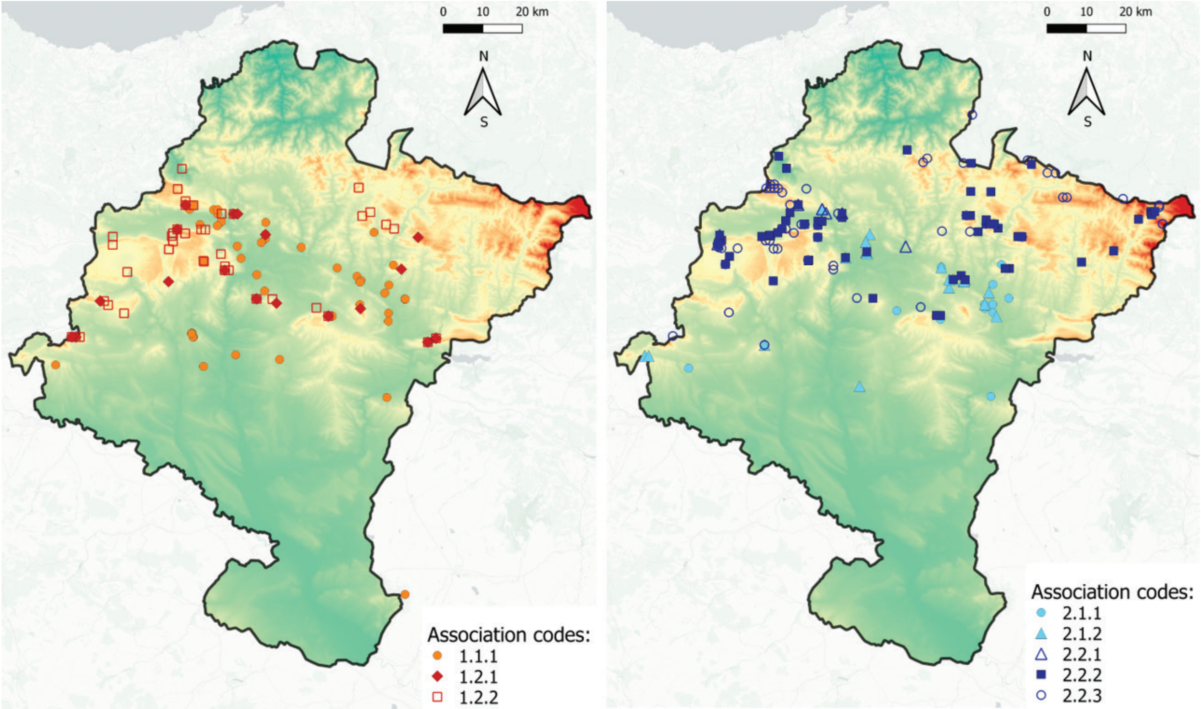

Figure 9. Location of the relevés from the class *Festuco-Brometea*: Order 1 (left) and Order 2 (right).

Table 5. Climatic structural, ecological and diversity characteristics of the orders and alliances within the *Festuco-Brometea*. The *p*-values and significance levels refer to ANOVAs.

Parameter	Alliances				*p*-value	Sig.
	1.1	1.2	2.1	2.2		
Total number of relevés	52	87	40	160		
Number of relevés from EDGG FW	18	5	8	33		
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD		
	Parameters calculated for all relevés					
Geographical and climatic parameters						
Elevation [m a.s.l.]	602±151	1030±215	561±139	912±273	<0.001	***
Mediterranity index	0.83±0.19	0.6±0.12	0.91±0.15	0.58±0.15	<0.001	***
Annual mean temperature [°C]	11.9±1.0	9.9±1.0	12.1±0.7	10.0±1.5	<0.001	***
Mean annual precipitation [mm]	1025±205	1287±210	920±167	1346±27.0	<0.001	***
	Parameters calculated for relevés from EDGG Field Workshop					
Vegetation structure						
Cover vegetation total [%]	74±27	68±16	91±7	85±14	0.033	*
Cover shrub layer [%]	4±4	0±0	1±2	0±1	<0.001	***
Cover herb layer [%]	69±22	62±15	79±26	81±16	0.068	.
Cover cryptogam layer [%]	15±17	9±7	34±32	14±12	0.021	*
Cover litter [%]	11±13	3±4	26±27	5±7	0.001	**
Herb layer maximum height [cm]	77±32	38±15	86±33	58±27	0.005	**
Species richness						
Species richness (total)	48.2±10.1	50.6±1.5	55.3±17.9	59.8±15.4	0.041	*
Species richness (vascular plants)	42.9±8.9	46.0±3.8	50.6±16.8	50.5±12.2	0.151	n.s
Species richness (cryptogams)	5.3±2.7	4.6±2.6	4.6±3.0	9.4±5.7	0.004	**
Species richness (bryophytes)	4.7±2.4	3.4±2.1	4.5±2.9	8.0±4.8	0.007	**
Species richness (lichens)	0.6±0.8	1.2±0.8	0.1±0.4	1.4±1.5	0.029	*
Topography						
Southing (cosine of aspect)	-0.1±0.7	0.8±0.2	-0.5±0.6	-0.5±0.5	<0.001	***
Inclination [°]	19±11	14±5	11±7	16±15	0.563	n.s
Maximum microrelief [cm]	7±4	9±7	7±7	11±9	0.240	n.s
Soil parameters						
Soil depth mean [cm]	14±6	8±5	21±9	17±9	0.034	*
Soil depth CV	48±26	100±82	35±29	46±35	0.020	*
Cover rocks and stones [%]	6±11	9±13	1±4	8±16	0.600	n.s
Cover gravel [%]	10±21	15±17	0±0	3±10	0.112	n.s
Cover fine soil [%]	84±26	76±18	99±4	89±22	0.261	n.s
Coarse fragments [%]	17±15	30±25	30±19	22±16	0.278	n.s
Fine fragments < 2mm [%]	83±15	70±25	70±19	78±16	0.278	n.s
pH	7.65±0.37	7.31±0.86	7.32±0.36	7.52±0.38	0.229	n.s
Electrical conductivity [µS/cm]	188±60	213±141	225±103	261±80	0.031	*
CaCO3 [%]	42.9±9	27.3±23.2	17.9±11.6	19.5±19	<0.001	***
Organic matter [%]	0.8±0.3	1.8±1.5	1.3±0.4	1.6±0.8	0.001	**

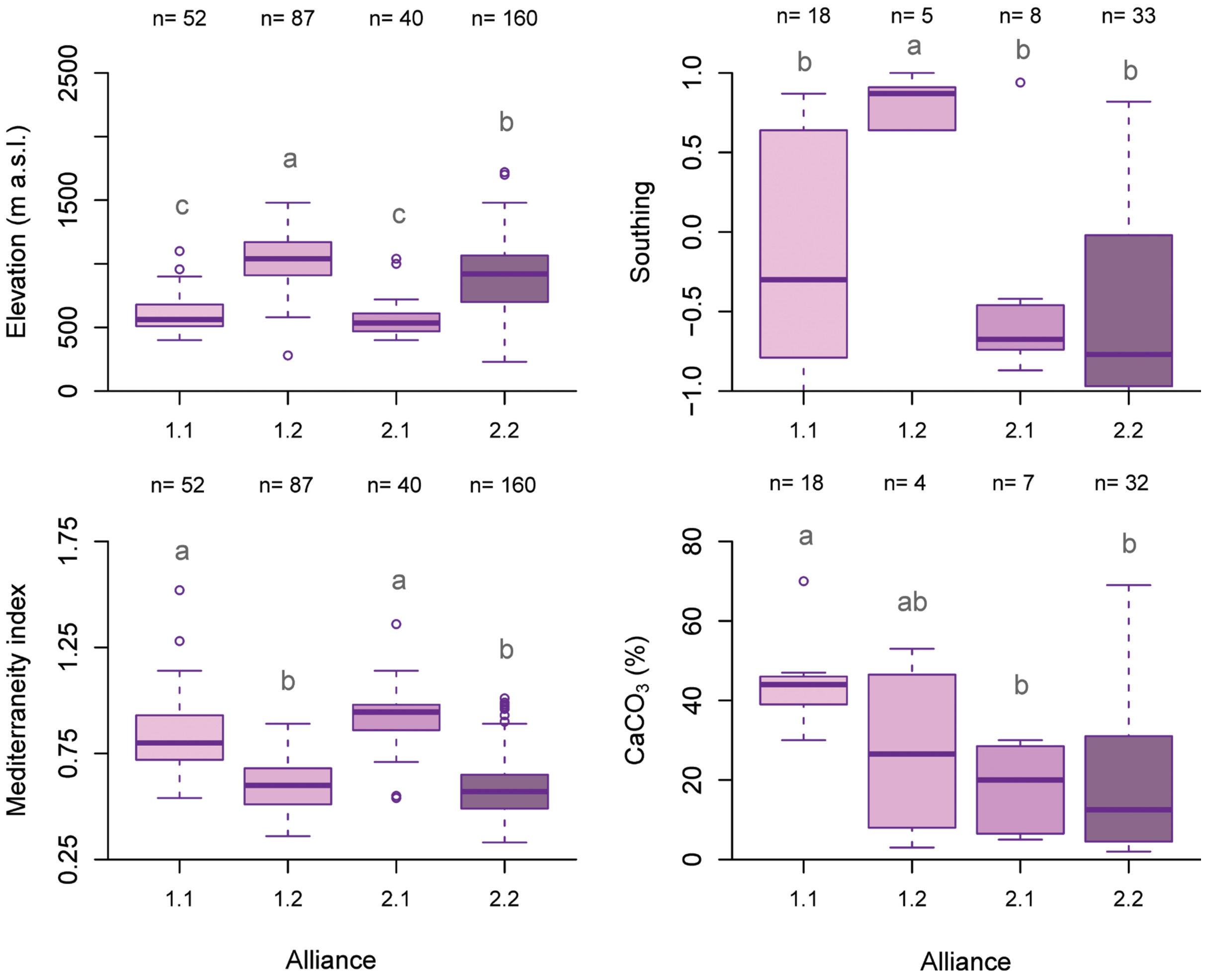

Figure 10. Comparison of four ecological variables among the four alliances. For elevation and Mediterraneity Index, all relevés were analysed, whereas for the rest of variables only relevés from EDGG Field Workshop were used. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

Table 6. Ecological characteristics of the associations within the *Festuco-Brometea*. The *p*-values and significance levels refer to ANOVAs.

Parameter	Association								*p*-values	Sig.
	1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3		
Total number of relevés	52	25	61	14	26	12	78	69		
Elevation [m a.s.l.]	602	1113	989	578	552	800	797	1060	<0.001	***
Mediterraneity index	0.83	0.61	0.59	0.89	0.91	0.57	0.64	0.51	<0.001	***
Annual mean temperature [°C]	11.8	9.8	9.9	12.1	12.1	10.5	10.5	9.4	<0.001	***
Mean annual precipitation [mm]	1025	1242	1302	905	928	1369	1258	1445	<0.001	***

Description of the *Festuco-Brometea* associations

Association 1.1.1 – *Thymelaeo ruizii-Aphyllanthetum monspeliensis*

(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 13)

Characterisation: Grasslands usually growing on the middle part of slopes, characterised by the dominance of *Brachypodium retusum* and *Bromopsis erecta* subsp. *erecta*. Typical Mediterranean grasses such as *Brachypodium retusum, B. phoenicoides, Dactylis glomerata* subsp. *hispanica, Festuca marginata* subsp. *andres-molinae* and *Helictochloa bromoides*, and chamaephytes as *Helianthemum apenninum* subsp. *apenninum, Lavandula latifolia* and *Thymus vulgaris* subsp. *vulgaris* are frequent in this association. In addition, typical species of submediterranean and temperate grasslands are also common: *Carex humilis, Koeleria vallesiana*, *Plantago lanceolata*, *Potentilla tabernaemontani*, *Sanguisorba minor*, and *Teucrium pyrenaicum*.

Ecology and distribution: These grasslands are typical of temperate submediterranean transitional areas, at elevations between 400 to 1,100 m a.s.l. The sampled stands are grazed or recently abandoned. They are distributed in the middle part of Navarre region, as serial stages of *Quercus faginea, Q. pubescens* and *Q. rotundifolia* forests, and main land use are the cereal crops. They are usually found in carbonate soils developed on marls, limestones, flysch,

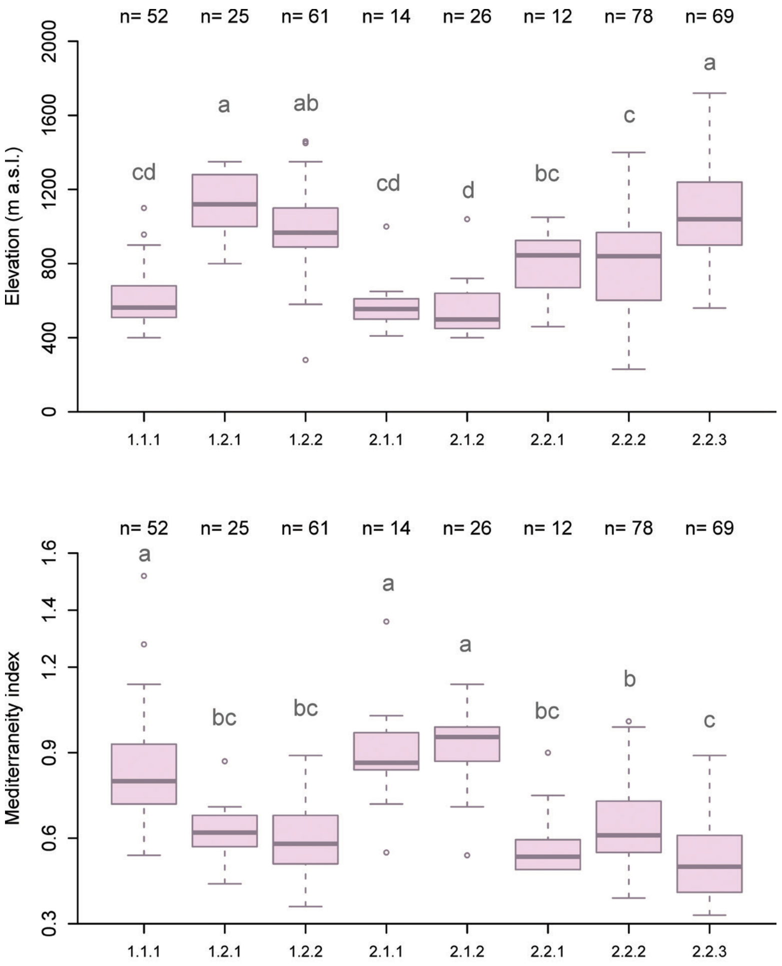

Figure 11. Comparison of elevation and Mediterraneity Index among the associations using all relevés from *Festuco-Brometea*. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

conglomerates and sandstones, in the meso-supramediterranean and mesotemperate-supratemperate sub-humid to humid belts (Berastegi et al. 2005).

Syntaxonomy: This unit matches quite well with the association *Thymelaeo ruizii-Aphyllanthetum monspeliensis,* described from the submediterranean central areas in Navarre by Braun-Blanquet (1966) as a dwarf-shrub community. However, Berastegi (2013) did not sample communities of the typical stands rich in dwarf shrubs, and our dataset only includes relevés of the subassociation *brachypodietosum retusi*. Therefore, the identity of this unit is mostly based on this subassociation dominated by hard-leaved grasses (*Brachypodiun retusum, Helictochloa bromoides*) and other hemicryptophytes such as *Bromopsis erecta* subsp. *erecta, Carex flacca* subsp. *flacca, C. humilis, Helictochloa pratensis* subsp. *iberica* and *Sanguisorba minor* aggr. (Berastegi et al. 2005). Although the type relevé assigned by Braun-Blanquet was also placed by the expert system in the same cluster, we would like to acknowledge that it is only one relevé and thus that the identity of this unit with the whole *Thymelaeo-Aphyllanthetum* is only provisional. Chamaephyte-rich stands should be included in new analyses to draw a final conclusion.

Association 1.2.1 – *Jurineo humilis-Festucetum hystricis* (relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 13)

Characterisation: These grasslands grow on ridges and flat summit areas that are very windy, in mountain ranges usually above 900 m a.s.l. located in the transition between temperate and Mediterranean climates, in areas where cryoturbation phenomenon usually occurs. *Carex humilis, Helianthemum canum* subsp. *canum* and *Koeleria vallesiana* show a very high constancy in these open grasslands, but they are characterised by species like *Anthyllis montana, Arenaria grandiflora* subsp. *grandiflora, Festuca hystrix, Jurinea humilis* and *Klasea nudicaulis,* most of them typical of the high Mediterranean mountains.

Ecology and distribution: These communities can be found at elevations between 650 and 1,350 m a.s.l., although more commonly above 900 m, in the supramediterranean and supratemperate subhumid-humid belts (Berastegi 2013). They grow on different calcareous rocks such as limestones, calcarenites, marl limestones and conglomerates, on very windy ridges and flat summit areas. Due to the landforms and the elevation at which they are

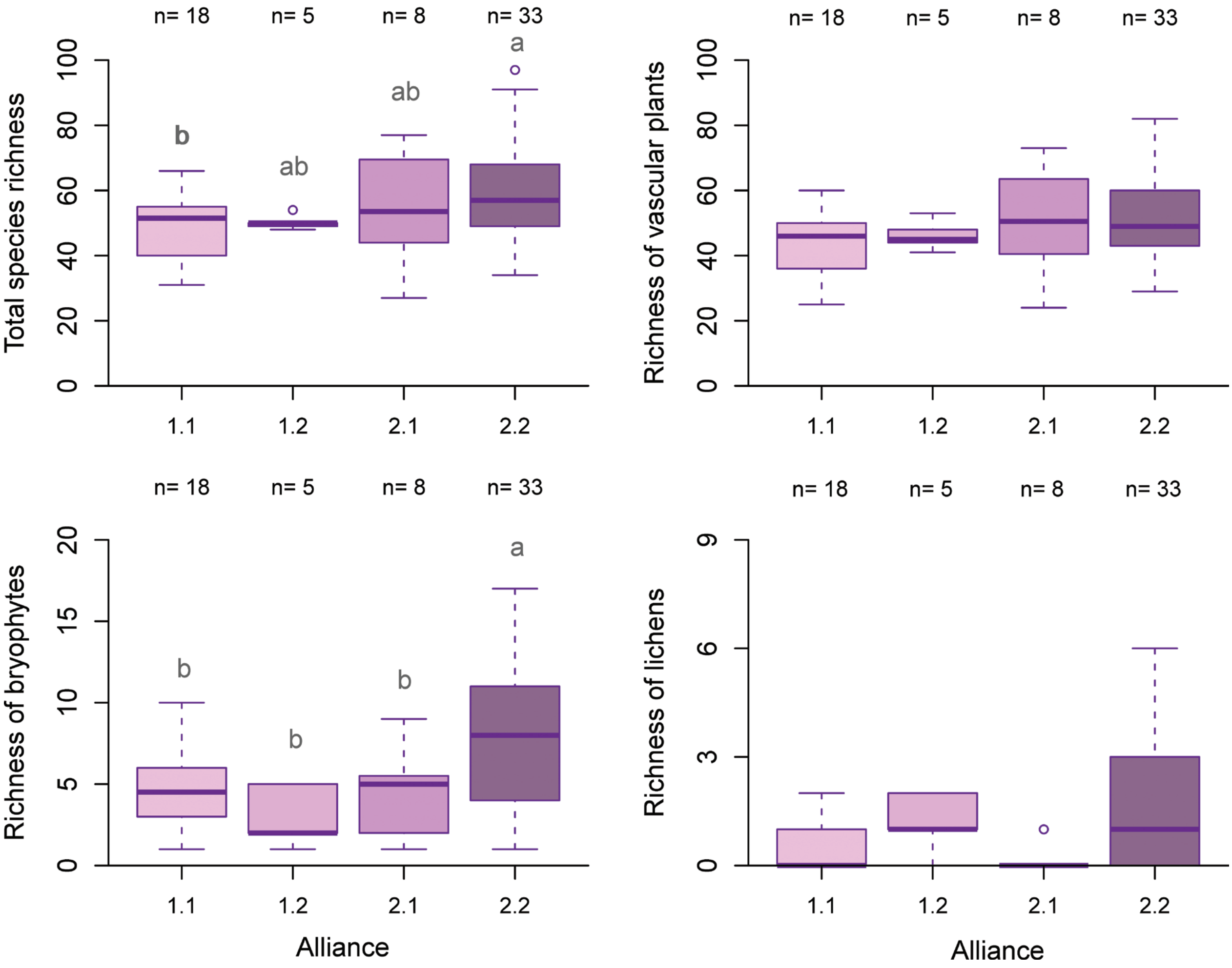

Figure 12. Comparison of species richness divided into four groups (total species, vascular plants, bryophytes and lichens) among the four alliances in *Festuco-Brometea* using the relevés from EDGG Field Workshop. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

found, the soils are usually stony due to the disintegration processes of the parent rock. Although the ombrotype of this area, e.g., the humidity type, is subhumid to humid, water availability for plants is very low, due to the low water retention capacity of the soils. They are often permanent natural communities, but they may also represent an initial successional stage, colonizing eroded soils after the elimination of more mature stages of the vegetation series in which they are integrated: *Fagus sylvatica, Quercus pubescens* and *Q. rotundifolia* series.

Syntaxonomy: This unit fits quite well with the association *Jurineo humilis-Festucetum hystricis*. Berastegi (2013) included these rocky grasslands in the class *Festuco-Ononidetea*, order *Festuco-Poetalia ligulatae* and alliance *Plantagini-Thymion mastigophori*, due to their affinity to the communities of the associations *Koelerio vallesianae-Thymetum mastigophori* García-Mijangos et al. 1994 and *Festuco hystricis-Genistetum eliassennenii* García-Mijangos et al. 1994 from submediterranean territories west of Navarre, where they are widely represented in the landscape (Loidi et al. 1997). These communities reach the central-western area of Navarre, but in specific geographical and ecological conditions, interspersed among other communities with which they share many species. For this reason, they do not achieve enough differential characteristics in the classification analysis to be considered in a different phytosociological class. It is therefore provisionally proposed that they should be included in the *Festuco-Brometea*, at least in Navarre context.

Association 1.2.2 – *Helianthemo incani-Koelerietum vallesianae*

(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 13)

Characterisation: These communities are dominated by dry grassland species such as *Carex humilis*, *Coronilla minima, Festuca rectifolia*, *Helianthemum canum* subsp. *canum*, *Helictochloa pratensis* subsp. *iberica*, *Koeleria vallesiana*, *Potentilla tabernaemontani,* or *Thymus praecox*. Typical species of meso-xeric grasslands such as *Bromopsis erecta* subsp. *erecta* or *Carthamus mitissimus* are also common. From a physiognomic point of view, they are characterised by being short grasslands, with a cover of around 70-90%, in which some creeping chamaephytes can be important.

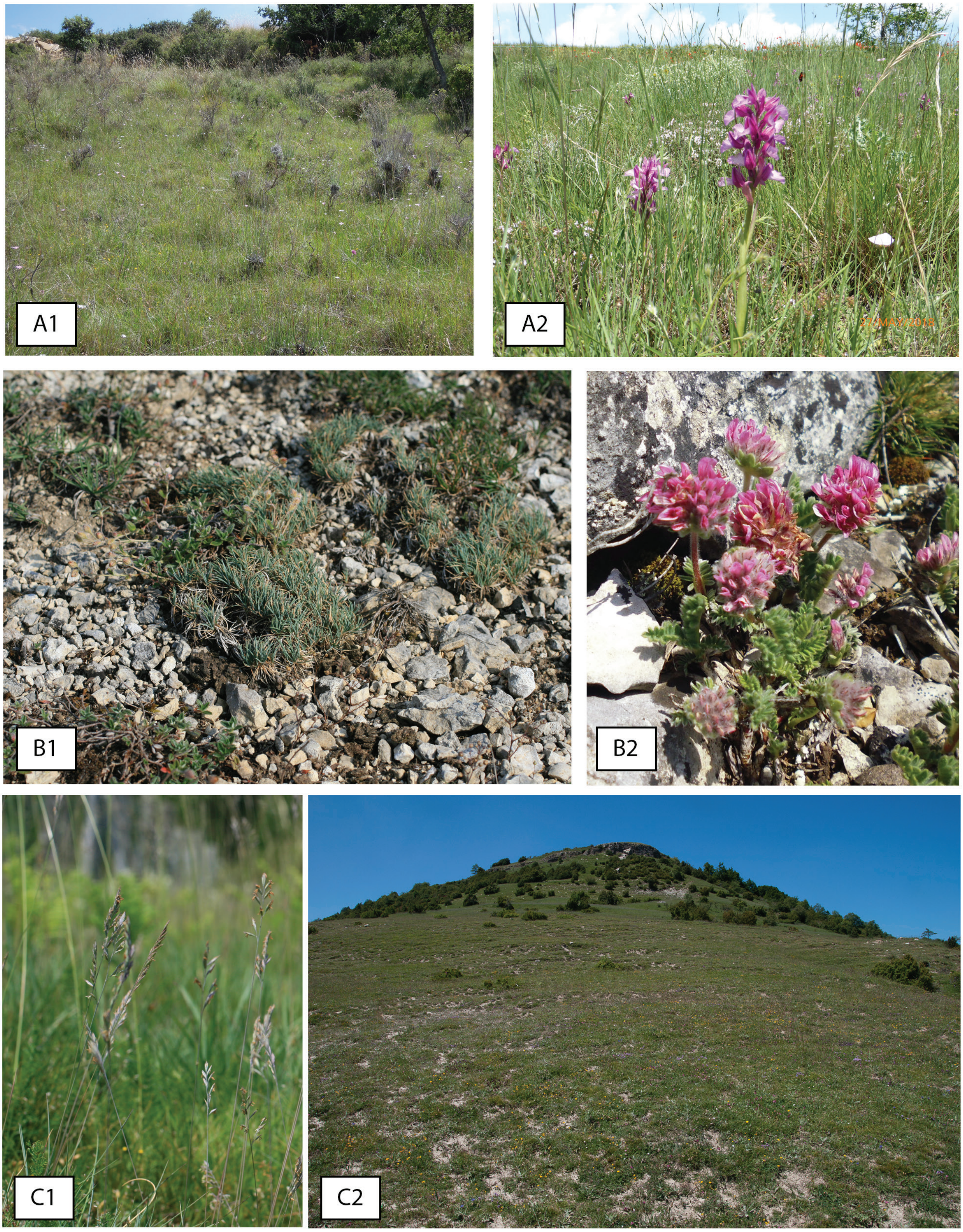

Figure 13. Photo plate showing typical stands of the associations included in order 1 of the *Festuco-Brometea*. A *Thymelaeo ruizii-Aphyllanthetum monspeliensis*, A1 Overview, A2 *Orchis papilionacea*, endangered in Navarre; B *Jurineo humilis-Festucetum hystricis*, B1 *Festuca hystrix*, B2 *Anthyllis montana*; C *Helianthemo incani-Koelerietum vallesianae*, C1 *Festuca rectifolia*, C2 overview. Photos: A. Berastegi (A2, B1, B2, C1); J. Dengler (A1, C2).

Ecology and distribution: The association represents pastures which are subject to intense livestock use, mainly by sheep, especially in the summer period. It occurs on different types of carbonate substrates (limestones, calcarenites, conglomerates, flysch), although mainly on limestone. They develop in the mountain ranges of the transition between the Atlantic and Mediterranean regions, also reaching the westernmost Pyrenean mountains, mostly in the montane belt.

Syntaxonomy: This unit matches well with the association *Helianthemo incani-Koelerietum vallesianae*, which was originally included in the class *Festuco-Ononidetea*, order *Ononidetalia striatae*, alliance *Genistion occidentalis* (Berastegi 2013), due to the floristic and ecological affinities to other rocky dry grasslands also included in this alliance. However, we would like to acknowledge that *Genistion occidentalis* originally included cushion shrub communities from Cantabrian mountains and Western Pyrenees (Díaz and Fernández-Prieto 1994), and only recently rocky dry grasslands from the Basque-Cantabrian mountains (*Helictotricho-Seslerietum hispanicae* and *Carici-Teucrietum pyrenaici*) were moved to this alliance and consequently to the class *Festuco-Ononidetea* (Rivas-Martínez 2011) from the class *Festuco-Brometea* where they had been previously placed (Rivas-Martínez et al. 1991a).

Association 2.1.1 – *Prunello hyssopifoliae-Plantaginetum serpentinae*

(relevès in Suppl. material 14; distribution in Figure 9)

Characterisation: These communities are characterised by species like *Festuca capillifolia*, *Jasonia tuberosa, Plantago maritima* subsp. *serpentina* or *Prunella hyssopifolia*. Other species with high frequency are *Blackstonia perfoliata*, *Carex flacca* subsp. *flacca*, *Centaurea jacea* or *Dorycnium pentaphyllum* subsp. *pentaphyllum*.

Ecology and distribution: They are typical of the submediterranean climate and can be found at elevations from 410 to 1,000 m a.s.l., in the colline and montane belts. These communities develop in micro-depressions in loamy or clayey soils, which, due to their impermeable nature, are subject to temporary waterlogging. During the rainy season, these areas can become flooded, while in periods of strong sunshine they dry out completely. They are relatively frequent in the areas of blue-grey loams in the central part of Navarre, as serial stages of *Quercus pubescens* and *Q. faginea* forests, and main land use are the cereal crops.

Syntaxonomy: This unit matches quite well with the *Prunello hyssopifoliae-Plantaginetum serpentinae* association, originally placed in the class *Molinio-Arrhenatheretea,* although as a quite deviant community from the alliance *Deschampsion mediae* that often occurs in mosaic with meso-xeric grasslands; thus, typical dry grassland species are common (Biurrun 1999; Berastegi 2013).

Association 2.1.2 – *Carduncello mitissimi-Brachypodietum phoenicoidis*

(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 14)

Characterisation: Grasslands growing usually on the middle or bottom part of slopes, characterised by *Blackstonia perfoliata, Brachypodium phoenicoides* (including its hybrid with *B. rupestre*), *Bromopsis erecta* subsp. *erecta, Carex flacca* subsp. *flacca, Eryngium campestre* or *Phleum pratense.* Some other typical *Festuco-Brometea* species also occur: *Carthamus mitissimus, Centaurea jacea, Ranunculus bulbosus* subsp. *bulbosus* or *Trifolium ochroleucon.* Species of the class *Molinio-Arrhenatheretea* are also common, including *Lotus corniculatus*, *Plantago lanceolata, Trifolium campestre* and *T. pratense.*

Ecology and distribution: These dry grasslands are typical for the submediterranean climate type and can be found at elevations between 400 and 1,040 m a.s.l., in the supramediterranean and mesotemperate belts. They appear on clayey soils developed from calcareous materials (marl and limestone). They are distributed in the middle area of Navarre region, as serial stages of *Quercus pubescens* and *Q. faginea* forests, and main land use are the cereal crops. The sampled stands are grazed with low intensity or have been recently abandoned.

Syntaxonomy: This unit matches well with the association *Carduncello mitissimi-Brachypodietum phoenicoidis*, originally included in the order *Brachypodietalia phoenicoidis* (Berastegi 2013).

Association 2.2.1 – *Helictotricho cantabrici-Seslerietum hispanicae*

(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 14)

Characterisation: These communities, dominated by the grasses *Brachypodium rupestre*, *Helictotrichon cantabricum* or *Sesleria autumnalis,* develop on rocky, steep slopes on limestone, usually with large crevices. In addition to the abovementioned species, it is common to find species such as *Bromopsis erecta* subsp. *erecta*, *Carex flacca* subsp. *flacca, Dactylis glomerata, Galium pumilum, Teucrium pyrenaicum* or *Vincetoxicum hirundinaria* subsp. *intermedium*. Some scrub species such as *Dorycnium pentaphyllum* subsp. *pentaphyllum, Erica vagans* or *Genista hispanica* subsp. *occidentalis* are also present, sometimes with relevant cover.

Ecology and distribution: These rocky grasslands are typical for the temperate climate and can be found at elevations between 460 and 1,050 m a.s.l., in the colline and montane belts These communities develop mainly in the context of the series of *Quercus ilex*, *Fagus sylvatica* and *Quercus pubescens*. However, their main role is as a permanent natural community on steep calcareous slopes.

Syntaxonomy: This unit roughly matches with the association *Helictotricho cantabrici-Seslerietum hispani-*

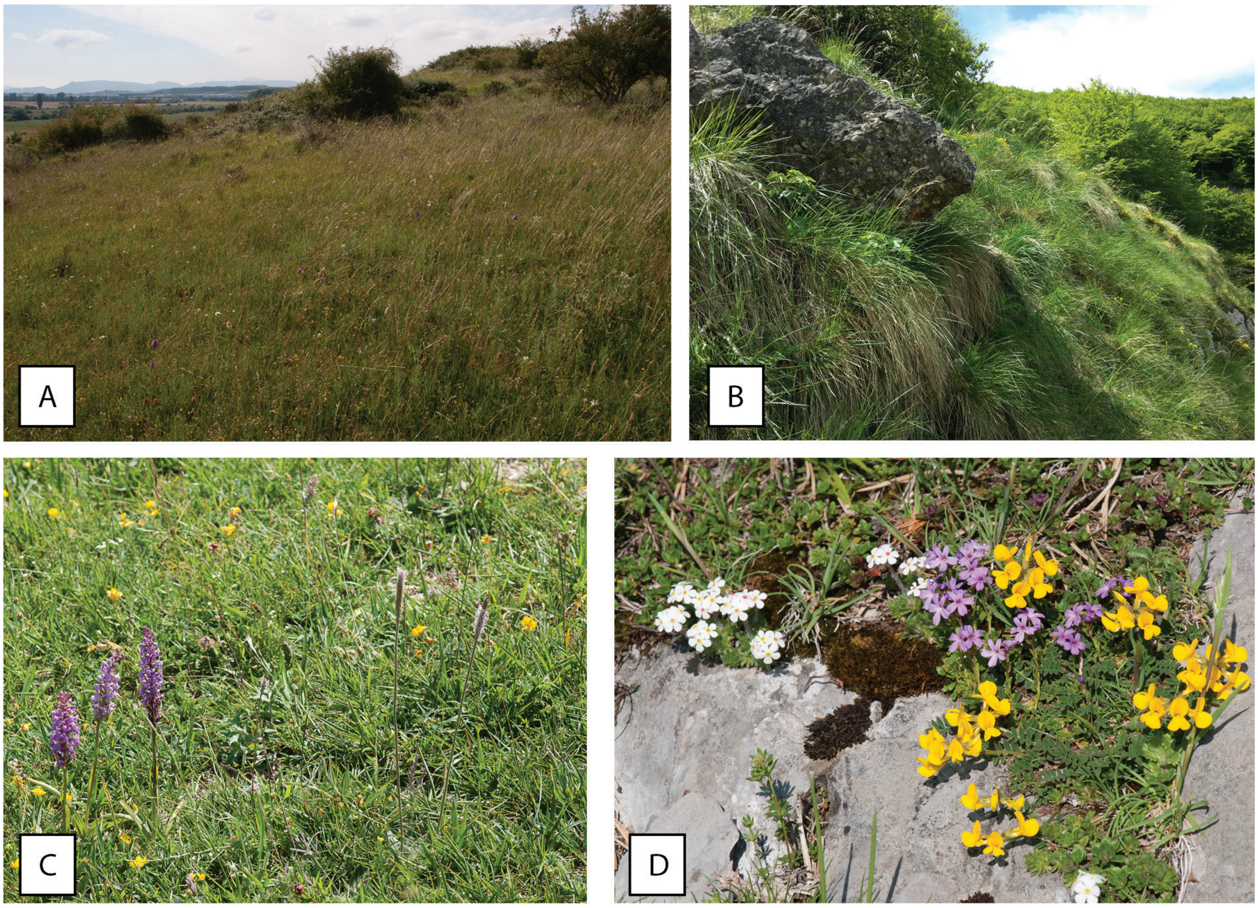

Figure 14. Photo plate showing typical stands of the associations included in order 2 of the *Festuco-Brometea*. A *Carduncello mitissimi-Brachypodietum phoenicoidis*; B *Helictotricho cantabrici-Seslerietum hispanicae*; C *Calamintho acini-Seselietum montani*, D *Carici ornithopodae-Teucrietum pyrenaici*. Photos: J. Dengler (A, C, D); A. Berastegi (B).

cae described by Braun-Blanquet (1967) in more atlantic areas of nearby Basque Country. Originally placed in the *Potentillo-Brachypodion pinnati* (Braun-Blanquet 1967; Rivas-Martínez et al. 1991a), the Spanish checklist of phytosociological syntaxa (Rivas-Martínez 2011) included it in the alliance *Genistion occidentalis*, therefore in the class *Festuco-Ononidetea*, although, it has also been assigned to the alliance *Bromo erecti-Teucrion pyrenaici* Rivas-Mart. et al. 1997 (Loidi et al. 1997).

Association 2.2.2 – *Calamintho acini-Seselietum montani*

(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 14)

Characterisation: Basophilous grasslands characterised by *Brachypodium rupestre, Briza media* subsp. *media, Bromopsis erecta* subsp. *erecta, Carex flacca* subsp. *flacca, Lotus corniculatus* or *Plantago media.* Some other taxa typical in these communities are *Carthamus mitissimus, Helictochloa pratensis* subsp. *iberica, Linum catharticum* subsp. *catharticum, Potentilla tabernaemontani, Ranunculus bulbosus* subsp. *bulbosus, Thymus praecox* and *Trifolium ochroleucon.* Species such as *Achillea millefolium* or *Trifolium pratense* are also common within the most mesic stands.

Ecology and distribution: These meso-xeric grasslands are typical for the temperate climate with submediterranean features and can be found at elevations between 230 and 1,400 m a.s.l., in the colline and montane belts. They develop on more or less deep soils, as serial stages of *Fagus sylvatica* and *Quercus pubescens* forests.

Syntaxonomy: This unit matches quite well with the association *Calamintho acini-Seselietum montani* described by Braun-Blanquet (1967) from temperate areas in Navarran inner valleys. In the Atlantic valleys in Navarre and nearby Basque Country it is replaced by the association *Seseli cantabrici-Brachypodietum rupestris* Br.-Bl. 1967 corr. Rivas-Mart. et al. 1984 (Rivas-Martínez et al. 1991a), linked to a more oceanic and humid climate. However, we could not reproduce this unit in our classification, as we had very sparse data from these Atlantic valleys.

Association 2.2.3 – *Carici ornithopodae-Teucrietum pyrenaici*

(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 14)

Characterisation: These grasslands are characterised by species such as *Clinopodium alpinum* subsp. *pyrenaeum, Festuca rectifolia, Helictochloa pratensis* subsp. *iberica, Ses-*

eli montanum subsp. *montanum* or *Teucrium pyrenaicum*, and some orophilous plants such as *Poa alpina* and *Vicia pyrenaica*. Typical elements of *Festuco-Brometea* such as *Bromopsis erecta* subsp. *erecta*, *Carex caryophyllea*, *Helianthemum nummularium*, etc. also occur, as well as others of *Nardetea* and *Molinio-Arrhenatheretea* such as *Festuca microphylla*, *Lotus corniculatus* or *Plantago lanceolata*.

Ecology and distribution: They are typical for the temperate climate and can be found at elevations between 560 and 1,720 m a.s.l., mostly in the montane belt. They usually grow on shallow soils (rendzina) developed on limestones, in the beech forest belt, and main land use is summer grazing (transterminant herds).

Syntaxonomy: This unit roughly matches with the association *Carici ornithopodae-Teucrietum pyrenaici* described by Loidi (1983), although it also includes some relevés originally included in *Festucion scopariae* and an important number of relevés originally classified in *Helianthemo incani-Koelerietum vallesianae*. Originally placed in the alliance *Potentillo-Brachypodion pinnati* (Loidi 1983; Rivas-Martínez et al. 1991a), the Spanish checklist of phytosociological syntaxa (Rivas-Martínez 2011) included it in the alliance *Genistion occidentalis*, therefore in the class *Festuco-Ononidetea*, although it has also been assigned to the alliance *Bromo erecti-Teucrion pyrenaici* Rivas-Mart. et al. 1997 (Loidi et al. 1997).

Discussion

Delimitation of the grassland classes

Although our results largely concur with the previous classification of grasslands in Navarre (Berastegi 2013), our analyses suggest a different treatment of the classes *Festuco-Brometea*, *Festuco-Ononidetea* and *Ononido-Rosmarinetea* compared to the Iberian tradition (Rivas-Martínez et al. 1991b; Rivas-Martínez 2011). Dry and rocky grasslands and dwarf-shrub communities have been traditionally assigned to the class *Festuco-Ononidetea* and those scrublands with a more Mediterranean character to *Ononido-Rosmarinetea*. Nevertheless, we could not recognise any of these two classes in Navarre in the context of the grasslands. Rather, they would remain within the communities dominated by dwarf shrubs and chamaephytes, while the communities dominated by grasses would belong to *Festuco-Brometea* or *Elyno-Seslerietea*. This new arrangement would tally with the European perspective of placing rocky grasslands in *Festuco-Brometea* (Willner et al. 2017, 2019; Dengler et al. 2020b), although their distinction from the remaining units in the classes *Festuco-Ononidetea* and *Ononido-Rosmarinetea* mentioned above, is still to be clarified.

The class *Festuco-Ononidetea* was proposed by Rivas-Martínez et al. (1991b) to separate grasslands rich in tussock grasses and dwarf shrubs with submediterranean continental supra-oromediterranean distribution from the communities dominated by nanophanerophytes and dwarf shrubs with broad Mediterranean distribution of the class *Rosmarinetea officinalis* Rivas-Mart. et al. 2002. The authors recognised two orders within the class, *Ononidetalia striatae* and *Festuco hystricis-Poetalia ligulatae*. Subsequently, Mucina et al. (2016) also included in *Festuco-Ononidetea* the order *Erysimo-Jurineetalia bocconei*, which includes submediterranean xeric calcicolous grasslands on skeletal soils of the Apennine Peninsula and the oromediterranean belt of Sicily. Nevertheless, the assignment of the orders *Ononidetalia* and *Erysimo-Jurineetalia* to the class *Festuco-Ononidetea* has been controversial (Bardat et al 2004; Biondi et al. 2014). In the Iberian Peninsula, the order *Ononidetalia striatae* has a Pyrenean and Cantabrian distribution, encompassing seven alliances that include a very heterogenous set of communities: dry grasslands, dwarf shrublands and cushions, occurring from the sea level to the subalpine belt (Rivas-Martínez 2011). According to our results, grasslands of *Ononidetalia* in Navarre should be included either in *Festuco-Brometea* or in *Elyno-Seslerietea*. The full set of communities of this order, including its type alliance *Ononidion striatae*, should be analysed together with dry grasslands in order to decide on its potential complete integration in *Festuco-Brometea*.

The class *Elyno-Seslerietea* gathers alpine and subalpine calcicolous swards of the nemoral mountain ranges of Europe. In Navarre, they belong to the Alpine-Pyrenean order *Seslerietalia caeruleae* and the alliance *Primulion intricatae* (Mucina et al. 2016). However, our analyses pose the question whether subalpine grasslands of *Festucion scopariae* should also be included in this class. Actually, this alliance had been originally included by Braun-Blanquet (1948) in *Elyno-Seslerietea*, but subsequently Rivas-Martínez et al. (1991b) transferred it to *Ononidetalia striatae*. Peyre and Font (2011) conducted a syntaxonomic revision by means of numerical analysis of the subalpine and alpine grasslands of the Pyrenees and Cantabrian Mountains and concluded that *Festucion scopariae* should be included in the order *Seslerietalia caeruleae,* even though it contains some thermophilous species. Our results also support the reclassification of *Festucion scopariae* into the class *Elyno-Seslerietea* as it presents a number of species of this class (*Euphrasia salisburgensis, Gentiana verna* subsp. *verna, Helictotrichon sedenense* subsp. *sedenense, Trifolium thalii*), which differentiates them from the rest of the *Festuco-Ononidetea* communities.

As regards the class *Carici-Kobresietea bellardii*, although our analysis included these communities in *Elyno-Seslerietea*, we kept it as a separate class, as it was only represented by two relevés in our dataset. Actually, these cryophytic alpine grasslands are very scarce in Navarre, so our geographic scope is not suitable to decide on the separation or grouping of both classes.

The class *Nardetea strictae* was defined as secondary oligotrophic grasslands and groups mesophilous or acidophilous, fairly grazed, tussock grasslands dominated by *Nardus stricta* from the montane to alpine belts with humid and hyper-humid ombroclimate (Rivas Goday and Rivas-Martínez 1963). Our relevés were included by Berastegi (2013) in the alliances *Violion caninae* and *Carici macrostylidi-Nardion strictae* (sub suballiance *Carici-Nardenion strictae*), following the classification of Rivas-Martínez (2011). However, the *Carici macrostylidi-Nardion,* grouping mat-grass chionophilous swards at high elevations of the Pyrenees and the Cantabrian Mountains (Rivas-Martínez et al. 1984) was transferred by Mucina et al. (2016) to the class *Juncetea trifidi*, within the order *Festucetalia spadiceae.* This new classification is based on the differentiation of the secondary mat-grass swards growing at low and mid-elevations included within the class *Nardetea*, from the primary oligotrophic pastures/grasslands occurring at high elevations, placed within the *Juncetea trifidi* (Mucina et al. 2016). Further analyses supported the separation of high and mid-low elevation swards (Rodriguez-Rojo et al. 2020), although Gavilán et al. (2017) included *Nardus stricta* grasslands from high elevations in the Pyrenees in the *Festucion eskiae* alliance, not in *Carici macrostylidi-Nardion*. Our analyses do not support the separation of low and high elevation swards, as all relevés originally assigned to the alliances *Violion caninae* and *Carici macrostylidi-Nardion* were grouped in the same cluster. In Navarre, the class *Juncetea trifidi* according to Rivas-Martínez (2011, as *Caricetea curvulae*) is represented by the association *Carici pseudotristis-Festucetum eskiae*, within the alliance *Festucion eskiae*. These communities have a central Pyrenean distribution and only occasionally reach the highest siliceous peaks in Navarre (Lakora Mountain). The scarcity of data from this alliance does not allow us to establish a clear differentiation between the classes *Nardetea* and *Juncetea trifidi* in the territory, as only one relevé from *Juncetea trifidi* was available, which was of course included in *Nardetea.* A more in-depth study would be necessary to decide definitively in this respect, since the high presence of acidophilous species in the communities of *Violion caninae, Carici macrostylidi-Nardion* and *Festucion eskiae* (Berastegi 2013) determines their grouping compared to the rest of the grasslands and pastures analysed in the context of this study.

According to our results, the association *Merendero-Cynosuretum* should also be included in the class *Nardetea strictae*. This association was originally included in the alliance *Cynsurion cristati* of the *Molinio-Arrhenatheretea* class (Tüxen and Oberdorfer 1958), although the high constancy of *Nardus stricta* and *Danthonia decumbens* is noteworthy. These pastures originate from the oligotrophic grasslands after intense grazing (Berastegi 2013). The position of this association within *Nardetea* would be justified by the high presence of acidophilous species diagnostic of this group, such as *Festuca microphylla, Galium saxatile* and *Polygala serpyllifolia*. However, they are enriched by species of the alliance *Cynosurion* due to livestock pressure.

Our analysis included relevés previously classified in the alliance *Sedion pyrenaici* from the class *Sedo-Scleranthetea* in *Nardetea strictae*. However, we have to consider the reduced context of our study, so we kept this class as a separate unit. In Navarre, these communities shaped by succulent species and dwarf chamaephytes growing on siliceous lithosols and rock surfaces (Rivas-Martínez et al. 2002) develop in montane and subalpine areas forming mosaics with grasslands of *Nardetea strictae.* Consequently, they share some acidophilous plants such as *Agrostis curtisii, Festuca microphylla* and *Galium saxatile*.

Molinio-Arrhenetheretea is the most diverse class in Navarre regarding the number of associations. Berastegi (2013) recognised twelve alliances grouped within four orders. Although some associations were not well represented in our data, especially the most hygrophilous ones, the TWINSPAN analysis did reproduce a structure with three branches interpreted as corresponding to the orders *Arrhenatheretalia elatioris, Molinietalia caeruleae* and *Holoschoenetalia.* The only changes regarding this class are the new positions of the associations *Merendero-Cynosuretum* (*Cynosurion, Arrhenatheretalia*) and *Prunello-Plantaginetum serpentinae* (*Deschampsion mediae, Holoschoenetalia*). We suggest moving the former to the class *Nardetea strictae*, as explained above, while the latter should be placed in *Festuco-Brometea*, as has been also explained in the results section.

The class *Lygeo-Stipetea* gathers Mediterranean pseudo-steppes on calcareous substrates and relict Mediterranean steppes on deep clayey soils (Mucina et al. 2016). In Navarre this class encompasses communities dominated by *Lygeum spartum* on the one hand and *Brachypodium retusum* grasslands on the other (Berastegi 2013). The former develops on the bottom of slopes receiving regular downslope input of fine materials (silt, clay) and can tolerate short periods of hydromorphy. *Lygeum spartum* communities are characterised by the co-occurrence of many annual species (*Asterolinon linum-stellatum, Filago pyramidata, Linum strictum, Trachynia distachya*) (Marcenò et al. 2019). However, the delimitation of *Brachypodium retusum* grasslands is another unresolved syntaxonomic issue (Apostolova et al. 2014). Two associations belonging to two different classes are recognised in the territory (Berastegi 2013), which is also reflected in our results. Within *Lygeo-Stipetea*, the association *Ruto angustifolio-Brachypodietum retusi* groups the typically Mediterranean grasslands of the Ebro valley (Braun-Blanquet and Bolòs 1958). The other syntaxon including grasslands rich in *Brachypodium retusum* is *Thymelaeo-Aphyllanthetum brachypodietosum retusi,* which was classified in *Festuco-Brometea* and is thus discussed in the next section.

Our analyses placed relevés of the classes *Poetea bulbosae* and *Stipo-Trachynietea distachyae* in *Lygeo-Stipetea*. However, our dataset contained only a small number of relevés from these classes and thus we cannot make any decision about the grouping of these classes within *Lygeo-Stipetea*. Therefore, we kept both classes as independent units.

Subdivision of the *Festuco-Brometea*

In Navarre, the class *Festuco-Brometea* is composed of dry grasslands dominated by hemicryptophytes that develop on non-hygromorphic soils in temperate and submediterranean climates (Berastegi 2013). According to our results, the class *Festuco-Brometea* in Navarre includes, besides the associations previously assigned to this class (*Calamintho-Seselietum montani* and *Carduncello-Brachypodietum phoenicoidis*), several associations that had been included in the class *Festuco-Ononidetea striatae* (Rivas-Martínez 2011; Berastegi 2013): *Carici-Teucrietum pyrenaici*, *Helianthemo-Koelerietum vallesianae* and *Helictotricho-Seslerietum hispanicae* from the order *Ononidetalia striatae,* and *Jurineo-Festucetum hystricis* from the order *Festuco-Poetalia ligulatae.* Additionally, the association *Thymelaeo-Aphyllanthetum monspeliensis,* classified in *Ononido-Rosmarinetea* by the Spanish checklist (Rivas-Martínez 2011) has also been included in *Festuco-Brometea*, as well as the association *Prunello-Plantaginetum serpentinae*, previously classified in *Molinio-Arrhenatheretea* (Rivas-Martínez 2011)

The numerical analysis clearly separates two groups that can be interpreted as two orders. Order 1 groups the more xerophytic relevès with Mediterranean influence which occupy an intermediate position between the orders *Brachypodietalia pinnati* and the more Mediterranean communities of *Festuco-Ononidetea* and *Ononido-Rosmarinetea*. This order would be a vicariant of *Astragalo-Potentilletalia* and *Stipo-Festucetalia pallentis* from central-southern Europe (Aćić et al. 2015).

Communities in this order 1 are included in two alliances. Alliance 1 includes the association *Thymelaeo-Aphyllanthetum monspeliensis,* originally included in the alliance *Helianthemo italici-Aphyllanthion monspeliensis* (class *Ononido-Rosmarinetea*) by Braun-Blanquet (1966). Subsequently most Spanish phytosociologists have also placed it there, including the Spanish checklist (Rivas-Martínez 2011), where it sits well due to the high cover of dwarf shrubs in the typical subassociation. A new comprehensive analysis including all basophilous grasslands and dwarf-shrublands from Mediterranean and submediterranean areas in Europe would help us decide not only on the syntaxonomic position of *Thymelaeo-Aphyllanthetum*, but also on the position of the alliance *Helianthemo-Aphyllanthion*. Consequently, we put forward the question whether a new alliance and order should be proposed for these grasslands rich in dwarf shrubs which would be transitional to *Lygeo-Stipetea* and *Ononido-Rosmarinetea*.

Alliance 2 in this order 1 includes two associations that were previously classified in two different orders of the class *Festuco-Ononidetea*: *Jurineo humilis-Festucetum hystricis* in the order *Festuco-Poetalia ligulatae* and *Helianthemo incani-Koelerietum vallesianae* in *Ononidetalia striatae* (Berastegi 2013). These communities contain a number of species diagnostic for perennial rocky calcareous grasslands of subatlantic-submediterranean Europe belonging to the *Xerobromion,* the *Festuco-Bromion* or the *Artemisio-Dichantion* (Chytrý et al. 2020), which justifies their inclusion within *Festuco-Brometea.* The identity of this alliance also remains unresolved until a comprehensive analysis including all basophilous grasslands and dwarf-shrublands in southern Europe is conducted.

Order 2 is related to *Brachypodietalia pinnati* and includes grasslands that usually develop in areas with a temperate climate, in well-constituted soils with relatively good water retention capacity and normally high total vegetation cover. *Calamintho-Seselietum* represents one of the typical associations of this order. This order also includes grasslands growing in rocky steep slopes from areas of high rainfall (*Helictotricho-Seslerietum hispanicae* and *Carici-Teucrietum pyrenaici*), as well as dry grasslands from submediterranean areas, but the latter ones are restricted to soils or topographic situations that allow relatively good water retention (*Prunello-Plantaginetum serpentinae* and *Carduncello-Brachypodietum phoenicoidis*).

Rocky grasslands from this order 2 (*Helictotricho-Seslerietum hispanicae* and *Carici-Teucrietum pyrenaici*) are included in *Ononidetalia striatae* in the Spanish checklist, but our analysis has shown that they have a strong floristic relationship with grasslands of *Brachypodietalia pinnati.* In fact, both associations were originally included in this order (Braun-Blanquet 1967; Loidi 1983).

Alliance 2.1, which includes the associations *Prunello-Plantaginetum serpentinae* and *Carduncello-Brachypodietum phoenicoidis* in Navarre, could be assigned to the alliance *Brachypodion phoenicoidis*. More comprehensive analyses would be needed to confirm, as this alliance is distributed along the Western Mediterranean region, and its type association *Brachypodietum phoenicoidis* Br.-Bl. 1924 was described in Mediterranean France (Rivas-Martínez 2011).

Proposed syntaxonomic scheme for the class *Festuco-Brometea* in Navarre

Class: *Festuco-Brometea* Br.-Bl. et Tx. ex Klika et Hadač 1944
  Order 1: ???
    Alliance 1.1: ???
      1.1.1: *Thymelaeo ruizii-Aphyllanthetum monspeliensis* Br.-Bl. et P. Montserrat in Br.-Bl. 1966
    Alliance 1.2: ???
      1.2.1: *Jurineo humilis-Festucetum hystricis* Peralta et al. in Berastegi 2013
      1.2.2: *Helianthemo incani-Koelerietum vallesianae* Berastegi et al. in Berastegi 2013
  Order 2: *Brachypodietalia pinnati* Korneck 1974 nom. cons. propos. (= *Brometalia erecti* Koch 1926)
    Nomenclatural remark: Dengler et al. (2003) proposed to reject the name *Brometalia erecti* Koch 1926 as nomen ambiguum, and Kuzemko et al. (2014) proposed to conserve the name *Brachypodietalia pinnati* Korneck 1974. This proposal was also adopted by Mucina et al. (2016), but no formal proposal has been submitted so far.

Alliance 2.1: ???
  - 2.1.1: *Prunello hyssopifoliae-Plantaginetum serpentinae* F. Prieto et al. ex Biurrun 1999
  - 2.1.2: *Carduncello mitissimi-Brachypodietum phoenicoidis* García-Mijangos et al. in Berastegi 2013

Alliance 2.2: *Potentillo montanae-Brachypodion pinnati* Br.-Bl. 1967
  - 2.2.1: *Helictotricho cantabrici-Seslerietum hispanicae* Br.-Bl. 1967
  - 2.2.2: *Calamintho acini-Seselietum montani* Br.-Bl. 1967
  - 2.2.3: *Carici ornithopodae-Teucrietum pyrenaici* Loidi 1983

Biodiversity

Grasslands of *Festuco-Brometea* showed the highest total species richness, and specifically meso-xeric grasslands of the association *Calamintho-Seselietum montani*, which have previously been highlighted as species rich grasslands (Dengler et al. 2016b; Boch et al. 2020). However, differences with mesic grasslands are not significant. In fact, only bryophyte richness is significantly higher in *Festuco-Brometea* than in *Molinio-Arrhenatheretea* in the Navarran context. This may be due to the continued agricultural extensive management of these secondary mesic grasslands, at least in part of the region, as it has been demonstrated that intensively managed grasslands tend to be species poor (Hilpold et al. 2018). In any case, the high bryophyte richness of *Festuco-Brometea* grasslands is comparable to that of alpine grasslands of *Elyno-Seslerietea*, which is the richest vegetation type when both bryophytes and lichens are considered. This significant cryptogam-richness of alpine grasslands was already shown by Dengler et al. (2020c) and has recently been evidenced using a very large dataset by Biurrun et al. (2021). We would also like to highlight the high lichen richness in the Mediterranean grasslands of *Lygeo-Stipetea*, which is comparable in this respect to *Elyno-Seslerietea*. Our results show that these Mediterranean grasslands, although being quite species-poor regarding total species richness and richness of vascular plants, host a high proportion of bryophytes and especially lichens, which was already observed by Biurrun et al. (2021).

Relevance of bryophytes and lichens

Up to now vegetation ecologists in the Southern European countries, and particularly in the Mediterranean region, rarely considered bryophytes and lichens as part of the vegetation - unlike many of their colleagues in temperate and boreal Europe. This is reflected by the fact that for example, Rivas-Martínez et al. (2002) in their overview of the syntaxa of the Iberian Peninsula did not list any non-vascular plant species (apart from few *Characeae* spp. and *Sphagnum* spp.) as diagnostic for any of the hundreds of syntaxa of the region. Also, Mucina et al. (2016), while listing some bryophytes and lichens as diagnostic for temperate and boreal classes, do not mention any for the Mediterranean classes. Even Dierßen (2001), who characterised the phytosociological prevalences of all European bryophyte species, systematically under-reported their presence in Mediterranean classes. As already highlighted by Guarino et al. (2012) in the report from the EDGG Field Workshop in Sicily, the non-vascular flora of Mediterranean grasslands can be quite rich. In fact, while amongst all grasslands of Navarre, those of the Mediterranean class *Lygeo-Stipetea* were poorest in vascular plants, they hosted the highest lichen diversity together with the *Elyno-Seslerietea*. We also found that bryophytes and lichens are not randomly distributed across communities but have clear and often narrow prevalences which makes them equally effective diagnostic species as many vascular plants. All this calls for a better consideration of non-vascular plants in syntaxonomic studies in South European countries.

Conclusions and outlook

The combination of numerical methods allows a standardisation of the classification of grassland types. In fact, with our expert system we could largely reproduce the associations previously recognised in the region. Moreover, some often "diagnostic" species mentioned in the literature could be confirmed by our numerical analyses of a large dataset, while others were not supported by the data. However, at the class level, we found significant deviations from the Iberian syntaxonomic tradition (Rivas-Martínez et al. 2002; Rivas-Martínez 2011) and we propose a new system that matches the Iberian data more appropriately, and is consistent with the European concept of the class *Festuco-Brometea*. In any case, questions still remain regarding classification at order and alliance level, which can only be solved by means of a comprehensive analysis of all basophilous grasslands and dwarf-shrub communities in southern Europe. This analysis will also allow for the delimitation of the controversial class *Festuco-Ononidetea*.

Our study provides, for the first time, an electronic expert system for the grasslands of Navarre, which allows a standardised assignment of any new relevé, thus is of enormous value, particularly for practitioners. We provide, also for the first time, a detailed databased characterisation and comparison of the syntaxa in terms of their environmental conditions and biodiversity. We were also able to show that bryophytes and lichens, contrary to past assumptions, are core elements of these grasslands and in particular, the Mediterranean ones of *Lygeo-Stipetea*, both in terms of biodiversity and of diagnostic species. Therefore, they should also be taken into account in Mediterranean phytosociology.

Once the main five phytosociological classes were differentiated, our study focused on the analysis of the *Festuco-Brometea*. Therefore, an in-depth analysis based on expert systems of the rest of the classes would be desirable. Moreover, classes whose status could not be resolved due to a small/marginal dataset or due to plot sizes being too small, should be specifically addressed in future studies with better/more data from a larger area.

Finally, it can be emphasised that we have provided important insights from the western part of Europe that complement the extensive studies of Willner et al. (2017, 2019) from Central and Eastern Europe. Thus, we have taken a new step on the pan-European classification of the *Festuco-Brometea*. With this aim, we acknowledge that these comprehensive analyses would be facilitated if the hierarchical expert system and hierarchical determination of diagnostic species could be directly implemented in JUICE.

Data availability

The vegetation-plot data underlying this study are stored and available in the GrassPlot database (https://edgg.org/databases/GrassPlot; dataset code ES_A; Dengler et al. 2018a, Biurrun et al. 2019), from which they can be requested according to the GrassPlot Bylaws, and in the Vegetation-Plot Database of the University of the Basque Country (BIOVEG) (Biurrun et al. 2012), which is available in the European Vegetation Archive (Chytrý et al. 2016) and the Global Vegetation Database sPlot (Bruelheide et al. 2019) as dataset EU-00-011.

Author contributions

I.G.M, I.B. and A.B. organized the 7th EDGG Field Workshop in Navarre (Spain); as EDGG Field Workshop Coordinator during the Field Workshop, J.D. ensured consistent application of the EDGG methodology, I.G.M. identified the vascular plant species collected during the Field Workshop, J.E. identified the lichens, R.N. identified the bryophytes and added ecological aspects, and O.Y. analysed the soil samples and described methodological aspects; A.B. compiled 839 relevés used in the paper from 1996 to 1999; I.G.M. together with J.D. developed the numerical classification, implemented the expert system and identified the diagnostic species with the collaboration of I.B., A.B., A.K., M.J., and D.V.; M.J. developed the NMDS ordination, I.D. and D.V. analysed differences between syntaxa by means of ANOVAs and J.D. calculated and analysed biodiversity patterns; I.G.M. led the writing of the manuscript with substantial inputs from A.B., I.B. and J.D.; all authors critically revised the manuscript.

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Supplementary material

Supplementary material 1
Geographic, environmental and structural data of the relevés
Link: https://doi.org/10.3897/VCS/2021/69614.suppl1

Supplementary material 2
Ordered relevé table and complete constancy table of the five classes
Link: https://doi.org/10.3897/VCS/2021/69614.suppl2

Supplementary material 3
Definition of the aggregates used
Link: https://doi.org/10.3897/VCS/2021/69614.suppl3

Supplementary material 4
Confusion matrix comparing TWINSPAN and original classification
Link: https://doi.org/10.3897/VCS/2021/69614.suppl4

Supplementary material 5
Information on type relevés
Link: https://doi.org/10.3897/VCS/2021/69614.suppl5

Supplementary material 6
Expert system for the five classes
Link: https://doi.org/10.3897/VCS/2021/69614.suppl6

Supplementary material 7
Expert system for the *Festuco-Brometea* orders
Link: https://doi.org/10.3897/VCS/2021/69614.suppl7

Supplementary material 8
Expert system for the *Festuco-Brometea* order 1 alliances
Link: https://doi.org/10.3897/VCS/2021/69614.suppl8

Supplementary material 9
Expert system for the *Festuco-Brometea* order 2 alliances
Link: https://doi.org/10.3897/VCS/2021/69614.suppl9

Supplementary material 10
Expert system for the *Festuco-Brometea* alliance 1.2 associations
Link: https://doi.org/10.3897/VCS/2021/69614.suppl10

Supplementary material 11
Expert system for the *Festuco-Brometea* alliance 2.1 associations
Link: https://doi.org/10.3897/VCS/2021/69614.suppl11

Supplementary material 12
Expert system for the *Festuco-Brometea* alliance 2.2 associations
Link: https://doi.org/10.3897/VCS/2021/69614.suppl12

Supplementary material 13
Synoptic table with seven clusters from TWINSPAN
Link: https://doi.org/10.3897/VCS/2021/69614.suppl13

Supplementary material 14
Ordered relevé table and complete constancy table of the *Festuco-Brometea*
Link: https://doi.org/10.3897/VCS/2021/69614.suppl14

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NOMENCLATURAL PROPOSAL PHYTOSOCIOLOGICAL NOMENCLATURE

Request (3) for a binding decision on the valid publication of the names *Xerobromion* and *Mesobromion* in Zoller 1954

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Abstract

The two alliances *Xerobromion* and *Mesobromion* derive from the change of rank of two suballiances of the *Bromion* Koch 1926 (*Xerobromenion* and *Mesobromenion*). Zoller (1954a) recognized that those suballiances could not belong to the same alliance (i.e. *Bromion*) and treated them as two separate alliances, although some doubts can be raised that he did not clearly adopted them at the rank of alliance. Zoller's work having been overlooked, other authors proposed subsequently to rise the *Xerobromenion* and *Mesobromenion* to the rank of alliances. Accordingly, the alliances *Xerobromion* and *Mesobromion* are often cited with author citations other than Zoller 1954. The present paper requests a binding decision on the valid publication of the names *Xerobromion* and *Mesobromion* in Zoller (1954a).

Abbreviations: EVC = EuroVegChecklist; ICPN = International Code of Phytosociological Nomenclature.

Keywords

Artemisio albae-Brometalia erecti, *Bromion erecti*, *Festuco-Brometea*, ICPN, phytosociological nomenclature, syntaxonomy

Introduction

The name *Mesobromion erecti* (Br.-Bl. et Moor 1938) Oberd. 1957 was recently proposed as *nomen conservandum* against the name *Bromion erecti* W. Koch 1926 (Proposal 22; Theurillat et al. 2017). On the other hand, Terzi et al. (2016, pp. 313–314) considered that earlier than Oberdorfer (1957), Zoller (1954a) had validly raised the suballiances *Mesobromenion* and the *Xerobromenion* to the alliance level. This issue concerns a controversial interpretation of the article 3b of the ICPN (Theurillat et al. 2021). A binding decision (definition XIV of ICPN) would be useful to resolve the different interpretations regarding the first valid publication of the names *Mesobromion* and *Xerobromion*. Therefore, the present request can be considered an addition to Proposal 22, presented by Theurillat et al. (2017).

Xerobromion (Braun-Blanquet et Moor 1938) Zoller 1954 and *Mesobromion* (Braun-Blanquet et Moor 1938) Zoller 1954

The two suballiances *Xerobromenion* and *Mesobromenion* were originally proposed by Braun-Blanquet and Moor (1938) to separate the xerophilous associations from the meso-xerophilous ones within the alliance *Bromion* Koch 1926. Terzi et al. (2016) suggested to retain the name *Xerobromion*

(Braun-Blanquet et Moor 1938) Zoller 1954 as the correct name at the alliance level over the later name *Xerobromion* (Braun-Blanquet et Moor 1938) Moravec in Holubet al. 1967 that was published in overlooking Zoller's publication (J. Moravec to J.-P. Theurillat, pers. comm.). On p. 314, Terzi et al. (2016) typified the *Xerobromion erecti* (Braun-Blanquet et Moor 1938) Zoller 1954 with the association *Xerobrometum rhenanum* Braun-Blanquet in Braun-Blanquet et Moor 1938. [The earliest available name for the illegitimate *Xerobrometum rhenanum* would be the *Cerastio-Brometum* Zoller 1954.] Zoller's work having been overlooked, the name *Xerobromion erecti* is mostly referred to Moravec in Holub et al. 1967 (e.g., Royer 1991; Pott 1992; Mucina et al. 1993; Biondi et al. 1995; Rivas-Martínez et al. 2011). However, the author citation '*Xerobromion erecti* (Braun-Blanquet et Moor 1938) Zoller 1954' is retained in Theurillat et al. (1995), and in the EVC (Mucina et al. 2016), and it was selected as the holotype of the order *Artemisio albae-Brometalia erecti* Ubaldi ex Dengler et Mucina in Mucina et al. 2009 (Mucina et al. 2009, p. 269) in the form '*Xero-Bromion erecti* Zoller 1954' [recte: *Xerobromion* (Braun-Blanquet et Moor 1938) Zoller 1954]. However, the *Artemisio albae-Brometalia erecti* Ubaldi ex Dengler et Mucina in Mucina et al. 2009 is a superfluous name (Art. 29c) for the validly published *Artemisio albae-Brometalia erecti* (Biondi, Ballelli, Allegrezza et Zuccarello 1995) Ubaldi 1997. Since the name by Dengler and Mucina includes Ubaldi's name, it is automatically typified by the type of Ubaldi's name (Art. 18b), namely the '*Xerobromion* (Br.-Bl. and Moor 1938) Moravec in Holub et alii 1967'.

The situation is different with the name *Mesobromion erecti* (Braun-Blanquet et Moor 1938) Zoller 1954 that was almost completely overlooked. In this case, the correct name according to the rules (Art. 24) should be *Bromion erecti* Koch 1926. However, that name has been proposed as a *nomen ambiguum* (see Theurillat et al. 2017). Consequently, Theurillat et al. (2017) proposed to retain the name *Mesobromion erecti*, yet not the earlier name *Mesobromion erecti* (Braun-Blanquet et Moor 1938) Zoller 1954 but the later, independently published *Mesobromion erecti* (Braun-Blanquet et Moor 1938) Oberdorfer 1957, which has been used by the majority of authors.

However, there could be a doubt about the validity of Zoller's names, an issue raised by W. Willner in Theurillat et al. (2017, p. 385). That is, Art. 3b could apply because, albeit explicitly proposed by Zoller, the names might not be clearly adopted by the author.

The reasoning to consider Zoller's names as validly or invalidly published were given in Terzi et al. (2016) and Theurillat et al. (2017). As pointed out by Terzi et al. (2016, p. 313), Zoller (1954a, 34–36), in a critic of the syntaxonomy of the order *Brometalia* in Braun-Blanquet and Moor (1938), found great difficulties in considering the "*Xerobromion*" and the "*Mesobromion*" as two suballiances of the same alliance, namely the *Bromion* sensu Braun-Blanquet and Moor (1938), due to the important floristic, ecological, chorological, and structural differences between them: "*Xerobromion und Mesobromion sind sowohl in floristischer und arealtypischer als auch in ökologischer Hinsicht so verschieden, daß sie nicht in einer höheren Einheit zusammengefaßt werden können*" [*Xerobromion* and *Mesobromion* are so different in floristic and chorological as well as in ecological respect that they can not be combined in one higher unit] (Zoller 1954a, p. 293). Therefore, Zoller (1954a, p. 36) refused to consider the two suballiances as belonging to the same alliance, and instead he implicitly retained the two syntaxa, *Xerobromion* and *Mesobromion*, as two separate alliances: "*Einer Vereinigung von Xerobromion, Mesobromion und Violion calaminariae in einem Bromion-Verband stellen sich deshalb zahlreiche Schwierigkeiten entgegen. Eine solche Zusammenfassung kann angesichts der großen Verschiedenheiten nur mit Zwang vorgenommen werden, weshalb wir auch hier davon absehen*" [A combination of *Xerobromion*, *Mesobromion* and *Violion calaminariae* within a *Bromion* alliance therefore faces numerous difficulties. In view of the great differences, such a pooling can only be done with force, which is why we refrain from doing it here]. Although Zoller (1954a) did not explicitly say that *Xerobromion* and *Mesobromion* are two separate alliances, it should be noted that he wrote in the indicative ("... they can not be combined in one higher unit"). If he would not be affirmative about having two different alliances, he would have used the conditional (e.g., "... they should perhaps not be combined in one higher unit"). Moreover, the two syntaxa are consistently treated as well separated objects throughout Zoller's work, as is particularly clear from the table of contents (pp. 3–6).

In addition to having the *Xerobromion* and the *Mesobromion* as two separate alliances, Zoller (1954a, p. 38) also wrote that he refrained from classifying the numerous *Bromus erectus* meadow associations of the Swiss Jura in the higher units of the Braun-Blanquet sociological system, referring to a previous article (Zoller 1954b): "*Wenn wir auf eine Einordnung der zahlreichen, im Schweizer Jura vorkommenden Assoziationen der Bromus erectus-Wiesen in die höheren Einheiten des soziologischen Systems von Braun-Blanquet verzichten, so stellt sich an dieser Stelle die wichtige Frage, wie wir sonst eine folgerichtige Eingliederung dieser Rasen in die Vegetation Europas erreichen. Die Lösung dieser Probleme wurde schon früher eingehend besprochen. Ich verweise hier auf die ausführlicheren Erörterungen in der arealtypischen Arbeit* (Zoller 1954, S.39ff.),…" [If we refrain from classifying the numerous associations of the *Bromus erectus* meadows occurring in the Swiss Jura in the higher units of the sociological system of Braun-Blanquet, then the important question arises how we can otherwise integrate these meadows into the vegetation of Europe in a coherent way. The solution to this problem has already been discussed in detail. I refer here to the detailed discussion in the chorological work.]. In that work, Zoller (1954b, p. 39) claimed to have refrained from using a hierarchical sociological system of classification ("*Ich sehe deshalb bewußt ab von einer konsequenten Einordnung der verschiedenen Typen der Trockenwiesen in das hierarchisch soziologische System mit Ordnungen und Klassen analog der Sippensystematik, wie es heute zwar von vielen Autoren angestrebt wird*" [I therefore deliberately refrain from classifying the various types of dry meadows consistently in the hierarchical sociological system with orders and classes in analogy to the taxonomy of species, as many authors aim today]).

However, Theurillat et al. (2017, p. 385) observed that, although Zoller (1954a) explicitly refused to consider the "*Xerobromion*" and the "*Mesobromion*" as two suballiances of the *Bromion*, he nevertheless mentioned "*Xerobromion*-Unterverbandscharakterarten" [characteristic species of the suballiance *Xerobromion*] in his tables 1 and 2 to indicate such species in accordance with Braun-Blanquet and Moor (1938). Therefore, it could be argued that Zoller did not formally accept the two names *Xerobromion* and *Mesobromion* at the new rank since he did not formally wrote it, besides questioning the higher ranks of order and class of the syntaxonomic scheme, as mentioned above.

In conclusion, on the one hand, when Zoller said that the *Xerobromion* and the *Mesobromion* do not belong to the same alliance *Bromion*, he implicitly stated that they are two separate alliances. On the other hand, Zoller did not formally say that the *Xerobromion* and the *Mesobromion* are two separate alliances, and he mentioned "characteristic species of the suballiance *Xerobromion*" in two tables. Therefore, a binding decision is requested whether the two names are clearly adopted or not (Art. 3b) by Zoller.

Author contributions

All the authors contributed to the nomenclature research and critically revised the manuscript.

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NOMENCLATURAL PROPOSAL PHYTOSOCIOLOGICAL NOMENCLATURE

Request (4) and Proposal (28): to conserve the name *Molinio arundinaceae-Quercetum roboris* Neuhäusl et Neuhäuslová-Novotná 1967

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Abstract

We propose (i) to select *Quercus robur* as the name-giving taxon of the associations *Molinio arundinaceae-Quercetum* Samek 1962 and *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967 and (ii) to conserve the younger name *Molinio arundinaceae-Quercetum roboris* Neuhäusl et Neuhäuslová-Novotná 1967, representing hygrophytic Central European acidophilous oak forests (*Quercion roboris* alliance).

(28) *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967: 17–23, table 2.

Typus: Neuhäusl and Neuhäuslová-Novotná (1967), table 2, rel. 11 (lectotypus; Pallas 1996: 51).

(H) *Molinio arundinaceae-Quercetum* Samek 1962: 134–135, table V on p. 156–160.

Typus: Samek (1962), Table V, rel. 28 (lectotypus; Moravec 1998: 33).

Taxonomic reference: Marhold et al. (1998).

Abbreviations: ICPN = International Code of Phytosociological Nomenclature.

Keywords

conserved name, phytosociological nomenclature, *Quercion roboris*, syntaxonomy, vegetation classification

Introduction

This proposal deals with hygrophytic Central European acidophilous oak forests. They are characterized by a dominance of *Quercus robur* agg. in the tree layer and the presence of *Frangula alnus* in the well-developed shrub layer. In addition to acidophilous and acidic-tolerant species, their herb layer contains primarily species indicating seasonal fluctuations in the groundwater table (e.g., *Deschampsia cespitosa*, *Molinia caerulea* agg., *Potentilla erecta*), accompanied by indicators of air humidity (mainly ferns). These stands usually inhabit wet flatlands with poorly drained soils or wet terrain depressions (Slezák et al. 2020).

In accordance with the published syntaxonomic revision of acidophytic oak forests in Slovakia (Slezák et al. 2020), we propose to conserve the association name *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967. The idea for conserving this name was originally recommended by Jens Pallas

(Münster, Germany) as a possible solution to nomenclatural questions and the syntaxonomic interpretation of hygrophytic acidophilous oak forests in the eastern part of Central Europe. Some authors have recently classified these stands into the broadly defined association *Holco mollis-Quercetum roboris* Scamoni 1935, but its protologue (Scamoni 1935) and neotype-relevé (Pallas 1996) do not fully correspond to a periodically wet acidophilous oak forests with a dominance of *Molinia* species.

Nomenclatural discussion

In a vegetation study of the Brdské hřebeny Mts (Czech Republic), Samek (1962) described the new association '*Molinio-Quercetum*'. He applied this name for oak forests with species adapted to an intermittent moisture regime (i.e., species of *Molinia* meadows) and a constant occurrence of some acidophytes. Since all three relevés in the phytosociological table include only *Molinia arundinacea*, Moravec (1998) added the species epithet according to Recommendation 10C of the ICPN and wrote the name as '*Molinio arundinaceae-Quercetum* Samek 1962'.

Neuhäusl and Neuhäuslová-Novotná (1967) described hygrophytic acidophilous oak forests dominated by *Molinia* species under the identical name *Molinio arundinaceae-Quercetum*, without reference to Samek. However, in both original diagnoses of the association name, the name-giving *Quercus* species was not indicated by the authors of the name. Therefore, a binding decision (Art. 40b of ICPN) is required for selecting the name-giving taxa.

Samek (1962) used a "double form" of the oak species name *Quercus robur-sessilis* in the phytosociological Table V (pages 156–160). It seems that the author did not distinguish the two oak species present in the relevés, i.e., *Q. robur* vs. *Q. sessilis* (synonym of *Q. petraea*). However, we assume that the first position of the oak species name "*robur*" indicates the dominant and/or typical oak species of the tree layer for this association, because in the Samek study, the oak species name *Quercus sessilis-robur* is reported, for example, in the case of the *Luzulo-Carpinetum* association (Table II, pages 146–149). We therefore propose *Q. robur* as the name-giving taxon of the association *Molinio arundinaceae-Quercetum* Samek 1962.

Neuhäusl and Neuhäuslová-Novotná (1967) published this association name based on 33 phytosociological relevés (in table 2) collected in the Czech Republic. It is clear from the author's description of the species composition that the forest overstory of well-developed hygrophytic stands consists mainly of the species *Q. robur* (present in 28 relevés), while *Q. petraea* is less common and reaches higher percentage values only on drier sites. Thus, we propose to select *Q. robur* as the name-giving taxon for the association *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967.

The authors (Samek 1962; Neuhäusl and Neuhäuslová-Novotná 1967) did not typify the association name at that time. The lectotype of the *Molinio arundinaceae-Quercetum* Samek 1962 designated by Moravec (1998) actually corresponds to a thermophilous oak forest on acidic substrates belonging to the *Melico pictae-Quercetum roboris* (*Quercion petraeae* alliance; Roleček 2013). The other two relevés of the Samek protologue are not oak-dominated forests, as *Quercus* has a very low cover or is completely absent. Moreover, there are also many more forest mesophytes (e.g., *Ajuga reptans*, *Anemone nemorosa*, *Melica nutans*, *Viola reichenbachiana*) and nutrient-demanding species (e.g., *Scorzonera humilis*) in the published relevés compared to the study of Neuhäusl and Neuhäuslová-Novotná (1967). On the other hand, lectotypification of the *Molinio arundinaceae-Quercetum* Neuhäusl et Neuhäuslová-Novotná 1967 carried out by Pallas (1996) follows the original concept of Neuhäusl and Neuhäuslová-Novotná (1967), and the type-relevé unambiguously represents a hygrophytic acidophilous oak forest. The name was adopted and traditionally used in this sense in various Central European countries (e.g., Wallnöfer et al. 1993; Moravec 1998; Pallas 2003; Jarolímek et al. 2008; Matuszkiewicz 2012).

If our proposal for a binding decision of the name-giving taxa will be accepted, the name *Molinio arundinaceae-Quercetum roboris* Neuhäusl et Neuhäuslová-Novotná 1967 becomes a later homonym. To promote nomenclatural stability and maintenance of the well-known and long-used association name, we therefore propose to conserve the name *Molinio arundinaceae-Quercetum roboris* Neuhäusl et Neuhäuslová-Novotná 1967 against the older name *Molinio arundinaceae-Quercetum roboris* Samek 1962.

Author contributions

MS led the writing, but all authors contributed to the nomenclatural research and revision of the manuscript.

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RESEARCH PAPER — INTERNATIONAL VEGETATION CLASSIFICATION

Poplar box woodlands of Eastern Australia: an assessment of a threatened ecological community within the IVC framework

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Abstract

Aims: Ecosystems nationally at risk in Australia are listed under the Environmental Protection and Biodiversity Act (EPBC Act), and many cross State jurisdictional boundaries. The determination of these ecosystems across the State boundaries are based on expert knowledge. The International Vegetation Classification has the potential to be useful as a cross-jurisdictional hierarchy which also gives global perspective to ecosystems. **Study Area:** All bioregions that include *Eucalyptus populnea* as a dominant or major component of woodlands across the species known distribution. **Methods:** We use plot-based data (455 plots) from two states (Queensland and New South Wales) in eastern Australia and quantitative classification methods to assess the definition and description for the Poplar Box Woodland ecosystem type (hereafter "ecological community" or "community") that is listed as endangered under the EPBC Act. Analyses were conducted using kR-CLUSTER methods to generate alliances. Within these alliances, analyses were undertaken to define associations using agglomerative hierarchical clustering and similarity profile testing (SIMPROF). We then explore how assigning this community into the IVC hierarchy may provide a mechanism for linking Australian communities, defined at the association and alliance levels, to international communities at risk. **Results:** We define three alliances and 23 associations based on the results of floristic analysis. Using the standard rule-set of the IVC system, we found that the IVC hierarchy was a useful instrument in correlating ecological communities across jurisdictional boundaries where different classification systems are used. It is potentially important in giving a broader understanding of communities that may be at risk continentally and globally. **Conclusions:** We conclude that the IVC hierarchy can incorporate Australian communities at the association level into useful units at higher levels, and provides a useful classification tool for Australian ecosystems.

Taxonomic reference: PlantNET (http://plantnet/10rbgsyd.nsw.gov.au/) [accessed June 2019].

Abbreviations: EPBC Act = Environmental Protection and Biodiversity Act; IVC = International Vegetation Classification; NMDS = non-metric multidimensional scaling; NSW = New South Wales; PCT = Plant Community Type; QLD = Queensland; RE = Regional Vegetation Community; SIMPER = similarity percentage analysis; SIMPROF = Similarity profile analysis.

Keywords

Australia, ecological community, International Vegetation Classification, New South Wales, Queensland, woodland

Introduction

One of the core methods for tackling the loss of biodiversity is the listing of threatened ecological communities on international, national and regional lists (IPBES 2019). However, this necessarily requires that such communities are defined and are identifiable. Without clear definitions of inclusion or exclusion we risk conservation priorities being misdirected (Hunter 2021a; Saunders et al. 2021). One key impediment to the process of listing threatened ecological communities is a lack of jurisdictional conformity in typology (Gellie et al. 2018; Muldavin et al. 2021; Saunders et al. 2021). Only through the unification of terminology and procedure, at least with some critical components of survey and naming across jurisdictions, can a clearer understanding of the distribution and threats to communities occur (De Cáceres et al. 2015; Gellie et al. 2018; Luxton et al. 2021).

A lack of jurisdictional conformity is a global issue within many regions and concerted efforts are being made to unify classificatory procedures at all levels to allow greater regional, continental and global understandings (Faber-Langendoen et al. 2014; De Cáceres et al. 2018; Luxton et al. 2021; Muldavin et al. 2021). Though many early attempts at classifying vegetation within Australia were continental in focus (e.g. Carnahan 1976; Beadle 1981; Walker and Hopkins 1990; Specht et al. 1995), classification within Australia has become strongly State and Territory led, each with their own individualistic approaches (Gellie et al. 2018; Luxton et al. 2021). In most instances, intuitive qualitative supervised methodologies have been used to create typologies, often with minimal hierarchical structures that are used primarily for mapping (Gellie et al. 2018). As such, difficulty arises when a threatened ecological community is listed at the continental scale on the Federal Environmental Protection and Biodiversity Act 1999 (EPBC Act; https://www.environment.gov.au/epbc) and is known to occur across jurisdictional boundaries within Australia. An intent of threatened community listings is to channel and prioritise limited resources towards those systems that are in urgent need of immediate protection, however, listings are often constrained by limited knowledge, outdated taxonomy and jurisdictional differences (Wallace and Fluker 2015; Dovey and Walker 2018; Saunders et al. 2021). Currently the *EPBC* Act contains 92 threatened ecological communities (4 Nov 2021). Any organisation or community member can nominate a listing which goes to a scientific committee for discussion. Potential listings are then refined and placed on public exhibition for comment before finally being presented to the federal minister for acceptance or rejection. Although guidelines suggest that communities should be defined based on numerical classification this has not been applied to many currently listed, some of which are clearly defined based on geomorphological features with only a generalised concept of a floristic assemblage (see, e.g., Hunter and Hunter 2020; Hunter 2021a). Without a full comprehension of all floristic and ecological components and interrelationships with co-occurring types, a real understanding cannot be gained of threats and persistence (Franklin et al. 2016; Jansen et al. 2016).

Although adjacent to each other and sharing approximately 1,500 km of border the vegetation classification methodologies between New South Wales (NSW) and Queensland (QLD) (Gellie et al. 2018) are highly divergent. Within QLD communities are defined as regional ecosystems (RE) that are classified at a thematic level considered equivalent to association. Unlike traditional concepts of an association, which strongly emphasize floristics, REs in QLD are named based firstly on the bioregion (IBRA7; Thackway and Cresswell 1995) in which they occur, secondarily by geology, landform and soils and only thirdly by the most dominant stratum in terms of biomass (not height) and then dominant floristics within strata (Gellie et al. 2018; Addicott et al. 2021). The approach is mapping based and created predominantly through expert opinion, with more than 1300 types currently defined (Gellie et al. 2018), although recently quantitative classification approaches are being implemented (Addicott et al. 2018; Addicott et al. 2021). In NSW, the vegetation classification has three hierarchical levels, of which the Plant Community Type level (PCT) was derived under a separate process to the other thematic levels of class and formation (Keith 2004; Benson 2006; Gellie et al. 2018). PCTs are based on floristics, unlike REs, and thus are closer to the traditional concept of association *sensu* Braun-Blanquet (Benson 2006). Un-supervised, semi-supervised, and, more rarely, fully supervised methods were used to define PCTs, depending on the density of qualitative data (Benson 2006). In contrast to REs, the PCT approach was not mapping based. Currently, approximately 1500 PCTs are defined for NSW. Independently developed classes and formations have also been defined for NSW through largely supervised and semi-supervised methods, with the relationships between the thematic levels based on expert opinion (Gellie et al. 2018). Overall NSW and QLD typologies have been developed through expert opinion; rarely do plot-based analyses underpin the circumscription of units.

Plot-based techniques are needed to better circumscribe communities within and across jurisdictions for greater consistency. Several tests have been completed within select vegetation types (e.g. Hunter and Lechner 2017; Addicott et al. 2018; Hunter 2020; Hunter and Hunter 2021a; Muldavin et al. 2021). Here we introduce an additional test based on the Poplar Box Woodland dominated by *Eucalyptus populnea. Eucalyptus populnea* is a widespread species with a wide edaphic tolerance but is generally restricted to annual rainfalls between 300 and 500 mm (Beeston et al. 1980; Beadle 1981) with a distribution almost equally divided across NSW and QLD and is restricted to these two jurisdictions. Beeston et al. (1980) subjectively defined 31 *Eucalyptus populnea* communities based on structure primarily for mapping purposes. Beadle (1981) defined a *Eucalyptus populnea* alliance with seven sub-alliances. These subjective cross jurisdictional works have been replaced by the Qld RE and the NSW PCT classifications. Within QLD, 34 REs have been circumscribed that are either dominated by, or have *Eucalyptus populnea*, as a characteristic canopy species, and they are found in 4 bioregions and a number of land zones (Suppl. material 1). Within NSW, 56 PCTs have *Eucalyptus populnea* as the dominant overstorey species or listed as a diagnostic element. These PCTs are placed within 23 Classes and 10 Formations (see Suppl. material 1).

In 2013, Poplar Box (*Eucalyptus populnea*) Grassy Woodland on Alluvial Plains was nominated as a nationally threatened ecological community within Australia and was accepted as such in 2019 under the Commonwealth EPBC Act 1999. At the time of listing no independent numerical classification was undertaken but existing state-based classifications were used as a guide for what should be included within listing advice for identification. Although there are 90 PCTs and REs types across both states that have *Eucalyptus populnea* as a defined diagnostic component, the current conservation listing advice for the endangered community only lists four PCTs and five REs as being characteristic of the endangered community. The listing advice was based on expert opinion and no cross jurisdictional analyses were performed to justify the conclusions made or to assess the interrelationships of the types incorporated. The differences between classification systems and methodologies in NSW and QLD and a lack of plot-based analysis limits our understanding of communities dominated by *Eucalyptus populnea* across its range. To address conservation priorities and to better place limited management resources, the interrelationships of these communities need to be better understood from a local, continental and global perspective. Hierarchical classification schema allow for a better understanding of interrelationships between communities and the conceptualisation of different ranks allows the scale of management to be applied at appropriate scales (Faber-Langendoen et al. 2018; Luxton et al. 2021).

One such hierarchical classification schema is the International Vegetation Classification (IVC) system, which is based on the EcoVeg approach (Faber-Langendoen et al. 2014) and was developed to characterise the world's vegetation. Due to its hierarchical structure, which includes eight thematic levels (indigenous and anthropogenic), the IVC enables vegetation types to be defined locally, regionally, and globally, without regard to jurisdictions (Gellie et al 2018; Muldavin et al. 2021). Here we propose to resolve the issues of differences between state-based classification schema and the lack of knowledge of their interrelationships by using plot based analytical techniques and defining types using the IVC criteria and structure across the full range of systems in which *Eucalyptus populnea* is a characteristic dominant. The results are used to assess the current circumscription of the listed endangered Poplar Box Grassy Woodlands on Alluvial Plains.

Methods

Study region

The study region incorporates the full range of environments across NSW and QLD in which *Eucalyptus populnea* is found to be a dominant or a characteristic species. This includes the eastern Australian bioregions of: Brigalow Belt North, Brigalow Belt South, Desert Uplands, Darling Riverine Plains, Nandewar, Mulga Lands, Cobar Peneplains, NSW South Western Slopes and the Murray Darling Basin (Figure 1) covering over 960,000 sq km and 14 degrees of latitude (Beeston et al. 1980).

Data and statistical analysis

Different Australian jurisdictions (States and Territories) have different protocols for plot-based vegetation sampling, using different sized plots and scoring systems (Gellie et al. 2018). There currently is no Australian national vegetation database system, although data exchange protocols for incorporating data from individual databases are under development (TERN AEKOS). Thus, vegetation data from the different databases were used to cover the extent of *Eucalyptus populnea* dominated communities within eastern Australia. These databases included the QLD government 'CORVEG' database, which is the most comprehensive database covering QLD, and a private database curated by one of the authors (JTH; listed in GIVD as Au-Au-003 – https://www/givd.info/databses.xhtml), which primarily covered NSW but includes some parts of QLD. Use of the private database was considered appropriate as it contained much of the data already incorporated in state-based databases and had the additional benefit of having a single surveyor providing consistency in identification and scoring of species.

Floristic data was extracted from plots in which *Eucalyptus populnea* was a dominant or co-dominant from CORVEG and Au-Au-003. From each database, plots were extracted where *Eucalyptus populnea* had >10% canopy cover. Within the Australian context, woodlands are defined as having a canopy cover of between 10–30% and thus at minimum the plots chosen for analysis had to have *Eucalyptus populnea* occupying a third of the canopy cover. Plots where less than six taxa were recorded within plots were removed. Plots where a misidentification with the closely related *Eucalyptus brownii* was made were also removed. Misidentification was determined by knowledge of the distribution and habitat preferences of the two species. Taxa not identified to species level were removed. The final dataset incorporated 455 plots (151 from CORVEG) and 1326 species (native and introduced) (see Figure 1 for distribution). IVC protocols specify using percentage cover of all species in all strata for the description of types (Jennings et al. 2009).

Within the CORVEG protocol, species cover can be recorded differentially across strata and there is a standard

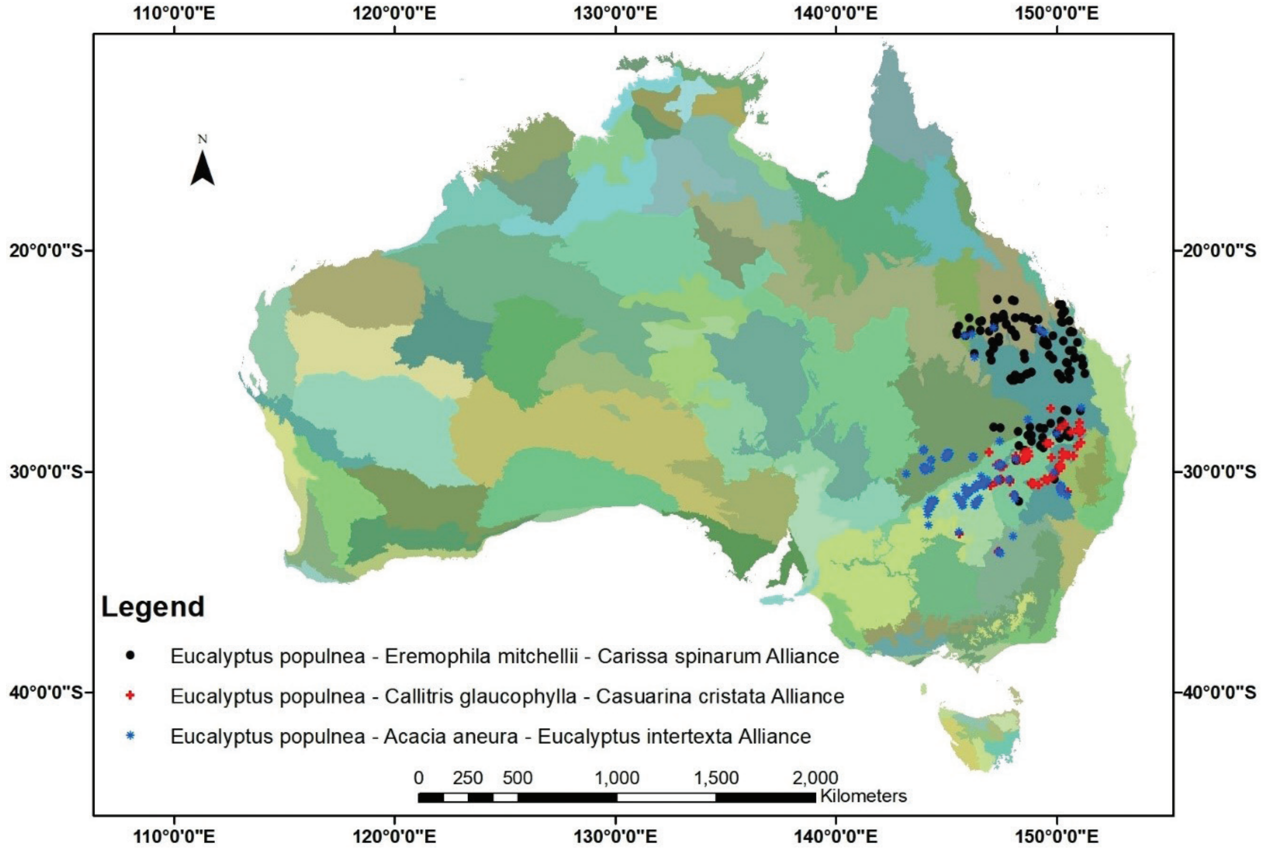

Figure 1. Location of plots from Poplar Box Woodlands in New South Wales and Queensland, Australia incorporated in analyses with proposed alliances. The boundaries of the bioregions of Australia from the IBRA version 7 (2012) are also shown.

plot size of 50 × 10 m. This plot size has been shown to adequately capture species richness in Eucalypt woodlands in Queensland (Neldner and Butler 2008). Within QLD plots, species were recorded using percent cover down to fractional percentages (0.1%). Plots surveyed within NSW most commonly were recorded using a modified six-point Braun-Blanquet cover abundance method (Westhoff and van der Maarel 1980) or percent cover and are of a 20 × 20 m dimension. Later protocols within NSW were changed to record percent cover down to 1%. Differences in recognised nomenclature were noted between jurisdictions. In order to assist compatibility across datasets, the following protocols were used; a) Braun-Blanquet scores were rescored to the mid-percent of each category, b) all fractional percentage scores were increased to a minimum of 1%, c) cover scores between strata of the same taxa were summed, d) nomenclature was standardised.

Primer E (ver. 7.0.11; Quest Research Limited; Ivybridge, Devon, UK) was used for data exploration, as commonly utilised within the target jurisdictions (e.g. Hunter and Lechner 2017; Addicott et al. 2018; Hunter and Hunter 2020; Muldavin et al. 2021). Due to the size of the dataset, an initial analysis was performed using kR-CLUSTER to generate major groups based on lowest stress (R = 0.77188). From this analysis three groups were defined, which were visually assessed secondarily via projection in 3-D using non-metric multidimensional scaling ordination (nMDS). The three groups were then separated for within group analysis. Removing sparse species from a dataset is also recommended (McCune and Grace 2002; Clarke et al. 2014). To avoid removing species which may occur infrequently but contribute a large component to the cover, species occurring only once and contributing 1% to the total cover across each of the major groups were removed.

Each of the major groups was analysed using the Bray-Curtis similarity co-efficient after square root transformation of cover values, and agglomerative hierarchical clustering was applied using group averaging. The similarity was profile tested using similarity profile analysis (SIMPROF) permutation tests (9999 iterations) in order to assess a relevant statistically significant cut-off dissimilarity for defining vegetation types at the association level. 3-D ordinations were generated using nMDS and defined groups were further assessed based on group projection and associated ordination stress. Where plots were found to be outliers within the group analyses, they were removed and placed within analyses of other groups to assess if the original analyses had caused a misallocation. Occasionally individual plots were reallocated to different proposed associations based on nMDS 3-D projection and visual assessment of species occurrence if they were deemed to have been misallocated during initial clustering. Once preliminary associations were determined, all plots within each association were combined and their scores averaged to form a single sample. A further cluster, SIMPROF, and ordination was performed against all associations to determine higher level relatedness between groups.

Similarity percentage analysis (SIMPER) identifies the species that drive differences between selected types. SIMPER uses the Bray–Curtis similarity measure to identify positively and negatively diagnostic taxa across vegetation types. Taxa with combined high frequency and cover were also identified and listed for diagnostic purposes and type delineation.

Alignment within the IVC hierarchy

The IVC schema is based on a hierarchy of natural physiognomic-ecological types at the upper levels, physiognomic-biogeographic-floristic characteristics at the middle levels and floristic-ecological characteristics at the lower level (Faber-Langendoen et al. 2016). For incorporation into the IVC hierarchy, expert knowledge and qualitative application of the criteria is often used at upper level, whereas quantitative analysis of plot-based data is used to distinguish vegetation types at the mid to lower levels (Faber-Langendoen et al. 2014). For the current study, allocation of proposed vegetation types into the IVC hierarchy was achieved by combining the key to IVC formation classes and brief definitions provided by Faber-Langendoen et al. (2016), the criteria of the IVC (Jennings et al. 2009; Faber-Langendoen et al. 2014) and expert knowledge with reference to environmental datasets and existing sub-continental scale vegetation classification systems. Sources of expert knowledge include publications by other authors, including Beadle (1981), Beeston (1980), Keith and Tozer (2017) and Neldner et al. (2019). In applying the key to IVC formation classes (Faber-Langendoen et al. 2016), we included scleromorphic trees in the mesomorphic tree concept, as the descriptions of Forest and Woodland (C01) and Shrub and Herb Vegetation (C02) formations include scleromorphic growth forms.

Crosswalk of Plant Community Types and Regional Ecosystem types to associations

In order for the IVC to provide a link between classification systems used by different jurisdictions, we crosswalked existing PCTs from NSW and REs from QLD to the associations recognised in this study. To do this we did two things: (i) allocated REs to associations using the RE attribution in the metadata of CORVEG plots from QLD and allocated PCTs from NSW to associations based on the metadata held within BioNET (https://www.environment.nsw.gov.au/research/Visclassification.htm) (see Suppl. material 1), and (ii) listed REs and PCTs that would make up the *E. populnea* woodlands based on the descriptions given online (see Suppl. material 1). In addition to providing a cross-walk table between jurisdictional classifications, this enabled us to indicate REs and PCTs that are most likely to be part of the *E. populnea* woodlands. PCTs and REs are maintained on a searchable databases by the respective state governments (https://apps.des.QLD.gov.au/regional-ecosystems; https://www.environment.nsw.gov.au/research/Visclassification.htm; both accessed 27 June 2021). *Eucalyptus populnea* was used as a key search term to find all REs and PCTs where this species was used in describing types.

Results

Alignment with the IVC hierarchy

The *E. populnea* woodlands range in height from 8–16 metres and from 12–38% in cover and are dominated by scleromorphic trees. This puts it into the IVC formation class 1. Forest and Woodland. The *E. populnea* woodlands are referred to as occurring in the subtropical and sub-humid climate zones of Australia (Fensham et al. 2017; Keith and Tozer 2017) and both climate zones are included in the Warm Temperate climatic zone of the IVC (Faber-Langendoen et al. 2016). We therefore suggest they be placed within the formation 1.B.1 Warm Temperate Forest and Woodland of the IVC. This is supported by Eucalypt woodlands of Australia having been specifically identified as part of the Temperate Forest and Woodlands formation by Faber-Langendoen et al. (2016). This contrasts with Keith and Tozer (2017)'s placement of subtropical woodlands in Savanna, which they have aligned with 1.A.1 Tropical dry forest and/or woodland and 2.A.1 Tropical lowland, grassland and savanna IVC formations. Although the Eucalypt woodlands of Australia have been referred to in formation level descriptions of the IVC types (Faber-Langendoen et al. 2014), there is currently no formal recognition of the eucalypt dominated woodlands at the division and lower levels of the IVC hierarchy within the Warm Temperate Forest and Woodlands formation. There is, however, informal recognition of the woodlands suggesting an Australian division of 1.B.1.La.4 Australian Warm Temperate Subhumid Woodland which would accommodate the *E. populnea* woodlands (Faber-Langendoen pers comm 2020). Although the IVC protocols recommend quantitative analyses to determine the mid-levels of the hierarchy, based on the criteria and descriptions given for the mid-level IVC types (Faber-Langendoen et al. 2014) we suggest the "Brigalow Forests and Associated Eucalypt Woodlands of Subtropical Eastern Australia" (Fensham et al. 2017) would be placed as a 'macrogroup' within this division. This 'macrogroup' is identified by the diagnostic species of *Acacia harpophylla* – *Eucalyptus populnea* – *Eucalyptus crebra/melanophloia* occurring on deep soils formed predominantly on sedimentary rocks on the western side of the Great Dividing Range of eastern Australia. Within this the *E. populnea* woodlands match the criteria of a 'group', in having a limited set of diagnostic species

Table 1. Circumscription of Poplar Box Woodlands (*Eucalyptus populnea*) of New South Wales and Queensland within eastern Australia. Descriptions of the 3 alliances and 23 associations include positive and negative diagnostic and negatively associated species, common dominant taxa (based on cumulative frequency and cover) and notes for each unit. Positive diagnostic species are listed in order of decreasing contribution to group identity. Negative diagnostic taxa are those not found within plots and should not occur or only occasionally within the defined type.s Common taxa are listed in decreasing order of cumulative frequency and cover within each identified group. Non-native taxa are indicated by '*'.

Hierarchy	**Positive diagnostic (SIMPER)**	**Negative diagnostic (SIMPER)**	**Common taxa**	**Notes and distribution**
Alliance 1: *Eucalyptus populnea – Eremophila mitchellii – Carissa spinarum / Heteropogon contortus – Eragrostis lacunaria* alliance	*Eremophila mitchellii, Cenchrus ciliaris*, Panicum effusum, Carissa spinarum, Heteropogon contortus, Eragrostis lacunaria, Aristida calycina, Chrysopogon fallax, Bothriochloa decipiens, Fimbristylis dichotoma, Cyperus gracilis, Evolvulus alsinoides.*	*Austrostipa aristiglumis, Paspalidium jubiflorum, Sclerolaena muricata, Austrostipa scabra, Austrostipa verticillata, Callitris glaucophylla, Acacia aneura, Carex inversa,*	*Eremophila mitchellii, Cenchrus ciliaris, Heteropogon contortus, Eragrostis lacunaria, Themeda triandra, Carissa spinarum, Aristida calycina, Panicum effusum, Enneapogon lindleyanus, Bothriochloa decipiens.*	More common in the northern half of the distribution. Widespread from the Belyando Downs and northern Bowen Basin south to Castlereagh-Barwon region. Does not occur in the more western areas of NSW.
Association 1: *Eucalyptus populnea - E. tereticornis – E. crebra / Themeda triandra – Heteropogon contortus*	*Themeda triandra, Heteropogon contortus, Sida hackettiana, Eremophila debilis, Cyperus gracilis, Dichanthium sericeum, Dinebra decipiens, Eucalyptus tereticornis, Dichatnium foecundum, Eucalyptus cambageana.*	*Eremophila mitchellii, Cenchrus ciliaris*, Chloris divaricata, Chloris ventricosa, Aristida calycina, Geijera parvifolia, Enteropogon acicularis, Enteropogon ramosus, Eucalyptus melanophloia, Thyridolepis xerophyila.*	*Themeda triandra, Heteropogon contortus, Aristida ramosa, Eucalyptus tereticornis, Eucalyptus crebra, Dinebra decipiens, Sporobolus creber, Dichanthium foecundum, Bothriochloa decipiens, Paspalum distans.*	Found on quaternary alluvial clay, sand, silt, and gravel. From Bloomsbury south of Proserpine south to Rockhampton west to Biloela in QLD. Brigalow Belt North, Brigalow Belt South and South East Queensland Bioregions.
Association 2: *Eucalyptus populnea – E. melanophloia – Corymbia dallachiana / Eremophila mitchellii – Archidendropsis basaltica*	*Eremophila mitchellii, Archidendropsis basaltica, Eragrostis leptocarpa, Chloris ventricosa, Eucalyptus melanophloia, Eragrostis tenella, Dodonaea viscosa, Corymbia dallachiana, Acacia leiocalyx.*	*Cenchrus ciliaris*, Corymbia dallachyana, Heteropogon contortus, Bothriochloa decipiens, Chloris divaricata, Geijera parviflora, Eucalyptus crebra, Casuarina cristata, Paspalidium caespitosum, Eragrostis lacunaria, Enteropogon acicularis.*	*Eremophila mitchellii, Archidendropsis basaltica, Eragrostis leptocarpa, Chloris ventricosa, Eucalyptus melanophloia, Eragrostis tenellula, Bothriochloa ewartiana, Dodonaea viscosa, Aristida calycina, Corymbia dallachiana.*	Found on Quartzose to lithic sandstone, siltstone and shale. A restricted community with only a few characteristic sites located in the Rubyvale and Capella areas of eastern central QLD. Brigalow Belt North Bioregion.
Association 3: *Eucalyptus populnea / Eragrostis lacunaria – Aristida caput-medusae*	*Eragrostis lacunaria, Aristida caput-medusae, Eragrostis sororia, Cyanthillium cinereum, Dinebra decipiens, Enneapogon lindleyanus, Heteropogon contortus, Aristida queenslandica, Dodonaea viscosa, Eriochloa fatmensis, Enteropogon unispiceus.*	*Cenchrus ciliaris, Themeda triandra, Bothriochloa decipiens, Chloris ventricosa, Aristida calycina, Geijera parviflora, Casuarina cristata, Paspalidium caespitosum.*	*Eragrostis lacunaria, Aristida lignosa, Aristida caput-medusae, Dodonaea viscosa, Melinis repens*, Eriochloa fatmensis, Enteropogon unispeceus, Eragrostis sororia, Aristida queenslandica, Enneapogon lindleyanus.*	Found on pebbly quart sandstone, conglomerate, shale, and siltstone. Restricted to the Brigalow Belt North within the Springsure and Fairburn State Forest area. Brigalow Belt North Bioregion.
Association 4: *Eucalyptus populnea – Casuarina cristata – E. largiflorens / Thyridolepis xerophila – Aristida jerichoensis*	*Eremophila mitchellii, Casuarina cristata, Aristida jerichoensis, Thyridolepis xerophila, Acacia aneura, Eucalyptus largiflorens.*	*Bothriochloa decipiens, Heteropogon contortus, Geijera parviflora, Aristida calycina, Chloris ventricosa, Enteropogon acicularis, Paspalidium caespitosum, Dichanthium sericeum, Cyperus gracilis.*	*Casuarina cristata, Thyridolepis xerophila, Acacia aneura, Eucalyptus largiflorens, Cenchrus ciliaris*, Chloris divaricata, Eremophila mitchellii, Aristida jerichoensis, Eucalyptus melanophloia, Themeda triandra.*	Found on Tertiary-Quaternary and Cainozoic sands and weathered sandstones. Widespread occurrences from Mt Wyatt area to Alpha and south to Bollon, St George, Texas in QLD and south to the Walgett (Wilgavale) area of NSW. Brigalow Belt North, Brigalow Belt South, Desert Uplands and Mulga Lands Bioregions.
Association 5: *Eucalyptus populnea – Corymbia clarksoniana / Cassia brewsteri – Carissa spinarum*	*Cassia brewsteri, Evolvulus alsinoides, Stylosanthus scabra, Paspalidium gracile, Carissa spinarum, Chrysopogon fallax, Denhamia cunninghamii, Aristida calycina, Bothriochloa decipiens, Corymbia clarksoniana, Eragrostis sororia.*	*Chloris divaricata, Geijera parviflora, Paspalidium caespitosum, Casuarina cristata, Enteropogon acicularis, Eucaliptus melanophloia, Dichanthium sericeum, Thyridolepis xerophila, Cymbopogon refractus, Aristida ramosa.*	*Chloris ventricosa, Cenchrus ciliaris, Aristida calycina, Paspalidium gracile, Chrysopogon fallax, Stylosanthus scabra, Bothriochloa decipiens, Abutilon oxycarpum, Panicum effusum, Carissa spinarum, Cassia brewsteri.*	Found on soils from deep sands. In the Logan and Peak Downs area of the Bowen Basin of the Brigalow Belt North within QLD.
Association 6: *Eucalyptus populnea / Bothriochloa decipiens – Chloris divaricata*	*Cyperus gracilis, Bothriochloa decipiens, Aristida calycina, Brunoniella australis, Cymbopogon refractus, Eremophila mitchellii, Cenchrus ciliaris*, Sida hackettiana, Chloris divaricata, Cyanthillium cinereum, Chloris ventricosa, Heteropogon contortus.*	*Geijera parviflora, Casuarina cristata, Aristida personata, Thyridolepis xerophila, Acacia aneura, Triodia pungens.*	*Cenchrus ciliaris*, Chloris divaricata, Chloris ventricosa, Heteropogon contortus, Bothriochloa decipiens, Aristida calycina, Eremophila mitchellii, Dichanthium sericeum, Paspalidium caespitosum, Cymbopogon refractus.*	One of the most widespread associations occurring within QLD. From Rockhampton west to Barcaldine and Tambo and south to Taroom and Gayndah with a contracted occurrence around Dalby to Tara and south to Goondiwindi. Found on Quaternary sand, silt, clay, and gravel in floodplains and alluvial fans. Also known from granites and porphyrite. Brigalow Belt North, Brigalow Belt South and Desert Uplands.

Hierarchy	Positive diagnostic (SIMPER)	Negative diagnostic (SIMPER)	Common taxa	Notes and distribution
Association 7: _Eucalyptus populnea – Casuarina cristata – Acacia harpophylla / Eremophila mitchellii – Geijera parviflora_	_Eremophila mitchellii, Geijera parviflora, Enteropogon acicularis, Abutilon oxycarpum, Sporobolus caroli, Cenchrus ciliaris_*_, Eragrostis lacunaria, Enchylaena tomentosa, Boerhavia dominii._	_Themeda triandra, Heteropogon contortus, Carissa spinarum, Eucalyptus melanophloia, Melinis repens_*_, Sida hackettiana._	_Eremophila mitchellii, Geijera parviflora, Cenchrus ciliaris_*_, Enteropogon acicularis, Bothriochloa decipiens, Acacia harpophylla, Paspalidium caespitosum, Sporobolus caroli, Casuarina cristata, Paspalidium constrictum, Ancistrachne uncinata._	A common association from Clermont in QLD south in an arc from Taroom to Mitchell, Tara, Goondiwindi, St George in QLD and further south to Lightning Ridge, Narrabri and north of Gilgandra in NSW. Known from Quaternary alluvia of clay, sand, silt, and gravel and sandstones. Brigalow Belt North, Brigalow Belt South, Darling Riverine Plains, Mulga Lands.
Association 8: _Eucalyptus populnea – E. melanophloia / Triodia pungens – Triodia mitchellii (Cenchrus ciliaris_*_)_	_Cenchrus ciliaris_*_, Eremophila mitchellii, Eragrostis lacunaria, Archidendropsis basaltica, Enneapogon lindleyanus, Psydrax oleifolia, Geijera parviflora, Triodia pungens, Carissa lanceolata, Triodia mitchellii, Eriachne mucronata._	_Bothriochloa decipiens, Chloris divaricata, Chloris ventricosa, Casuarina cristata, Paspalidium caespitosum, Cyperus gracilis, Aristida ramosa._	_Cenchrus ciliaris_*_, Melinis repens_*_, Triodia pungens, Eucalyptus melanophloia, Thyridolepis xerophylla, Heteropogon contortus, Aristida calycina, Carissa lanceolata, Eremophila mitchellii, Aristida jerichoensis._	Restricted to QLD and most common South of Mt Coolon to Blackwater, Springsure, Tambo, and west to Barcaldine with a disjunct occurrence near Nindgully and Thallon south to Engonia in NSW. Found on sand sheets, red hard setting sandy clay, aeolian sands and sandstone. Brigalow Belt North, Brigalow Belt South and Desert Uplands Bioregion.
Association 9: _Eucalyptus populnea – Eucalyptus crebra / Carissa spinarum – Alectryon diversifolius_	_Cenchrus ciliaris_*_, Carissa spinarum, Bothriochloa decipiens, Eucalyptus crebra, Enneapogon lindleyanus, Erythroxylum australe, Alectryon diversifolius._	_Heteropogon contortus, Chloris divaricata, Chloris ventricosa, Geijera parviflora, Paspalidium caespitosum, Casuarina cristata, Enteropogon acicularis, Cymbopogon refractus, Eucalyptus melanophloia, Dichanthium sericeum, Thyridolepis xerophila._	_Cenchrus ciliaris_*_, Carissa spinarum, Bothriochloa decipiens, Eremophila mitchellii, Themeda triandra, Enneapogon lindleyanus, Eucalyptus crebra, Erythroxylum australe, Alectryon diversifolius, Chloris truncata._	Found primarily within the Yeppoon, Mirandbah, Clermont, and south to Moura region of QLD. Found on deeply weathered course grained sandstone, Quaternary and Tertiary alluvia and sediments. Brigalow Belt North and Brigalow Belt South Bioregions.
Alliance 2: _Eucalyptus populnea – Callitris glaucophylla – Casuarina cristata / Geijera parviflora – Eremophila mitchellii_ alliance	_Geijera parviflora, Callitris glaucophylla, Cyperus gracilis, Austrostipa scabra, Eremophila mitchellii, Brunoniella australis, Einadia nutans, Casuarina cristata, Abutilon oxycarpum, Maireana microphylla, Enchylaena tomentosa, Cheilanthes sieberi._	_Austrostipa aristiglumis, Paspalidium jubiflorum, Sclerolaena muricata, Acacia aneura._	_Eremophila mitchellii, Callitris glaucophylla, Geijera parviflora, Austrostipa scabra, Einadia nutans, Sclerolaena birchii, Cyperus gracilis, Enteropogon acicularis, Casuarina cristata, Calotis lappulacea Eucalyptus largiflorens, Carissa spinarum._	Primarily restricted to the central and eastern parts of the range. Most common from Carbelago region of the Cobar Peneplain to the Tara Downs and Inglewood Sandstone region.
Association 10: _Eucalyptus populnea – Acacia harpophylla – Casuarina cristata / Geijera parviflora – Eremophila glabra_	_Acacia harpophylla, Setaria paspalidioides, Abutilon oxycarpum, Apophyllum anomalum, Austrostipa setacea, Brachyscome dentata, Brunoniella australis, Einadia nutans, Enchylaena tomentosa, Eremophila mitchellii._	_Eremophila mitchellii, Callitris glaucophylla, Austrostipa scabra, Sclerolaena birchii, Einadia nutans, Enteropogon acicularis, Calotis cuneifolia, Paspalidium constrictum, Eucalyptus largiflorens, Eremophila debilis._	_Acacia harpophylla, Brachyscome ciliaris, Setaria paspalidioides, Geijera parviflora, Enchylaena tomentosa, Casuarina cristata, Sporobolus caroli, Rytidosperma longifolium, Eremophila glabra, Eremophila mitchellii._	Found as disjunct distributions within the northern Pilliga Outwash south west to Culgoa in NSW and north to the Expedition and Carnarvon Ranges usually on gilgai clay soils. Brigalow Belt South, Darling Riverine Plains and Mulga Lands Bioregions.
Association 11: _Eucalyptus populnea – Callitris glaucophylla – E. melanophloia / Calotis cuneifolia - Pimelea trichostachya_	_Callitris glaucophylla, Calotis cuneifolia, Pimelea trichostachya, Einadia nutans, Calandrinia eremaea, Sida cunninghamii, Fimbristylis dichotoma, Austrostipa scabra, Chenopodium curvispicatum, Glossocardia bidens, Rhodanthe moschata, Euphorbia drummondii._	_Eremophila mitchellii, Geijera parviflora, Sclerolaena birchii, Einadia nutans, Enteropogon acicularis, Casuarina cristata, Paspalidium constrictum, Eucalyptus largiflorens, Chenopodium desertorum._	_Callitris glaucophylla, Dodonaea viscosa, Pimelea trichostachya, Calotis cuneifolia, Cheilanthes sieberi, Eucalyptus melanophloia, Centipeda cunninghamii, Aristida ramosa, Dysphania melanocarpa, Glycine canescens._	Known from Collarenebri, the Narran Lakes region and Culgoa Floodplains. Occurring on low lying clay floodplains. Brigalow Belt South, Darling Riverine Plains and Mulga Lands Bioregions.
Association 12: _Eucalyptus populnea – Allocasuarina luehmannii – Callitris glaucophylla / Cymbopogon refractus – Aristida_ spp.	_Allocasuarina luehmannii, Cymbopogon refractus, Callitris glaucophylla, Brunoniella australis, Aristida caput-medusae, Chloris divaricata, Aristida ramosa, Eucalyptus conica, Aristida jerichoensis, Paspalidium caespitosum._	_Eremophila mitchellii, Sclerolaena birchii, Einadia nutans, Enteropogon acicularis, Paspalidium constrictum, Chenopodium desertorum._	_Cymbopogon refractus, Allocasuarina luehmannii, Eucalyptus largiflorens, Callitris glaucophylla, Chloris divaricata, Aristida ramosa, Austrostipa scabra, Aristida caput-medusae, Geijera parviflora, Eucalyptus crebra._	Found within southern QLD from Glenmorgan south to Texas. Known from Quaternary alluvia, sand sheets, clayey sandstone and aeolian sands. Primarily within the Brigalow Belt South but also within the Nandewar Bioregion.
Association 13: _Eucalyptus populnea – Casuarina cristata – Allocasuarina luehmannii / Aristida scabra – Cymbopogon refractus_	_Austrostipa scabra, Cyperus gracilis, Eremophila debilis, Dichanthium sericeum, Leptochloa ciliolata, Abutilon oxycarpum, Aristida caput-medusae, Cymbopogon refractus, Sporobolus creber, Casuarina cristata, Chloris truncata._	_Sclerolaena birchii, Calotis cuneifolia, Eucalyptus largiflorens, Eucalyptus melanophloia, Paspalidium constrictum, Chenopodium desertorum._	_Cymbopogon refractus, Aristida caput-medusae, Austrostipa scabra, Cyperus gracilis, Leptochloa ciliolata, Dichanthium sericeum, Callitris glaucophylla, Allocasuarina luehmannii, Eremophila debilis, Notelaea microcarpa._	Found within NSW from Croppa Creek south to Terry Hie Hie. Generally, on sandy clays or within and surrounding small wetlands on sandy clay or loamy clay soils. Brigalow Belt South Bioregion.

Hierarchy	**Positive diagnostic (SIMPER)**	**Negative diagnostic (SIMPER)**	**Common taxa**	**Notes and distribution**
Association 14: *Eucalyptus populnea – Eucalyptus albens – Eucalyptus blakelyi / Eremophila mitchellii – Carisa spinarum*	*Carissa spinarum, Notelaea microcarpa, Cheilanthes distans, Eucalyptus albens, Acacia deanei, Chloris ventricosa, Psydrax odoratum, Eucalyptus blakelyi, Teucrium junceum.*	*Austrostipa scabra, Sclerolaena birchii, Enteropogon acicularis, Calotis cuneifolia, Eucalyptus largiflorens, Chenopodium desertorum, Calotis lappulacea.*	*Geijera parviflora, Eremophila mitchellii, Carissa spinarum, Casuarina cristata, Notelaea microcarpa, Cheilanthes distans, Callitris glaucophylla, Eucalyptus melanophloia, Eucalyptus albens, Chloris ventricosa.*	Known from north of Millmerran in QLD south to Narrabri and west to the western Pilliga outwash near Gwabegar in NSW. Known from sandy clays or loam clay outwash plains and around small wetlands within broader sandy soils landscapes. Brigalow Belt South Bioregion.
Association 15: *Eucalyptus populnea – Callitris glaucophylla – Casuarina cristata / Geijera parviflora – Eremophila mitchellii*	*Geijera parviflora, Eremophila mitchellii, Austrostipa scabra, Callitris glaucophylla, Sclerolaena birchii, Einadia nutans, Chenopodium desertorum.*	*Cyperus gracilis, Carissa spinarum, Cymbopogon refractus, Acacia harpophylla, Cadellia pentastylis, Notelaea microcarpa, Enchylaena tomentosa, Aristida ramosa.*	*Geijera parviflora, Eremophila mitchellii, Carissa spinarum, Casuarina cristata, Notelaea microcarpa, Cheilanthes distans, Callitris glaucophylla, Eucalyptus albens, Eucalyptus melanophloia, Chloris ventricosa.*	Known from south of Texas, Mungindi and Lightning Ridge to Gunnedah in the east and Brewarrina in the west and as far south as Mount Hope and Lake Cowal. Association with clay and cracking clay alluvial soils within floodplains Brigalow Belt South and Darling Riverine Plains Bioregions.
Association 16: *Eucalyptus populnea – Callitris glaucophylla – Cadellia pentastylis / Geijera parviflora – Carissa spinarum*	*Callitris glaucophylla, Cyperus gracilis, Brunoniella australis, Austrostipa scabra, Calotis lappulacea, Aristida personata, Geijera parviflora, Lomandra multflora, Sida corrugata, Evolvulus alsinoides, Austrostipa verticillata, Boerhavia dominii, Maireana microphylla, Notelaea microcarpa, Acacia deanei.*	*Eremophila mitchellii, Geijera parviflora, Einadia nutans, Enteropogon acicularis, Eucalyptus largiflorens, Chenopodium desertorum.*	*Callitris glaucophylla, Austrostipa scabra, Cyperus gracilis, Carissa spinarum, Cadellia pentastylis, Aristida personata, Eucalyptus pilligaensis, Acacia decora, Chloris truncata, Dichondra* sp. A.	A similar geographic distribution of association 15 but occurring on higher parts of the landscape on clay loam and sandy clay loam soils. Nandewar, Brigalow Belt South and Darling Riverine Plains Bioregions.
Alliance 3: *Eucalyptus populnea – Acacia aneura – Eucalyptus intertexta / Enteropogon acicularis – Austrostipa verticillata* alliance	*Acacia aneura, Enteropogon acicularis, Austrostipa verticillata, Dodonaea viscosa, Paspalidium jubiflorum, Senna zygophylla, Carex inversa, Eremophila sturtii, Austrostipa aristiglumis, Eucalyptus intertexta.*	*Eremophila mitchellii, Callitris glaucophylla, Cenchrus ciliaris*, Austrostipa scabra, Sclerolaena birchii, Cyperus gracilis, Einadia nutans, Themeda triandra, Carissa spinarum.*	*Acacia aneura, Eremophila mitchellii, Geijera parviflora, Enteropogon acicularis, Austrostipa verticillata, Senna zygophylla, Carex inversa, Paspalidium jubiflorum, Austrostipa aristiglumis, Dodonaea viscosa.*	Occurring throughout the range but more common in more western regions. Occurring as far west as the Ursino Sandplains.
Association 17: *Eucalyptus populnea / Paspalidium jubiflorum – Sclerolaena muricata*	*Medicago polymorpha*, Rapistrum rugosum*, Hordeum glaucum, Paspalidium jubiflorum, Sclerolaena muricata, Austrostipa aristiglumis.*	*Acacia aneura, Eremophila mitchellii, Geijera parviflora, Senna zygophylla, Carex inversa, Dodonaea viscosa, Eremophila sturtii, Eucalyptus intertexta, Casuarina cristata, Callitris glaucophylla.*	*Austrostipa aristiglumis, Medicago polymorpha*, Hordeum glaucum*, Paspalidium jubiflorum, Lolium perenne*, Rapistrum rugosum*, Sclerolaena muricata, Enteropogon acicularis, Sisymbrium erysimoides*, Malva parviflora*.*	Found in the Gunnedah and Boggabri regions on alluvial clay loam and loamy clay soils. An association of heavily grazed and disturbed soils with many associated introduced species.
Association 18: *Eucalyptus populnea – Casuarina cristata – Eucalyptus camaldulensis / Austrostipa verticillata – Paspalidium jubiflorum*	*Carex inversa, Austrostipa verticillata, Paspalidium jubiflorum, Casuarina cristata, Cynodon dactylon, Austrostipa scabra, Paspalidium constrictum, Phyla canescens*, Enteropogon acicularis, Sonchus oleraceus*, Sisymbrium erysimoides*, Sclerolaena muricata.*	*Acacia aneura, Eremophila mitchellii, Geijera parviflora, Dodonaea viscosa, Austrostipa aristiglumis, Eremophila sturtii, Eucalyptus intertexta, Senna filifolia.*	*Austrostipa verticillata, Carex inversa, Cynodon dactylon, Casuarina cristata, Paspalidium jubiflorum, Enteropogon acicularis, Austrostipa scabra, Paspalidium constrictum, Phyla canescens*, Lolium perenne*, Eucalyptus camaldulensis, Eucalyptus melliodora.*	Widespread from Dalby in QLD south as far west as Yantabulla and east to Gunnedah and as far south as Lake Cowal in NSW. generally found clay, clay loam and loamy clay soils but often higher parts of floodplains. Brigalow Belt South, Darling Riverine Plains, Mulga Lands and NSW South Western Slopes Bioregions.
Association 19: *Eucalyptus populnea – Eucalyptus crebra – Allocasuarina luehmannii / Austrostipa aristiglumis – Sporobolus mitchellii*	*Austrostipa aristiglumis, Centipeda thespidioides, Allocasuarina luehmannii, Eucalyptus crebra, Sporobolus mitchellii, Corymbia clarksoniana, Rorippa eustylis*, Panicum laevinode.*	*Eremophila mitchellii, Geijera parviflora, Enteropogon acicularis, Austrostipa verticillata, Paspalidium jubiflorum, Dodonaea viscosa, Senna zygophylla, Eremophila sturtii.*	*Austrostipa aristiglumis, Centipeda thespidioides, Allocasuarina luehmannii, Eucalyptus crebra, Sporobolus mitchellii, Panicum laevinode, Corymbia clarksoniana, Rorippa eustylis*, Austrostipa nitida.*	Widespread but disjunct occurrences from west of Duaringa to east of Alpha in QLD and from Gunnedah and Parkes in the east to Yantabulla and east of Wilcannia in NSW. Associated with and fringing ephemeral wetlands usually on clay soils. Brigalow Belt North, Brigalow Belt South, Mulga Lands, NSW South Western Slopes and Murray Darling Depression Bioregions.

Hierarchy	Positive diagnostic (SIMPER)	Negative diagnostic (SIMPER)	Common taxa	Notes and distribution
Association 20: *Eucalyptus populnea – Eucalyptus intertexta – Acacia aneura / Eremophila mitchellii – Geijera parviflora*	*Eremophila mitchellii*, *Geijera parviflora*, *Acacia aneura*, *Eucalyptus intertexta*, *Dodonaea viscosa*, *Cenchrus ciliaris**, *Senna sturtii*.	*Austrostipa verticillata*, *Paspalidium jubiflorum*, *Carex inversa*, *Austrostipa aristiglumis*, *Casuarina cristata*, *Senna filifolia*, *Acacia brachystachya*.	*Eremophila mitchellii*, *Geijera parviflora*, *Acacia aneura*, *Eucalyptus intertexta*, *Dodonaea viscosa*, *Callitris glaucophylla*, *Senna zygophylla*, *Enteropogon acicularis*, *Acacia excelsa*, *Senna sturtii*.	Most commonly restricted to the more western districts. Found from south of Barcaldine to Tambo and St George to Goondiwindi in QLD and within NSW from Ledknapper Carinda south to Cobar. Generally associated with low lying ephemerally wet areas within higher landscape elements. Desert Uplands, Brigalow Belt South, Mulga Lands, Darling Riverine Plains and Cobar Peneplain.
Association 21: *Eucalyptus populnea – Acacia aneura – Acacia brachystachya / Senna* spp. – *Eremophila gilesii*	*Acacia aneura*, *Cheilanthes sieberi*, *Tripogon loliiformis*, *Senna zygophylla*, *Acacia brachystachya*, *Eragrostis eriopoda*, *Eremophila gilesii*, *Fimbristylis dichotoma*, *Eragrostis laniflora*.	*Austrostipa verticillata*, *Paspalidium jubiflorum*, *Carex inversa*, *Austrostipa aristiglumis*, *Casuarina cristata*, *Cynodon dactylon*, *Sclerolaena birchii*.	*Acacia aneura*, *Senna zygophylla*, *Cheilanthes sieberi*, *Senna filifolia*, *eragrostis eriopoda*, *Geijera parviflora*, *Enteropogon acicularis*, *Eremophila sturtii*, *Acacia brachystachya*, *Eremophila gilesii*.	Restricted to far western areas of NSW from Narran Lake south to Cobar to west of Hungerford and Wannaring. This assemblage is generally found growing around small ephemeral semi-arid wetlands and small ephemeral creeklines. Often on clay soils. Brigalow Belt South, Mulga Lands, Cobar Peneplain and Murray Darling Depression Bioregions.
Association 22: *Eucalyptus populnea / Enchylaena tomentosa – Dissocarpus paradoxus*	*Enchylaena tomentosa*, *Dissocarpus paradoxus*, *Senna filifolia*, *Carractera annua**, *Duma florulenta*, *Roepera similis*.	*Acacia aneura*, *Eremophila mitchellii*, *Geijera parviflora*, *Austrostipa verticillata*, *Senna zygophylla*, *Carex inversa*, *Austrostipa aristiglumis*, *Eucalyptus intertexta*, *Callitris glaucophylla*, *Casuarina cristata*.	*Sisymbrium erysimoides**, *Medicago laciniata** *Enchylaena tomentosa*, *Dissocarpus paradoxus*, *Carrichtera annua**, *Senna filifolia*, *Eremophila sturtii*, *Duma florulenta*, *Dodonaea viscosa*, *Roepera similis*, *Sclerolaena birchii*, *Enteropogon acicularis*, *Salvia verbenaca**.	Found only in the most western extent of *Eucalyptus populnea* distribution in NSW. From Yantabulla in the north, south to Wanaaring and the Paroo Darling wetlands to north of Ivanhoe. Restricted to shallow ephemeral semi-arid wetlands. Usually on clay soils. Mulga Lands and Murray Darling Depression Bioregions.
Association 23: *Eucalyptus populnea / Sclerolaena birchii – Eragrostis lacunaria*	*Sclerolaena birchii*, *Sida trichopoda*, *Eragrostis lacunaria*, *Nicotiana simulans*, *Teucrium racemosa*, *Centipeda thespidioides*, *Cyperus iria*, *Wahlenbergia gracilis*, *Stemodia florulenta*, *Marsilea costulifera*, *Sporobolus actinocladus*, *Tetragonia moorei*.	*Acacia aneura*, *Eremophila mitchellii*, *Geijera parviflora*, *Enteropogon acicularis*, *Austrostipa verticillata*, *Paspalidium jubiflorum*, *Senna zygophylla*, *Dodonaea viscosa*, *Carex inversa*, *Austrostipa aristiglumis*.	*Wahlenbergia gracilis*, *Cyperus iria*, *Sclerolaena birchii*, *Eragrostis lacunaria*, *Stemodia florulenta*, *Teucrium racemosum*, *Sporobolus actinocladus*, *Tetragonia moorei*, *Nicotiana simulans*, *Enchylaena tomentosa*.	Restricted to western NSW from Narran Lakes west to Yantabulla and Wanaaring and south to Yathong. Restricted to the margins of ephemeral semi-arid wetlands and small ephemeral semi-arid creeklines. Brigalow Belt South, Mulga Lands and Cobar Peneplains Bioregions.

(*E. populnea*, *Callitris glaucophylla* and *Acacia aneura*), a diagnostic growth form (trees) with broadly similar composition, and a distribution that reflects a regional mesoclimate and soil characteristics (sub-humid / subtropical climate and largely on soils with sodic sub-soils; Fensham et al. 2017). We propose that the major vegetation types within this *E. populnea* woodlands group are alliances and describe the vegetation types within those alliances as associations. Confirming these proposed mid-levels of the hierarchy using plot-based data remains to be done.

Vegetation types

Analysis of our data of 455 plots in which *Eucalyptus populnea* was a major component of the canopy enabled us to define three interim alliances and 23 associations. We propose the types as interim and refrain from adding proper formal and colloquial names that are generally provided for alliances and associations within the IVC as we would prefer standardised naming to be provided based on a wider decision-making process than the authors alone. Table 1 highlights for each community type the positive and negative diagnostic taxa, along with their most common taxa (i.e., those with high summed cover) (Suppl. material 2 and 3). The *Eucalyptus populnea – Eremophila mitchellii – Carissa spinarum / Heteropogon contortus – Eragrostis lacunaria* alliance (Figure 2), primarily of the Brigalow Belt (IBRA7; Thackway and Cresswell 1995), was prominent in QLD and incorporated most of the plots from this state. It was generally widespread

Figure 2. *Eucalyptus populnea – Eremophila mitchellii – Carissa spinarum / Heteropogon contortus – Eragrostis lacunaria* alliance.

Figure 3. *Eucalyptus populnea – Callitris glaucophylla – Casuarina* spp. / *Geijera parviflora – Eremophila mitchellii* alliance.

Figure 4. *Eucalyptus populnea – Acacia aneura – Eucalyptus intertexta / Enteropogon acicularis – Austrostipa verticillata* alliance.

across the whole geographic range of *Eucalyptus populnea* and contains nine associations. The *Eucalyptus populnea – Callitris glaucophylla – Casuarina* spp. / *Geijera parviflora – Eremophila mitchellii* alliance (Figure 3) contains seven associations, and it was primarily restricted to southern QLD, though also found in the most southern locations sampled within the range of *Eucalyptus populnea*. This alliance was commonly found within the Brigalow Belt South and the Darling Riverine Plains Bioregions and thus had general south easterly distribution (IBRA7; Thackway and Cresswell 1995). The *Eucalyptus populnea – Acacia aneura – Eucalyptus intertexta / Enteropogon acicularis – Austrostipa verticillata* alliance (Figure 4) also includes seven associations and while occurring across the entire geographic range sampled, was primarily found in the most western semi-arid districts of southwestern QLD and northwestern NSW and the only alliance distributed in these areas (Figure 4).

Although the listing advice for the endangered Poplar Box Grassy Woodlands on Alluvial Plains only includes the six REs 11.3.2, 11.3.17, 11.4.7, 11.4.12, 12.3.10, and the four PCTs 56, 87, 101, and 244 (https://www.environment.gov.au/cgi-bin/sprat/public/publicshowcommunity.pl?id=141&status=Endangered), there are fifteen PCTs and 34 REs that have *Eucalyptus populnea* as a diagnostic species within the title or detailed descriptions of the type (Suppl. material 1). All of these types were found to correspond to our associations directly or in part within our classification. Thus, all described *Eucalyptus populnea* dominant PCTs or REs were sampled and incorporated within our analyses (Table 2). However, a few of our defined associations had no direct correlates and thus could not be placed within the current state-based classifications (association 19, 22 and 23; Tables 1 and 2) and thus may require new RE and PCT designations. Many of the defined PCTs had a 1:1 or a 2:1 relationship with our defined types. Only association 20 appeared to incorporate multiple PCTs (6 in total) suggesting this PCT maybe overly split at the association level. There was less correlation found between the NSW classes and formations compared to that found for PCTs and there is little direct relationship between REs and our proposed types, with most associations having multiple REs (up to 13), as potentially synonymous. Additionally, REs were found to occur across multiple associations. RE 11.3.2 in particular was found to be attributed to nearly half of our associations (9 in total) and to all three alliances, and it is listed as an assemblage that typifies the listed endangered Poplar Box Grassy Woodlands on Alluvial Plains (Table 2). Thirteen of the associations defined here are synonymous with the nine REs and PCTs contained in the listing advice for the endangered Poplar Box Woodlands. Based on our analysis the listing of the endangered Poplar Box Grassy Woodland on Alluvial Plains does not correspond to any particular level of a classification hierarchy and incorporates multiple associations and crosses alliances but not in a consistently applicable way. We also found that at the RE and PCT diagnostic level some areas that could be included or excluded as part of the endangered community in one state would not in the other if based purely on the listed REs considered synonymous. Thus, from a floristic perspective there is a lack congruence within the current definition of the listed endangered community and plot-based analyses but also between jurisdictions if using PCTs and REs. Basing listed communities on plot-based classifications could present a better approach and allow for greater cross jurisdictional alignment when categorising what is and isn't included in the definition on ground.

Discussion

Here we present one of the few examples of cross jurisdictional vegetation classification analyses that have been conducted within Australia. Our results highlight two issues; firstly, the difficulty in trying to align vegetation types across borders when such divergent systems are used (in this case between NSW and QLD), particularly when it involves the determination of an endangered ecological community, and secondly, the benefits of using a hierarchical quantitative plot-based classification system that identifies the relationships between ecological com-

Table 2. Legacy existing classification equivalents to plant associations proposed under the IVC hierarchy in this study. Plant Community Types (PCT), class and formation are part of the current New South Wales vegetation classification schema; Regional Ecosystems (RE) comprise the Queensland equivalent of associations.

Hierarchy Level and Type	**NSW (PCT/Class/Formation) Classification**	**QLD (RE) Classification**
Alliance 1: *Eucalyptus populnea – Eremophila mitchellii – Carissa spinarum / Heteropogon contortus – Eragrostis lacunaria* alliance		
Association 1: *Eucalyptus populnea – E. tereticornis – E. crebra / Themeda triandra – Heteropogon contortus*	NA	11.3.2; 11.5.1; 11.8.15; 11.11.9; 12.3.10; 12.12.26
Association 2: *Eucalyptus populnea – E. melanophloia – Corymbia dallachiana / Eremophila mitchellii – Archidendropsis basaltica*	NA	11.10.7; 11.4.2
Association 3: *Eucalyptus populnea / Eragrostis lacunaria – Aristida caput-medusae*	NA	11.10.12.
Association 4: *Eucalyptus populnea – Casuarina cristata – E. largiflorens / Thyridolepis xerophila – Aristida jerichoensis*	PCT87; PCT 55. North west Floodplain - Woodlands Semi-arid Woodlands Grassy sub-formation.	6.5.2; 10.5.12; 11.4.10; 11.5.3; 11.5.13
Association 5: *Eucalyptus populnea – Corymbia clarksoniana / Cassia brewsteri – Carissa spinarum*	NA	11.5.3; 11.10.12
Association 6: *Eucalyptus populnea / Bothriochloa decipiens – Chloris divaricata*	NA	10.3.27; 11.3.2; 11.10.7; 11.11.9; 11.12.17; 11.4.12; 11.5.1; 11.5.13; 11.9.7.
Association 7: *Eucalyptus populnea – Casuarina cristata – Acacia harpophylla / Eremophila mitchellii – Geijera parviflora*	PCT 35, Brigalow Clay Plain Woodlands - Semi-arid Woodlands Grassy sub-formation.	6.3.24; 6.4.3; 6.5.1; 6.5.3; 11.3.2; 11.3.17; 11.4.2; 11.4.3; 11.4.7; 11.4.12; 11.5.1; 11.9.10; 11.9.7
Association 8: *Eucalyptus populnea – E. melanophloia / Triodia pungens – Triodia mitchellii* (*Cenchrus ciliaris**)	PCT 117, Sub-tropical Semi-arid Woodlands – Semi-arid Woodlands Shrubby sub-formation.	10.3.27; 10.5.12; 11.3.2; 11.3.17; 11.4.2; 11.4.12; 11.5.3;11.5.13; 11.9.2; 11.11.9
Association 9: *Eucalyptus populnea – Eucalyptus crebra / Carissa spinarum – Alectryon diversifolius*	NA	11.3.2; 11.3.36; 11.4.2; 11.5.3; 11.10.7; 11.10.12
Alliance 2: *Eucalyptus populnea – Callitris glaucophylla – Casuarina cristata / Geijera parviflora – Eremophila mitchellii* alliance		
Association 10: *Eucalyptus populnea – Acacia harpophylla – Casuarina cristata / Geijera parviflora – Eremophila glabra*	PCT 35, Brigalow Clay Plain Woodlands - Semi-arid Woodlands Grassy sub-formation.	No equivalent in QLD
Association 11: *Eucalyptus populnea – Callitris glaucophylla – E. melanophloia / Calotis cuneifolia - Pimelea trichostachya*	PCT 192, Subtropical Semi-arid Woodlands – Semi-arid Woodlands Shrubby sub-formation.	6.5.17; 11.5.5
Association 12: *Eucalyptus populnea – Allocasuarina luehmannii – Callitris glaucophylla / Cymbopogon refractus – Aristida* spp.	PCT 71, North-west Alluvial Sand Woodlands – Semi-arid Woodlands Shrubby sub-formation.	11.3.2; 11.3.16; 11.3.18; 11.5.1
Association 13: *Eucalyptus populnea – Casuarina cristata – Allocasuarina luehmannii / Aristida scabra – Cymbopogon refractus*	PCT 55, North west Floodplain - Woodlands Semi-arid Woodlands Grassy sub-formation; PCT 56, Floodplain Transitional Woodlands – Grassy Woodlands.	No equivalent in QLD
Association 14: *Eucalyptus populnea – Eucalyptus albens – Eucalyptus blakelyi / Eremophila mitchellii – Carisa spinarum*	no real equivalent in NSW but possibly close to PCT 710 Semi-arid Floodplain Grasslands – Grasslands.	11.5.1
Association 15: *Eucalyptus populnea – Callitris glaucophylla – Casuarina cristata / Geijera parviflora – Eremophila mitchellii*	Though widespread no clear match but similar to PCT 98; PCT 244 Floodplain Transitional Woodlands – Grassy Woodlands.	No clear equivalent in QLD, but possibly close to 11.5.3
Association 16: *Eucalyptus populnea – Callitris glaucophylla – Cadellia pentastylis / Geijera parviflora – Carissa spinarum*	PCT 113 North-west Alluvial Sand Woodlands – Semi-arid Woodlands Shrubby sub-formation; PCT 98 North-west Alluvial Sand Woodlands – Semi-arid Woodlands Shrubby sub-formation.	No equivalent in QLD
Alliance 3: *Eucalyptus populnea – Acacia aneura – Eucalyptus intertexta / Enteropogon acicularis – Austrostipa verticillata* alliance		
Association 17: *Eucalyptus populnea / Paspalidium jubiflorum – Sclerolaena muricata*	Possibly a derived form of PCT 101 Brigalow Clay Plain Woodlands – Semi-arid Woodlands Grassy sub-formation.	No equivalent in QLD
Association 18: *Eucalyptus populnea – Casuarina cristata – Eucalyptus camaldulensis / Austrostipa verticillata – Paspalidium jubiflorum*	PCT 36 Inland Riverine Forests – Freshwater Wetlands; PCT 74 Floodplain Transitional Woodlands – Grassy Woodlands.	11.3.2
Association 19: *Eucalyptus populnea – Eucalyptus crebra – Allocasuarina luehmannii / Austrostipa aristiglumis – Sporobolus mitchellii*	In part PCT 88 Pilliga Outwash Dry Sclerophyll Forests – Dry Sclerophyll Forests shrubby sub-formation.	11.3.2; 11.5.3; 11.9.7
Association 20: *Eucalyptus populnea – Eucalyptus intertexta – Acacia aneura / Eremophila mitchellii – Geijera parviflora*	PCT 72, PCT 103 North-west Alluvial Sand Woodlands – Semi-arid Woodlands shrubby sub-formation; PCT 82 Floodplain Transitional Woodlands – Grassy Woodlands; PCT 100 Desert Woodlands – Semi-arid Woodlands shrubby sub-formation; PCT 229 North West Plain Shrublands – Arid Shrublands Acacia sub-formation; PCT 258 Inland Rocky Hills – Semi-arid Woodlands shrubby sub-formation.	6.3.18; 6.5.3; 6.5.5; 6.5.7; 10.5.12; 11.5.1; 11.9.7
Association 21: *Eucalyptus populnea – Acacia aneura – Acacia brachystachya / Senna* spp. *– Eremophila gilesii*	PCT 105, PCT 109 North-west Alluvial Sand Woodlands – Semi-arid Woodlands shrubby sub-formation; PCT 207 North-west Floodplain Woodlands – Semi-arid Woodlands grassy sub-formation.	6.5.15
Association 22: *Eucalyptus populnea / Enchylaena tomentosa – Dissocarpus paradoxus*	Possibly PCT 25 Inland Floodplain Wetlands – Freshwater Wetlands or PCT 144 North West Plain Shrublands – Arid Shrublands Acacia sub-formation.	No equivalent in QLD
Association 23: *Eucalyptus populnea / Sclerolaena birchii – Eragrostis lacunaria*	No direct equivalents.	No direct equivalents.

munities at local, continental and global levels as opposed to classification systems which rely on correlative environmental gradients or cross-walked map-based systems (ESCAVI 2003; Keith and Tozer 2017; Luxton et al. 2021).

The congruence between our associations and the types in existing classifications varied between the different jurisdictions. Most PCTs types (NSW) were found to form a closer relationship with our proposed associations than REs (QLD). This may not be surprising as the methods used to define PCTs were either based on previous published and unpublished un-supervised analyses or, where fully supervised means were used, types were defined based on floristic composition and dominance, whereas the REs in the bioregions included in this study have been derived by fully supervised means and incorporate historical units derived from disparate studies. There are some notable exceptions within the PCTs, in particular those generally listed for the Cobar Peneplain Bioregion, where association 20 was potentially synonymous with six PCTs suggesting these PCTs are over-split at the association level. The lack of correlation on the Cobar Peneplain may be due to previous limited plot data within this bioregion. A lack of congruence was more apparent between our types and the NSW class and formation types. The situation was much more complicated for REs, where we also found little congruence between our associations and REs. Under the RE classification system, similar plant associations are divided by geomorphological categories, reflecting the assumption that there will be different biodiversity values associated with different substrates which are not necessarily reflected in plant diversity (Sattler and Williams 1995). This means that ideally, there should not be plots from one RE occurring in multiple associations, such as found in this study; for example, all plots attributed to RE 11.3.2 should match only one association, rather than nine (Table 2). When this mismatch does occur, it is likely reflecting the qualitative nature of the current classification of REs within each bioregion of QLD. The lack of hierarchical quantitative delineation of the NSW classes and formations and their relationship to PCTs is also likely to be the reason for their lack of congruence between our alliances and associations. One use of the results of this study, and future associations recognised under the IVC hierarchy, is to provide feedback into the individual jurisdictional classification systems to improve the delineations of individual vegetation types. Conversely, in identifying a possible new division, macrogroup, group, alliances, and associations within the IVC, analysis such as in this study feed back into the flexible design of the IVC, modifying it to include new levels in the hierarchy which accurately reflect the diversity of vegetation globally.

Under the *EPBC* Act 1999 an ecological community is defined as "*The extent in nature in the Australian jurisdiction of an assemblage of native species that inhabits a particular area in nature*" and is defined by the co-occurrence and interactions of species with overlapping distributions (Threatened Species Scientific Committee 2017). Furthermore, listing guidelines state that threatened communities should be defined based on classification of (dis-) similarities between vegetation types preferably based on composition (Threatened Species Scientific Committee 2017). Thus, the intent is to include in the classification vegetation types that are defined by composition. Our analysis indicates that the endangered community listing is largely based on a landscape element with an emphasis on alluvial plains, excluding types that were not predominantly grassy, reflected in its title and the REs and PCTs characterising this landscape element and structural type, rather than plant associations, to which it bears little relationship. It thus cannot be placed directly within a hierarchical classification scheme. Although low lying floodplain landscapes are commonly the most highly impacted within the Australian landscape, the emphasis on this landscape element over floristic coherence raises a number of important questions regarding conservation targets, with consideration of the whole distribution of the plant association required rather than one particular element of its distribution. Concentration on one landscape element does not help to increase our understanding of these communities or their interrelationships. Furthermore, restriction to a predominantly grassy understorey can be complicated in systems where this is transitory in nature due to natural climatic variation, disturbances both natural and human induced (Hunter 2021b; Saunders et al. 2021). It is possible that consideration of the threatened community at the alliance level may provide a more useful level of protection for the Poplar Box Grassy Woodlands than disparate sections of numerous associations.

Our relationship of synonymous types (Table 2) with the associations in this study highlights an important function of using a consistent national classification system, such as one based on the EcoVeg approach and integrated with the IVC. Adherence to the rules and processes of quantitative classification systems such as the IVC provides a clear and repeatable process when defining vegetation units and also allows for interrelationships to be recognised across jurisdictions. This is obscured within both the current NSW and QLD systems from a purely floristic-ecological classification perspective, and compounded when comparing across jurisdictions. For instance, our comparison table shows that the RE types 11.3.2 and 11.3.17, which are included in the definition of the listed endangered community description, align in part with PCT 35 yet this PCT is not one listed as defining the endangered community. The strength of using a national classification system based on quantitative plot-based analysis is in showing the relationships between floristic assemblages across jurisdictions. These may not show up in classification systems that are mapping oriented and not quantitatively based, such as the National Vegetation Inventory System, which is the current Australian national classification system (ESCVAI 2003). The strength of the IVC is that it also puts the individual threatened ecological community in a global perspective. If many of the plant associations within any given level of the IVC are listed as threatened communities it helps provide a continental and global perspective for communities within any level of the hierarchy.

Conclusion

This investigation highlights how a rigorous rule-based hierarchical classification system, where the lower schematic levels are based on plot-based vegetation analyses of floristic and ecological data, should underpin our understanding of Australian vegetation. Such processes allow for a better understanding of distribution, interrelatedness, rarity, and threat of ecological communities at lower levels and inform mid to broad levels of vegetation pattern. Our study also suggests that state-based systems should not, in and of themselves, be the only basis for the listing of endangered ecological communities. Lack of clear guidelines and a similar process applied across state and territory borders only adds further confusion leaving practitioners to rely on intuition and opinion. Using a classification system such as the IVC allows an understanding of the threats to, and status of, communities both at local and regional levels and within a continental and global perspective.

Data availability

The NSW data is contained within Version 3 of sPlot (https://www.idiv.de/?id=176&L=0) (Bruelheide et al. 2019) and is listed on GIVD as AU-AU-003 (https://www.givd.info/databases.xhtml). The Queensland data is contained within the Queensland government QBEIS database and is publicly available on request.

Author contributions

JTH collected all NSW plot data, entered all of NSW data, analysed the data and co-wrote the manuscript. EA contributed equally to writing of the manuscript and in particular the incorporation of the IVC hierarchy to the results presented.

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Supplementary material

Supplementary material 1
NSW PCTs and Qld REs that use *Eucalyptus populnea* as a diagnostic or community associated overstorey species
Link: https://doi.org/10.3897/VCS/2021/71216.suppl1

Supplementary material 2
Frequency table
Link: https://doi.org/10.3897/VCS/2021/71216.suppl2

Supplementary material 3
Images of *Eucalyptus populnea* plant associations
Link: https://doi.org/10.3897/VCS/2021/71216.suppl3

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

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RESEARCH PAPER
CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC

Regional typology of spring vegetation in Parc Ela (Grisons, Switzerland)

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Abstract

Aims: The spring habitats of Central Europe are insular biotopes of high ecological value. Although subject to severe exploitation pressures, they do not yet have a comprehensive protection status in Switzerland. Contributing to this challenge is the controversy involved with their syntaxonomic classification. In the context of the development of a regional conservation strategy and the establishment of a national inventory of Swiss springs, we carried out a regional survey of spring vegetation and aimed to translate this into a classification system. **Study area:** Montane and subalpine zones of Parc Ela (Grisons, Switzerland). **Methods:** We selected 20 springs to cover different regions, elevations and bedrock types within the park. In each of them we recorded complete vascular plant and bryophyte composition as well as a range of environmental variables in three 1-m² plots that were placed to reflect the heterogeneity within the spring. After running an unsupervised classification with modified TWINSPAN, the distinguished vegetation units were characterized in terms of diagnostic species, species richness and environmental variables and placed within the syntaxonomic system. **Results:** Species richness was high (total species 264, mean 21.7 species in 1 m²). The two most important environmental gradients of the ordination were elevation/water conductivity and insolation/water pH/soil reaction EIV. We distinguished seven communities within two main groups. **Conclusions:** All unshaded springs, including those over siliceous bedrock, could be assigned to a broadly defined *Cratoneurion*. The petrifying springs were not strongly distinguishable floristically from other base-rich springs. The forest springs, although often not clearly differentiated from their unshaded counterparts, could be provisionally divided into the alliances *Caricion remotae* and *Lycopodo europaei-Cratoneurion commutati*. As there is a certain threat to these habitats in the park due to anthropogenic influence, protection measures are recommended, most importantly the appropriate management of alpine pastures.

Taxonomic reference: Juillerat et al. (2017) for vascular plants, Meier et al. (2013) for bryophytes.

Abbreviations: ANOVA = analysis of variance; DCA = detrended correspondence analysis; EIV = ecological indicator value; FOEN = Federal Office of the Environment (Switzerland); NCHO = Ordinance on the Protection of Nature and Cultural Heritage; SD = standard deviation; TWINSPAN = Two Way Indicator Species Analysis; WPA = Federal Act on the Protection of Waters.

Keywords

bryophyte, helocrene, montane, *Montio-Cardaminetea*, Parc Ela, phytosociology, regional typology, rheocrene, spring vegetation, subalpine, Switzerland, unsupervised classification

Introduction

Central European springs are small but complex island biotopes. Their unique environmental conditions exert great influence on the vegetation and allow colonization by many highly specialized organisms, including glacial relicts (Wilmanns 1998). Around the spring outlet, environmental conditions remain relatively constant over time: spring water temperature remains close to the annual mean air temperature (Pott and Remy 2000), and humidity near the surface of the substrate is high, but the substrate is rarely fully saturated (Zechmeister and Mucina 1994). Strong ecological gradients (Brunke et al. 2015) and spatial heterogeneity (Illies and Botosaneanu 1963; Weigand 1998) result in great species richness.

Because of these conditions, as well as their small size and relative isolation (Zollhöfer 1997; Weigand 1998), springs are sensitive habitats. Zollhöfer (1999) estimated that 95% of the springs on the Swiss Plateau had been tapped or otherwise impaired by 1999; this number has likely increased in the intervening 20 years. Specialized spring-habitat species are particularly disadvantaged by habitat degradation (Heino et al. 2005; Juutinen 2011). Threats also exist in the sparsely populated Alps, where springs contribute strongly to regional biodiversity (Reiss et al. 2016): in structural surveys of the springs in Parc Ela (Grisons, CH), 24% were classified as moderately to severely impaired (Küry 2020, unpublished). Although spring habitats are ecologically valuable and subject to strong anthropogenic pressures, they do not have a comprehensive protection status in Switzerland. Unshaded spring habitats are listed in the Ordinance on the Protection of Nature and Cultural Heritage (NCHO) as "habitats worthy of protection" (Annex 1 NCHO, see also Delarze et al. 2016), but this unfortunately offers only limited protection, e.g., that encroachment must meet "an overriding need" (Art. 14 NCHO). The provisions of the Water Protection Act implicitly apply to spring habitats (Art. 1–4 WPA), but this protection is "so broad and general as to be ineffective" (Zollhöfer 1997).

In order to develop a differentiated conservation strategy for springs, it would be useful to put spring habitats into a universal scheme. Although phytocoenoses are particularly useful as reference units for conservation (Dengler 2003), phytosociology has been of limited use for spring conservation to date because the class *Montio-Cardaminetea* Br.-Bl. et Tüxen ex Klika et Hadač 1944 is fraught with controversy (e.g., Beierkuhnlein and Gollan 1999). The importance of insolation and water chemistry for species composition are particularly contentious points. The classification of spring habitats is even more challenging in the mountains, where the differences between hard- and soft-water springs are less pronounced (Braun-Blanquet 1949; Geissler 1976; Pott 1995; Pignatti and Pignatti 2014). In these habitats, local climatic conditions gain importance for the formation of spring vegetation (Beierkuhnlein and Gollan 1999).

Switzerland, unlike many other European countries or regions (e.g. Valachovič 2001; Berg et al. 2004; Chytrý 2011), lacks a data-based, country-wide syntaxonomic overview. For practical conservation purposes, parts of the TypoCH habitat typology (Delarze et al. 2015) have been adopted post-hoc into the List of Biotope Types deserving Protection (NCHO Annex 1) and other official documents. However, this typology is poorly resolved. The description of the base-rich and base-poor alliances *Cratoneurion commutati* Koch 1928 and *Cardamino-Montion* Br.-Bl. 1926 hardly reflect the geological complexity of Switzerland. Forest springs are not treated separately, but rather blanketly assigned to the forest association *Fraxinion* in agreement with Ellenberg and Klötzli (1972). Such forests hardly occur above the montane level; thus, the numerous springs within Swiss mountain forests are excluded from the classification system entirely.

In general, the distinction between springs and their contact associations is often ambiguous because of their strong spatial variation and interlock with adjacent habitats (Warncke 1980; Beierkuhnlein and Gollan 1999). There are few diagnostic plant species that are not also common in other habitats (e.g., fens) (Oberdorfer 1992; Beierkuhnlein and Gollan 1999), and spring habitats with similar environmental conditions often have very different species compositions, especially in the mountains (Cantonati et al. 2006). The following general methodological problems also arise in the syntaxonomic treatment of the *Montio-Cardaminetea*:

- Older typologies are usually not based on sufficiently large datasets (Dengler et al. 2005);
- The recording of bryophytes is rudimentary in some works;
- Most studies comprise geographically narrowly restricted regional surveys (Cantonati et al. 2006);
- Extreme variation in relevé size affects fidelity values (Dengler et al. 2009).

Due to these difficulties, there is a need for a Europe-wide systematic review of the class *Montio-Cardaminetea*, based on a comprehensive data basis. Hájek et al. started a project to this end in 2020 (pers. comm.). The data of this study will be included in Hájek's project.

Springs of the Swiss Alps have been the subject of various vegetation surveys, mostly in the context of regional studies of alpine vegetation in Grisons (Braun-Blanquet 1949; Trepp 1968) or of international studies of alpine springs (e.g. Sekulová et al. 2012). Other hydrobiological studies of Swiss springs do not comprise detailed vegetation surveys (e.g. Nadig 1942; Zollhöfer 1997). Geissler (1976) identified typical associations for the eastern part of the Swiss Alps, sampling in 27 localities and citing a gap in the otherwise thorough investigation of Swiss alpine vegetation which seems to have persisted to the present day. It is hoped that the records of this study contribute to a more complete understanding of spring vegetation in the Swiss Alps.

Parc Ela's plan to develop a conservation concept for their spring habitats, as well as the commission of a national inventory of spring habitats by the Federal Office for the Environment FOEN (Küry et al. 2019), provide the impetus for this work. To increase knowledge of spring habitats, Audorff et al. (2011) cite the importance of regional studies including physico-chemical parameters and multiple organism groups. Since the patterns of spring biodiversity differ greatly between mountain regions, local studies can also be helpful in identifying the relevant parameters (Sekulová et al. 2012). In this sense, this work aims to characterize the diversity of spring habitats in Parc Ela and identify the underlying environmental factors so that effective conservation measures can be developed.

Study area

As the largest nature park in Switzerland, Parc Ela covers 548 km^2 in the canton of Grisons (Figure 1). The park area includes the Surses and Albula valleys and the surrounding Albula, Plessur and Oberhalbsteiner Alps. As inner-alpine valleys in central Grisons, the Surses and Albula valleys have a continental climate (Figure 2). The year has up to 190 days of frost, which shortens the vegetation period to about 6 months.

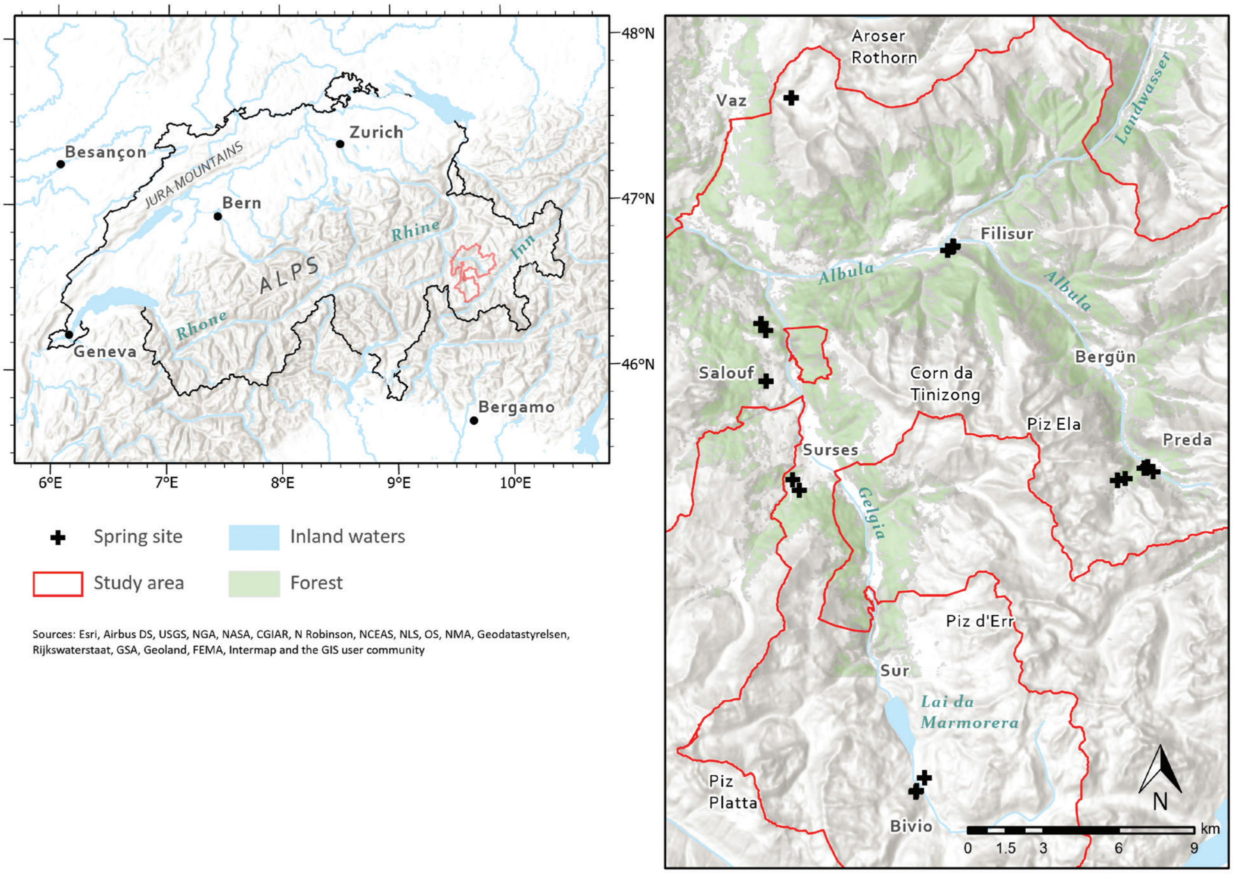
The park is located on the Pennine and Eastern Alpine nappes, with the Surses valley lying in the middle. A large part of the park lies on basic bedrock, mainly biogenic sediments and evaporites (Federal Office of Topography swisstopo 2020). To the south, around the Albula, Septimer and Julier passes, sedimentary and crystalline rocks (granodiorite, gneiss) alternate on a small scale. In the valleys, especially in the Surses valley, alluvial debris and landslide deposits occur over large areas. The mountain landscape is glacially influenced, its soils shallow and young (ibid.). The springs of this study are located between 956 and 2,115 m a.s.l, as shown in Figure 1.

The park is only sparsely populated. Agricultural use consists mainly of alpine pasture. Park habitats include moorlands, heathland, mountain grasslands, and richly structured landscapes which had been historically cultivated for subsistence agriculture. Tourism is of great importance for the local economy and regional development.

Methods

Vegetation survey

Sites were selected in accordance with the presumed main environmental gradients of shading, elevation, and



Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community

Figure 1. Maps of the study area. Left – location of Parc Ela in Switzerland; right – overview of all studied springs. Thematic layers by the Federal Office of the Environment FOEN and swisstopo.

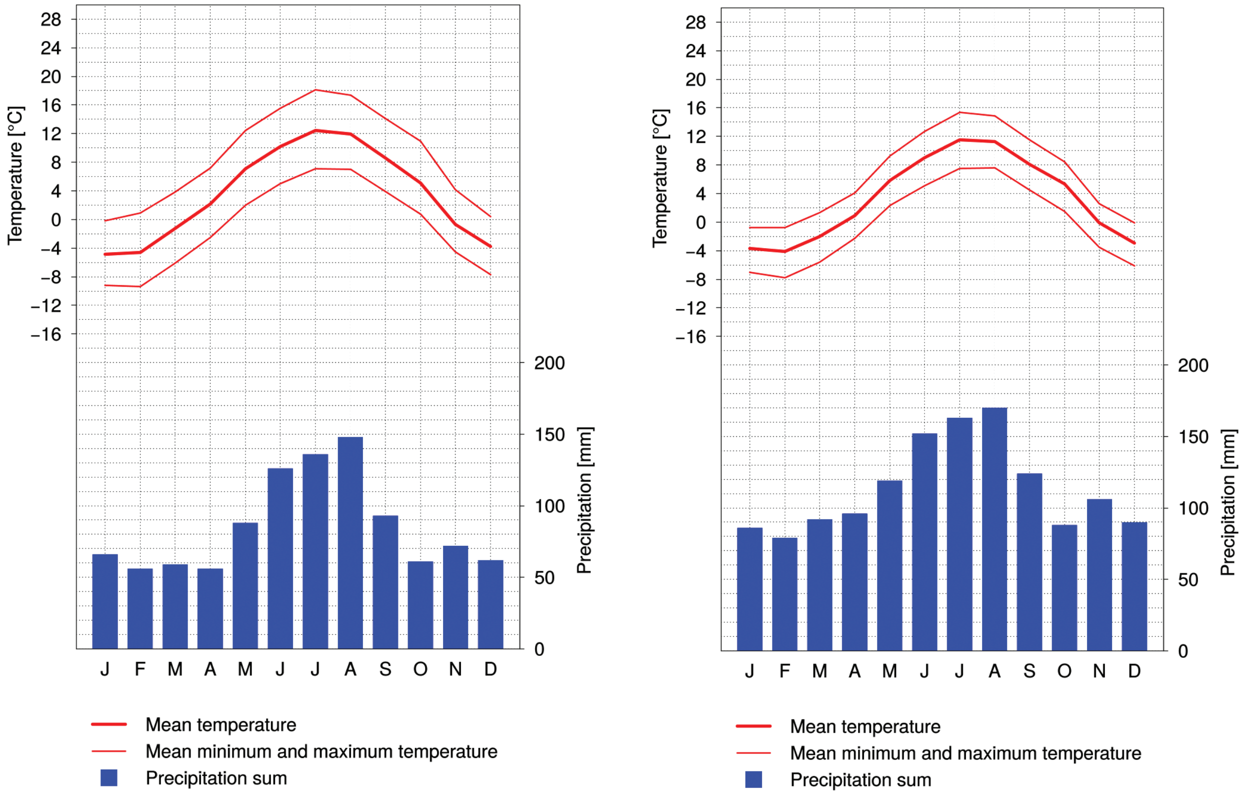


Figure 2. The climate at Arosa (1,878 m, left) and Davos (1,594 m, right) is taken as representative for central Grisons. The climate diagrams show mean values for the standard period 1981–2010. Annual precipitation Arosa 1,365 mm; annual mean temperature Arosa 3.6°C; annual precipitation Davos 1,022 mm; annual mean temperature Davos 3.5°C (Federal Office of Meteorology and Climatology MeteoSwiss 2020).

spring water chemistry. The cantonal spring inventory (GeoGR 2020) was used as a basis, as well as data from the structural surveys of the springs of the Grisons parks 2016–2018 (Küry 2020, unpublished). Sites of natural to semi-natural quality with high or medium conservation priority were preferred. Each spring was assigned a hydrologic type based on the Steinmann-Thienemann concept (Steinmann 1915; Thienemann 1922); in some cases, springs were assigned to the so-called linear or wandering type (Zollhöfer 1997; Küry et al. 2019). Because natural limnocrenes are rare in the region, they were omitted from the study.

Vegetation surveys were conducted in July and August 2020. Three plots (relevés) of 1 m^2 were recorded per spring site, arranged to best cover the variability evident in the field. Although single plots were intended to be as homogeneous as possible, neither ostensibly "fragmentary" nor "atypical" sites were excluded from the surveys in order to capture the real situation as completely as possible (Dengler et al. 2005). All vascular plants and bryophytes were recorded, with percent cover as importance measure. The nomenclature followed Juillerat et al. (2017) for vascular plants and Meier et al. (2013) for bryophytes. Vascular plants were determined using works by Hess et al. (2015) and Eggenberg and Möhl (2013). For the bryophyte determinations, the following works were drawn upon: Burck (1947), Paton (1999), Frahm and Frey (2004), Smith (2004), Frey et al. (2006), Atherton et al. (2010), and Lüth (2019). The species *Bryum pseudotriquetrum* and *B. bimum* are summarized as *B. pseudotriquetrum* aggr., since hardly any fertile samples were found. Conservation status of the species follows Schnyder et al. (2004) and Bornand et al. (2016).

A variety of structural and physico-chemical parameters were included as possible explanatory variables for species composition (Table 1). Water temperature at the outlet, water pH, water conductivity (as an indicator of mineral content, analogous to Sekulová et al. 2012), oxygen content, and oxygen saturation were measured at three locations per plot in open water. Signs of human or animal use were noted in the field and compared with federal and cantonal geodata (Federal Office of Topography swisstopo 2020; GeoGR 2020).

Structural survey

The structural surveys followed the method developed on behalf of the FOEN for the national inventory of spring habitats (Lubini et al. 2014; Küry et al. 2019) and the instructions for the structural surveys in the nature parks of Grisons (Küry 2018, unpublished). Several parameters from the structural records were included in the analysis (Table 1).

Table 1. Examined environmental parameters.

Parameter	Unit	Comment
Coordinates	°	World Geodetic System WGS 1984
Topography		
Elevation	m	Values extracted from the Swiss topographical model TLM25
Slope	°	
Maximum microrelief	cm	Perpendicular deviation of the surface from the plane
Hydrology		
Spring size	m²	Area of open water immediately around the spring outlet (Küry et al. 2019)
Discharge	l/s	Field approximation (Küry et al. 2019)
Maximum water depth	cm	
Vegetation		
Vegetation cover	%	Total vegetation; tree, shrub, herb, and cryptogam layers (shoot presence)
Canopy cover	%	App. % cover
Maximum height of herb layer	cm	
Substrate		
Coverage values	%	Open water, litter, dead wood, stones / rocks, gravel / coarse sand, fine soil
Carbonate content of soil	-	Ordinal scale (HCl test) (Bodenmann et al. 1997, modified)
Spring water		
Water temperature at outlet	°C	Multiprobe HQ40d (Hach)
Water conductivity	µS/cm	Multiprobe HQ40d (Hach)
Water pH	-	Multiprobe HQ40d (Hach)
Oxygen content	mg/l	Multiprobe HQ40d (Hach)
Oxygen saturation	%	Multiprobe HQ40d (Hach)

Classification

Unsupervised classification was performed using the modified TWINSPAN (Two Way Indicator Species Analysis) algorithm (Roleček et al. 2009) in the software JUICE (Tichý 2002) (v.7.1.25, 2020), with a minimum group size of 3 and the average Sørenson coefficient as similarity index. Pseudospecies cut levels of 0, 5, and 40% coverage were used to achieve the clearest possible diagnostic species for the groups and to optimize the spatial distribution of types in the ordination. Diagnostic species were determined based on the standardized phi coefficient (Chytrý et al. 2002; Tichý and Chytrý 2006), where phi values of 0.25 or greater were considered diagnostic, those equal to 0.5 or greater were considered highly diagnostic. Diagnostic species were tested for significance with Fisher's exact test (Fisher 1922). Species with a frequency greater than 50% in the corresponding type were defined as constant species. The resulting units were compared with syntaxa from the literature in order to classify them and characterize them ecologically. The dataset is not representative of all vegetation types in the region, nor of all spring types in Switzerland.

Statistical analysis

The data were managed using Vegedaz (Küchler 2019). Statistical analyses were performed in R (v.3.1.2, R Core Team 2017) within the RStudio environment (v.1.1.383, RStudio Team 2016). All alternative hypotheses were two-sided unless specifically stated. The significance level was set at $\alpha = 0.05$.

In Vegedaz, the square root-weighted means of ecological indicator values (EIV) for moisture, soil reaction, temperature, light, soil aeration, nutrient content (hereafter "nutrient EIV"), and humus content were calculated for each relevé (Landolt et al. 2010). In accordance with the Central Limit Theorem (Quinn and Keough 2002), verification of normal distribution was not required. If variances differed greatly (i.e., by a factor of 4), data were transformed using decadic logarithm or square root; if variances could not be brought within an acceptable range through transformation, significance of differences was tested using Welch's ANOVA (one-way), with Games-Howell tests for post-hoc analyses. Otherwise, the significance of differences in means was tested via one-way analysis of variance (ANOVA). Tukey tests were performed for the post-hoc analyses. In a few cases, Welch's *t*-test was used to determine the significance of differences between two independent groups.

Detrended correspondence analysis (DCA) was performed on the vegetation data using the R package "vegan" (v.2.5), with rare species downweighted (Oksanen et al. 2019). Indicator values and recorded environmental factors were passively projected onto a visualization of the ordination.

Results

Species richness

A total of 95 bryophytes and 164 vascular plant species were recorded. The mean species richness was 21.7 species in 1 m^2. The most species-rich plot was located on a large helocrene system used as summer pasture, characterized by 31 vascular plant and 10 bryophyte species in 1 m^2. The most common species were *Bryum pseudotriquetrum* aggr. (occurring in 70% of the relevés) and *Aster bellidiastrum* (62%). *Palustriella commutata* was recorded in about half of the plots, over both limestone and silicate. Seven species in the vegetation plots are endangered or potentially endangered in Switzerland, including *Tofieldia pusilla*, *Bryoerythrophyllum alpigenum* and *Catoscopium nigritum*.

Classification

Comparing different divisions, seven was the highest number of types for which each of the terminal groups yielded a well floristically defined unit of more than five relevés (Figure 3); this excludes Type 1, an outlier consisting of one relevé. For the assignment to higher syntaxa, types were grouped to best yield ecologically interpretable units. For most springs, all three relevés belonged to a common type; for six springs, the relevés were split across

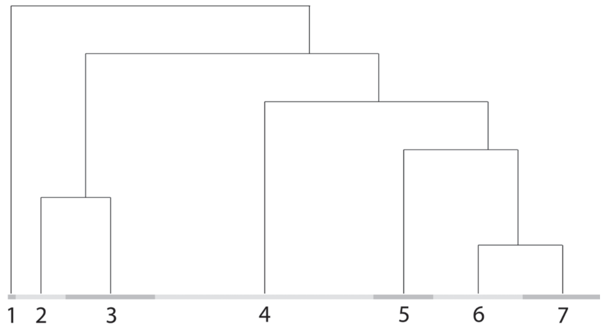


Figure 3. Dendrogram of the TWINSPAN-classification. The width of the bars is proportional to the number of vegetation plots included (one plot in case of cluster 1).

two types. Table 2 displays an abbreviated synoptic table (see Suppl. material 1 for full synoptic table and complete relevé table).

Comparison of vegetation types

Water pH differed little between vegetation types (mean 7.5–7.9) and oxygen content was mostly high (Suppl. material 3). Springs were mostly cold (water temperature at outlet 3.7–7.0°C) to slightly warm (7.0–11.0°C) (Suppl. material 3). The plots ranged from fully insolated to heavily shaded. The maximum height of the herb layer, often

Table 2. Abbreviated synoptic table from the numerical classification. Constancies are given as percentages; diagnostic (> 0.25) phi values are marked with (*), highly diagnostic (> 0.5) values with (**). Significant values are marked in light grey, highly significant values in dark grey. Diagnostic species (upper part of the table) passed Fisher's exact test, companion species did not pass the test. No diagnostic species are marked for Type 1 because it consists of a single relevé.

Type	**1**	**2**		**3**		**4**		**5**		**6**		**7**	
No. relevés	*1*	*5*		*9*		*21*		*5*		*6*		*13*	
Taxon													
Rhizomnium magnifolium	-	100	**	22		10		-		-		-	
Geranium sylvaticum	-	60	**	-		-		-		-		-	
Calamagrostis villosa	100	80	**	-		-		-		-		-	
Epilobium alsinifolium	-	20		78	**	-		-		-		-	
Saxifraga stellaris	-	-		67	**	14		-		-		-	
Brachythecium rivulare	-	80		100	*	14		20		-		15	
Chaerophyllum hirsutum	-	80		67	*	-		-		-		-	
Pinguicula alpina	-	-		-		71	**	-		-		-	
Selaginella selaginoides	-	-		-		67	**	-		-		15	
Salix foetida	-	-		-		52	**	-		-		-	
Palustriella falcata	-	20		-		52	**	-		-		-	
Arabis subcoriacea	-	-		22		52	**	-		-		-	
Juncus alpinoarticulatus	-	-		-		52	*	20		-		15	
Philonotis tomentella	-	-		22		43	*	-		-		-	
Fissidens dubius	-	-		-		5		80	**	-		15	
Platydictya jungermannioides	-	-		-		-		60	**	-		-	
Plagiochila asplenioides	-	-		-		-		80	**	33		8	
Knautia dipsacifolia	-	20		-		-		80	**	33		8	
Brachythecium glareosum	-	-		-		5		-		83	**	-	
Plagiomnium medium	-	-		-		-		-		50	**	-	
Carex davalliana	-	-		-		24		20		-		69	**
Cephalozia spec.	-	-		-		5		-		-		-	
Amblystegium serpens	-	-		-		-		-		-		8	
Agrostis stolonifera	-	-		56		5		40		-		38	
Alchemilla alpina aggr.	-	-		-		14		-		-		-	
Equisetum variegatum	-	-		11		43		-		-		31	
Aneura pinguis	-	-		33		57		20		67		46	
Aster bellidiastrum	-	40		33		76		100		67		54	
Anastrophyllum minutum	100	-		-		-		-		-		-	
Achillea millefolium aggr.	-	-		-		5		-		-		-	
Amblystegium tenax	-	20		11		-		-		-		-	
Amblystegium fluviatile	-	40		44		-		-		-		-	
Adenostyles alliariae	-	20		11		-		-		-		-	
Blindia acuta	-	-		-		29		-		-		-	
Alchemilla conjuncta aggr.	-	-		11		-		-		-		-	
Bartsia alpina	-	-		-		19		-		-		-	
Adenostyles alpina	-	-		-		5		-		33		-	
Alnus viridis	-	-		-		10		-		-		-	
Cephaloziella varians	-	-		11		-		-		-		-	
Carex sempervirens	-	-		-		14		-		-		-	
Angelica sylvestris	-	-		-		-		-		-		8	
Caltha palustris	-	20		-		5		-		-		15	
Briza media	-	-		-		-		-		-		8	
Brachypodium rupestre	-	-		-		-		20		-		8	
Aulacomnium palustre	-	-		11		-		-		-		-	
Avenella flexuosa	-	-		-		5		-		-		-	
Blepharostoma trichophyllum	100	20		-		5		-		-		-	
Calypogeia azurea	-	20		-		5		-		-		-	
Cardamine amara	-	-		-		-		-		-		15	

Table 3. Arithmetic mean, minimum, and maximum values of environmental variables over the entire survey. Significant differences are noted as follows: (***), highly significant ($p < 0.001$); (**), moderately significant ($0.001 \leq p < 0.01$); (*), significant ($0.01 \leq p < 0.05$); (n.s.), not significant. The ordinal scale of the carbonate content of the soil should be interpreted as follows: 0, no carbonate present; 1, only traces of carbonate; 2, < 2% carbonate; 3, 2–10% carbonate; 4, > 10% carbonate (Bodenmann et al. 1997, modified).

Topography	**Mean**	**Min.**	**Max.**	**Test, Transformation**	***p*-value**	**Significance**
Elevation (m)	1,575	964	2,122	Welch's ANOVA	< 0.001	***
Slope (°)	19	4	46	ANOVA	0.911	n.s.
Maximum microrelief (cm)	22	4	77	ANOVA, log10	0.010	*
Hydrology						
Spring size (m²)	7	1	20	Welch's ANOVA	0.183	n.s.
Discharge (l/s)	5	0.03	25	Welch's ANOVA	0.005	**
Maximum water depth (cm)	5	0	26	ANOVA, log10	0.005	**
Vegetation						
Canopy cover (%)	28	0	82	ANOVA	0.415	n.s.
Maximum height of herb layer (cm)	54	16	150	ANOVA	0.559	n.s.
Coverage herb layer (%)	46	0.2	92	ANOVA	0.574	n.s.
Coverage moss layer (%)	50	5	96	Welch's ANOVA	0.503	n.s.
Species richness	21.7	10	41	ANOVA	0.845	***
Vascular plant species richness	13.6	5	31	Welch's ANOVA	< 0.001	
Bryophyte species richness	7.3	1	17	ANOVA	0.130	n.s.
Substrate						
Open water (%)	22	0	69	ANOVA	0.103	n.s.
Litter (%)	17	0.1	95	Welch's ANOVA	0.047	*
Dead wood (%)	3	0	20	Welch's ANOVA	0.792	n.s.
Stone, rock (%)	29	0	95	Welch's ANOVA	< 0.001	***
Gravel, coarse sand (%)	22	0	85	ANOVA	0.531	n.s.
Fine soil (%)	49	0	100	ANOVA	0.006	**
Carbonate content of soil	1.6	0	4	ANOVA	< 0.001	***
Spring water						
Water temperature at outlet (°C)	8.5	3.7	13.0	Welch's ANOVA	< 0.001	***
Water conductivity (μS/cm)	487	131	1299	Welch's ANOVA	< 0.001	***
Water pH	7.7	6.8	8.6	Welch's ANOVA	0.046	*
Oxygen content (mg/l)	7.37	0.17	10.81	Welch's ANOVA	< 0.001	***
Oxygen saturation (%)	78.7	1.9	108.6	Welch's ANOVA	< 0.001	***

measured on culms of *Deschampsia cespitosa*, averaged 54 cm. In the following passages, the types of the numerical classification are described and provisionally assigned to likely syntaxa. The full header data can be found in Suppl. material 2, characterization of the surveyed environmental parameters per vegetation type in Suppl. material 3. Boxplots of a selection of ecological parameters are displayed in Figure 4, while representative photos of each type are shown in Figure 5.

Type 1: strongly flowing rheocrene over boulders

This type consisted of a single plot in sparse mountain forest: a deep outlet of very cold water (3.8°C) under a massive rock overhang with mostly saxicolous vegetation. Many of the species present were unique in the survey (e.g. *Sphagnum capillifolium*, *Bryoerythrophyllum alpigenum*). In the ordination, this relevé lies more than 2 SD (standard deviation) away from its nearest neighbor (DCA axis 1). This type was excluded post-hoc from classification and final ordination for these reasons. The other relevés of this heterogeneous spring area belong to Types 2 and 3.

Type 2: Rhizomnium magnifolium-Chaerophyllum hirsutum community: mineral-poor springs in subalpine forest clearings

Diagnostic species: *Calamagrostis villosa*, *Geranium sylvaticum*, *Rhizomnium magnifolium*

This type was composed of many species that prefer sheltered sites. *Brachythecium rivulare* occurred frequently, while *Palustriella commutata* was absent. Litter cover was high, and the herb layer was vigorous (mean cover 58%, mean maximum height 88 cm). The spring water had low conductivity, was often oxygen-rich and very cold (mean water temperature at outlet 5.2°C). The type mostly consisted of rheocrenes with moderate to strong flow (mean discharge 6.2 l/s). The average maximum microrelief was 48.2 cm, significantly greater than in many other types (Figure 4D). Nutrient EIV was also significantly greater than in many other types (Figure 4G).

This type is difficult to classify. According to Hinterlang (1992) and Mucina et al. (2016), the *Cardamino-Chrysosplenietalia* Hinterlang 1992 always occurs below the spruce stage. The well-developed herb layer, predominance of shade-loving species, and strong flow suggest the *Caricion remotae* Kästner 1941 (Table 3). This alliance, although mostly associated with the montane zone, is also recorded at higher elevations (e.g., Grabherr and Mucina 1993; Chytrý 2011). Some traditional character species of the *Cardamino-Chrysosplenietum alternifolii* Maas 1959 are not present here, but that should not exclude the community: *Carex remota* does not grow above the montane level, and *Chrysosplenium alternifolium* rarely occurs in the area (Info Flora 2020). Some characteristic and dominant species of the community described by

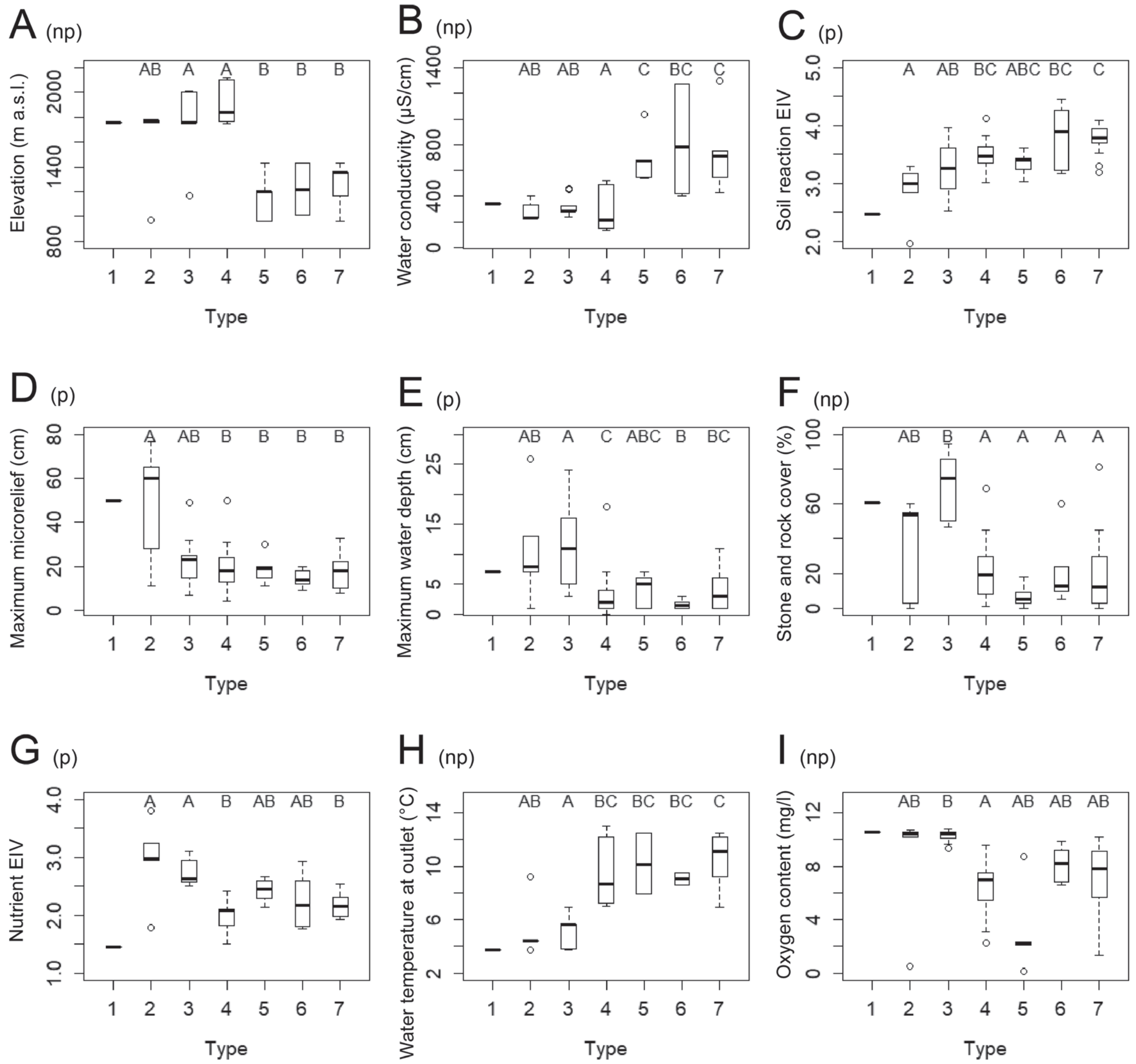


Figure 4. Boxplots of a selection of ecological parameters. Bars without common letters differ significantly from each other. Variables with (p) were assessed with parametric procedures (ANOVA, Tukey test), for variables with (np) non-parametric tests were used (Welch's ANOVA, Games-Howell test).

Chytrý (2011) are present (e.g. *Chaerophyllum hirsutum*, *Brachythecium rivulare*, *Conocephalum conicum*).

Type 3: Epilobium alsinifolium-Brachythecieum rivulare community: mineral-poor, cold-stenothermic, unshaded springs

Diagnostic species: *Brachythecium rivulare*, *Chaerophyllum hirsutum*, *Epilobium alsinifolium*, *Saxifraga stellaris*

This vegetation developed around rheocrenes of the subalpine zone under the influence of oxygen-rich, cold spring water (mean water temperature at outlet 5.1°C). Compared to other unshaded springs in the study, the water was significantly richer in oxygen (mean oxygen content 10.2 mg/l) (Figure 4I). The mean cover of the moss layer was comparatively high at 60%, and *Palustriella commutata* strongly dominated in many plots, which may explain the relatively low species richness. These relevés were mostly strongly flowing rheocrenes, with stone and rock cover exceeding many other types significantly (Figure 4F). Mosses dominated over vascular plants more strongly than in the other types.

This vegetation type shares a diagnostic species (*Epilobium alsinifolium*) with the *Cratoneuro-Philonotidetum seriatae* Geissler 1976. *E. alsinifolium* makes no special demands on substrate chemistry, but prefers very wet, cold sites (Geissler 1976; Oberdorfer 2001). The character species *Saxifraga stellaris* is also a cold-water specialist. Since there are certain similarities with the *Cratoneuro-Philonotidetum calcarae* Geissler 1976, the type may be an intermediate form between the two associations. Although the mean water conductivity of 319 µS/cm is high relative to other studies, Geissler gives 16 °dH (about 480 µS/cm) as the maximum value of total hardness for the association. The *Cratoneuro-Philonotidetum seriatae* is mostly found in the subalpine zone, where it is represented mainly by rheocrenes with considerable flow velocities. The *Brachythecium rivulare-Cardamine amara* variant described by Geissler (1976) includes stands along rapidly flowing headwater streams with strong stands of *Brachythecium rivulare*, as well as scattered occurrences of *Cardamine amara* and tall shrubs (e.g. *Petasites paradoxus* in this case).

Figure 5. Representative photographs of each vegetation type. **A** Type 2, mineral-poor springs in subalpine forest clearings; **B** Type 3, mineral-poor, cold-stenothermic, unshaded springs; **C** Type 4, mineral-poor springs in alpine pastures; **D** Type 5, mineral-rich, montane forest springs; **E** Type 6, mineral-rich forest springs; **F** Type 7, montane rich-fen springs. Photographs by Hallie Seiler (**A–E**) and Jürgen Dengler (**F**).

Type 4: Palustriella falcata-Pinguicula alpina community: mineral-poor springs in alpine pastures

Diagnostic species: *Arabis subcoriacea*, *Juncus alpinoarticulatus*, *Palustriella falcata*, *Philonotis tomentella*, *Pinguicula alpina*, *Salix foetida*, *Selaginella selaginoides*

These relevés included oligotrophic springs on pastures in the subalpine to alpine zones. The plots were evenly divided between rheo- and helocrenes. The most species-rich relevés in the survey belonged to this type (mean 24.3 species in 1 m^2). These springs were mostly fully insolated or were only lightly shaded. In some cases, very high water temperatures were recorded in shallow pools. Water was significantly shallower than in Types 2 and 3 (Figure 4E). The nutrient EIV was significantly lower than the other high elevation springs (Figure 4G).

The records of this type are similar to *Philonoto fontanae-Montietum rivularis* Büker et Tx. 1941. This community is found in moderately warm alpine springs over siliceous bedrock and is associated with grazing. The character species *Philonotis tomentella* is also diagnostic here, and the calcifuge *Diobelonella palustris* occurs sporadically. Compared to *Pinguicula vulgaris*, the diagnostic species *P. alpina* is more likely to occur in high mountains and is less bound to limestone (Oberdorfer 2001). However, it is questionable whether this vegetation type could be assigned to a siliceous alliance: although the substrate is carbonate-poor, many typical species of the *Cratoneurion* are present, including the character species *Pinguicula alpina* and *Palustriella falcata*, which are diagnostic for this type. One possible solution would be to understand the alliance *Cratoneurion* as a collection of subalpine-alpine spring communities over both limestone and silicate, as proposed by Geissler (1976). The *Cratoneuro-Philonotidetum calcareae* Geissler 1976 appears to be a suitable match. Diverse calcicoles are present, and the differential species *Arabis subcoriacea* is diagnostic and common. This species colonizes base-rich, humic soils as well as weakly trickling springs over gravel (Oberdorfer 2001). *Brachythecium rivulare* is conspicuously rare, and *Saxifraga aizoides* is more common than *S. stellaris*, as is characteristic for the association.

Type 5: Fissidens dubius-Cratoneuron decipiens community: mineral-rich, montane forest springs

Diagnostic species: *Fissidens dubius*, *Knautia dipsacifolia*, *Plagiochila asplenioides*, *Platydictya jungermannioides*

These helocrenes were found in forests of the montane zone. The substrate was basic (soil reaction EIV), nutrient-rich (nutrient EIV), and fine. The oxygen content of the spring water was significantly lower than many other types (mean 3.1 mg/l) (Figure 4I). Canopy cover varied widely. Relevés included springs with severe trampling damage from wildlife. Springs tended to be small and weakly flowing (mean discharge 0.2 l/s). Herb layer cover was mostly higher than that of the moss layer, which is unusual for this study.

The alliance *Lycopodo europaei-Cratoneurion commutati* Hadač 1983 could be considered here. These calcareous forest springs, although mostly associated with the colline and montane zones, occur almost to the timberline according to Chytrý (2011), and have been recorded in the Italian Alps (Giacomini 1939, assigned by Dierssen 1973). The only association of the alliance, *Brachythecio rivularis-Cratoneuretum* Dierssen 1973, has a similar ecomorphology and species assemblage (e.g., *Palustriella commutata* (diagnostic), *Eucladium verticillatum* (diagnostic) and *Equisetum palustre* (dominant)). According to Hájek (1998), this community occurs in both heavily and lightly shaded habitats. Tufa does not occur in the relevés, probably due to local climatic conditions, although microscopic carbonate crystals were observed in many bryophyte samples. For three springs, assignments were split across Types 5 and 7, presumably due to varying light conditions in the spring area.

Type 6: Plagiomnium medium-Palustriella commutata community: mineral-rich forest springs

Diagnostic species: *Brachythecium glareosum*, *Plagiomnium medium*

These records were superficially similar to Type 5: they were also base-rich, shaded springs of the montane stage. The springs were either rheocrenes or linear springs. Half of the relevés were tufaceous, and the relevés were species-poor on average (mean 18.3 species in 1 m^2). Water was better oxygenated in contrast to type 5 (Figure 4I), and nutrient EIVs were low. These large springs occurred on steep, wooded slopes.

The relevés of this type belong to two forest springs with very different environmental conditions: a linear spring without tufa formation and a very large, complex rheocrene system with cascade tufa. The question arises as to why they were combined in the classification. There are only a few species that can persist under strong tufa formation; however, these can often occur on other base-rich, wet sites, so they are usually not strictly tied to petrifying springs (Zemp et al. 2016). The rarity of true character species for petrifying springs leads to them being distributed here over two types (6 and 7). Lyons and Kelly (2017) note that the definition of *Cratoneurion* vegetation has long been problematic, and that transitions between petrifying springs and other habitats are poorly characterized, although widely recognized in the literature. The linear forest spring could probably be assigned to the *Brachythecio rivularis-Cratoneuretum*, while the large tufaceous spring potentially belongs to the *Eucladietum verticillati* Allorge 1922. This community occurs on steep, wet limestone rock faces, often in partial shade (Grabherr and Mucina 1993). Grabherr and Mucina (1993) found the second association at elevations up to 1,500 m in Austria, although the community has otherwise rarely been recorded there. The character species *Eucladium verticillatum* is present, but not dominant, as indicated in the literature. Otherwise, many of the numerous companion species of the association are present: *Tofieldia calyculata*, *Carex flacca*, *Palustriella commutata*, and *Agrostis stolonifera*. *Catoscopium nigritum*, a pioneer species of tufa cascades (Schubert et al. 2001), was found in one plot. Although tufaceous springs also belong to Type 7, those formations consist of terraces rather than slabs.

Type 7: Carex davalliana-Palustriella commutata community: montane rich fen-springs

Diagnostic species: *Carex davalliana*

This vegetation type was influenced by warm, base-rich spring water, sometimes with tufa formation. With the exception of one plot, this type was located in helocrenes (69%) or linear springs. Canopy cover varied from 14 to 68%, but species mostly had moderately high light EIVs (mean 3.34). The water temperatures at the outlet were significantly higher than in Type 3 (Figure 4H). The fine, calcareous substrate was rather weakly percolated.

This type shares many species with rich fens, including *Carex davalliana* (diagnostic), *Carex lepidocarpa* (constant), and *Tofieldia calyculata*. However, character species of the *Cratoneurion* (*Palustriella commutata* and *Aneura pinguis*) occur frequently, and *Hymenostylium recurvirostrum* (character species) and *Pinguicula vulgaris* (companion species) are also present. The *Cratoneuretum commutati* Aichinger 1913 could be considered: this vegetation occurs in calcareous springs of the montane stage and possesses the character species *Cratoneuron filicinum* aggr., present in the relevés, a rather nitrophilous species that tolerates desiccation better than *Palustriella commutata* (Lyons and Kelly 2017).

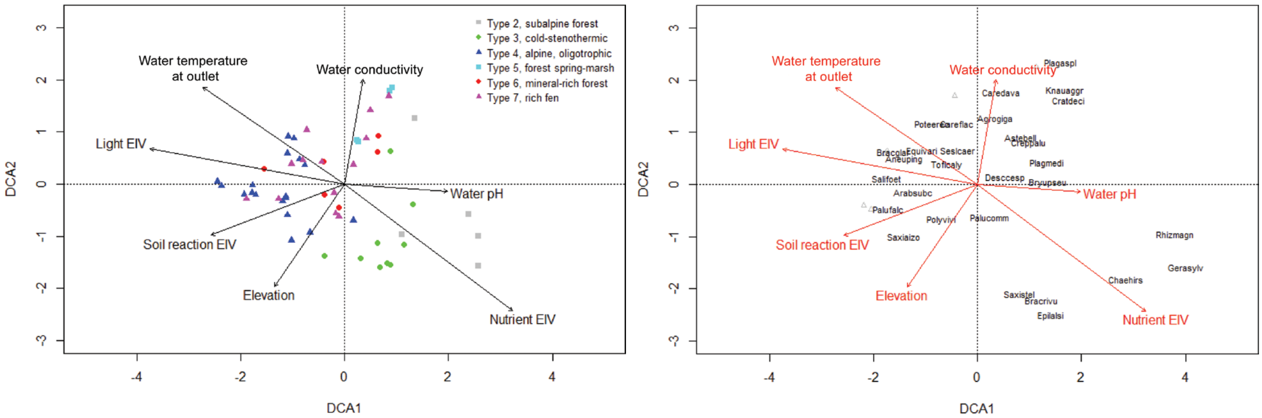


Figure 6. Gradient analysis (DCA) of the dataset. Environmental variables and EIVs are projected over the ordination. The vectors shown correlate with at least |r| = 0.80 with one of the two axes. Above – vegetation types; below – the 20 most common species in the relevés, as well as the diagnostic species of the numerical classification, are shown: "Arabsubc" – *Arabis subcoriacea*; "Agrogiga" – *Agrostis gigantea*; "Aneuping" – *Aneura pinguis*; "Astebell" – *Aster bellidiastrum*; "Bracglar" – *Brachythecium glareosum*; "Bracrivu" – *Brachythecium rivulare*; "Bryupseu" – *Bryum pseudotriquetrum* aggr.; "Caredava" – *Carex davalliana*; "Careflac" – *Carex flacca*; "Chaehirs" – *Chaerophyllum hirsutum*; "Cratdeci" – *Cratoneuron decipiens*; "Desccesp" – *Deschampsia cespitosa*; "Epilalsi" – *Epilobium alsinifolium*; "Equivari" – *Equisetum variegatum*: "Gerasylv" – *Geranium sylvaticum*; "Knauaggr" – *Knautia dipsacifolia*; "Palufalc" – *Palustriella falcata*; "Palucomm" – *Palustriella commutata*; "Plagaspl" – *Plagiochila asplenioides*; "Plagmedi" – *Plagiomnium medium*; "Polyvivi" – *Polygonum viviparum*; "Poteerec" – *Potentilla erecta*; "Rhizmagn" – *Rhizomnium magnifolium*; "Salifoet" – *Salix foetida*; "Saxiaizo" – *Saxifraga aizoides*; "Seslcaer" – *Sesleria caerulea*; "Toficaly"– *Tofieldia calyculata*.

The frequent interlocking with the *Caricion davallianae* is also mentioned in the literature (Knapp and Stoffers 1962; Grabherr and Mucina 1993); indeed, some plots of this type might be better assigned to that alliance. This type includes spring sites whose relevés were sometimes assigned to Types 2 and 3 (both mineral-poor types of the subalpine zone), underscoring the difficulty of differentiating spring vegetation on the basis of water chemistry.

Environmental gradients

DCA axes 1 and 2 explain much of the variation in species composition (eigenvalues 0.66 and 0.54, respectively, Figure 6). The length of axis 1 is 5.09 standard deviations (SD), signaling high β-diversity, so the two ends of the gradient share few common species. Axis 2 has gradient length 3.51, justifying the use of DCA. DCA axis 1 correlates most strongly with water pH ($|r| = 0.998$), light EIV ($|r| = 0.984$), soil reaction EIV ($|r| = 0.935$), and nutrient EIV ($|r| = 0.799$), while DCA axis 2 correlates most strongly with water conductivity ($|r| = 0.984$) and elevation ($|r| = 0.825$). Vegetation Type 1 ($n = 1$) was omitted from the ordination.

Discussion

Species richness

The species richness of the records (95 moss species, 164 vascular plant species) is high compared to similar studies. In Gesäuse National Park (AT), 97 vascular plants and 60 bryophyte species were recorded in 46 plots of less than 1 m^2 (Suanjak 2007). Mogna et al. (2015) found 135 species of bryophytes and vascular plants in 48 springs in the Ligurian Alps (Italy). In the Kalkalpen (Austria), Weigand (1998) recorded 77 bryophyte species in 22 springs. In a study of 19 springs in the Adamello-Brenta Regional Park (Italy), Cantonati and Ortler (1998) found only 58 bryophyte species, but an astonishing 245 vascular plant species. For springs in the Swiss Alps, western Carpathians, and mountains of Bulgaria, Sekulová et al. (2012) found a mean species richness of 25.0, 22.2, and 17.3 species in 16 m^2, respectively. The GrassPlot database (Dengler et al. 2018; Biurrun et al. 2019) gives a mean total species count of 15.4 species in 1 m^2 ($n = 493$) for wetlands in alpine, boreal, and temperate climates (GrassPlot Diversity Explorer v. 2.10; https://edgg.org/databases/GrasslandDiversityExplorer; see Biurrun et al. 2021); in this study, a mean species count of 21.7 species in 1 m^2 was recorded. However, few records of *Montio-Cardaminetea* are represented in the database at present, and other wetlands (e.g., reedbeds and riparian habitats) are generally species-poorer on average. It is unclear why the records in Parc Ela were so species rich, especially when the species-area relationship is considered (Chytrý and Otýpková 2003). One possible explanation is the inclusion of springs with widely varying environmental conditions.

Site conditions

The ecological conditions of springs are generally difficult to assess because they are small habitats characterized by strong ecotones (Brunke et al. 2015). For this study, only a single measurement of the physico-chemical parameters was made, although Cantonati et al. (2006) recommend that these parameters be recorded over at least one year. Although spring water generally undergoes only minor physico-chemical changes during the course of a year (Odum 1971), it is unknown how parameters vary seasonally within the study area. The FOEN method (Küry et al. 2019) is practical for rapid survey of key characteristics, but many parameters are rough estimates.

Vegetation types are clearly separated by elevation and water conductivity (Figure 4A and 4B). The first group (Types 1 to 4) includes springs of the subalpine-alpine levels with a mean water conductivity around 297 µS/cm (SD = 126 µS/cm). The moderately low conductivity could be related to the geology of the aquifer and/or short groundwater residence time (Catonati and Ortler 1998). The mean soil reaction EIV corresponds to a pH between weakly acidic and neutral (mean 3.31, SD = 0.43). The second group consists of montane springs with higher water conductivities (mean 748 µS/cm, extreme values up to 1,299 µS/cm). Here, according to the soil reaction EIV, the substrate is somewhat more base-rich than in the first group (mean 3.68, SD = 0.37). The differences within mean elevation and water conductivity are statistically significant ($p < 0.001$ and $p = 0.002$, Welch's *t*-test, one-sided). The average temperature EIV of the second group is significantly higher ($p = 0.018$, Welch's *t*-test, one-sided), but the difference in means is not large (mean group 1 = 2.27, group 2 = 2.60).

There is an apparent gradient of shading within the main groups, but it is not statistically significant in the overall data set, although it explains much of the variability in the ordination (light EIV, $|r| = 0.984$ with DCA axis 1).

Classification and syntaxonomy

This study was affected by the oft-cited paucity of diagnostic species particular to spring habitats (Oberdorfer 1992; Beierkuhnlein and Gollan 1999). Of the 21 diagnostic species calculated, less than half belong to the classic character species for syntaxa of the *Montio-Cardaminetea*. However, this is presumably related to methodological limitations: since only spring vegetation data were included, many of the diagnostic species are probably differential species that are more common in other habitats.

Epilobium alsinifolium, listed as a class character species of *Montio-Cardaminetea*, appears in these records only in the Types 2 and 3, presumably due to temperature-related effects. The class character species *Stellaria alsine* and *Bryum schleicheri* (Schubert et al. 2001) do not occur in the records; *Stellaria alsine* is a calcifuge forest species which does not occur in the region. According to Oberdorfer (2001), *Cardamine amara* prefers humic, nutrient-rich sites, and occurs only sporadically in springs; in this study, it was encountered in only three relevés. In addition, Pott (1995) notes that the species transgresses too much into reedbeds and alder carrs to be a strong character species of the class.

Although the water conductivity was mostly not very low (Figure 4), species of the *Cardamino-Montion* did occur. The alliance character species *Diobelonella palustris* was observed sporadically, but the main distributional range of *Montia* spp. ceases north of the Alps (Hinterlang 2017) and the genus, like the alliance character species *Epilobium obscurum*, is rare in the mountains of Switzerland (Info Flora 2020). Other differential species of the alliance, *Calliergonella cuspidata* and *Juncus articulatus* (Hinterlang 2017), occur as well, but are not strictly tied to siliceous substrate (Oberdorfer 2001; Atherton et al. 2010). The species assemblage of the unshaded springs mostly agrees with the classic *Cratoneurion commutati*; the problem is rather that the typical species of the alliance (e.g. *Palustriella commutata*, *Saxifraga aizoides*) are also quite common over siliceous bedrock in the Alps.

The delimitation between spring and contact community is challenging, which complicates the selection of areas for vegetation surveys: in the literature, very different area sizes are recorded, between 0.04 to 80 m^2 (Chytrý and Otýpková 2003; see also Pott 1995). Fragmentary or weakly developed stands are often ignored in favor of homogeneous small-scale sites (Cantonati et al. 2006), which was not done in this study; therefore, comparisons with existing syntaxa should be viewed critically.

The numerical classification results in seven vegetation types which seem to occupy a rank between alliance and association. For this classification, the forest springs were neither simply split off into a separate alliance, nor were they merged with unshaded springs of similar chemistry. Although some researchers (e.g., Delarze et al. 2015) treat forest spring synusia as components of forest communities, we share the view of Kästner (1941). The vegetation of forest springs, although dependent on shading, has characteristic species compositions which have been attested by numerous authors as separate types (e.g. Braun-Blanquet 1926; Tüxen 1937; Maas 1959; Hinterlang 1992).

The description and comparison of types results in the proposed syntaxonomy in Table 4. All unshaded communities can be assigned to the *Cratoneurion*, a TypoCH-alliance which is listed in the Ordinance on the Protection of Nature and Cultural Heritage as "deserving of protection." These communities can be provisionally divided into two "suballiances" of the *Cratoneurion*: a montane group, and a group sensu Geissler (1976), which includes subalpine-alpine springs over calcareous and siliceous bedrock. The position of the alliances is controversial. Mucina et al. (2016) place the *Caricion remotae* within a separate order (*Cardamino-Chrysosplenietalia* Hinterlang 1992) and note that the *Cratoneurion* may better be placed in the *Adiantetea* Br.-Bl. et al. 1952. Additionally, they suggest reducing the *Lycopodo-Cratoneurion* to a synonym of the *Cratoneurion*. This may be justified in our case, since no clear separation between shaded and unshaded springs over limestone could be shown.

Table 4. Proposed syntaxonomy for the studied spring sites.

Montio-Cardaminetea Br.-Bl. et Tüxen ex Klika et Hadač 1944
  Montio-Cardaminetalia Pawłowski et al. 1928
    Cratoneurion commutati Koch 1928
      Montane associations
        ° _Eucladietum verticillati_ Allorge 1922
        ° _Cratoneuretum commutati_ Aichinger 1913
      Subalpine-alpine associations
        ° _Cratoneuro-Philonotidetum calcareae_ Geissler 1976
        ° _Cratoneuro-Philonotidetum seriatae_ Geissler 1976
    Lycopodo europaei-Cratoneurion commutati Hadač 1983
        ° _Brachythecio rivularis-Cratoneuretum_ Dierssen 1973
  Cardamino-Chrysosplenietalia Hinterlang 1992
    Caricion remotae Kästner 1941
        ° _Cardamino-Chrysosplenietum alternifolii_ Maas 1959

Environmental gradients

The two visualized DCA axes show high heterogeneity along their lengths. DCA axis 1 can be interpreted as a gradient from highly insolated, oligotrophic springs to somewhat more nutrient-rich forest springs with base-rich water (Figure 6). Nutrient EIV increases with increasing shading, possibly due to the allochthonous input of organic material. Temperature EIV also increases slightly in association with this gradient, as shaded springs are better sheltered from cold and usually occur below the timberline. As the axis value increases, typical species of forests and tall forb communities occur (e.g. *Geranium sylvaticum*, *Chaerophyllum hirsutum*). At the lower end of the axis, species of the subalpine-alpine unshaded springs are more likely to be found, such as *Palustriella falcata* and *Saxifraga aizoides*. DCA axis 2 is most strongly correlated with water conductivity and elevation. In the lowest range of values are the species of cold springs, such as *Saxifraga stellaris* and *Epilobium alsinifolium*. *Carex davalliana*, as a calcicole, lies in the highest range of the axis.

In the ordination it can be clearly seen that elevation is a sum parameter which integrates diverse factors and catchment processes (Strohbach et al. 2009). As elevation increases, the mineral content of the spring water decreases and the mean annual temperature decreases. Habitats become more strongly insolated and nutrient-poor. However, no strong pattern is evident in the ordination with respect to soil reaction, despite high correlation with DCA axis 1. The intermingling of calcifuges and calciphiles in the ordination is consistent with the observed reality in the field. As in other studies (e.g., Beierkuhnlein and Gräsle 1998; Hájek et al. 2002; Hájkova et al. 2008), water pH was found to be an important parameter for species composition, although the effect is likely obscured by the discrepancy between spring water chemistry and substrate chemistry at the sites.

Implications for conservation efforts

The ordination confirms that nutrient EIV is an important factor for species composition ($|r| = 0.799$ with DCA axis 1). Since eutrophication quickly leads to the depletion of specialized bryophytes in oligotrophic wetlands (Bergamini and Pauli 2001; Hedenäs et al. 2003), local farmers in Parc Ela carry particular responsibility for these sites. Interestingly, the most species-rich areas in the study were on low-intensity grazed pastures; however, it is possible that highly specialized spring species are adversely affected by this disturbance. Trampling by game or livestock was observed in 20% of the relevés in this study, with the most severely damaged springs located in montane forests. Helocrenes were observed to be impacted by forest management, through trampling and inputs of forest debris during timber harvesting. Zollhöfer (1997) reports that such springs also fall victim to logging trails. For this reason, we consider it necessary to involve forestry operations in conservation projects.

Parc Ela has a good ecological infrastructure which is continuously being reinforced. Spring restoration projects, rare in Switzerland to date, likely have a good chance of success within the park; however, Cantonati et al. (2006) note that research is needed to understand how typical spring flora can be effectively restored, if at all. This survey was limited to relatively natural springs of the montane and subalpine levels, providing basic knowledge on the ecological potential of many local springs. For further development of a protection concept, comparable studies for impaired springs or those near settlements are recommended.

Outlook

This study confirms the oft-cited species richness of spring habitats. For the protection of these valuable habitats, many new developments can be expected in the coming years, such as the planned European revision of the class *Montio-Cardaminetea* (cf. Hájek et al., pers. comm.) and completion of the national inventory of spring habitats in Switzerland. However, regional projects remain important. Since many species of bryophytes are highly specialized to springs (Cantonati et al. 2006), they should be used for monitoring and evaluations of the effectiveness of conservation measures.

In the future, a refined typology must be considered for spring conservation. This study identifies three major challenges to typifying the montane-subalpine springs of the central Alps: the complex geological and topographical conditions prevent simple division by groundwater chemistry; petrifying springs are floristically hardly distinguishable from other base-rich springs (and definition based on tufa formation is unsatisfactory; Lyons and Kelly 2017); and subalpine forest springs, although clearly distinguishable, are not taken into account in the existing Swiss classification system. These points should be considered for future conservation efforts.

Although the network of spring habitats is more intact in the high mountains than in the lowlands, many threats still exist. In this study, the importance of nutrient balance for plant species composition is confirmed; however, for the numerous oligotrophic springs on alpine pastures, the extent of the ecological influence of this type of land use is still unclear. Climatic conditions may also become problematic in the coming years: because high-elevation springs depend on catchment snowpack and glaciers (Brown et al. 2003; Hannah et al. 2007), these disjunct habitats and their communities will react strongly to climate change (Woodward et al. 2010; Küry et al. 2018). Further studies of alpine springs, including long-term monitoring, could provide important information.

As the "water castle of Europe," Switzerland bears a strong responsibility to preserve its natural springs. Although there are many challenges facing spring conservation, renewed national scientific interest should do much to protect these valuable habitats.

Data availability

The data are provided as supplementary material and also included in the GrassPlot database (https://edgg.org/databases/GrassPlot).

Author contributions

The project was planned jointly by H.S., J.D., and D.K.; H.S. carried out the field sampling and plant determination with support from J.D. and D.K.; H.S. performed the analyses and drafted the manuscript under the guidance of J.D.; all authors checked, improved, and approved the manuscript.

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Supplementary material

Supplementary material 1
Complete relevé table and combined synoptic table
Link: https://doi.org/10.3897/VCS/2021/69101.suppl1

Supplementary material 2
Header data
Link: https://doi.org/10.3897/VCS/2021/69101.suppl2

Supplementary material 3
Environmental parameters within the seven vegetation types
Link: https://doi.org/10.3897/VCS/2021/69101.suppl3

VEGETATION CLASSIFICATION AND SURVEY

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REVIEW AND SYNTHESIS
INTERNATIONAL VEGETATION CLASSIFICATION

Braun-Blanquet meets EcoVeg: a formation and division level classification of European phytosociological units

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Abstract

Aims: To link the Braun-Blanquet units of the EuroVegChecklist (EVC) with the upper levels of the International Vegetation Classification (IVC), and to propose a division level classification for Europe. **Study area:** Europe. **Methods:** We established a tabular linkage between EVC classes and IVC formations and identified mismatches between these two levels. We then proposed IVC division level units to organize EVC classes. **Results:** We organized the EVC classes into 21 formations and 30 divisions. We flagged classes that did not fit comfortably within an existing formation, either because its content corresponded to more than one formation or because it did not fit any formation description. In a few cases, we split EVC classes because they seemed too heterogenous to be assigned to a single formation. **Conclusions:** The IVC approach adds a set of physiognomic and ecological criteria that effectively organizes the EVC classes, which are already being increasingly informed by physiognomy. Therefore, the formation concepts are relatively natural extensions of concepts already embedded in the classes. However, physiognomic placement of Braun-Blanquet classes can be difficult when the sampling of the vegetation is at finer grain than usual in the respective formation (tall-scrub, annual pioneer communities). Some EVC classes seem too heterogenous to fit into the IVC formation system. Delimitation of these classes has often been a matter of debate for many decades, and the IVC perspective might help to solve these intricate issues. In other cases, mismatches between phytosociological classes and IVC formations might better be solved by emending the current formation concepts.

Abbreviations: BB = Braun-Blanquet; EVC = EuroVegChecklist; IVC = International Vegetation Classification.

Keywords

Braun-Blanquet approach, class, division, EcoVeg approach, Europe, EuroVegChecklist, formation, International Vegetation Classification, macrogroup

Introduction

There is an increasingly wide array of tools that permit ecologists to describe, classify, and map the diversity of ecosystems around the globe, including large scale plot datasets and remotely sensing imagery. These tools have led to a renewed interest in global hierarchical typologies of vegetation types ("bioecosystems"). Such typologies provide a knowledge structure for interpreting ecosystem diversity, and guiding resource management, conservation assessments, and species-habitat relationships. A commonly used set of criteria used to organize these hierarchies are physiognomy and structure, ecological functions and factors, floristics, and biogeography (Faber-Langendoen et al. 2014, 2020; Moncrief et al. 2016; Guo et al. 2018; Mucina 2018; Keith et al. 2020); less commonly, zonal criteria are introduced based on vegetation-climatic relationships (Luebert and Pliscoff 2006; Mucina et al. 2016; MacKenzie and Meidinger 2018). These global classification efforts are strongest when building on existing, data driven, extensive, plot-based / inventory-based classifications at regional to continental scales.

A recent European synthesis at the continental scale – the "EuroVegChecklist" (EVC) – brought together a comprehensive hierarchical system of alliances, orders, and classes of Braun-Blanquet (BB) syntaxonomy, briefly characterizing each unit in ecological and geographic terms, and providing a list of diagnostic species for all classes (Mucina et al. 2016). However, the Braun-Blanquet approach, by relying on floristic composition and similarity for its hierarchy, lacks a coherent global framework. This is because, at upper levels, vegetation types are largely equally distinct in their floristic differences – i.e., they have no or very few species in common, and there is no clear basis to organize the classes within the system. Various proposals have been made over the years on how to organize BB classes using external criteria, beginning with the "sociological progression" and the "circle of vegetation" (Braun-Blanquet 1921, 1964), to a new division level above class (Jakucs 1967), to formation concepts (Passarge 1966; Theurillat et al. 1995; Rodwell et al. 2002) and, most recently, zonal concepts (Mucina et al. 2016). Fundamentally, the system is open to any of these external approaches.

The International Vegetation Classification (IVC) maintained by NatureServe and partners, which uses the EcoVeg approach (Faber-Langendoen et al. 2014, 2018, 2020), has developed a global set of formations (Faber-Langendoen et al. 2016) and an increasingly comprehensive set of division level units (e.g., Sayre et al. 2013; Dixon et al. 2014; Muldavin et al. 2021). The formation is physiognomic-structural in character with supplementary ecological information and defined by dominance of a given growth form in the uppermost stratum of the community, or by a combination of dominant growth forms (Whittaker 1975). These formations have also been widely used to define biomes (Moncrieff et al. 2016; Faber-Langendoen et al. 2020). The term "division" was adopted from the Braun-Blanquet approach, and it was originally proposed as a level above the class (Jakucs 1967; Westhoff and van der Maarel 1973). It unites related phytosociological classes (or, in the EcoVeg hierarchy, macrogroups) within a biogeographic region on the basis of common division-level character species, growth forms, and ecology. The division concept introduces floristic criteria, by which the upper-level formation types can be subdivided by continental scale biogeographic species pools. In turn, from the bottom-up, shared growth forms among division types, which reflect a set of shared climatic and edaphic factors, lead to their placement within the same formation.

The Braun-Blanquet approach places a strong emphasis on plant species composition. Specifically, the approach deals with plant species co-occurrences, or, in other words, species compositional patterns and gradients at the scale of the plant community. It works with empirical, plot-based data and techniques to compare floristic composition among communities and relates these patterns to environmental factors (Westhoff and Van der Maarel 1973; Ewald 2003; Dengler et al. 2008). It organizes vegetation types in a hierarchical system based on floristic composition and similarity.

The EcoVeg approach places a strong emphasis on both plant species composition and growth form, interpreting the role of both through the lens of biogeographic and ecologic factors. Specifically, the EcoVeg approach works with the same plot-based data and techniques of the Braun-Blanquet approach but expands the analyses to include local to global gradients of both composition and growth form. In turn, it organizes vegetation types in a hierarchical system based on the patterns and relationships of vegetation to ecological and biogeographic gradients. Thus, e.g., plant communities occurring in Mediterranean climates around the globe have convergent adaptations in structure, life forms and flora evolution (Dallman 1998; Pignatti et al. 2002), which provide the basis for placing these vegetation units together in the "Mediterranean Scrub & Grassland" formation of the IVC, despite sharing no species in common.

Despite the primary focus of the Braun-Blanquet approach on floristic composition and similarity, its fundamental goals align with that of the EcoVeg approach: to describe the patterns of plant communities that form a matrix of global, regional and local vegetation cover, and to investigate and explain the ecological context of these communities (Mueller-Dombois and Ellenberg 1974; Faber-Langendoen et al. 2014; Guarino et al. 2018). However, to be successful, some consistency is needed in extending the floristic criteria to allow for recognition of continental and global patterns of vegetation. The Braun-Blanquet approach still lacks an agreed upon set of constraining attributes at the class level (Pignatti et al. 1995; Mucina et al. 2016). These could well include physiognomic or growth form criteria, which are largely determined by the dominant species, as well as biogeographic criteria, which integrate the full suite of species.

Although the primary attributes of the EcoVeg approach include plant species composition and growth form, and their interpretation in light of biogeographic and ecologic factors, there is as of yet, little systematic documentation of these attributes. The IVC is largely heuristic, relying on practical judgement as to the most probable organizing factors that guide the definition and placement of vegetation types. It thereby achieves a reasonable framework for addressing the urgency of conservation and resource management issues, while being open to rigorous long-term improvement. That said, these judgements are often firmly grounded in the integration of existing information on a wide range of local, regional, continental, and global vegetation types. Thus, the units form effective hypotheses open to further testing.

The IVC formations (Faber-Langendoen et al. 2016) provide suitable concepts that can be used to assess their strengths and limits for organizing BB classes, which have well described diagnostic concepts (Mucina et al. 2016). By contrast, the equivalent unit in the EcoVeg approach to the BB class is the macrogroup, which rarely contains a definitive list of diagnostic species, relying instead on expert-based descriptions of regional dominant, constant, and diagnostic species, along with growth form, structure, and ecology (Faber-Langendoen et al. 2014). Thus, the two approaches are now well positioned to benefit from a mutual collaboration focused on the class level of the Braun-Blanquet approach and the division and formation levels of the EcoVeg approach. In addition, whereas the phytosociological classes described between 1926 and 1950 were often quite heterogeneous in terms of physiognomy and dominant growth forms, the Braun-Blanquet system has been evolving towards a synthesis between a purely floristic and a formation system during the last 50 years (Guarino et al. 2018). We seek here to demonstrate the merits of this trend.

More specifically, we link the BB units of the EuroVegChecklist 1 (EVC1; vegetation dominated by vascular plants) with the upper levels of the International Vegetation Classification (IVC), asking the following questions:

(1) Which classes do or do not fit comfortably within an existing formation?
(2) Are there any classes which are too heterogeneous in terms of ecology or physiognomy and therefore should be split?
(3) Are there formations which are too broad (i.e., include classes that should be separated) or, on contrary, too narrow (i.e., separate classes that should be placed together), or which should be amended in another way?

Finally, we propose a division level classification for Europe.

Methods

The concept of Formation and Division in the IVC

We here provide the definitions of the EcoVeg formation and division levels relevant to this study (from Faber-Langendoen et al. 2014; links to descriptions of formations applicable to Europe are provided in Appendix 1).

- Formation Class (L1): broad combinations of dominant general growth forms adapted to basic moisture, temperature, and/or substrate or aquatic conditions.
- Formation Subclass (L2): combinations of general dominant and diagnostic growth forms that reflect global macroclimatic factors driven primarily by latitude and continental position, or that reflect overriding substrate or aquatic conditions.
- Formation (L3): combinations of dominant and diagnostic growth forms that reflect global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions (cf. “formation-type” and “biome-type” of Whittaker 1975).
- Division (L4): combinations of dominant and diagnostic growth forms and a broad set of diagnostic plant species that reflect biogeographic differences in composition and continental differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes. Whereas the formation level (L3) is more strictly physiognomic, the division level includes both physiognomic and floristic criteria. (cf. “biome” of Whittaker 1975, “continental biome” of Faber-Langendoen et al. 2020).

Assessment of placement of EVC classes within IVC formations

We established a tabular linkage between EVC classes and IVC formations and identified mismatches between these two levels. We assessed the relative acceptability of each EVC class within a formation based on four criteria: (i) growth form, (ii) biogeography (including macroclimate), (iii) ecology (edaphic site conditions and disturbance, both natural and anthropogenic), (iv) floristics (i.e., the floristic coherence of the class, with special emphasis on the dominant layer). We placed classes within a formation whenever class concepts largely contained the attributes of a formation, while noting various difficulties with the boundaries of concepts. We assessed class fit within the formation using three categories: good (G), fair (F) and poor (P), and we flagged any classes that did not fit comfortably within an existing formation, either because its content corresponded to more than one formation or because it did not fit any formation description. In cases of poor fit, we checked whether splitting the EVC class would lead to an increase in the fit.

To assess class characteristics, we mainly relied on the description of the classes in Mucina et al. (2016), which contain descriptors for accepted syntaxa, including (1) the physiognomy of the vegetation classified within the given unit (e.g. forest, grassland, ericaceous scrub, aquatic vegetation, etc.), sometimes with indication of dominant plant species or growth form (e.g. grass-dominated); (2) their unifying ecological context (e.g. mesic, nutrient-poor soils, coastal cliffs under sea-spray influence); and (3) their distribution. Classes of pioneer and seral communities that often occur as small patches within a matrix of vegetation belonging to another class (e.g., patches of tall scrub within a grassland matrix, fringe vegetation on forest edges; Chytrý and Otýpková 2003) were placed into the formation corresponding to large (≥ 100 m^2) patches of these classes, even though such large patches might be relatively rare. Classes occurring under both semi-natural and strongly anthropogenic site conditions were placed in formations of semi-natural vegetation, while classes exclusively found on anthropogenic sites were placed in the formation class "Agricultural & Developed Vegetation" (Faber-Langendoen et al. 2016).

Finally, we evaluated the homogeneity of formations with respect to the attributes of the included classes.

Recognition of IVC divisions for European vegetation

We reviewed prior division concepts developed for European forests (Faber-Langendoen et al. 2020) and grasslands (Dixon et al. 2014). The grassland divisions were developed globally, providing some guidance on scaling the concepts for Europe. We developed divisions that organize the EVC classes and represent distinct physiognomic, biogeographic, climatic, and edaphic types within a formation. For the naming of divisions, we follow the biogeographic terminology of the European Environment Agency where appropriate (Cervellini et al. 2020).

Results

Here we summarize the placement of all European classes into IVC formations and our proposed divisions for organizing all BB classes. We briefly explain issues of moderate to poor fit between formations and classes. Possible solutions are addressed in the Discussion. The detailed assessment of class fit (based on growth form, biogeography, ecology, and floristics) within formations is provided in Suppl. material 1.

The formation names strictly follow Faber-Langendoen et al. (2016). In cases where these names do not fully reflect the content of the included BB units, we additionally provide a short diagnosis below the formation name. An overview including all hierarchical levels is provided in Appendix 1.

1.B.1. Warm Temperate Forest & Woodland

[Mediterranean and warm temperate forest, woodland and tall scrub]

Macaronesian Warm Temperate Forest & Tall Scrub

- OLE: *Oleo cerasiformis-Rhamnetea crenulatae* p.p. [excl. OLE-02 *Cisto canariensis-Micromerietalia hyssopifoliae*]
  Remark: While the core of this class are tall shrub and woodland communities, the order OLE-02 *Cisto canariensis-Micromerietalia hyssopifoliae* includes low scrub, which rather corresponds to formation 2.B.1. Mediterranean Scrub & Grassland.
- LAU: *Pruno lusitanicae-Lauretea azoricae*
- AZO: *Lauro azoricae-Juniperetea brevifoliae*
  Remark: This class contains both evergreen laurophyll forest and heath seral to forest. Some adjustments in the circumscription of the class might be necessary to fit it into this formation.
- CAN: *Cytiso-Pinetea canariensis*

Mediterranean Basin Warm Temperate Sclerophyllous Forest & Tall Scrub

- QUI: *Quercetea ilicis*
- CYT: *Cytisetea scopario-striati*
  Remark: This class contains broomy shrub communities seral to forest and woodland. *Cytisus scoparius* is up to 3 m high, the same as *Prunus spinosa*, *Rosa canina* and other *Crataego-Prunetea* species. Therefore, we preliminarily consider this class as a tall scrub. The order CYT-03 *Spartio juncei-Cytisetalia scoparii* is not Mediterranean, but an oceanic warm-temperate unit.

1.B.2. Cool Temperate Forest & Woodland

[Cool temperate forest, woodland and tall scrub]

Western Eurasian Cool Temperate Forest & Tall Scrub

Here we propose to organize the classes by three division groupings, zonal, seral, and dry pine forests. These groupings account for the major gradients within this division that historically dominated much of the temperate European landscape. The one challenge may be that the seral grouping contains shrub/small tree physiognomy that straddles the shrub and tree formations. Floristically, ecologically, and biogeographically, those classes mostly belong together with the zonal temperate forest class grouping. However, low scrub cannot be accommodated in this formation and should be excluded (see Remarks under individual classes below).

Western Eurasian Cool Temperate Forest & Tall Scrub 1 (zonal)

- FAG: *Carpino-Fagetea sylvaticae*
- PUB: *Quercetea pubescentis*
- QUE: *Quercetea robori-petraeae*

Western Eurasian cool Temperate Forest & Tall Scrub 2 (seral scrub)

- RHA: *Crataego-Prunetea* p.p.max.
  Remark: The low scrub of the steppe zone (RHA-01J *Prunion fruticosae*) better fits in formation 2.B.2. Temperate Grassland & Shrubland.
- ARE: *Salicetea arenariae* p.p.min.
  Remark: This class mostly includes low scrub, which corresponds to formation 2.B.4. Temperate to Polar Scrub & Herb Coastal Vegetation.
- LON: *Lonicero-Rubetea plicati*
- ROB: *Robinietea*

Western Eurasian Cool Temperate Forest & Tall Scrub 3 (azonal dry pine forests)

- ERI: *Erico-Pinetea*

- PYR: *Pyrolo-Pinetea sylvestris*
- SAB: *Junipero-Pinetea sylvestris*

Southern Siberian Cool Temperate Forest

The Southern Siberian Cool Temperate Forest division is the classic example of "hemiboreal" vegetation. Hemiboreal refers to the northernmost subzone of the temperate zone, so when paralleling the latitudinal zones with the elevational belts of temperate mountains, hemiboreal would be middle montane, and boreal would be high montane to subalpine. Temperate high montane to subalpine forests are here proposed to be included within 1.B.4. Boreal Forest & Woodland. The hemiboreal forests of Eastern Europe are not well studied from a BB perspective, and it is unclear which class they belong to. They are transitional between the *Carpino-Fagetea* and *Vaccinio-Piceetea*.

- ASA: *Asaro europaei-Abietetea sibiricae*
- BRA: *Brachypodio pinnati-Betuletea pendulae*

1.B.3. Temperate Flooded & Swamp Forest

[Mediterranean, temperate and boreal forest, woodland, and tall scrub on base-rich, flooded or permanently wet soils]

Western Eurasian Rich Flooded & Swamp Forest & Tall Scrub

The classes below fit fairly well within this formation but are not restricted to the temperate zone.

- POP: *Alno glutinosae-Populetea albae*
- PUR: *Salicetea purpureae*
- ALN: *Alnetea glutinosae*
- FRA: *Franguletea*

Eurasian Arid Flooded Forest & Tall Scrub

The classes included here vary from scrub to small tree.

- NER: *Nerio-Tamaricetea*
- TAM: *Tamaricetea arceuthoidis*

1.B.4. Boreal Forest & Woodland

[Temperate high montane to subalpine and boreal forest, woodland, and tall scrub]

Eurasian Boreal & Temperate High Montane Forest & Tall Scrub

This division accommodates the vast areas of boreal forest across Eurasia. We here propose to include both the boreal forest proper, as well as temperate high montane to subalpine spruce-fir-pine vegetation. Strictly speaking the current formation concept treats the latter as part of the Cool Temperate Forest & Woodland formation (I.B.2).

- PIC: *Vaccinio-Piceetea* p.p.max. [excl. *Vaccinio uliginosi-Pinetea*]
  Remark: This class, while having its main distribution in the boreal zone, also includes montane and subalpine forests of the temperate zone. The orders of oligotrophic wooded mires (PIC-07 *Vaccinio uliginosi-Pinetalia sylvestris* and PIC-08 *Calamagrostio purpureae-Piceetalia obovatae*) are excluded (see Formation 1.B.5.).
- MUG: *Roso pendulinae-Pinetea mugo*
  Remark: Despite being restricted to the subalpine belt of temperate mountains, this unit ecologically corresponds to boreal forest and scrub. The *Roso pendulinae-Pinetea mugo* is a controversial class concept. Traditionally, it was treated as part of the *Vaccinio-Piceetea*.
  Placement of this class is more acceptable if the formation concept is revised to be "Boreal & Temperate High Montane Forest & Woodland" (cf. Keith et al. 2020).
- VIR: *Betulo carpaticae-Alnetea viridis*
  Remark: This class includes both boreal and temperate subalpine communities.

1.B.5. Boreal Flooded & Swamp Forest

[Boreal and temperate forest, woodland, and tall scrub on wet, acidic soils]

Eurasian Boreal Acidic Flooded & Swamp Forest & Tall Scrub

- PIC: *Vaccinio-Piceetea* p.p.min. [*Vaccinio uliginosi-Pinetea*]
  Remark: Here we preliminarily accept the class *Vaccinio uliginosi-Pinetea*, comprising oligotrophic wooded mires included in the *Vaccinio-Piceetea* by Mucina et al. (2016) (PIC-07 *Vaccinio uliginosi-Pinetalia sylvestris* and PIC-08 *Calamagrostio purpureae-Piceetalia obovatae*). Boreal flooded forest and tall scrub on rich soils belong to the classes *Alno glutinosae-Populetea albae* and *Salicetea purpureae*, which are accommodated in the temperate flooded and swamp Formation 1.B.3. The order *Vaccinio uliginosi-Pinetalia sylvestris* also includes oligotrophic wooded mires of eastern Central Europe.

2.B.1. Mediterranean Scrub & Grassland

[Mediterranean low scrub and grassland]

Mediterranean Basin Scrub & Grassland

- ROS: *Ononido-Rosmarinetea*
- LAV: *Cisto-Lavanduletea stoechadis*
- LYG: *Lygeo sparti-Stipetea tenacissimae*
- SAC: *Stipo giganteae-Agrostietea castellanae*
- BUL: *Poetea bulbosae*

- TUB: *Helianthemetea guttati*
  Remark: This class includes annual vegetation, often forming small patches within larger perennial scrub and grassland.
- TRA: *Stipo-Trachynietea distachyae*
  Remark: This class includes annual vegetation, often forming small patches within larger perennial scrub and grassland.

Macaronesian Scrub & Grassland

- OLE: *Oleo cerasiformis-Rhamnetea crenulatae* p.p. [OLE-02 *Cisto canariensis-Micromerietalia hyssopifoliae*]
  Remark: This class includes pioneer vegetation dominated by annuals and succulents, often forming small patches within larger perennial scrub and grassland.

2.B.2. Temperate Grassland & Shrubland

[Temperate and southern boreal low scrub, heath, and grassland vegetation]

Azorean Warm Temperate Grassland & Heath

- TOL: *Tolpido azoricae-Holcetea rigidi*
  Remark: Endemic class of the Azores. Its floristic-biogeographic relationship to other grassland classes remains to be evaluated.

European Temperate Grassland & Heath

These are a diverse group of classes, including both lowland and montane grasslands and heath. In contrast to the situation in eastern North America, where there is a clear demarcation between native and planted grasslands, traditional European pastures and hay meadows of the *Molinio-Arrhenatheretea* are semi-natural communities and therefore included here rather than under 7.B.2 Pasture & Hay Field Crop. However, they are grouped with other ruderal classes to reflect their intermediate position between more strictly cultural grasslands and native grasslands.

European Temperate Grassland & Heath 1 (natural & semi-natural)

- RHA: *Crataego-Prunetea* p.p.min. [*Amygdaletea nanae*]
  Remark: The low scrub of the steppe zone (RHA-01J *Prunion fruticosae*) is placed under this formation while we include tall scrub in formation 1.B.2. Cool Temperate Forest & Woodland (see above).
- ULI: *Calluno-Ulicetea*
- NAR: *Nardetea strictae*
- FES: *Festuco-Brometea*
- GER: *Trifolio-Geranietea sanguinei*
- ONO: *Festuco hystricis-Ononidetea striatae*
  Remark: Submediterranean dry calcicolous grasslands, similar to the rocky grasslands of the *Festuco-Brometea*. Delimitation against alpine grasslands of the class *Elyno-Seslerietea* needs further revision.
- COR: *Koelerio-Corynephoretea canescentis*
- SED: *Sedo-Scleranthetea*

European Temperate Grassland & Heath 2 (ruderal & strongly anthropogenic)

- MOL: *Molinio-Arrhenatheretea*
  Remark: This class is a poor fit to this formation because it contains both more natural and strongly anthropogenic grasslands, some of which may fit into cultural grassland formation Pasture & Hay Field Crop (7.B.2). Moreover, it contains both upland grasslands and wet meadows, the latter which may better fit the concept of Temperate to Polar Freshwater Marsh, Wet Meadow & Shrubland (2.C.4).
- ART: *Artemisietea vulgaris*
  Remark: Perennial forb vegetation, mostly of ruderal and strongly anthropogenic habitats.
- EPI: *Epilobietea angustifolii*
  Remark: Perennial forb vegetation of ruderal or seral habitats, including tall-herb vegetation along rivers.

2.B.3. Boreal Grassland & Shrubland

[Temperate high montane to subalpine and boreal low scrub, grassland, and forb vegetation]

European Boreal & Temperate High Montane Scrub & Herb Vegetation

This formation needs further review in Europe. We here propose to include both the boreal grasslands and shrublands proper, as well as boreo-temperate high montane to subalpine grassland and shrubland vegetation. Strictly speaking, the current formation treats the latter within the Temperate Grassland & Shrubland formation (2.B.2.). As further explained below, these three open classes correspond to the forest classes in the boreal forest and scrub formation 1.B.4.

- LOI: *Loiseleurio procumbentis-Vaccinietea* p.p. [excl. LOI-03A *Loiseleurio-Arctostaphylion*]
  Remark: This class is quite heterogenous. It mostly corresponds to the *Vaccinio-Piceetea*, to which it is floristically closely related. However, the arctic and boreo-alpine tundra scrub of LOI-03A cannot be accommodated here; rather, it is included in formation 4.B.2.
- RHO: *Rhododendro hirsuti-Ericetea carneae*
  Remark: This class corresponds to the *Roso pendulinae-Pinetea mugo*, to which it is floristically closely related. Despite being restricted to the subalpine belt of temperate mountains, this unit ecologically corresponds to boreal scrub and herb vegetation.
- MUL: *Mulgedio-Aconitetea*
  Remark: This class corresponds to the *Betulo-Alnetea viridis*, to which it is floristically closely related.

2.B.4. Temperate to Polar Scrub & Herb Coastal Vegetation

[Mediterranean, temperate, boreal, and arctic low scrub, grassland and forb vegetation of coastal cliffs and dunes]

Euro-Atlantic Coastal Scrub & Herb Vegetation

- ARE: *Salicetea arenariae* p.p.max.
  Remark: Tall scrub on older dunes is placed in 1.B.2. Cool Temperate Forest & Woodland.
- AMM: *Ammophiletea*
- CRU: *Helichryso-Crucianelletea maritimae*
- CRI: *Crithmo-Staticetea*
- CAK: *Cakiletea maritimae*

Macaronesian Coastal Scrub & Herb Vegetation

- MOQ: *Polycarpaeo niveae-Traganetea moquini*

2.C.2. Temperate to Polar Bog & Fen

Eurasian Bog & Fen

- OXY: *Oxycocco-Sphagnetea*
- SCH: *Scheuchzerio palustris-Caricetea fuscae*

2.C.4. Temperate to Polar Freshwater Marsh, Wet Meadow & Shrubland

[Mediterranean, temperate, boreal and arctic freshwater springs and marshes]

Eurasian Freshwater Marsh, Wet Meadow & Shrubland

For wet meadows see remark under MOL *Molinio-Arrhenatheretea* above.

- PHR: *Phragmito-Magnocaricetea*
- MON: *Montio-Cardaminetea*
- LIT: *Littorelletea uniflorae*
- ISO: *Isoëto-Nanojuncetea*
- BID: *Bidentetea*

2.C.5. Salt Marsh

Eurasian Interior Wet Saline Marsh

Some inland saline marshes are placed in the European Coastal Salt Marsh division below.

- FEP: *Festuco-Puccinellietea*
- CRY: *Crypsietea aculeatae*
- KAL: *Kalidietea foliati*
- AEL: *Aeluropodetea littoralis*

European Coastal Salt Marsh

The separation of inland versus coastal salt marshes is not always made at the class level, as with the *Therosalicornietea*.

- JUN: *Juncetea maritimi*
- SAL: *Salicornietea fruticosae*
- SPA: *Spartinetea maritimae*
- THE: *Therosalicornietea*
- SAG: *Saginetea maritimae*

3.A.2. Warm Desert & Semi-Desert Scrub & Grassland

Mediterranean-Macaronesian Warm Semi-Desert Scrub & Grassland

- PEG: *Pegano harmalae-Salsoletea vermiculatae*
- KLE: *Kleinio neriifoliae-Euphorbietea canariensis*
- SUP: *Spartocytisetea supranubii*
  Remark: This class occupies the high altitudes on the Canary Islands above the cloud belt where Macaronesian Warm Temperate Forest & Scrub are found. Therefore, the climatic conditions are relatively cool.

3.B.1. Cool Semi-Desert Scrub & Grassland

Eurasian Cool Semi-Desert Scrub & Grassland

- LER: *Artemisietea lerchianae*

4.B.1. Temperate & Boreal Alpine Vegetation

European Alpine Dwarf-Shrub & Grassland

This division is quite distinct from the Oromediterranean alpine division described below, and placing these two together in one formation hides the close relationship of this division to the Arctic Tundra & Barrens Division in the Polar Tundra & Barrens formation (4.B.2) (see Discussion for more details).

- SES: *Elyno-Seslerietea*
- TRI: *Juncetea trifidi* p.p. [excl. TRI-01 *Juncetalia trifidi*]
  Remark: The concept adopted for this class in Mucina et al. (2016) does not fit into the current IVC formation system. Without prejudging a future revision, we exclude here the boreo-arctic order TRI-01 *Juncetalia trifidi* (see Formation 4.B.2.).
- IND: *Festucetea indigestae*
- PIL: *Saginetea piliferae*

Oromediterranean Alpine & Subalpine Grassland & Scrub

See comment above under European Alpine Dwarf-shrub & Grassland. This division largely contains cushion-tragacanthic alpine scrub.

- RUM: *Rumici-Astragaletea siculi*
- ANA: *Trifolio anatolici-Polygonetea arenastri*
- GEN: *Carici-Genistetea lobelii*
- DAP: *Daphno-Festucetea*
- CYP: *Diantho troodi-Teucrietea cyprii*

4.B.2. Polar Tundra & Barrens

[Temperate high alpine to arctic vegetation]

Arctic Tundra & Barrens

Some classes that extend into the temperate high alpine zone have close floristic relation to classes in the European Alpine Dwarf-shrub & Grassland division of the alpine formation 4.B.1. (see remarks under specific classes).

- KOB: *Carici rupestris-Kobresietea bellardii*
  Remark: Also occurs in the high alpine belt of cool temperate mountains.
- LOI: *Loiseleurio procumbentis-Vaccinietea* p.p. [LOI-03A *Loiseleurio-Arctostaphylion*]
  Remark: Delimitation between the *Loiseleurio-Vaccinietea* and *Juncetea trifidi* is controversial, and a broad-scale phytosociological revision would be needed to clarify the issue. Most of the class corresponds to the Boreal Grassland & Shrubland formation (2.B.3.).
- TRI: *Juncetea trifidi* p.p. [TRI-01 *Juncetalia trifidi*]
  Remark: The order TRI-01 *Juncetalia trifidi* includes arctic swards, but also extends into the alpine belt of Northern Europe (i.e., the boreal zone) and even includes “glacial relict” communities in the Hercynic Mountains of Central Europe.
- HER: *Salicetea herbaceae*
  Remark: Also widespread in the high alpine belt of cool temperate mountains.
- PAP: *Drabo corymbosae-Papaveretea dahliani*
- COC: *Saxifrago cernuae-Cochlearietea groenlandicae*
- SAX: *Saxifrago tricuspidatae-Calamagrostietea purpurascentis*
- ARC: *Matricario-Poetea arcticae*

5.A.3. Benthic Vascular Saltwater Vegetation

Temperate Atlantic Seagrass Aquatic Vegetation

- HAL: *Halodulo wrightii-Thalassietea testudinum*
- RUP: *Ruppietea maritimae*
- ZOS: *Zosteretea*

5.B.2. Temperate to Polar Freshwater Aquatic Vegetation

Temperate Eurasian Freshwater Aquatic Vegetation

This division concept might need further revision as the class *Lemnetea* is described in Mucina et al. (2016) as having a Holarctic distribution (though its one order has a temperate European distribution). The classes *Platyhypnidio-Fontinalietea antipyreticae* (listed in EVC2) and *Charetea intermediae* (listed in EVC3) should also be included here.

- LEM: *Lemnetea*
- POT: *Potamogetonetea*

6.B.1. Temperate & Boreal Cliff, Scree & Other Rock Vegetation

Macaronesian Cliff, Scree & Other Rock Vegetation

- AEO: *Aeonio-Greenovietea*
- VIO: *Violetea cheiranthifoliae*

Western Eurasian Cliff, Scree & Other Rock Vegetation

Various classes of epilithic bryophyte and lichen communities (listed in EVC2) should also be included here (see also Berg et al. 2020).

- ADI: *Adiantetea*
- POD: *Polypodietea*
- ASP: *Asplenietea trichomanis*
- CYM: *Cymbalario-Parietarietea diffusae*
- PHA: *Phagnalo saxatilis-Rumicetea indurati*
- DRY: *Drypidetea spinosae*
- THL: *Thlaspietea rotundifolii*
  Remark: This is a rather heterogenous class, spanning a gradient from thermophilous submediterranean to temperate nival and arctic communities. The latter would better fit into the Polar Tundra & Barrens formation (4.B.2.).
- LAM: *Lamio tomentosi-Chaerophylletea humilis*

7.B.4. Fallow Field & Weed Vegetation

Eurasian Fallow Field & Weed Vegetation [cultural]

- PAR: *Papaveretea rhoeadis*
- CHE: *Chenopodietea*
- DIG: *Digitario sanguinalis-Eragrostietea minoris*
- SIS: *Sisymbrietea*
- POL: *Polygono-Poetea annuae*

7.B.5. Herbaceous Wetland Crop

Eurasian Fallow Field & Weed Vegetation [cultural, wet]

- ORY: *Oryzetea sativae*

Discussion

Evaluation of class concepts

From a Braun-Blanquet approach perspective, it has been proposed (Pignatti et al. 1995; Willner 2006, 2020) to consider syntaxa as acceptable only if they have, on the one hand, a floristic basis (i.e., a sufficient set of diagnostic species), but on the other hand also an ecological basis (i.e., a measurable range of climatic and edaphic preferences with little or no overlap with the neighbouring community types) and an evolutionary significance (i.e., chorological and biogeographical information). For our purposes, we expand the “floristic basis” to include growth forms and structural attributes. Acceptable vegetation types should be clearly discriminated along environmental gradients.

Our approach is not unlike that of Pignatti et al. (1995) who evaluated European vegetation classes in terms of their status of class character species, ecological characterization, coherence of the geographical distribution of character species and common physiognomy-structure. However, our goal was to assess whether mismatches in placement of classes within formations relate to relative weaknesses in any of the mismatched class or formation concepts. When the fit is poor, the class definition might be too broad, or the formation definitions might be too narrow, or both.

EVC classes which seem to be too heterogenous to fit into the IVC formation system include the *Oleo cerasiformis-Rhamnetea crenulatae*, *Crataego-Prunetea*, *Vaccinio-Piceetea*, *Loiseleurio-Vaccinietea*, *Juncetea trifidi* and *Thlaspietea rotundifolii*. Delimitation of *Vaccinio-Piceetea*, *Loiseleurio-Vaccinietea* and *Juncetea trifidi* has been a matter of debate for many decades (e.g., Grabherr and Mucina 1993; Daniëls 1994; Dierßen 1996). The IVC perspective might help to solve these intricate issues.

Mesomorphic unfertilized subalpine grasslands (partly natural, e.g., in avalanche gullies, partly maintained by grazing) are currently included in the same classes as typical alpine tundra (*Juncetea trifidi*, *Elyno-Seslerietea*) due to some common species. However, this concept is not unchallenged (especially concerning the placement of subalpine *Nardus stricta* swards). From a physiognomic point of view, the subalpine grasslands would better fit in the Temperate Grassland & Shrubland formation (2.B.2).

More fundamentally, the European grassland classes (*Nardetea strictae*, *Molinio-Arrhenatheretea*, *Festuco-Brometea* etc.) span a much larger natural to anthropogenic gradient than in eastern North America, where all seeded pastures (of which the vast majority are of introduced European grasses) are placed in 7.B.2 Pasture & Hay Field Crop. These pastures may be grazed by cattle or used as hay meadows. In addition, in North America, urban and park lawns, sport fields, golf courses, and the like are included in 7.C.1. Lawn, Garden and Recreational Vegetation. In Europe, pastures and hay meadows are composed of native European species, and they are a product of long "co-evolution" between nature and human land use. Therefore, there is no sharp border between natural and anthropogenic grasslands, and all traditionally managed grasslands must be regarded as semi-natural. "Artificial" (or cultural) grasslands that mainly consist of sown plants exist as well. However, similar to plantations of non-native trees, they are not treated as communities in the Braun-Blanquet system and therefore have no corresponding EVC class.

Wet meadows are currently included in the class *Molinio-Arrhenatheretea*. However, several authors have considered wet meadows as classes in their own right (*Molinio-Juncetea acutiflori*, *Agrostietea stoloniferae*). The same is true for megaforbic fringes on wet sites (*Filipendulo ulmariae-Calystegietea*). The position of wet communities dominated by rather low-growing shrubs (e.g., *Salix repens*) should also be reconsidered. They are currently included in tall-shrub classes such as the *Franguletea*. As a consequence, Formation 2.C.4. Temperate to Polar Freshwater Marsh, Wet Meadow & Shrubland currently contains no classes that represent wet meadows, nor wet shrubland.

The class *Thlaspietea rotundifolii* comprises scree vegetation from the submediterranean and temperate colline belt up to the nival belt and arctic barrens, with the extremes having not a single species in common. A revision of the whole phytosociological class seems necessary.

Evaluation of formation concepts

There are cases of mismatches between phytosociological classes and IVC formations that might better be solved by emending the current formation concepts:

Tall shrubs/scrub and Forest & Woodland

We included tall shrub communities (dominated by shrubs > 2 m, cover of tall shrubs and trees > 50%) in the Forest & Woodland formation class because they are not separated from forests and woodlands at higher phytosociological levels. There are physiognomic, floristic, and ecological arguments supporting this approach: Some species can be either trees or tall shrubs; they often have very similar companion species in the herb layer; from the perspective of understorey herbs and animals, there is not much difference between a tree and a tall shrub. Another advantage is that the extremely heterogeneous Grassland & Shrubland formation class becomes physiognomically more uniform. On shallow soils, or near the treeline, tall shrub communities (as well as krummholz of *Fagus sylvatica* and *Pinus mugo*) may have only 1–2 m height, without corresponding floristic differences.

Boreal and temperate high montane

Eurasian boreal and temperate-montane *Picea* forests have always been included in the same class *Vaccinio-Piceetea*, and even in the same alliance (e.g., PIC-01A *Piceion excelsae* – European boreo-montane spruce forests and subalpine open pine woods on nutrient-poor podzolic soils; Mucina et al. 2016). The floristic core of temperate high montane–subalpine coniferous forests is very similar to boreal forests, although they are enriched by species with nemoral distribution. Basically, the temperate high montane–subalpine coniferous forest belt can be considered as extrazonal. In general, high montane–subalpine coniferous forests of the cool temperate zone are usually either dominated by the same species as in the boreal zone (e.g., *Picea abies* in Europe, *Abies lasiocarpa* in North America), or by very closely related species (e.g. *Pinus cembra* – *P. sibirica* in Eurasia, *Picea engelmannii* – *P. glauca* in North America). The understorey of these subalpine forests also shows strong affinities with the boreal forest. We therefore include both the boreal forest proper, as well as temperate high montane to subalpine forest and tall scrub in the same formation. Analogous considerations suggest that boreal and temperate high montane–subalpine grassland vegetation could be included within one formation.

Review of this decision with eastern Eurasian and North American colleagues is needed to confirm placement of these extrazonal types within this formation.

Boreal and temperate flooded and swamp forests

Separation of boreal and temperate flooded & swamp forests (formations 1.B.3. and 1.B.5.) is difficult as their floristic composition reflects the gradient from oligotrophic to eutrophic rather than macroclimate. Therefore, phytosociological classes are present in both zones, and it may be best to combine the two formations into a "Temperate & Boreal Flooded & Swamp Forest". This would also be consistent with how other wetland formations are defined (e.g., shrub and herb wetlands typically range from Temperate to Polar).

Polar tundra and alpine grasslands

The delimitation of Temperate & Boreal Alpine Vegetation (formation 4.B.1.) and Polar Tundra & Barrens (4.B.2.) may need revision. Arctic and alpine tundra and snowbed vegetation share the same floristic core of arctic-alpine species, though the temperate alpine vegetation is enriched by species that are not present in the arctic. Therefore, they are not separated at the level of phytosociological classes (*Carici-Kobresietea*, *Juncetea trifidi*, *Loiseleurio-Vaccinietea*, *Salicetea herbaceae*). Boreal alpine and arctic vegetation are even placed in the same alliances. In contrast, the oromediterranean thorn cushion scrub, typical for the alpine belt of warm-temperate regions with dry summers (from the Mediterranean in the west to Central Asia in the east), is physiognomically and ecologically very different from the arctic and boreo-temperate alpine tundra. As with the extrazonal classes of the boreal forest, a global review of the placement of boreo-temperate alpine vegetation is needed.

Floristically heterogeneous formations

Finally, some formations might appear quite lumpy, comprising phytosociological classes that, at first glance, do not have much in common. Formation 1.B.2. Cool Temperate Forest & Woodland includes deciduous and coniferous forests as well as tall scrub. However, separation of these three structural types is often difficult, even at the level of phytosociological classes, so placement within a single formation seems appropriate. The Grassland & Shrubland Formations 2.B.2., 2.C.4. and 2.C.5. include pioneer communities rich in annuals (e.g., *Helianthemetea guttati*, *Sedo-Scleranthetea*, *Isoëto-Nanojuncetea*, *Saginetea maritimae*), which often grow in gaps within perennial scrub and grassland communities (see also Pignatti et al. 1995). It might be argued that these communities do not fit into the current formation scheme, as they correspond to communities usually sampled with plots of 1–4 m² (Chytrý and Otýpková 2003). This kind of small-scale communities have not been recognized in the EcoVeg approach, and their placement in the formation system might need revision (see also next section below). However, they can cover larger areas in strongly disturbed habitats. Perennial forb vegetation of ruderal habitats and forest clearings (*Artemisietea vulgaris*, *Epilobietea angustifolii*) is often grouped with weed vegetation (also in Mucina et al. 2016), but from a physiognomic point of view, the vegetation better fits in the Temperate Grassland & Shrubland formation. Importantly, these two classes do not only occur in anthropogenic habitats but also on sites naturally disturbed by animals or storms.

Annual weed vegetation

The formation assignment of annual weed vegetation is problematic. By definition, these communities only comprise spontaneously growing plant species; thus, in Europe, they are not considered cultural ("artificial") vegetation. However, their habitat is strongly determined by anthropogenic activities, and crops may be present with high cover. Therefore, they are here assigned to the formation class Agricultural & Developed Vegetation, which also includes cultural vegetation not considered in the Braun-Blanquet system. Apart from weed communities of rice fields, all weed vegetation classes have been assigned to formation 7.B.4. Fallow Field & Weed Vegetation. Indeed, weed vegetation is not directly dependent on the cultivated crops, and often the communities are best developed on young fallow fields or along the margin of crop fields.

Scale of plot sampling and formation placement

Occasionally, physiognomic placement of classes is difficult when the sampling of the vegetation is conducted at a fine grain. In Europe, plot sizes for all non-forested vegetation are typically less than 100 m². Plots of this size may be physiognomically uniform, even when the physiognomic pattern at a larger scale is more complex. For example, we placed *Cytisetea scopario-striati*, *Crataego-Prunetea*, *Salicetea arenariae*, *Lonicero-Rubetea plicati*, and *Franguletea* in the Forest & Woodland formation class. The concept of these tall-scrub units refers only to shrub-dominated patches and excludes grassland and low-scrub patches in between (which may belong to the *Cisto-Lavanduletea*, *Festuco-Brometea*, *Nardetea strictae* etc.). Tall shrubs only rarely form up to one hectare of pure tall-scrub; more often, patches are intermingled with grasslands or form linear structures along forest edges or free-standing hedges, with no grassland context (Figure 1). The ecological reasoning behind these tall-scrub classes is that they represent a successional stage between grassland and woodland or are squeezed in between them along an environmental gradient. Biogeographically, they are strongly linked to the temperate forest climate. The tall shrubs are considered aliens in the grassland, and they outcompete the herb layer in the absence of disturbances, ultimately transforming the grassland into a woodland. In dense forests, they are outcompeted themselves, but in light oak woodland they usually find enough space to survive. Still, if their shrub structure is partly based on natural disturbance processes that maintain the larger scale shrubland-grassland mosaic, then an argument could be made that physiognomically and ecologically, they belong in the Shrub and Herb Vegetation class.

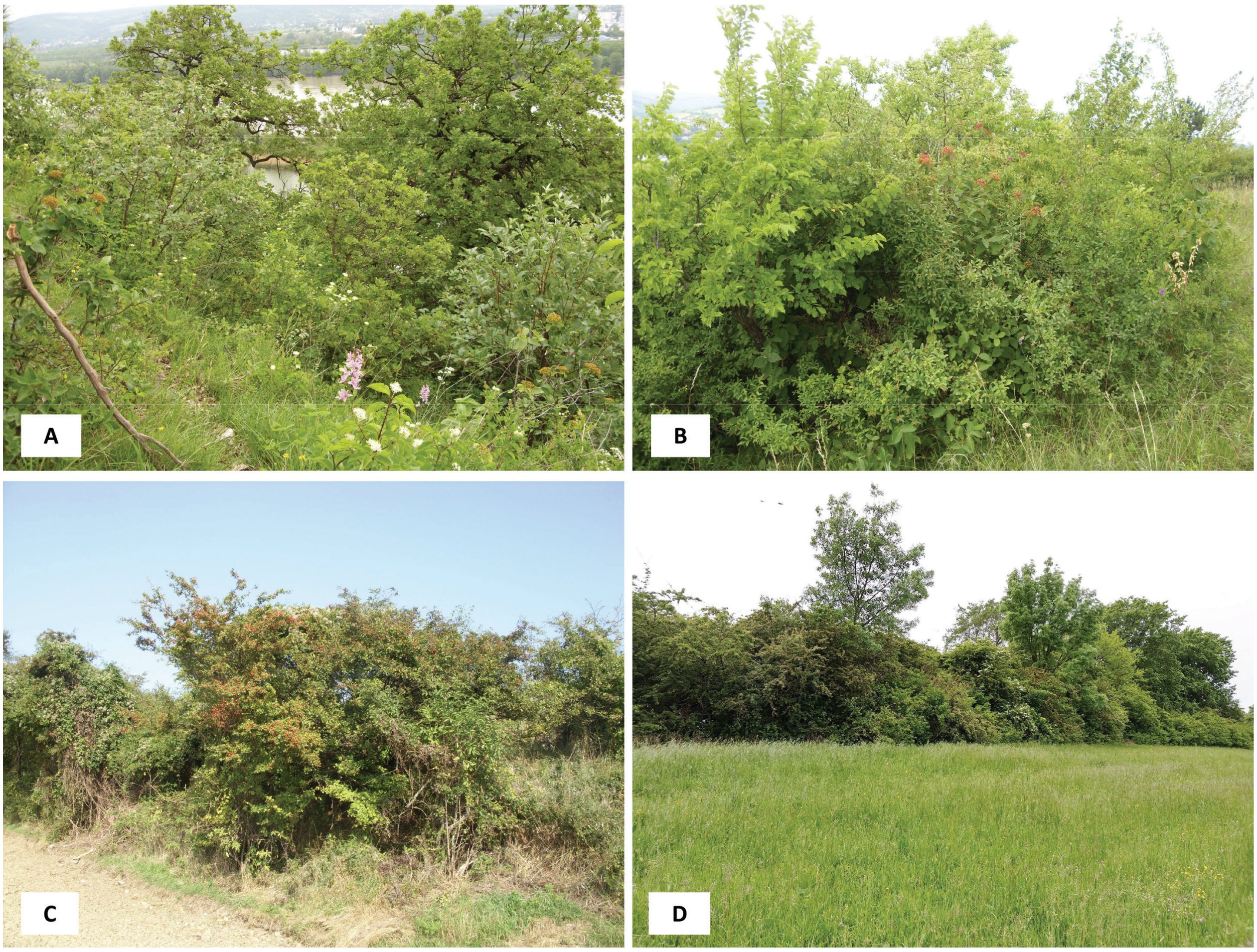

Figure 1. Open *Quercetea pubescentis* woodland in eastern Austria with high abundance of thermophilous shrubs (**A**) and various stands of seral tall-scrub of the *Crataego-Prunetea* (**B–D**). Note that the grasslands adjacent to the tall-scrub is not included in the *Crataego-Prunetea* but belongs to other classes such as the *Festuco-Brometea*, *Trifolio-Geranietea*, *Molinio-Arrhenatheretea* etc. (all photos by W. Willner).

Plot sampling traditions in the U.S. rarely use plot samples less than 100 m^2; more often the plot is between 100 and 1,000 m^2 (Peet and Roberts 2013). In contrast, 16 m^2 have been suggested as standard plot size for grasslands within the framework of the Braun-Blanquet approach (Chytrý and Otýpková 2003). Thus, in the first case the physiognomy of a plot may be described as a shrub grassland, while in the second case it may be considered a mosaic of grassland and tall-scrub.

Small-scale pioneer communities such as the *Sedo-Scleranthetea*, *Isoëto-Nanojuncetea* or *Saginetea maritimae* are usually sampled at even smaller scales. The same is true for vegetation dominated by bryophytes and lichens, most of which is included in EVC2 in Mucina et al. (2016). Chytrý and Otýpková (2003) recommended 4 m^2 for small-scaled vegetation, and a recent proposal suggested 1 m^2 as the minimum plot size for a phytocoenosis (Berg et al. 2020). Communities sampled with vastly different plot sizes cannot be directly compared, and in fact may represent different scales in the vegetation mosaic. Thus, merging these classes with grasslands is somewhat methodologically problematic. Accepting that various plot sample sizes will occur within formations, division subgroupings might be a pragmatic solution.

A common definition for the macrogroup/class level?

Perhaps surprisingly, there is no widely agreed upon definition for the vegetation class in the Braun-Blanquet approach (Pignatti et al. 1995; Mucina et al. 2016; Loidi 2020). While the rank was introduced as early as 1926 (Koch 1926), overviews of classes were not published before the 1940s (Braun-Blanquet and Tüxen 1943; Kilka and Hadač 1944), one or two decades after the description of most alliances and orders. Only then were these units organized into classes. The classes were developed in a bottom-up approach purely based on floristic similarity, independent from (and frequently even in contradiction to) earlier formation systems. From the 1960s onwards, physiognomic considerations started to slowly seep into the Braun-Blanquet approach, leading to a gradual splitting of physiognomically heterogeneous classes – a process which is still not finished (see Bonari et al. 2021).

Within the EcoVeg approach, the macrogroup level is constrained by the formation level and organized by the division level, as well as being informed by lower level units. Thus, it is useful to ask how similar the macrogroup concept is to the current BB class concept.

The Macrogroup (L5) is defined by moderate sets of diagnostic plant species and diagnostic growth forms that reflect biogeographic differences in composition and sub-continental to regional differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes (Faber-Langendoen et al. 2014). A macrogroup type typically contains a moderately large set (dozens) of strongly diagnostic species that share a broadly similar physiognomy and ecology in response to continental, sub-continental, or regional differences in ecological factors. Thus, the macrogroup expresses the floristic, growth form and regional ecological factors that separate vegetation types within a division.

Many EVC classes have distribution ranges covering the whole of western Eurasia, while biogeographical differences in species composition are reflected at the level of orders and alliances (Mucina et al. 2016). This seems to contradict the definition of the macrogroup given above and also the current practice in North America, where there are often two or more geographically vicariant macrogroups within a division. For instance, within the Eastern North American Forest & Woodland division there are four macrogroups of mesic forests: Appalachian-Interior-Northeastern Mesic Forest, Central Midwest Mesic Forest, Laurentian Mesic Forest, and Acadian-Northern Appalachian Mesic Forest (Faber-Langendoen et al. 2018). There could be several reasons for this seeming mismatch. One is the historic tradition in northeastern North America of distinguishing these classes based on strongly divergent tree composition (e.g., Braun 1950). This may reflect a higher biogeographical diversity in this region as compared to Europe. In this case, different ranges of macrogroups and EVC classes would reflect objective differences in the vegetation of both continents. On the other hand, the differences could also be the result of divergent methodological approaches: The class is the highest official unit in the Braun-Blanquet system, and often it is the only rank linking vegetation types in different parts of Europe together. Proposing a new class is a bold step and not easily accepted by the phytosociological community. Moreover, most dominant and constant species of associations have wide distribution ranges, and these species can only be considered as character species of vegetation units if these units have equally wide distribution ranges. Conversely (see also section below), because the EcoVeg approach has a division level, these intra-continental patterns are readily recognized, and testing of their diagnostic strength can be reviewed through large-scale plot-based analyses. Intercontinental comparisons are needed to further elucidate this issue. However, we believe that, in the long run, a common macrogroup/class concept would be beneficial for the global evaluation of vegetation diversity.

Merits of the division concept for organizing Braun-Blanquet classes

In the context of European vegetation (as covered by EVC), the strength of the IVC approach is largely that it adds a set of physiognomic and ecological criteria that effectively organizes the classes, which are already being increasingly informed by physiognomy (most recently see Bonari et al. 2021). That is, the formation concepts are relatively natural extensions of concepts embedded in the classes. Thus, as with Mucina (1997) and Rodwell et al. (2002), we advance the use of the formation, and its extension at the division level, as an organizing set of levels for EVC classes, using an international-based set of formations.

Given the geographical scope of EVC (i.e., the western part of Eurasia), it is perhaps not surprising that most European vegetation classes fall within one or a few divisions within a formation. The division level accounts for large biogeographically distinct expressions of formations, such that e.g., Mediterranean Basin forests are placed in the context of all Mediterranean type vegetation around the globe, Western Eurasian temperate forests are separated from those in East Asia, North America, and other parts of the globe, and Eurasian boreal forests from their North American counterpart. Most importantly, by organizing the classes within such a well-researched part of the globe, a hierarchical structure is provided to researchers in many other countries in how to seek consensus on class concepts based on the well-established traditions in Europe. In addition, groupings of classes ("division subtype") may be an important addition to the division level concept when many classes occur within a formation (e.g., see the division grouping within the Western Eurasian Cool Temperate Forest).

Conclusions

With the completion of division level concepts for Europe, there are now division concepts for Western Eurasia, all of the Americas (Faber-Langendoen et al. 2018), for Africa (Sayre et al. 2013), and for all grasslands and shrublands (Dixon et al. 2014). Macrogroup and/or BB class concepts are also largely complete for these areas, and Division and macrogroup concepts have also been piloted in Australia (Muldavin et al. 2021). Formation level concepts as developed for the IVC (Faber-Langendoen et al. 2016) already reflect a long tradition of well-established concepts, but extensions of ecological criteria to include ecological functions may enrich these concepts (Keith et al. 2020). It is now possible to consider compiling a compendium of BB class concepts, IVC macrogroup concepts, and closely related concepts, using division and formation level units. These compendiums could build on existing publicly available webtools in Europe (http://euroveg.org/) and in the Americas (https://explorer.natureserve.org/). Such an effort would more firmly establish a consistent set of guiding principles for the use of physiognomy, floristics, biogeography, and ecology in the construction of hierarchically consistent approaches. It would also further the aim of guiding IUCN Red Lists of Ecosystems for terrestrial and wetland ecosystems (e.g., Ferrer-Paris et al. 2018), as a complement to the recent global framework of Keith et al. (2020), which does not provide the needed lower-level units of that hierarchy.

The goal of comparing and compiling units across various classifications is not to develop a single authoritative system, but, in the mindset of Sterner et al. (2020), to collaborate based on the Coordinative Consensus Principle (CCP). Using that principle, the ground of consensus is communicative expediency, rather than metaphysical truth or epistemic agreement about a single classification hierarchy. The philosophical approach to coordinating the existing "classification dissent" (taxonomic pluralism) among vegetation ecologists is to bring the full spectrum of global vegetation in view using a few global backbone classifications that assist in the compilation, while still firmly anchoring all relationships of types with subnational or national partner classifications (e.g., by using established relationship methods, such as the RCC-5 method of Sterner et al. 2020). In this way the goal is to build reliable relationships between global and local classifications and to facilitate information exchanges, whether about types, plot data, or conservation information.

Author contributions

W.W. had the idea for this paper, and both authors equally contributed to the writing.

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Appendix 1

List of IVC Formations (from Faber-Langendoen et al. 2016), with draft Divisions and EVC Classes (the latter from Mucina et al. 2016). Links to the descriptions of all IVC formations are also provided.

IVC Class	IVC Subclass	IVC Formation	Draft Division	EVC Class	IVC link on NatureServe Explorer
1. Forest & Woodland					https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860217
	1.B. Temperate & Boreal Forest & Woodland				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860227
		1.B.1. Warm Temperate Forest & Woodland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860255
			Macaronesian Warm Temperate Forest & Tall Scrub		
				Oleo cerasiformis-Rhamnetea crenulatae p.p.	
				Pruno lusitanicae-Lauretea azoricae	
				Lauro azoricae-Juniperetea brevifoliae	
				Cytiso-Pinetea canariensis	
			Mediterranean Basin Warm Temperate Sclerophyllous Forest & Tall Scrub		
				Quercetea ilicis	
				Cytisetea scopario-striati	
		1.B.2. Cool Temperate Forest & Woodland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860241
			Western Eurasian Cool Temperate Forest & Tall Scrub 1 (zonal)		
				Carpino-Fagetea sylvaticae	
				Quercetea pubescentis	
				Quercetea robori-petraeae	
			Western Eurasian Cool Temperate Forest & Tall Scrub 2 (seral)		
				Crataego-Prunetea p.p.max.	

IVC Class	IVC Subclass	IVC Formation	Draft Division	EVC Class	IVC link on NatureServe Explorer
				Salicetea arenariae p.p.min.	
				Lonicero-Rubetea plicati	
				Robinietea	
			Western Eurasian Cool Temperate Forest & Tall Scrub 3 (azonal dry pine forest)		
				Erico-Pinetea	
				Pyrolo-Pinetea sylvestris	
				Junipero-Pinetea sylvestris	
			Southern Siberian Cool Temperate Forest		
				Asaro europaei-Abietetea sibiricae	
				Brachypodio pinnati-Betuletea pendulae	
		1.B.3. Temperate Flooded & Swamp Forest			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860261
			Western Eurasian Rich Flooded & Swamp Forest & Tall Scrub		
				Alno glutinosae-Populetea albae	
				Salicetea purpureae	
				Alnetea glutinosae	
				Franguletea	
			Eurasian Arid Flooded Forest & Tall Scrub		
				Nerio-Tamaricetea	
				Tamaricetea arceuthoidis	
		1.B.4. Boreal Forest & Woodland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860236
			Eurasian Boreal & Temperate High Montane Forest & Tall Scrub		
				Vaccinio-Piceetea p.p.max.	
				Roso pendulinae-Pinetea mugo	
				Betulo carpaticae-Alnetea viridis	
		1.B.5. Boreal Flooded & Swamp Forest			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860237
			Eurasian Boreal Acidic Flooded & Swamp Forest & Tall Scrub		
				Vaccinio uliginosi-Pinetea [*Vaccinio-Piceetea* p.p.min.]	
2. Shrub & Herb Vegetation					https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860211
	2.B. Temperate & Boreal Grassland & Shrubland				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860233
		2.B.1. Mediterranean Scrub & Grassland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860273
			Mediterranean Basin Scrub & Grassland		
				Ononido-Rosmarinetea	
				Cisto-Lavanduletea stoechadis	
				Lygeo sparti-Stipetea tenacissimae	
				Stipo giganteae-Agrostietea castellanae	
				Poetea bulbosae	
				Helianthemetea guttati	
				Stipo-Trachynietea distachyae	
			Macaronesian Scrub & Grassland		
				Oleo cerasiformis-Rhamnetea crenulatae p.p.	
		2.B.2. Temperate Grassland & Shrubland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860245
			Azorean Warm Temperate Grassland & Heath		
				Tolpido azoricae-Holcetea rigidi	
			European Temperate Grassland & Heath 1 (natural & semi-natural)		
				Amygdaletea nanae [*Crataego-Prunetea* p.p.min]	
				Calluno-Ulicetea	
				Nardetea strictae	
				Festuco-Brometea	
				Trifolio-Geranietea sanguinei	
				Festuco hystricis-Ononidetea striatae	
				Koelerio-Corynephoretea canescentis	
				Sedo-Scleranthetea	
			European Temperate Grassland & Heath 2 (ruderal & strongly anthropogenic)		
				Molinio-Arrhenatheretea	
				Artemisietea vulgaris	
				Epilobietea angustifolii	
		2.B.3. Boreal Grassland & Shrubland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860266
			European Boreal & Temperate High Montane Scrub & Herb Vegetation		
				Loiseleurio procumbentis-Vaccinietea p.p.	
				Rhododendro hirsuti-Ericetea carneae	
				Mulgedio-Aconitetea	
		2.B.4. Temperate to Polar Scrub & Herb Coastal Vegetation			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860238
			Euro-Atlantic Coastal Scrub & Herb Vegetation		
				Salicetea arenariae p.p.max	
				Ammophiletea	
				Helichryso-Crucianelletea maritimae	
				Crithmo-Staticetea	
				Cakiletea maritimae	
			Macaronesian Coastal Scrub & Herb Vegetation		
				Polycarpaeo niveae-Traganetea moquini	

IVC Class	IVC Subclass	IVC Formation	Draft Division	EVC Class	IVC link on NatureServe Explorer
	2.C. Shrub & Herb Wetland				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.926082
		2.C.2. Temperate to Polar Bog & Fen			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860253
			Eurasian Bog & Fen		
				Oxycocco-Sphagnetea	
				Scheuchzerio palustris-Caricetea fuscae	
		2.C.4. Temperate to Polar Freshwater Marsh, Wet Meadow & Shrubland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860268
			Eurasian Freshwater Marsh, Wet Meadow & Shrubland		
				Phragmito-Magnocaricetea	
				Montio-Cardaminetea	
				Littorelletea uniflorae	
				Isoëto-Nanojuncetea	
				Bidentetea	
		2.C.5. Salt Marsh			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860269
			Eurasian Interior Wet Saline Marsh		
				Festuco-Puccinellietea	
				Crypsietea aculeatae	
				Kalidietea foliati	
				Aeluropodetea littoralis	
			European Coastal Salt Marsh		
				Juncetea maritimi	
				Salicornietea fruticosae	
				Spartinetea maritimae	
				Therosalicornietea	
				Saginetea maritimae	
3. Desert & Semi-Desert					https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860216
	3.A. Warm Desert & Semi-Desert Woodland, Scrub & Grassland				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860224
		3.A.2. Warm Desert & Semi-Desert Scrub & Grassland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860252
			Mediterranean-Macaronesian Warm Semi-Desert Scrub & Grassland		
				Pegano harmalae-Salsoletea vermiculatae	
				Kleinio neriifoliae-Euphorbietea canariensis	
				Spartocytisetea supranubii	
	3.B. Cool Semi-Desert Scrub & Grassland				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860228
		3.B.1. Cool Semi-Desert Scrub & Grassland			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860250
			Eurasian Cool Semi-Desert Scrub & Grassland		
				Artemisietea lerchianae	
4. Polar & High Montane Scrub, Grassland & Barrens					https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860213
	4.B. Temperate to Polar Alpine & Tundra Vegetation				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860229
		4.B.1. Temperate & Boreal Alpine Vegetation			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860272
			European Alpine Dwarf-shrub & Grassland		
				Elyno-Seslerietea	
				Juncetea trifidi p.p.	
				Festucetea indigestae	
				Saginetea piliferae	
			Oromediterranean Alpine & Subalpine Grassland & Scrub		
				Rumici-Astragaletea siculi	
				Trifolio anatolici-Polygonetea arenastri	
				Carici-Genistetea lobelii	
				Daphno-Festucetea	
				Diantho troodi-Teucrietea cyprii	
		4.B.2. Polar Tundra & Barrens			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860248
			Arctic Tundra & Barrens		
				Carici rupestris-Kobresietea bellardii	
				Loiseleurio procumbentis-Vaccinietea p.p.	
				Juncetea trifidi p.p.	
				Salicetea herbaceae	
				Drabo corymbosae-Papaveretea dahliani	
				Saxifrago cernuae-Cochlearietea groenlandicae	
				Saxifrago tricuspidatae-Calamagrostietea purpurascentis	
				Matricario-Poetea arcticae	
5. Aquatic Vegetation					https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860214
	5.A. Saltwater Aquatic Vegetation				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860226
		5.A.3. Benthic Vascular Saltwater Vegetation			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.877228
			Temperate Atlantic Seagrass Aquatic Vegetation		
				Halodulo wrightii-Thalassietea testudinum	
				Ruppietea maritimae	
				Zosteretea	
	5.B. Freshwater Aquatic Vegetation				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860222
		5.B.2. Temperate to Polar Freshwater Aquatic Vegetation			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.877233
			Temperate Eurasian Freshwater Aquatic Vegetation		
				Lemnetea	
				Potamogetonetea	

IVC Class	IVC Subclass	IVC Formation	Draft Division	EVC Class	IVC link on NatureServe Explorer
6. Open Rock Vegetation					https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860218
	6.B. Temperate & Boreal Open Rock Vegetation				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860230
		6.B.1. Temperate & Boreal Cliff, Scree & Other Rock Vegetation			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860263
			Macaronesian Cliff, Scree & Other Rock Vegetation		
				Aeonio-Greenovietea	
				Violetea cheiranthifoliae	
			Western Eurasian Cliff, Scree & Other Rock Vegetation		
				Adiantetea	
				Polypodietea	
				Asplenietea trichomanis	
				Cymbalario-Parietarietea diffusae	
				Phagnalo saxatilis-Rumicetea indurati	
				Drypidetea spinosae	
				Thlaspietea rotundifolii	
				Lamio tomentosi-Chaerophylletea humilis	
7. Agricultural & Developed Vegetation					https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.860215
	7.B. Herbaceous Agricultural Vegetation				https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.867665
		7.B.4. Fallow Field & Weed Vegetation			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.867668
			Eurasian Fallow Field & Weed Vegetation [cultural]		
				Papaveretea rhoeadis	
				Chenopodietea	
				Digitario sanguinalis-Eragrostietea minoris	
				Sisymbrietea	
				Polygono-Poetea annuae	
		7.B.5. Herbaceous Wetland Crop			https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.877250
			Eurasian Fallow Field & Weed Vegetation [cultural, wet]		
				Oryzetea sativae	

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Supplementary material

Supplementary material 1
Class fit to IVC formations.
Link: https://doi.org/10.3897/VCS/2021/71299.suppl1

VEGETATION CLASSIFICATION AND SURVEY

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Vegetation Classification and Survey 2: 293–304
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RESEARCH PAPER **CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC**

Fine-grain beta diversity in Palaearctic open vegetation: variability within and between biomes and vegetation types

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Abstract

Aims: To quantify how fine-grain (within-plot) beta diversity differs among biomes and vegetation types. **Study area:** Palaearctic biogeographic realm. **Methods:** We extracted 4,654 nested-plot series with at least four different grain sizes between 0.0001 m^2 and 1,024 m^2 from the GrassPlot database spanning broad geographic and ecological gradients. Next, we calculated the slope parameter (z-value) of the power-law species–area relationship (SAR) to use as a measure of multiplicative beta diversity. We did this separately for vascular plants, bryophytes and lichens and for the three groups combined (complete vegetation). We then tested whether z-values differed between biomes, ecological-physiognomic vegetation types at coarse and fine levels and phytosociological classes. **Results:** We found that z-values varied significantly among biomes and vegetation types. The explanatory power of area for species richness was highest for vascular plants, followed by complete vegetation, bryophytes and lichens. Within each species group, the explained variance increased with typological resolution. In vascular plants, adjusted R^2 was 0.14 for biomes, but reached 0.50 for phytosociological

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classes. Among the biomes, mean *z*-values were particularly high in the Subtropics with winter rain (Mediterranean biome) and the Dry tropics and subtropics. Natural grasslands had higher *z*-values than secondary grasslands. Alpine and Mediterranean vegetation types had particularly high *z*-values whereas managed grasslands with benign soil and climate conditions and saline communities were characterised by particularly low *z*-values. **Conclusions:** In this study relating fine-grain beta diversity to typological units, we found distinct patterns. As we explain in a conceptual figure, these can be related to ultimate drivers, such as productivity, stress and disturbance, which can influence *z*-values via multiple pathways. The provided means, medians and quantiles of *z*-values for a wide range of typological entities provide benchmarks for local to continental studies, while calling for additional data from under-represented units.

Syntaxonomic references: Mucina et al. (2016) for classes occurring in Europe; Ermakov (2012) for classes restricted to Asia.

Abbreviations: ANOVA = analysis of variance; EDGG = Eurasian Dry Grassland Group; SAR = species-area relationship.

Keywords

biome, bryophyte, fine-grain beta diversity, GrassPlot, lichen, mean occupancy, Palaearctic grassland, phytosociological class, species–area relationship (SAR), vascular plant, vegetation type, *z*-value

Introduction

The Palaearctic biogeographic realm (*sensu* Olson et al. 2001) is the largest terrestrial realm on Earth, covering more than 52 million square kilometres or approximately 40% of the ice-free terrestrial surface of the globe. Its elevational extent ranges from the lowest (423 m b.s.l.; Dead Sea) to the highest (8,848 m a.s.l.; Mt. Everest) point of the terrestrial surface and is thus exceptionally large. The resulting environmental heterogeneity includes eight of the ten biomes recognised by Bruelheide et al. (2019) and translates into a huge diversity of vegetation types, ranging from single-species stands to those that hold the world records for vascular plant species richness at most grain sizes below 100 m^2 (Wilson et al. 2012; Roleček et al. 2021).

The GrassPlot database (Dengler et al 2018; Biurrun et al. 2019) contains high-quality, multi-scale vegetation-plot data of any type of grasslands and other non-forest habitats of the Palaearctic realm. The selection criteria of GrassPlot include 63% of the habitat diversity of Europe according to a current typology (Janssen et al. 2016), and the fraction probably would be higher for Northern Africa and extra-tropical Asia with their higher fractions of grasslands (Dengler et al. 2020b), tundras, semi-deserts and deserts. Through covering a diverse set of habitat types and providing high-quality data not only for vascular plants, but also for bryophytes and lichens sampled in the same plots, GrassPlot offers a unique framework to analyse plant diversity patterns and their drivers (Biurrun et al. 2021). This is readily evident for species richness, since GrassPlot provides thousands of comprehensively sampled plots at eight standard grain sizes from 0.0001 to 1,000 m^2, together with extensive environmental and structural *in situ* measured variables. However, even more unique is the fact that GrassPlot contains thousands of nested-plot series (see Biurrun et al. 2019), which allow the analysis of small-scale nested species-area relationships (SARs).

A recent study using GrassPlot (Dengler et al. 2020a) found that nested SARs at the mentioned spatial scales can be well described with a power law, $S = c\,A^z$, where *S* is species richness, *A* area and *c* and *z* modelled parameters (Arrhenius 1921; Dengler 2009). The exponent *z* only exhibits a small amount of scale dependence (Zhang et al. 2021), meaning that for most purposes it is adequate to assume *z* to be constant within the range of grain sizes included in GrassPlot. As well as being a parameter of the power-law SAR, the *z*-value, when calculated using nested-plot data, is also a measure of β-diversity (Jurasinski et al. 2009; Dembicz et al. 2021). In fact, the *z*-value measures multiplicative β-diversity, standardized by the grain size ratio (Polyakova et al. 2016; Dembicz et al. 2021). β-diversity quantifies the dissimilarity between local communities and, together with mean α-diversity, makes up the diversity of a larger area (γ-diversity) (Whittaker 1960). Understanding patterns and drivers of β-diversity is thus of high importance both for ecological theory and biological conservation.

According to Storch (2016), *z*-values are closely related to the mean occupancy of species, i.e. the rarer species are in the finest grain size on average, the higher the *z*-values are. Dembicz et al. (2021) analysed which factors influence small-grain *z*-values using the GrassPlot database and found that herb layer cover, elevation, rock and stone cover, latitude and land use had the greatest explanatory power. Based on these findings and mathematical considerations, the authors proposed a conceptual model of how different environmental factors jointly could influence *z*-values by modifying mean occupancy values. We now present a refined version (Figure 1) that summarizes our main hypotheses: While total vegetation cover and similarity of species in adjacent subplots should affect fine-grain *z*-values negatively, mean size of individuals should have a positive influence (Figure 1). Since productivity, stress or disturbance can influence these three variables via multiple pathways, the effects of the former can be amplified or cancelled out (Figure 1).

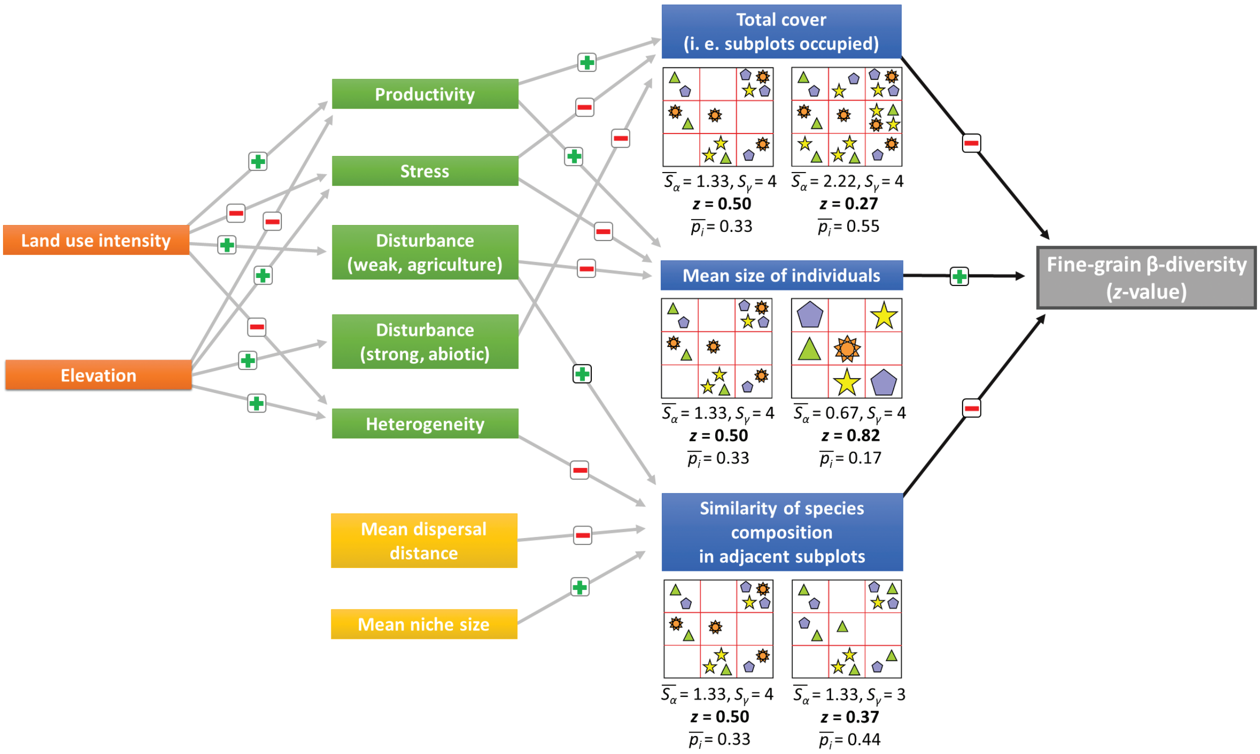

Figure 1. Conceptual figure summarizing our main hypotheses for how different drivers could influence fine-grain β-diversity via changing mean occupancy of species, based on the findings of Dembicz et al. (2021) and ecological theory. Fine-grain β-diversity (and likewise for larger grain sizes) is mathematically linked to mean occupancy, which can be decomposed into (i) total cover; (ii) mean size of individuals; and (iii) similarity of species composition between adjacent subplots. These three aspects of mean occupancy are affected by the environmental drivers, productivity, stress, disturbances and heterogeneity (green), as well as the mean traits of the analysed species group, namely dispersal distance and niche size (yellow). Note that disturbance can have contrasting effects depending on its type and intensity. To the very left we exemplify how two aggregated environmental parameters, land use intensity and elevation (orange), could influence fine-grain β-diversity via multiple pathways. What we mean with the three aspects that make up mean occupancy is illustrated with a pair of figures showing to the left a situation with low and to the right with high values of the respective aspect. The four different symbols represent individuals of four species distributed in a vegetation plot of a total extent of $A_\gamma = 9$ and assessed also at a grain size of $A_\alpha = 1$. Below each community, we provide the corresponding $\bar{S}_\alpha$-, S_γ-, z-values as well as the mean occupancies ($\bar{p}_i$). Since $z = \log(S_\gamma / \bar{S}_\alpha) / \log(A_\gamma / A_\alpha)$ and $\bar{p}_i = \bar{S}_\alpha / S_\gamma$, it is obvious that higher $\bar{p}_i$ means lower z and vice versa. Influences of one parameter are indicated by the arrows with their + and – symbols; grey arrows correspond to ecological hypotheses and black arrows to strict mathematical relationships. We did not aim to display all possible relationships in this figure, but concentrated on those that we consider most important. The expected effect of a certain driver or aggregated environmental parameter on fine-grain β-diversity can be estimated by multiplying the +/- symbols along the path. If several paths connect to fine-grain β-diversity, their products should be summed (modified from Dembicz et al. 2021).

Dembicz et al. (2021) analysed the effects of environmental variables, such as climate, soil, topography and land use, on z-values, but they did not assess how z-values vary across typological units. Here, we address this question, using the same data. For this purpose, we selected three different typologies that are widely used and carry different but complementary information: (a) biomes (reflecting the climax vegetation according to the macroclimate; Schultz 2005; Hunter et al. 2021), (b) ecological-physiognomic vegetation types (at two levels of resolution) and (c) phytosociological classes (reflecting the actual species composition; see Dengler et al. 2008; Mucina et al. 2016). Based on the findings regarding environmental predictors (Dembicz et al. 2021) and our hypotheses on causal pathways (Figure 1), we have the following *a priori* expectations:

1. Among biomes, “Dry tropics and subtropics”, “Subtropics with winter rain” and “Alpine” should have particularly high, and “Temperate mid-latitudes” particularly low, z-values.
2. Among vegetation types (ecological-physiognomic and phytosociological), those with more closed canopy should have lower z-values than those with more open ground; types of secondary grasslands should have lower z-values than those of natural grasslands.

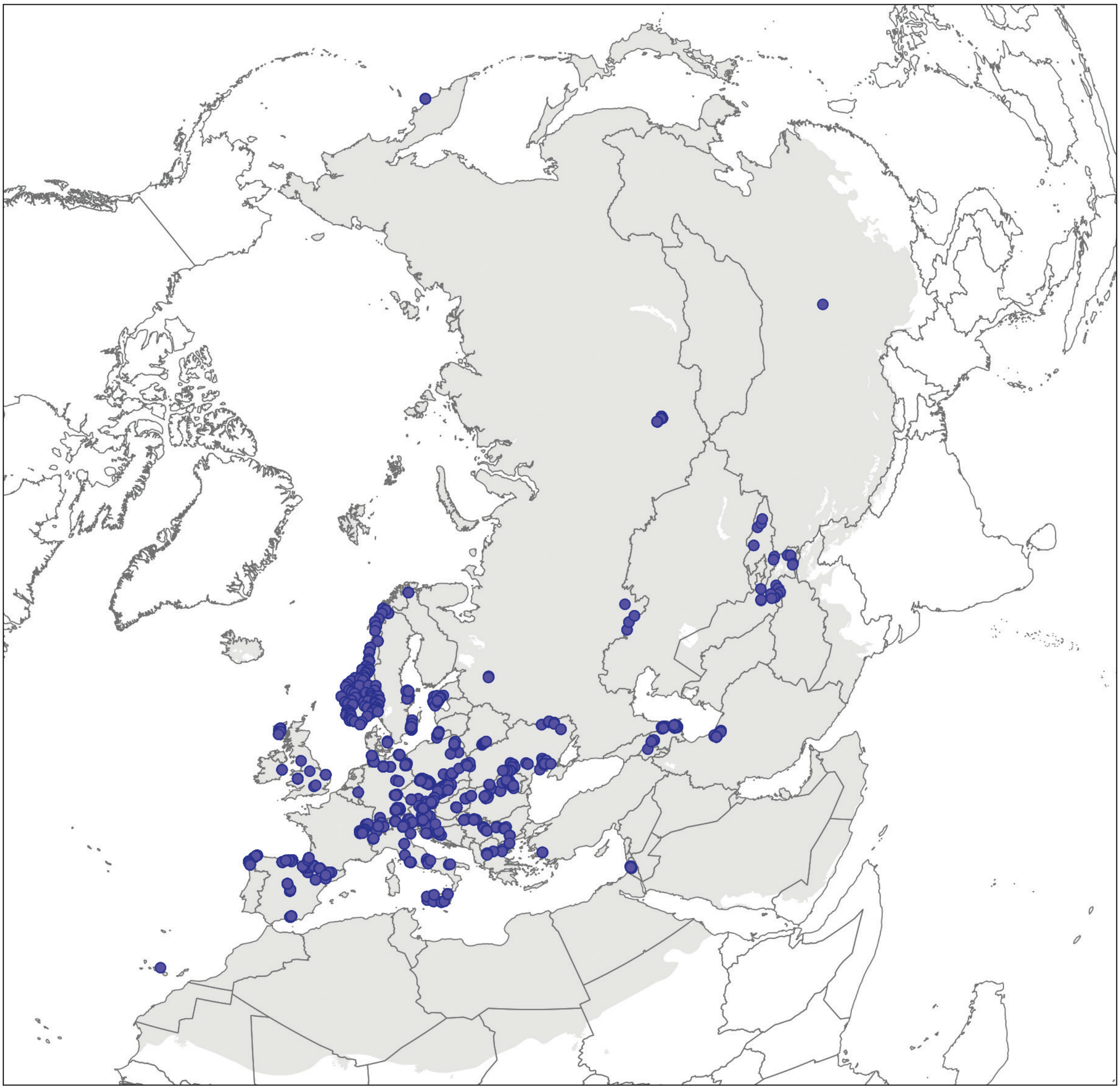

Figure 2. Geographic distribution of the 4,654 nested-plot series used in this study. The grey shading delimits the Palaearctic biogeographic realm.

Beyond testing these expectations, our aim is to provide information on typical *z*-values of biomes and vegetation types. This could help to detect habitat-specific deviations, related for example to anthropogenic disturbances (see, e.g., Tittensor et al. 2007) or invasive species (Powell et al. 2013).

Study area

The geographic scope of GrassPlot and of this study is the whole Palaearctic biogeographic realm. The nested-plot data used cover wide geographic gradients but have the highest density in Europe (Figure 2) with few plots in northern Africa or the eastern half of Asia. They are distributed across 34 different countries, from 28.5° to 70.0° N and 16.2° W to 161.8° E, and cover an elevation gradient from 0 to 4,387 m a.s.l. (Suppl. material 1).

Methods

Vegetation-plot data

We used plot data from the collaborative vegetation-plot database GrassPlot (Dengler et al. 2018; Biurrun et al. 2019; https://edgg.org/databases/GrassPlot). GrassPlot assembles vegetation-plot data from grasslands and other non-forest vegetation types (rocks and screes, deserts, ruderal communities, etc.) from the Palaearctic biogeographic realm. We retrieved all nested-plot series from GrassPlot (v. 2.04 on 20 March 2020) that contained at least four different grain sizes (4,654 series, consisting of 164,578 individual plots ranging from 0.0001 to 1,024 m^2). All series had information on *vascular plants*, 890 on terricolous (soil-dwelling) *bryophytes*, 894 on terricolous *lichens*, and 862 on all three taxonomic groups (i.e. total species richness of the vegetation, hereafter termed *complete vegetation*). We refer to the four categories (complete vegetation, vascular plants, bryophytes, lichens) together as the *four species groups*.

For those nested-plot series with more than one plot for a certain grain size, we averaged richness values per grain size. Thus, we obtained one single richness value for each grain size within each nested-plot series for each of the sampled species groups.

SAR modelling

We fitted a power function to each dataset (i.e. a species group within a nested-plot series) using the non-transformed "S-space" ($S = c\,A^z$) and the "logarithmic S-space" ($\log_{10} S = \log_{10} c + z \log_{10} A$) with S = species richness, A = area in m^2, and c and z the fitted "intercept" and "slope" parameters, respectively. Both approaches are valid, have been widely used in the literature, and have different advantages and limitations (see Dengler 2009; Dengler et al. 2020a). Due to the different treatment of the error structure, the parameter estimates in the two mathematical spaces usually deviate. Generally speaking, fitting in S-space gives more weight to a good fit at larger grain sizes, whereas fitting in log S-space gives more weight to a good fit at smaller grain sizes and typically reduces heteroscedasticity.

To fit the power model in log S-space, we used linear regression and the standard 'lm' function in R. The fitting in S-space followed the approach of Dengler et al. (2020a; see also Matthews et al. 2019). We applied non-linear regression using the 'mle2' function in the 'bbmle' R package (Bolker and R Core Team 2017). Starting parameter values were derived from the linear model in log S-space. In a small number of cases where the resultant S-space model did not converge, we iterated across a range of different starting parameter values to achieve convergence (see Dengler et al. 2020a). To avoid problems with fitting in log S-space, we assigned small, non-zero values to any subplot with observed values of $S = 0$ (Dengler et al. 2020a). For both the S-space and log S-space fitted models, we obtained the z-values for further analyses.

Analyses of the *z*-values

We excluded nested-plot series with zero reported species for the investigated species group as well as the very few nested-plot series where the model fitting did not converge or resulted in theoretically impossible values of $z > 1$ (Williamson 2003). The latter was true for 0.01% of all series across the four species groups in log S-space and 0.25% in S-space. Consequently, for log S-space we obtained z-values for 4,570 series for vascular plants, 719 for bryophytes, 417 for lichens and 862 for complete vegetation, while for S-space we estimated z-values for 4,554 series for vascular plants, 716 for bryophytes, 400 for lichens and 862 for the complete vegetation. Note that in some cases taxonomic groups were searched for but did not occur; therefore, the number of series for complete vegetation is higher than the numbers for bryophytes or lichens.

We tested how the modelled z-values depended on biome and vegetation types of three different typologies. First, as a biome typology, we used the ecozones of Schultz (2005) with additional separation of an Alpine biome (Körner et al. 2017) – as implemented by Bruelheide et al. (2019). Further, we used the coarse and fine vegetation typology of GrassPlot (Biurrun et al. 2019), which is mainly based on ecological and physiognomic criteria (for details see Suppl. material 2). Lastly, we used the phytosociological classes. Plots were assigned to classes based on the information provided by data contributors, as well as by expert judgement based on floristic composition. Classes occurring in Europe were named after Mucina et al. (2016), classes restricted to Asia according to Ermakov (2012).

As the visual inspection of the boxplots did not yield severe violations of the assumptions of linear models (see Quinn and Keough 2002), we applied analyses of variance (ANOVAs) with the 'aov' function (R package 'stats'), followed by Tukey's HSD *post hoc* test using the functions 'TukeyHSD' (R package 'stats') and 'multcompLetters4' (R package 'multcompView'; Graves et al. 2019) to produce a letter-based representation of all-pairwise group comparisons. For the ANOVAs, we excluded some categories that had very few observations only (see details below).

For visualisation of the distribution of the observed values, we used violin plots, a method of plotting numeric data that is a hybrid of boxplots and kernel density plots, able to identify multimodality (R package 'ggplot2'; Thrun et al. 2020). The scale of the violin plots was set to "width".

To avoid strong unequal sample sizes and heterogeneous variances among categories when comparing taxa, which could make F-tests unreliable, we restricted comparisons to biomes, vegetation types and phytosociological classes represented in complete vegetation by at least ten nested-plot series. All computations were performed with R 4.1.1 (R Core Team 2021).

Results

As the results were qualitatively similar for log S-space and S-space, and as we had slightly more replicates for log S-space, we present the results from the ANOVAs and violin plots only for log S-space in the main text. Descriptive statistics (number of replicates, means, medians, 10% and 90% quantiles) for both spaces are provided in Suppl. material 3.

Vascular plants

The mean and median z-values of most biomes and vegetation types were around 0.25, although the range was

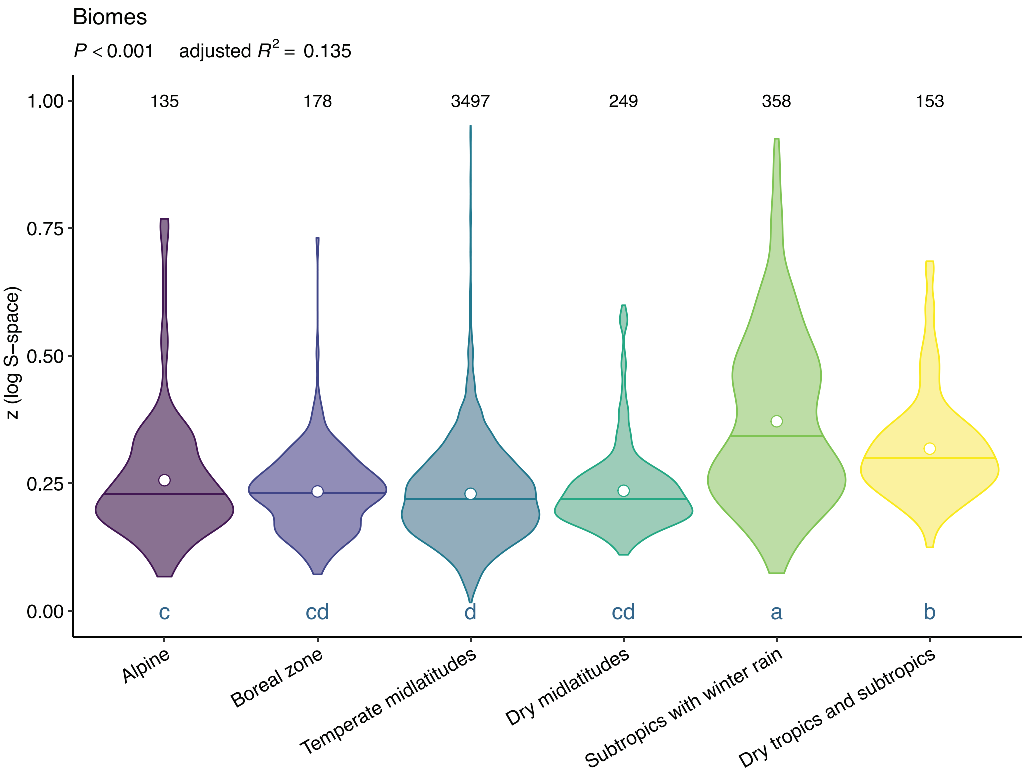

Figure 3. Comparison of fine-grain *z*-values of vascular plants between the biomes included in GrassPlot with suitable data. The biomes are sorted in descending order of latitude and elevation. The circles represent the means, the horizontal lines the medians and the letters homogeneous groups according to Tukey's HSD post hoc test following a significant ANOVA (in decreasing order). Numbers at the top of the violin plots indicate the number of nested-plot series in each biome.

from 0.15 to 0.50 (Figures 3–6). However, in most of the typological units, there was a large variation, with extreme values sometimes almost covering the entire theoretically possible range from 0 to 1 (Figures 3–6). Despite this variation, for each of the four typologies there were distinct groups that differed significantly in their mean *z*-values (Figures 3–6). The explanatory power of the typologies was relatively low for biomes and coarse-level vegetation types ($R^2 = 0.14$), intermediate for fine-level vegetation types ($R^2 = 0.36$) and high for phytosociological classes ($R^2 = 0.50$).

Among the biomes, the Temperate midlatitudes had the lowest mean *z*-value, but were hardly different from Alpine, Boreal zone and Dry midlatitudes (Figure 3). By contrast, the vegetation of the Dry tropics and subtropics, and particularly the Subtropics with winter rain, had clearly higher *z*-values (Figure 3). Among the coarse-level vegetation types, natural grasslands had clearly the highest mean *z*-values, followed by dwarf shrublands, whereas azonal communities had the lowest values (Figure 4). Among the fine-level vegetation types, Mediterranean grasslands, alpine grasslands and garrigues and thorn-cushion communities had particularly high *z*-values, while saline communities and saline steppes and semi-deserts had particularly low values (Figure 5). Among the phytosociological classes, the Mediterranean class *Stipo-Trachynietea* and the high-elevation classes *Festucetea indigestae* and *Carici-Kobresietea* had particularly high *z*-values, followed by *Juncetea trifidi* and *Sedo-Scleranthetea*, while the saline classes *Festuco-Puccinellietea* and *Juncetea maritimi*, as well as the mesic secondary grassland classes *Molinio-Arrhenatheretea* and *Nardetea strictae*, had particularly low *z*-values (Figure 6).

The four species groups in comparison

For all four vegetation typologies considered, the explained variance was highest for vascular plants, followed by complete vegetation, whereas it was relatively low in bryophytes and lowest in lichens (Suppl. material 4: Figures S4.1–S4.4). For the four biomes with sufficient data, the pattern was similar among all four species groups with the Subtropics with winter rain always being in the group of highest *z*-values (Suppl. material 4: Figure S4.1). For coarse-level vegetation types, vascular plants, bryophytes and complete vegetation showed a similar pattern of decreasing *z*-values from natural grasslands via secondary grasslands to azonal communities, whereas the three other categories (with much fewer observations) were at an intermediate position (Suppl. material 4: Figure S4.2). By contrast, lichens did not differ significantly in their mean *z*-values among coarse-level veg-

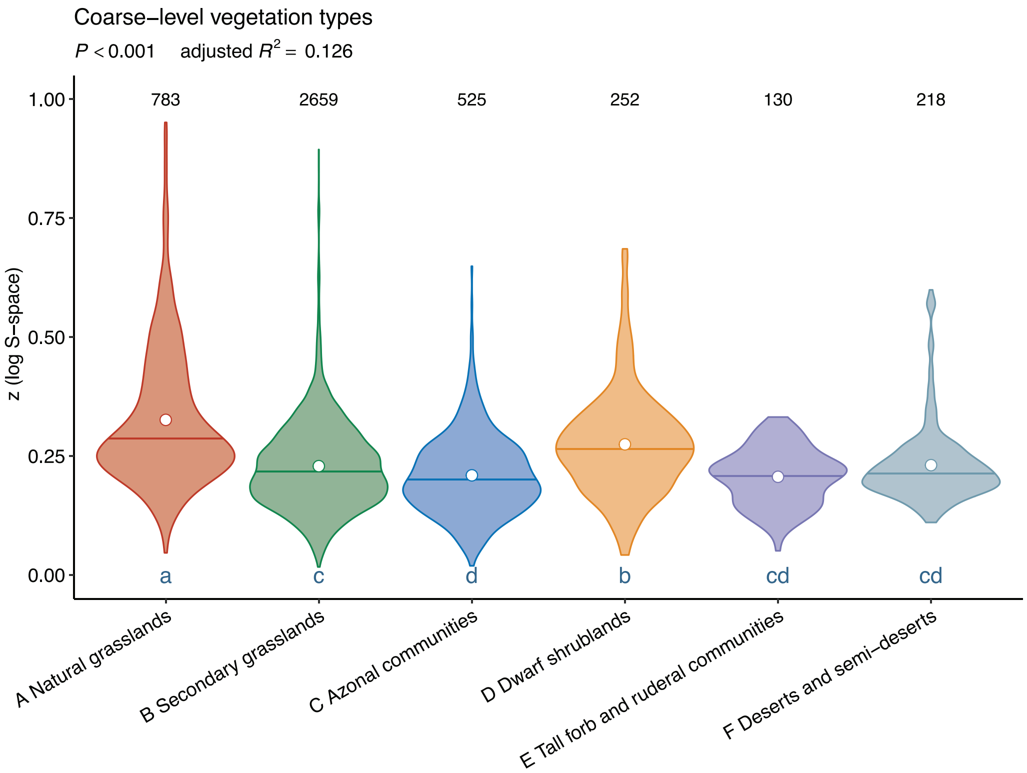

Figure 4. Comparison of fine-grain *z*-values of vascular plants between the six coarse-level vegetation types distinguished in GrassPlot. The circles represent the means, the horizontal lines the medians and the letters homogeneous groups according to Tukey's HSD post hoc test following a significant ANOVA (in decreasing order). Numbers at the top of the violin plots indicate the number of nested-plot series in each coarse-level vegetation type.

etation types (Suppl. material 4: Figure S4.2). Likewise, for fine-level vegetation types, the patterns for complete vegetation, vascular plants and bryophytes were similar, with Mediterranean and rocky grasslands having the highest *z*-values (Suppl. material 4: Figure S4.3). Finally, when analysing the phytosociological classes, across all four species groups, the *Sedo-Scleranthetea* had the highest *z*-values (sometimes together with other classes), whereas *Molinio-Arrhenatheretea*, *Nardetea strictae* and *Scheuchzerio-Caricetea* had particularly low *z*-values (Suppl. material 4: Figure S4.4).

Discussion

Overall patterns

Similar to previous studies, we found large variation in *z*-values within most of the typological units considered (Schmiedel et al. 2010; Dengler et al. 2012; Pedashenko et al. 2013). Whereas the only two previous studies that to our knowledge tested for differences in fine-grain *z*-values between vegetation types had not reported any significant differences (Dengler et al. 2012; Pedashenko et al. 2013), we found highly significant differences, which in the case of vascular plants explained more than half of the overall variance. These contrasting results can be attributed to (i) our much larger sample size, which allowed for detection of differences despite the strong variation within typological units, and (ii) our more diverse array of phytosociological classes, thus longer gradients. By contrast, the former study that compared *z*-values between biomes had also found significant differences (Schmiedel et al. 2010).

Second, we found that the explained variance increased the finer resolved our typology was: while biomes explained only around 14% of the variance, phytosociological classes accounted for more than 50%. This finding is not surprising and mainly reflects that our typological units are meaningful entities that differ in their vegetation patterns as well as their average productivity, stress and disturbance (see Dengler et al. 2008; De Cáceres et al. 2015), all of which affect *z*-values (see Figure 1). The relatively small amount of variance explained by biome indicates that, for *z*-values, macroclimate is less important than local conditions, such as soil and water conditions, as well as disturbance regimes due to management.

Third, we found a clear decrease in explained variance (or in other words, in distinctness of the patterns) from vascular plants via complete vegetation to bryophytes and lichens. This is consistent with findings of two previous GrassPlot studies that looked at other aspects of fine-grain *z*-values (Dembicz et al. 2021; Zhang et al. 2021). Partially, this might be explained by the fact that, due to the generally low replication of smaller plots within a nested plot series

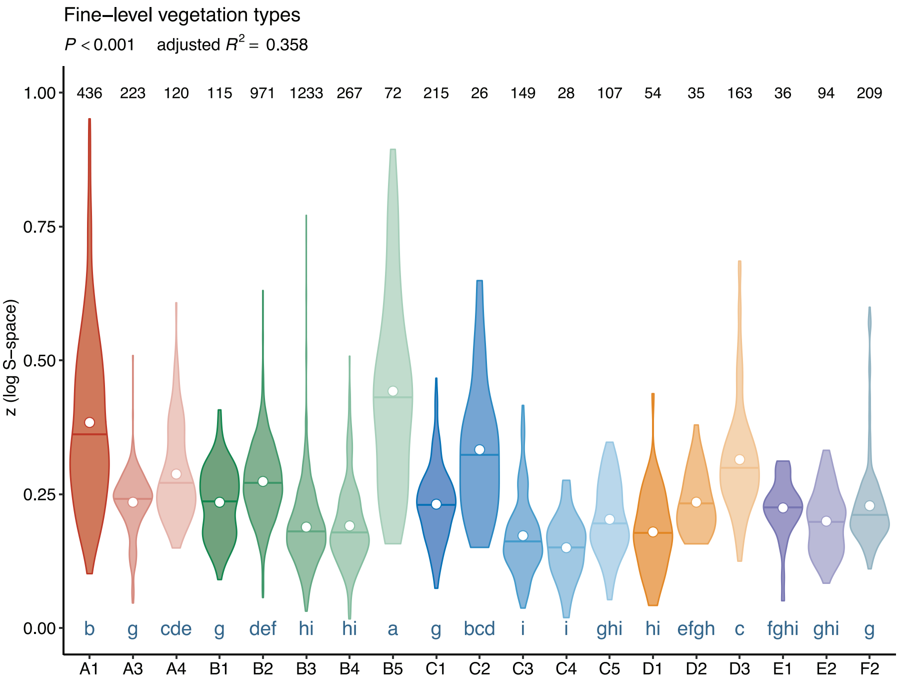

Figure 5. Comparison of fine-grain *z*-values of vascular plants between those fine-level vegetation types distinguished in GrassPlot that were represented by at least 10 observations. A1 = alpine grasslands, A3 = xeric grasslands and steppes, A4 = rocky grasslands, B1 = sandy dry grasslands, B2 = meso-xeric grasslands, B3 = mesic grasslands, B4 = wet grasslands, B5 = Mediterranean grasslands, C1 = dunes, C2 = rocks and screes, C3 = saline communities, C4 = saline steppes and semi-deserts, C5 = wetlands, D1 = lowland heathlands, D2 = arctic-alpine heathlands, D3 = garrigues and thorn-cushion communities, E1 = tall forb communities, E2 = ruderal communities, F2 = cold deserts and semi-deserts. The circles represent the means, the horizontal lines the medians and the letters homogeneous groups according to Tukey's HSD post hoc test following a significant ANOVA (in decreasing order). Numbers at the top of the violin plots indicate the number of nested-plot series in each fine-level vegetation type.

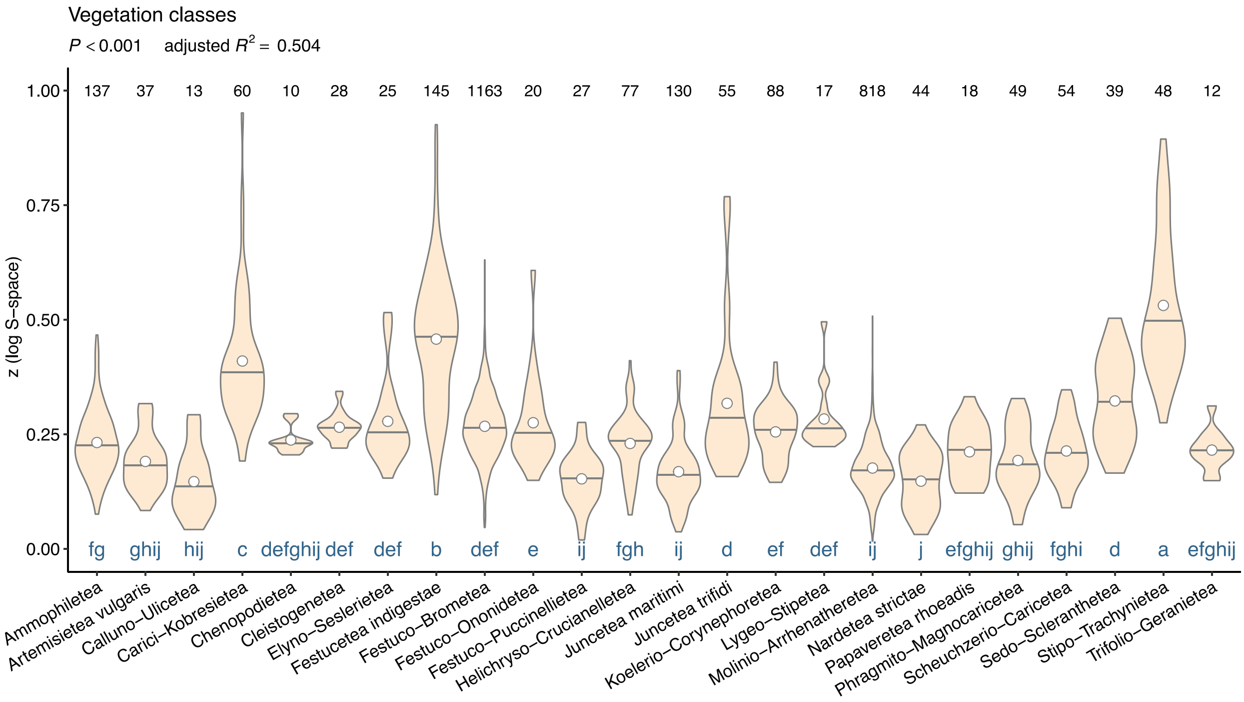

Figure 6. Comparison of fine-grain *z*-values of vascular plants between those phytosociological classes that were represented by at least 10 observations. The circles represent the means, the horizontal lines the medians and the letters homogeneous groups according to Tukey's HSD post hoc test following a significant ANOVA (in decreasing order). Numbers at the top of the violin plots indicate the number of nested-plot series in each phytosociological class.

(typically only two replicates), there were often mean richness values of zero reported for bryophytes or lichens in the smaller plots, while in reality the mean values always must be above zero. This leads to an interpretation of no difference in the SARs within these taxa, which might not have been the case with more replicates, given that we could have then established different mean richness values between 0 and 1 for the different grain sizes. On the other hand, an ecological reason for the lower explained variance might be that the spatial distribution of non-vascular species is more dependent on micro-structures than on the vegetation type.

Entities with high and low fine-grain *z*-values

The two subtropical biomes (Subtropics with winter rain, Dry tropics and subtropics) had clearly higher *z*-values than the rest, which is consistent with the increase in *z*-values from 50 °N southward reported by Dembicz et al. (2021). However, we did not find the (moderate) poleward increase (Dembicz et al. 2021), which might be due to the fact that a large fraction of our Boreal series was from the southern border of the Boreal zone and we did not have a sufficient number of Arctic series to include them. Dembicz et al. (2021) also reported a strong increase in *z*-values with elevation, whereas in our study the Alpine biome did not have higher *z*-values than the Boreal zone or the Dry midlatitudes, and only slightly higher values compared to the Temperate midlatitudes. This discrepancy points to the fact that mainly non-climatic factors (such as increased small-scale heterogeneity) are responsible for higher *z*-values at higher elevation, and thus a climatically defined “Alpine” biome (as used here, based on the definition of Körner et al. 2017) might not stand out as much as an alternative definition based on plots above 2,000 or 3,000 m a.s.l. (see Dembicz et al. 2021). Our results are similar to Schmiedel et al. (2010) who compared fine-grain *z*-values of biomes in Southern Africa. They found the by far highest values in the “Namib Desert” followed by the “Succulent Karoo”, both belonging to the Dry tropics and subtropics. At much larger grain sizes (1 to 1,000,000 km^2), Gerstner et al. (2014) also compared *z*-values of vascular plants among biomes. Among the biomes common to their and our study, they had particularly high values for “Mediterranean forests, woodlands, and scrub or sclerophyll forests” (0.280), medium for “Montane grasslands and shrublands” (0.215) and “Deserts and xeric shrublands” (0.205), low for “Temperate broadleaf and mixed forests” (0.161) and “Temperate grasslands, savannas, and shrublands” (0.144) and very low for “Boreal forest/taiga” (0.078). While the absolute numbers are lower, the ranking of biomes is relatively similar to ours (see Figure 3) – despite the many orders of difference in grain size, which makes it unlikely that the same drivers are relevant (see Shmida and Wilson 1985 for α-diversity).

Second, natural grasslands had systematically higher *z*-values than secondary grasslands. This corroborates the previously reported clear negative effects of land use intensity on *z*-values (Dembicz et al. 2021). At the lower typological level, the three units with particularly high z-values were Alpine grasslands, Mediterranean grasslands and garrigues and thorn-cushion communities. This outstanding position of two Mediterranean units and one Alpine unit is consistent with the extraordinary fine-grain β-diversity found for the Subtropics with winter rain (above) and for natural habitats combined with high elevation (Dembicz et al. 2021). The same pattern is reflected in the phytosociological classes where three of the five units with the highest *z*-values were natural grasslands above the timberline, one unit belonged to Mediterranean grasslands and one unit to temperate rocky outcrop communities, the latter two with rather open vegetation structure.

Reasons for variation in *z*-values

Nested-plot *z*-values are mathematically closely linked to mean occupancy (Storch 2016; Dembicz et al. 2021). Therefore, factors that increase mean occupancy at fine grains will decrease fine-grain *z*-values and vice versa (see Figure 1). Following Dembicz et al. (2021), we argue that there are three main factors that have a direct (mathematical) relationship with *z*-values (Figure 1). All other things being equal, *z*-values will increase with decreasing total cover, higher dissimilarity in species composition between adjacent patches and increasing mean size of plant individuals. These direct factors are influenced in different ways by various drivers, like disturbance and stress. In particular, disturbance can have opposing effects on *z*-values depending on the intensity (Figure 1). While disturbance as a result of agricultural land use (e.g., mowing or moderate grazing) will normally decrease *z*-values, more extreme disturbance (e.g., fire, flooding) might increase *z*-values (Figure 1). The reason for this assumption is that “proper” grassland management is conducted in a way that vegetation cover is not decreased (Dembicz et al. 2021).

Our findings with regard to the different typological entities fit well into the hypothetical schema of Figure 1. Just like Dembicz et al. (2021), we confirm the negative impact of typical grassland management on fine-grain β-diversity by demonstrating that *z*-values were systematically lower in secondary than in natural grasslands. We also confirm that, at the typological level, more stressful habitats, in particular those where the stress leads to a more open vegetation structure (i.e. lower total cover), typically have higher *z*-values, which is particularly true for Alpine and Mediterranean habitats. On the other hand, vegetation types with benign conditions, and thus high cover, combined with the effects of agricultural disturbances that reduce the mean size of individuals and homogenize the vegetation, like *Molinio-Arrhenatheretea* and *Nardetea strictae*, have rather low *z*-values. However, saline communities as well as saline steppes and semi-deserts, had even lower mean *z*-values. In relation to Figure 1 this was, at first glance, rather unexpected as these communities can be considered among the most stressed vegetation types included in the study, typically also having a very open vegetation structure. However, in these extreme cases, other factors may be relevant that are not reflected in Figure 1. For example, the extreme stress might filter the species pool so strongly that there are simply no additional species available that could grow in the large plot, thus limiting the slope of the SAR from the upper end.

Conclusions and outlook

This is the most comprehensive study to date that relates fine-grain β-diversity as measured using *z*-values to different vegetation typologies. We thus complement the recent study of Dembicz et al. (2021) who related nested-plot *z*-values to a wide range of environmental predictors, and demonstrated that *z*-values are a useful measure of multiplicative β-diversity as they are independent from the ratio of areas at the α- and γ-level. This characteristic was particularly useful in our case given that the sizes of the smallest and biggest plots varied substantially across series.

We found that despite important variation, there are clear differences in mean *z*-values among typological units. While there is not a single reason for low or high *z*-values, the values themselves can still be used as informative tools to assess the influence of certain drivers, particularly land-use intensity (see also Tittensor et al. 2007; Dembicz et al. 2021) and biotic invasions (Powell et al. 2013). Our results, broken down into different typologies (Suppl. material 3), provide a set of "benchmarks", which future local- oro continental-scale studies in Palaearctic open habitats can utilise, in a similar way to the α-diversity benchmarks provided in the GrassPlot Diversity Explorer (https://edgg.org/index.php/databases/GrasslandDiversityExplorer; Biurrun et al. 2021). For the missing or less represented units, Suppl. material 3 can be understood as a call to collect such nested-plot data, preferentially using the EDGG standard (Dengler et al. 2016), and contribute them to the collaborative GrassPlot database (Dengler et al. 2018; Biurrun et al. 2019) so that we can draw an even more complete picture in the future.

Data availability

The vegetation-plot data used are stored in and available from the GrassPlot database (https://edgg.org/databases/GrassPlot; Dengler et al. 2018) under version number 2.04 (20 March 2020).

Author contributions

J.D. initiated the data collection and, together with I.D. and S.B., conceived the idea for this paper. Most authors contributed data. J.D. served as custodian and I.B. as database manager of the GrassPlot database. F.G., M.J.S. and T.J.M. conducted the statistical analyses, while I.D. and J.D. led the writing. All authors checked, improved and approved the manuscript.

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Supplementary material

Supplementary material 1
Nested-plot datasets used in this study and their sources
Link: https://doi.org/10.3897/VCS/2021/77193.suppl1

Supplementary material 2
Overview of the coarse- and fine-level vegetation typology used in GrassPlot (including a few categories without nested-plot series in the current study)
Link: https://doi.org/10.3897/VCS/2021/77193.suppl2

Supplementary material 3
Descriptive statistics of *z*-values per typological unit for the four species groups and the two *S*-spaces
Link: https://doi.org/10.3897/VCS/2021/77193.suppl3

Supplementary material 4
Results in log *S*-space for the four species groups
Link: https://doi.org/10.3897/VCS/2021/77193.suppl4

VEGETATION CLASSIFICATION
AND SURVEY

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REPORT

PHYTOSOCIOLOGICAL NOMENCLATURE

Report 2 of the Committee for Change and Conservation of Names (CCCN)

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Abstract

In this Report, three previously published nomenclatural proposals are discussed, and recommendations on acceptance or rejection of these proposals are provided. The proposals concern the following syntaxa: *Berberidion* Braun-Blanquet 1950, *Aceretalia pseudoplatani* Moor 1976 and *Festucetalia valesiacae* Braun-Blanquet et Tüxen ex Braun-Blanquet 1950.

Abbreviations: CCCN = Committee for the Change and Conservation of Names; GPN = Working Group for Phytosociological Nomenclature; ICPN = International Code of Phytosociological Nomenclature.

Keywords

nomenclature, nomen conservandum, phytosociology, syntaxonomy

Introduction

The Committee for the Change and Conservation of Names (CCCN) is the successor of the Committee for Nomina Conservanda, Ambigua, Inversa and Mutata (CNC) established by the 3rd edition of the International Code of Phytosociological Nomenclature (ICPN) (Weber et al. 2000; Willner et al. 2015). A first Report was published in 2011, containing recommendations on 19 proposals submitted to the Committee (Willner et al. 2011). In 2015, the Assembly of the Working Group for Phytosociological Nomenclature (GPN) voted on three of these proposals (Gigante et al. 2019), and the accepted ones were published in appendix 3 and 4 of the ICPN, 4th edition (Theurillat et al. 2021). One proposal – which has not been submitted to vote yet – is re-evaluated here with some modifications (see proposal 17* below). The other proposals discussed in Willner et al. (2011), all of them referring to *nomina mutata*, are obsolete since the adaptation of syntaxon names to changes in the names of the name-giving taxa does no longer require submission of a proposal (see Art. 44 and Art. 45 in the 4th edition of the ICPN).

Following the publication of the new edition of the ICPN, the CCCN resumed its activity. Federico Fernández-González was elected as a member to replace Heinrich Weber who passed away in 2020. Therefore, the current members are: Wolfgang Willner (chair), Andraž Čarni, Federico Fernández-González, Jens Pallas and Jean-Paul Theurillat.

Some nomenclatural cases turned out to be quite complicated, so the progress in the Committee was slower than expected. In the following, we discuss three proposals and present our recommendations. Some published proposals (Theurillat et al. 2017; Novák 2019; Fernández-González et al. 2021) are still pending and will be treated in the next Report, which is scheduled for 2022. The Committee will also discuss the submitted requests for a binding decision (Silva and Molina 2021), a procedure newly introduced in the 4th edition of the ICPN.

Authors who wish to submit a proposal are asked to consult appendix 2 of the ICPN and the recently published proposals in *Vegetation Classification and Survey* (Fernández-González et al. 2021). Authors who wish to request a binding decision should consult appendix 6 and the request by Silva and Molina (2021).

Recommendations on published proposals

Note: An asterisk (*) after the number of the proposal 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. Modified version of the proposal published in Willner et al. (2011). Votes: 4 pro, 1 contra (recommended).

(17*) *Berberidion* Braun-Blanquet 1950 [Braun-Blanquet 1948–1950, part 6: 349].
Typus cons. propos.: *Berberido-Rosetum* Braun-Blanquet 1961: 189.
(=) *Prunion spinosae* Soó 1931: 294.
Typus: *Crataego monogynae-Prunetum spinosae* Soó 1931: 312 (holotypus).

The original diagnosis of the alliance *Berberidion* Braun-Blanquet 1950 includes two associations: "*Rosetum rhamnosum* Braun-Blanquet 1918" and "*Coryleto-Populetum* Braun-Blanquet (1919) 1938". Most authors, including Willner et al. (2011), have regarded the "*Rosetum rhamnosum*" as invalidly published, considering the "*Coryleto-Populetum*" (recte: *Corylo-Populetum*) as the holotype of the alliance. A closer look to the original diagnosis of the *Berberidion* Braun-Blanquet 1950 revealed that the previous evaluations were partly wrong. First, the name *Rosetum rhamnosum* is not invalid according to Art. 3e since the epithet "*rhamnosum*" does not have the termination *-etosum* indicating a subassociation. Instead, it should be interpreted as an epithet in the nominative case that indicates a morphological or other property (Art. 34a). In Braun-Blanquet (1918), the *Rosetum rhamnosum* was proposed as a subassociation of the "*Corylus*-Assoziation", so the name was indeed invalidly published in 1918 (Art. 3e). In Braun-Blanquet (1948–1950), the association *Rosetum rhamnosum* could be interpreted as validly published because there is a reference to Braun-Blanquet (1918: 19) where the *Rosetum rhamnosum* is synonymised with the "Muschnaformation von Hager" ("Muschna" is a Romansh name for a clearance cairn) and accompanied with a reference to Hager (1916). Indeed, Hager (l.c.: 211–212) published a species list with three semi-quantitative categories of frequency which can be considered as sufficient original diagnosis (Art. 7). However, Braun-Blanquet (1918) specifically referred to p. 212 of Hager, where there is a species list of one particular example of a "Muschnaformation" without quantitative indications. The chapter where both species lists are provided is titled "Die Assoziationen der Muschna-Hügel" (the associations of the Muschna hills) which in turn is part of the chapter on the "Formation von *Prunus padus*" (Formation of *Prunus padus*). While it is clear that Hager (1916) considered both species lists as belonging to the same abstract vegetation unit (the Formation of *Prunus padus* growing on Muschna hills), it is not clear whether Braun-Blanquet intended to refer specifically to the species list on p. 212 or to the whole formation described by Hager. To make things even more complicated, Braun-Blanquet (1948–1950) did not directly cite the "Muschnaformation" but a different page (p. 220) in Hager (1916) where another community with *Berberis* is described ("alluviale *Berberis*-Strauchheide"), which lacks a sufficient original diagnosis. Given this problematic situation, opinions about the validity of the name *Rosetum rhamnosum* Braun-Blanquet 1950 were not unanimous among the members of the CCCN.

The second association in the original diagnosis of the alliance *Berberidion*, the *Corylo-Populetum* Braun-Blanquet 1950, was also not correctly evaluated in previous nomenclatural analyses. The only element in the original diagnosis of the *Corylo-Populetum* arguably meeting the prescriptions of Art. 7 is the reference to Brockmann-Jerosch (1907) who published a single relevé of the "Haselstrauch-Formation" on page 265, although this relevé only contains the woody species, among which are both *Corylus avellana* and *Berberis vulgaris*. [The same reference to Brockmann-Jerosch (1907) was indicated by Braun-Blanquet (1918: 18–19, 80) for his "Assoziation von *Corylus avellana*". Hence the *Corylo-Populetum* Braun-Blanquet 1950 is a nomenclatural synonym of the *Coryletum avellanae* Braun-Blanquet 1918.] The other references given by Braun-Blanquet (1948–1950) contain only species lists or *nomina nuda*, including the species list of the *Coryletum* in Beger (1922) in which abundance values are indicated for less than half of the species.

Since the *Corylo-Populetum* has often been excluded from the *Berberidion* and classified within a separate alliance *Corylo-Populion* (see, e.g., Braun-Blanquet 1961), it is not a suitable type for the name *Berberidion*. Even if the *Rosetum rhamnosum* might be considered as validly published, choosing a neotype for this illegitimate name and then selecting this association as lectotype for the *Berberidion* does not appear the best solution to serve the goal of nomenclatural stability. Willner et al. (2011) recommended conserving the next valid publication of the name *Berberidion*, which appeared in Tüxen (1952), with the *Pruno-Ligustretum* Tüxen 1952 as lectotype. However, the 4th edition of the ICPN (Theurillat et al. 2021) offers a more elegant solution, namely a conserved type (Art. 53). The best choice for a conserved type of the *Berberidion* Braun-Blanquet 1950 is obviously the *Berberido-Rosetum* Braun-Blanquet 1961, which is the correct name for the "*Rosetum rhamnosum*".

Therefore, we recommend to conserve the name *Berberidion* Braun-Blanquet 1950 with a conserved type, as outlined above. As the original diagnosis of the *Berberido-Rosetum* Braun-Blanquet 1961 contains no direct reference to the *Rosetum rhamnosum*, it must be considered as a new association. Willner and Grabherr (2007: 224) selected the following lectotype for the *Berberido-Rosetum*: Braun-Blanquet (1961), table 40, relevé 6.

Another point that emerged during the discussion of this proposal is the name *Prunion spinosae* Soó 1931. Sádlo et al. (2013: 87, 92–93) considered it as a synonym of the *Berberidion* and proposed its rejection as *nomen ambiguum*. Indeed, the name *Prunion spinosae* has mostly been used in a sense that excludes its type, often with a wrong year (Wirth 1993; Borhidi et al. 2012). We refrain here from commenting on this proposal, that has not been officially submitted to the CCCN yet. However, it is clear that the name *Prunion spinosae* Soó 1931 poses a potential threat to the well-established name *Berberidion* Braun-Blanquet 1950, so we recommend to conserve the latter against this older name. Nevertheless, the adoption of this proposal would still allow to use the name *Prunion spinosae* if its type association (*Crataego monogynae-Prunetum spinosae* Soó 1931) is considered as not belonging to the *Berberidion*.

(20) To conserve the name *Aceretalia pseudoplatani* Moor 1976 against *Tilietalia* Moor 1973. Proposed by Willner (2015). Votes: 4 pro, 0 contra, 1 abstention (recommended).

This proposal (Willner 2015) means to conserve the name *Aceretalia pseudoplatani* (Moor 1976: 336) against the name *Tilietalia* (Moor 1973: 129) when European maple and lime forests are united within a single order. If the lime forests are treated as a separate order, the name *Tilietalia* Moor 1973 would still be available. The name *Aceretalia pseudoplatani* is widely accepted in the literature (e.g., Mucina et al. 2016), and the CCCN also agrees that *Acer pseudoplatanus* is a better name giving taxon for the united order. Therefore, acceptance of the proposal is recommended.

(21) To conserve the name *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 against *Festucetalia* Soó 1940. Proposed by Terzi et al. (2017). Votes: 1 pro, 4 contra (not recommended).

The name *Festucetalia valesiacae* is generally accepted for the order of continental grass steppes of western Eurasia. However, there is disagreement on the correct author citation of this name. Mucina et al. (2016) attribute it to Soó (1947), but as showed by Terzi et al. (2017), Soó (1947) simply emended and renamed his earlier, validly published order *Festucetalia* Soó 1940. The original diagnosis of this order is very heterogeneous, including communities that are currently placed in at least three orders belonging to two different classes. Even more problematic, *Festuca valesiaca* is absent from the original diagnosis of the type alliance "*Festucion sulcatae*" Soó 1930 (recte: *Festucion rupicolae* Soó 1930 nom. corr.). The name *Festucetalia valesiacae* was coined by Braun-Blanquet and Tüxen (1943), but not validly published due to the lack of bibliographical references. Indeed, even Soó (1964) accepted Braun-Blanquet's and Tüxen's name, putting his own *Festucetalia* Soó 1940 into the synonymy. Therefore, the majority of the CCCN agreed with the general proposal to conserve the later validation of the name *Festucetalia valesiacae* by Braun-Blanquet (1948–1950) against Soó's *Festucetalia*. However, there is a problem with the type of the order. Braun-Blanquet (1948–1950) did not provide a reference to the alliance *Festucion valesiacae* Klika 1931, which is included in the order in Braun-Blanquet and Tüxen (1943), and from which the order name obviously is derived. The holotype of the *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 is the alliance *Stipo-Poion xerophilae* Br.-Bl. et Tx. ex Br.-Bl. 1950, as this is the only alliance mentioned by Braun-Blanquet (1948–1950) within the order. It is an illegitimate, heterotypic homonym of the *Stipo-Poion xerophilae* Br.-Bl. et Richard 1950 (Braun-Blanquet and Richard 1950: 127). The type association of the *Stipo-Poion xerophilae* Br.-Bl. et Tx. ex Br.-Bl. 1950 is the *Astragalo onobrychidis-Brometum erecti* Br.-Bl. 1950, which – according to Willner et al. (2019) – belongs to the order *Brachypodietalia pinnati* (semi-dry grasslands of western Eurasia). Therefore, the conservation of the name *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 only makes sense if it is, at the same time, conserved with a conserved type reflecting the current use of the order name (see proposal 21*).

(21*) To conserve the name *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 with a conserved type and against *Festucetalia* Soó 1940. Modified version of the proposal by Terzi et al. (2017). Votes: 3 pro, 2 contra (recommended).

(21*) *Festucetalia valesiacae* Braun-Blanquet et Tüxen ex Braun-Blanquet 1950 [Braun-Blanquet 1948–1950, part 3: 312].
Typus cons. propos.: *Festucion valesiacae* Klika 1931: 376.
(=) *Festucetalia* Soó 1940: 32.
Typus: *Festucion rupicolae* Soó 1930 nom. corr. (lectotypus; Terzi et al. 2016).

As discussed above, the strict application of the ICPN leads to the conclusion that the name *Festucetalia valesiacae* Br.-Bl. et Tx. ex Br.-Bl. 1950 is based on an association most likely not belonging to the order as it is currently understood. Therefore, a conserved type has to be chosen. While the authors of the original proposal suggested the legitimate name *Stipo-Poion xerophilae* Br.-Bl. et Richard 1950, based on the *Festuco valesiacae-Caricetum supinae* Br.-Bl. 1936 (lectotypus selected by Terzi et al. 2016), the majority of the CCCN felt that the *Festucion valesiacae* Klika 1931 would be more suitable as conserved type of the order *Festucetalia valesiacae*. The following arguments are put forward for this decision: (1) Braun-Blanquet and Tüxen (1943) obviously derived the order name *Festucetalia valesiacae* from the *Festucion valesiacae* (in fact, the content of that order is identical with the previous, broader concept of the alliance); (2) everyone would expect the *Festucion valesiacae* being the type of the *Festucetalia valesiacae* by looking at the names (indeed, the *Festucion valesiacae* would be the automatic type of the order according to Art. 20 if there were a proper reference to Klika, either in Braun-Blanquet and Tüxen 1943 or in Braun-Blanquet 1948–1950); (3) the name *Festucetalia valesiacae* is attributed to Soó 1947 in the EuroVegChecklist (Mucina et al. 2016), and Soó (1947) referred to Klika's *Festucion valesiacae* as a corresponding name of his *Festucetalia valesiacae*; (4) the remote possibility that the alliance *Festucion valesiacae* ends up in a different order than the *Festucetalia valesiacae* should be excluded.

The alliance names *Festucion valesiacae* Klika 1931 and *Festucion rupicolae* Soó 1930 nom. corr. are currently considered as syntaxonomic synonyms (Mucina et al. 2016: 85). In the same publication it has been suggested that the name *Festucion rupicolae* Soó 1930 nom. corr. should be rejected as *nomen ambiguum*, but no such proposal has been submitted to the CCCN yet. However, conserving the name *Festucetalia valesiacae* with the *Festucion valesiacae* Klika 1931 as conserved type does not necessarily mean that the name *Festucion valesiacae* must be conserved as well or be accepted as the correct name of an alliance. The *Festucion valesiacae* Klika 1931 was lectotypified by Toman (1975) with the *Ranunculo illyrici-Festucetum valesiacae* Klika 1931, and he also selected a type relevé for the latter association (rel. 45).

Author contributions

All authors are members of the CCCN and participated in the evaluation and discussion of the proposals. W.W. planned the Report and wrote the first draft, which was commented and revised by all authors.

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