VEGETATION CLASSIFICATION AND SURVEY

A peer-reviewed open-access journal

1 2020

IAVS

PENSOFT

Vegetation Classification and Survey (VCS)

Chief Editors

Idoia Biurrun
University of the Basque Country UPV/EHU, Bilbao, Spain
idoia.biurrun@ehu.es

Jürgen Dengler
Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland
dr.juergen.dengler@gmail.com

Florian Jansen
University of Rostock, Rostock, Germany
florian.jansen@uni-rostock.de

Wolfgang Willner
University of Vienna, Vienna, Austria
wolfgang.willner@univie.ac.at

Editorial Secretary

Boryana Ovcharova
Pensoft Publishers, Sofia, Bulgaria
phone: +359-2-8704281
fax: +359-2-8704282
e-mail: vcs@pensoft.net

Associate Editors

Federico Fernández-González, Toledo, Spain
Melisa A. Giorgis, Córdoba, Argentina
John Hunter, Armidale, Australia
Flavia Landucci, Brno, Czech Republic
Zdeňka Lososová, Brno, Czech
David W. Roberts, Bozeman, USA
Jozef Šibík, Bratislava, Slovakia
Cindy Q. Tang, Kunming, China
Viktoria Wagner, Edmonton, Canada

Linguistic Editors

Don Faber-Langendoen, Syracuse, USA
Megan J. McNellie, Canberra, Australia
Emmeline Natalie Topp, Göttingen, Germany
Lynda Weekes, Dublin, Ireland
Valerie Whitworth, Winters, USA
Stephen Bell, Callaghan, Australia
Jim Martin, Dublin, Ireland
Michael Glaser, Vienna, Austria

Editorial Board

Miguel Alvarez, Bonn, Germany
Didem Ambarlı, Freising, Germany
Bianca Andrade, Lincoln, USA
Iva Apostolova, Sofia, Bulgaria
Stephen Bell, Callaghan, Australia
Christian Berg, Graz, Austria
Erwin Bergmeier, Göttingen, Germany
Amy L. Breen, Fairbanks, USA
Leslie R. Brown, Vienna, Austria
Jorge Capelo, Oeiras, Portugal
Victor Chepinoga, Novosibirsk, Russia
Heike Culmsee, Göttingen, Germany
Miquel de Cáceres, Solsona, Spain
Panayotis Dimopoulos, Patras, Greece
Romeo Di Pietro, Rome, Italy
Nikolai Ermakov, Russia
Don Faber-Langendoen, Syracuse, USA
Scott Franklin, Greeley, USA
Antonio Galán de Mera, Madrid, Spain
Daniela Gigante, Perugia, Italy
François Gillet, Besançon, France
Riccardo Guarino, Palermo, Italy
Michal Hájek, Brno, Czech Republic
Ute Jandt, Halle, Germany
Monika Janišová, Bratislava, Slovakia
Michael Kessler, Zurich, Switzerland
Zaal Kikvidze, Tbilisi, Georgia
Pavel Krestov, Vladivostok, Russia
Anna Kuzemko, Kyiv, Ukraine
Frank Yonghong Li, Hohhot, China
Javier Loidi, Vizcaya, Spain
Parastoo Mahdavi, Oldenburg, Germany
Yukito Nakamura, Tokyo, Japan
Michael P. Nobis, Birmensdorf, Switzerland
Arkadiusz Nowak, Opole, Poland
Vladimir Gertrudovich Onipchenko, Moscow, Russia
Gwendolyn Peyre, Bogotá, Colombia
Jan Roleček, Brno, Czech Republic
Ute Schmiedel, Hamburg, Germany
Urban Šilc, Ljubljana, Slovenia
Zhiyao Tang, Beijing, China
Ioannis Tsiripidis, Thessaloniki, Greece
Karsten Wesche, Görlitz, Germany

Vegetation Classification and Survey

2020. Volume 1

ISSN: 2683-0671 (online)
Abbreviated keys title: VCS

Cover photos credit
Jürgen Dengler

Vegetation Classification and Survey (VCS)
1 2020

Jansen F, Biurrun I, Dengler J, Willner W
Vegetation classification goes open access 1

Tang CQ, Shen L-Q, Han P-B, Huang D-S, Li S, Li Y-F, Song K, Zhang Z-Y, Yin L-Y, Yin R-H, Xu H-M
Forest characteristics, population structure and growth trends of *Pinus yunnanensis* in Tianchi National Nature Reserve of Yunnan, southwestern China 7

Abutaha MM, El-Khouly AA, Jürgens N, Oldeland J
Plant communities and their environmental drivers on an arid mountain, Gebel Elba, Egypt 21

Hunter JT, Hunter VH
Montane mire vegetation of the New England Tablelands Bioregion of Eastern Australia 37

Zervas D, Tsiripidis I, Bergmeier E, Tsiaoussi V
A phytosociological survey of aquatic vegetation in the main freshwater lakes of Greece 53

Attorre F, Cambria VE, Agrillo E, Alessi N, Alfò M, De Sanctis M, Malatesta L, Sitzia T, Guarino R, Marcenò C, Massimi M, Spada F, Fanelli G
Finite Mixture Model-based classification of a complex vegetation system 77

Zeballos SR, Giorgis MA, Cabido MR, Acosta ATR, Iglesias MR, Cantero JJ
The lowland seasonally dry subtropical forests in central Argentina: vegetation types and a call for conservation 87

Fungomeli M, Githitho A, Frascaroli F, Chidzinga S, Cianciaruso M, Chiarucci A
A new Vegetation-Plot Database for the Coastal Forests of Kenya 103

Hunter JT
Grasslands on Coastal Headlands in New South Wales, south eastern Australia 111

Franklin SB, Scheibout M, Šibik J
Vegetation Classification Exercise for the Pawnee National Grasslands, USA 123

Willner W
What is an alliance? 139

Biurrun I, Willner W
First Report of the European Vegetation Classification Committee (EVCC) 145

Vynokurov D, Didukh Y, Krasova O, Lysenko H, Goncharenko I, Dmytrash-Vatseba I, Chusova O, Shyriaieva D, Kolomiychuk V, Moysiyenko I
Eastern European Steppe Database 149

Vassilev K, Pedashenko H, Alexandrova A, Tashev A, Ganeva A, Gavrilova A, Macanović A, Assenov A, Vitkova A, Genova B, Grigorov B, Gussev C, Masic E, Filipova E, Gecheva G, Aneva I, Knolova I, Nikolov I, Georgiev G, Gogushev G, Tinchev G, Minkov I, Pachedzieva K, Mincheva K, Koev K, Lyubenova M, Dimitrov M, Gumus M, Nazarov M, Apostolova-Stoyanova N, Nikolov N, Velev N, Zhelev P, Glogov P, Natcheva R, Tzonev R, Barudanović S, Kostadinova S, Boch S, Hennekens S, Georgiev S, Stoyanov S, Karakiev T, Ilić T, Kalníková V, Shivarov V, Vulchev V
Balkan Vegetation Database (BVD) – updated information and current status 151

de Ronde I, Haveman R, van der Berg A, van Heusden T
DUMIRA – a management related vegetation plot database of Dutch military ranges 155

Loidi J
The concept of vegetation class and order in phytosociological syntaxonomy 163

Bürger J, Metcalfe H, von Redwitz C, Cirujeda A, Fogliatto S, Fried G, Fu Dostatny D, Glemnitz M, Gerowitt B, González-Andújar JL, Hernández Plaza E, Izquierdo J, Kolářová M, Ņečajeva J, Petit S, Pinke G, Schumacher M, Ulber L, Vidotto F
Arable Weeds and Management in Europe 169

Biurrun I, Font X
SIVIM Floodplain Forests – Database of riverine forests and scrubs from the Iberian Peninsula 171

Campos JA, Mercadé A, Font X
SIVIM Deciduous Forests – Database of deciduous forests from the Iberian Peninsula 173

Fanelli G, Hoda P, Mersinllari M, Mahmutaj E, Attorre F, Farcomeni A, Cambria VE, De Sanctis M
Phytosociological overview of the Fagus and *Corylus* forests in Albania 175

Nowak A, Świerszcz S, Nowak S, Nobis M
Classification of tall-forb vegetation in the Pamir-Alai and western Tian Shan Mountains (Tajikistan and Kyrgyzstan, Middle Asia) 191

Jiménez-Alfaro B, Font X
SIVIM Alpine – Database of high-mountain grasslands in the Iberian Peninsula 219

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 1–6
doi: 10.3897/VCS/2020/53445

EDITORIAL

Vegetation classification goes open access

Florian Jansen[1], Idoia Biurrun[2], Jürgen Dengler[3,4,5], Wolfgang Willner[6]

1 *Landscape Ecology, Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany*
2 *Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain*
3 *Vegetation Ecology, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Wädenswil, Switzerland*
4 *Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany*
5 *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany*
6 *Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria*

Corresponding author: Florian Jansen (florian.jansen@uni-rostock.de)

Academic editor: Wolfgang Willner ♦ **Received** 20 April 2020 ♦ **Accepted** 20 April 2020 ♦ **Published** 4 May 2020

Abstract

With this inaugural editorial, we introduce Vegetation Classification and Survey (VCS), the new gold open access (OA) journal of the International Association for Vegetation Science (IAVS). VCS is devoted to vegetation classification at any spatial and organisational scale and irrespective of the methodological approach. It welcomes equally case studies and broad-scale syntheses as well as conceptual and methodological papers. Two Permanent Collections deal with ecoinformatics (including the standardised Database Reports published in collaboration with GIVD, the Global Index of Vegetation-Plot Databases) and phytosociological nomenclature (edited in collaboration with the respective IAVS Working Group). We discuss the advantages of OA as well as challenges and drawbacks caused by the way it is currently implemented, namely "pay for flaws" and publication impediments for scientists without access to funding. Being a society-owned journal, editorial decisions in VCS are free from economic considerations, while at the same time IAVS offers significant reductions to article processing charges (APCs) for authors with financial constraints. However, it is recognised that sustainable OA publishing will require that payment systems are changed from author-paid APCs to contracts between the science funding agencies and publishers or learned societies, to cover the production costs of journals that meet both quality and impact criteria.

Abbreviations: APC = article processing charge, GIVD = Global Index of Vegetation-Plot Databases, IAVS = International Association for Vegetation Science, JVS = Journal of Vegetation Science, OA = open access, VCS = Vegetation Classification and Survey.

Keywords

article processing charge (APC), double-blind, learned society, open access, open data, peer review, phytosociological nomenclature, science funder, serial crisis, vegetation classification, vegetation-plot database

Introduction

Welcome to the first issue of the new journal Vegetation Classification and Survey (VCS).

After one year of intensive discussion, the Council of the IAVS decided in June 2019 to start VCS as a third association-owned journal, alongside the Journal of Vegetation Science (JVS) and Applied Vegetation Science (AVS), which means that now the whole spectrum of vegetation science is covered by IAVS-owned journals.

The scope of VCS is focused on **vegetation typologies and vegetation classification systems**, their methodological foundation, their development and their application. The journal publishes original papers that develop

PENSOFT.

Copyright *Florian Jansen et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

new typologies as well as applied studies that use such typologies, for example, in vegetation mapping, ecosystem modelling, nature conservation, land use management, or monitoring. We particularly encourage methodological studies that design and compare tools for vegetation classification and mapping, such as algorithms, databases and nomenclatural principles, or are dealing with the conceptual and theoretical bases of vegetation survey and classification. VCS is for the international audience, meaning that large-scale studies are preferred, but regional studies will be considered if they fill important knowledge gaps or are used to develop and present new methods. Apart from "regular" articles, VCS will include two special sections, called "Permanent Collections":

The Collection **Ecoinformatics** invites papers presenting vegetation-plot databases and other ecoinformatics data sources relevant for vegetation classification as well as concepts, methods and tools for using these. VCS has established a formal collaboration with the Global Index of Vegetation-Plot Databases (GIVD; http://www.givd.info) and it will serve as an outlet for reports on GIVD activities, Short Database Reports (1–2 printed pages, no text except abstract, no references) and Long Database Reports (3–15 printed pages). Submissions of Database Reports must be accompanied by a recent Fact Sheet from the GIVD website.

The Collection **Phytosociological Nomenclature** focuses on nomenclature issues for syntaxa. We encourage comprehensive nomenclatural revisions of major syntaxa, analyses of nomenclatural problems related with the names of wide-spread high-rank syntaxa as well as Forum Papers on general nomenclatural issues that are of interest to an international readership. Further, official documents issued by the Working Group for Phytosociological Nomenclature (GPN) of the IAVS, such as Reports, Decisions and Proposals, will be published in this section.

It has certainly not gone unnoticed that the editorial team of VCS is largely identical with the one that has been responsible for Phytocoenologia during the last five years (Jansen et al. 2016; Biurrun et al. 2019). The reasons why we and IAVS decided to start a new journal with a new publisher are manifold. The situation resembles the launch of JVS in 1990. Indeed, the words of Eddy van der Maarel in the inaugural editorial of JVS (referring to the journal Vegetatio, now Plant Ecology), could equally be applied to summarise our own decision: "not only did IAVS as a society lack a real influence on the journal, [...] the journal became a luxury for libraries in rich countries" (van der Maarel 1990). We hope that you as readers and authors will now follow us into a successful future of academic exchange and development. We, the Chief Editors of the old and the new journal, are excited about the new possibilities and we hope for your support. In particular, we want to thank the members of our very diverse editorial team. Representatives from many regions of the world have agreed to support the journal and will guarantee an unprecedented level of expertise to cover research on vegetation from all around the globe.

Together with the new journal title and the new publisher, we also decided to implement some additional major changes. The most important ones are to go **open access** and to introduce **double-blind peer review**.

Open research

It is acknowledged that research which is freely available has a greater impact than research hidden behind a payment wall (Antelman 2004), benefiting science by accelerating dissemination and the uptake of research findings (Eysenbach 2006), especially for developing countries (Evans and Reimer 2009). Other academic, economic or societal benefits of an open research approach have been identified (Tennant et al. 2016) and as part of this approach the availability of primary data is recognised as being crucial for the reproducibility of analyses (Reichman et al. 2011) and must be encouraged.

The development of the Internet and how it redefined communication and publishing has been the main driver of the open access (OA) movement (Laakso et al. 2011). Making printed versions of articles obsolete, the costs per research article theoretically should have decreased as a result of not investing material resources in publication printing and distribution. Instead, the subscription prices within the traditional publishing model have increased steadily, enabled by the inelastic demand for finding prestigious publication venues for authors.

The way towards open access

The resulting OA initiatives have led to "gold open access" venues, these are journals that solely publish open-access papers with the costs of publishing either marginalised by the publication work being undertaken on an unpaid voluntarily basis or paid for by the authors via APCs. At present, however, "green open access" (i.e., the publication of accepted but unformatted articles on personal webpages), and "hybrid" models are still more common. The latter have become standard in most traditional journals. Hybrid OA means that additional to the normal subscription fee for a journal, individual papers can be paid-off from the pay wall restrictions but in most cases without a reduction of the journal subscription fee. This effectively means "double dipping" for the publisher (Cheung 2015), making it attractive within traditional business models, but without generating momentum for a general shift towards OA. Therefore, such hybrid models have been excluded from the OA payment regulations of many science funding institutions.

The biggest challenge of OA is located outside of science and is a problem of financial cash flow. As exemplified in Geschuhn (2015) there probably is enough money in the system to cover all costs of OA publishing. Publication costs are much more transparent in OA than in traditional subscription models and average costs have

been estimated to be much lower. For 2015, a global expenditure of at least EUR 7.6 billion, mostly in the form of subscription fees, and a production of 1.5 to 2 million papers has been calculated, resulting in an allocation per article of EUR 3,800 to 5,000 (Geschuhn 2015). This money would need to be transferred from subscription fees paid by libraries (mainly for huge bundles of journals from a small number of mega-publishers) to the APCs for OA papers. Only if the money is re-purposed from subscription fees to individual or bundled APCs, transforming the underlying business model for publishers and overcoming the "serial crisis" (McGuigan and Russell 2008), will OA be as disruptive as predicted. Until recently the most target-oriented step has been the introduction of "offsetting" models instead of hybrid approaches. Offsetting means that for every OA article the subscription fee for the journal is effectively reduced, making the transition between subscription and pre-publication business models transparent and flexible.

A widely perceived step towards a complete transition to OA was the so-called project DEAL between German science organisations and major global publishers in 2019 and 2020 (Wiley and MPDL Services 2019; Springer-Nature and MPDL Services 2020). The core objective of this deal is open access to all research articles written by corresponding authors based at German science institutions, while paying for such services with a model based on the number of articles published by the institution. If this model could be adopted in more countries, it could become a very powerful driver for a fast shift to OA, because in this scenario APCs do not have to be covered by the authors of a paper but are being be paid by a country's research institutions.

Challenges of open access

While in the initial phase of the OA movement a broad believe was predominant among scientists, librarians, and science funders that "gold open access" would be the solution to many of the problems of the traditional subscription journal system, nowadays scientists are often disillusioned by how OA is implemented in practice:

Firstly, gold open access often only transfers the barriers from one place to another. While published science in an OA world is accessible to everybody, it does depend on the financial capabilities of authors and their institutions whether a relevant piece of science is published or not; as long as it is based on APCs and no non-discriminatory refunding mechanism exists. In the traditional publication system, libraries in rich countries subsidize the production of high-quality journals and good scientific work is accepted irrespective of the origin and financial capabilities of the authors. Getting access to a published non-OA article, even if your own library has not subscribed, is in practice much easier than securing funds for your own OA manuscript. In fact, APCs are not only prohibitive for authors from developing countries, but also for many authors in rich countries who are not associated with large scientific institutions.

Secondly, it has been widely perceived in the scientific community that a business model that is built on APCs might jeopardize the quality of scientific journals. Generally, APCs incentivize quantity rather than quality: the more articles are published, the more revenue is generated by the publisher, at least in the short to medium term. Accordingly, many new OA publishers have been established promising faster and higher acceptance rates. In order to ensure this promise, it is often the employees of the publisher, instead of respected and independent scientists, that make editorial decisions. However, also traditional scientific publishers have opened new low-profile OA journals to which they redirect those articles that did not reach the standards required for acceptance in their own high-profile subscription journals. We call this a "pay for flaws" model. It should also be recognised that there are still hardly any top-tier journals among the gold OA journals, neither in ecology nor in multidisciplinary sciences.

Ways to overcome the challenges

They are far from trivial, but there are ways out of this labyrinth. Science funders should not pay gold OA fees independent of the journal's quality, but should look more closely into editorial practices and base payment on the average quality of the outcome (e.g., citation rates). Editors have to be independent and not employees of the publisher. Usually reviewers and editors have made a big contribution to the quality of an article before it reaches the scientific public and there must be no incentives or pressure to shortcut this process. Journals that violate such ethical standards must be excluded from receiving APCs paid from public money. Moreover, for those journals meeting specific quality standards funding agencies should cover different levels of cost depending on the quality level of the journal, for example by setting different thresholds depending on the impact quantile of the respective discipline to which the journal belongs.

Science funders also need to nurture science as a whole, not only those scientists employed at high-profile institutions within their own country. Gold OA will only work properly when we overcome the current situation of individual APCs paid by authors and replace this with payments from consortia of science funders and institutions to publishers or learned societies, to produce high-quality gold OA journals.

The role of learned societies

Learned societies have always played a major role in scientific publishing. The first scholarly journals were founded by learned societies such as the Philosophical

Transactions by the Royal Society of London in 1665. Learned societies will also play an indispensable role in the transition to OA, fostering scientific excellence beyond economic stimulus. Currently, however, the incentives for learned societies are detrimental to OA as they are paid by publishers for the journals published under their name and editorial team, as is the case for the two long-standing IAVS journals. This is often the predominant source of income for a society which in turn is used to fund scientific activities, such as grants and prizes for young scientists or discounts on conference fees for participants with financial constraints. On the other hand, membership is coupled with discounts on journal subscription fees, which is often the major incentive to become a society member. At least the latter can be replaced by switching from an incentive for readers to incentives for authors by reducing the APCs, as is done by the IAVS in the form of a 10% discount for VCS for IAVS members.

How VCS addresses the challenges

We Chief Editors fully support the open research philosophy. However, we also see the drawbacks of the current implementation of OA for science in general and the problems that APC OA causes for many of our authors.

As VCS is owned by a respected scientific association, which controls the publication policy and appoints the Chief Editors, full economic independence from the publisher is guaranteed. This means that we do not promise that the acceptance of an article in our journal will be fast or the revisions easy. However, both authors and readers can trust on the quality of all articles when they are published.

It is important that authors consider the bigger picture if confronted with an APC bill. The whole scientific community is asked to work within sustainable financing and it should be recognised that the IAVS will do its best to distribute financial burdens fairly, by offering reductions and waivers for authors until more countries find solutions to refund the cost of pre-publication fees. Authors should discuss with co-authors the best solution for your manuscript. If in doubt, please contact the editors. The distribution of good scientific research should not be hindered by financial obstacles!

You can find the current APCs for VCS, set by the IAVS Publication Committee, at https://vcs.pensoft.net/about#Article-Processing-Charges. The comparatively low base price is further reduced for IAVS members, Editorial Board members, authors from countries with low income or with financial hardship. Please talk to your research institution about possibilities for refunding the costs. An increasing number of institutions and funding agencies are happy to cover the costs for gold open access journals such as VCS, knowing that in the long term this is an opportunity to move away from the serial crisis of traditional subscription pricing. We hope that the science funding bodies will recognise the opportunities that learned societies like the IAVS and medium-sized publishers such as Pensoft offer and consider implementing similar deals to the ones they have struck with some mega-publishers.

Open data

As important as open access to scientific articles is the access to the underlying data. In the last decade, we have seen how the availability of vegetation-plot data at the national (see Dengler et al. 2011) and international level (Chytrý et al. 2016; Dengler et al. 2018; Bruelheide et al. 2019) has fostered cooperation and enabled completely new avenues of research (Bruelheide et al. 2018; Dengler et al. 2020). Hoewever, for vegetation classification there is still much progress to be made. Many of the analytical methods utilised in the production of classifications can generate unstable results, as they are highly dependent on small parts of the input data. The availability of primary data is an indispensable requirement for the reproducibility of ecological research (Reichman et al. 2011).

VCS expects that data will be archived, if possible, in an appropriate public repository or in electronic Supplementary Information connected to the paper. The authors should make a statement of where the primary data are stored. If they are archived in a public repository, a reference to a DOI (digital object identifier) or permanent URL (uniform resource locator) should be provided. If the paper uses data from large multi-contributor databases such as sPlot, EVA (European Vegetation Archive) or TRY, which cannot be made publicly available because of the third-party ownership issues, the data selection released for the study should be stored in a permanent repository and made available for re-analyses upon request. As Chief Editors of VCS we are interested in making all underlying data permanently available to the scientific public on platforms where the data are easily located and in formats that preserve the rich and complex information that is contained within vegetation data. You can expect us, together with related journals, to spearhead the development of new approaches that will improve on the current scattered and inconsistent solutions.

Double-blind

The second significant change the editorial team have implemented, compared to our predecessor journal, regards the peer review system. Following other journals like Global Ecology and Biogeography, we now have a double-blind review system where not only the reviewers are unknown to the authors but also the other way round (i.e., the authors are unknown to the reviewers).

The discussion whether single-blind reviews discriminate specific authors based on their affiliation, gender and seniority is controversial and the findings context-dependent (Snodgrass 2006; Budden et al. 2008; Webb et al. 2008). However, whether a paper is accepted for publica-

tion should be made on the basis of the manuscript alone: Are the methods correct, the conclusions substantiated by the results and overall does the contribution advance science? It should not be dependent on circumstances such as who wrote the paper or the professional affiliations of the authors. We have experienced that biases in both directions can occur, whether manuscripts from young, female authors from developing countries are assessed over-critically compared to those from senior, well-known male authors, or the other way around are just waved through despite obvious weaknesses. By introducing double-blind peer review, we want to contribute our part to reducing such biases where they might exist. We are well aware that sometimes authors can be guessed from the manuscript content, but this does not make the approach invalid. Beyond double-blind reviews we will always try to do our best to be fair to all authors, fairness to unknown authors or institutions, fairness to prolific or to less-published authors, as well as gender equity.

The first papers of VCS

This Editorial goes online together with a group of papers, covering five continents and much of the journal's research spectrum. A study from China examines *Pinus yunnanensis* forests, a commercially, culturally and economically important tree of south-western China (Tang et al. 2020). We would like to see more vegetation studies from this species-rich region, from both natural and anthropogenically influenced vegetation types. Hunter and Hunter (2020) report on montane mire vegetation from the New England Tablelands Bioregion in Australia and how it fits into previous classifications. Zeballos et al. (2020) classify dry subtropical forests in the Espinal province, Argentina, using vegetation plots, and call for their urgent conservation. Abutaha et al. (2020) describe the plant communities and their environmental drivers on Gebel Elba, Egypt. Finally, Zervas et al. (2020) present a phytosociological survey of aquatic vegetation in the main freshwater lakes of Greece.

Classification methods in VCS are not limited to any specific approach. This is exemplified by the selection of papers published together with the Editorial. They range from phytosociology (Guarino et al. 2018) to the EcoVeg approach (Faber-Langendoen et al. 2014) and we hope to see many more approaches together with papers that try to unify different approaches. As explained in our scope (see Introduction), we also appreciate methodological papers, such as the one from Attorre et al. (2020), who compare finite mixture models to a more traditional classification method. Such comparisons are fundamental to advance our toolbox for vegetation classification and survey.

Author contributions

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

Acknowledgements

We thank James Martin for linguistic editing.

References

Abutaha M, Elkhouly A, Jürgens N, Oldeland J (2020) Plant communities and their environmental drivers on an arid mountain, Gebel Elba, Egypt. Vegetation Classification and Survey 1: 21–36. https://doi.org/10.3897/VCS/2020/38644

Antelman K (2004) Do open-access articles have a greater research impact? College & Research Libraries 65: 372–382. https://doi.org/10.5860/crl.65.5.372

Attorre F, Cambria VE, Agrillo E, Alessi N, Alfò M, De Sanctis M, Malatesta L, Sitzia T, Guarino R, … Fanelli G (2020) Finite Mixture Model based classification of a complex vegetation system using a large dataset. Vegetation Classification and Survey 1: 77–86. https://doi.org/10.3897/VCS/2020/48518

Biurrun I, Bergmeier E, Dengler J, Jansen F, Willner W (2019) Vegetation classification and its application are relevant globally. Phytocoenologia 49: 1–6. https://doi.org/10.1127/phyto/2019/0323

Bruelheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM, Botta-Dukát Z, Chytrý M, Field R, … Jandt U (2018) Global trait-environment relationships of plant communities. Nature Ecology & Evolution 2: 1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Bruelheide H, Dengler J, Jiménez-Alfaro B, Purschke O, Hennekens SM, Chytrý M, Pillar VD, Jansen F, Kattge J, … Zverev A (2019) sPlot – a new tool for global vegetation analyses. Journal of Vegetation Science 30: 161–186. https://doi.org/10.1111/jvs.12710

Budden A, Tregenza T, Aarssen L, Koricheva J, Leimu R, Lortie C (2008) Double-blind review favours increased representation of female authors. Trends in Ecology & Evolution 23: 4–6. https://doi.org/10.1016/j.tree.2007.07.008

Cheung M (2015) The costs of double dipping. Research Libraries, UK. https://www.rluk.ac.uk/the-costs-of-double-dipping [accessed 25 Mar 2020]

Chytrý M, Hennekens SM, Jiménez-Alfaro B, Knollová I, Dengler J, Jansen F, Landucci F, Schaminée JHJ, Aćić S, … Yamalov S (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. Applied Vegetation Science 19: 173–180. https://doi.org/10.1111/avsc.12191

Dengler J, Jansen F, Glöckler F, Peet RK, De Cáceres M, Chytrý M, Ewald J, Oldeland J, Lopez-Gonzalez G, … Spencer N (2011) The Global Index of Vegetation-Plot Databases (GIVD): A new resource for vegetation science. Journal of Vegetation Science 22: 582–597. https://doi.org/10.1111/j.1654-1103.2011.01265.x

Dengler J, Wagner V, Dembicz I, García-Mijangos I, Naqinezhad A, Boch S, Chiarucci A, Conradi T, Filibeck G, … Biurrun I (2018) GrassPlot – a database of multi-scale plant diversity in Palaearctic grasslands. Phytocoenologia 48: 331–347. https://doi.org/10.1127/phyto/2018/0267

Dengler J, Matthews TJ, Steinbauer MJ, Wolfrum S, Boch S, Chiarucci A, Conradi T, Dembicz I, Marcenò C, … Biurrun I (2020) Spe-

cies-area relationships in continuous vegetation: Evidence from Palaearctic grasslands. Journal of Biogeography 60: 72–86. https://doi.org/10.1111/jbi.13697

Evans JA, Reimer J (2009) Open access and global participation in science. Science 323: 1025–1025. https://doi.org/10.1126/science.1154562

Eysenbach G (2006) Citation advantage of open access articles. PLoS Biology 4: e157. https://doi.org/10.1371/journal.pbio.0040157

Faber-Langendoen D, Keeler-Wolf T, Meidinger D, Tart D, Hoagland B, Josse C, Navarro G, Ponomarenko S, Saucier JP, … Comer P (2014) EcoVeg: a new approach to vegetation description and classification. Ecological Monographs 84: 533–561. https://doi.org/10.1890/13-2334.1

Geschuhn K (2015) Disrupting the subscription journals' business model for the necessary large-scale transformation to open access: A Max Planck Digital Library Open Access Policy White Paper. SciencesOpen Research. [accessed 25 Mar 2020] https://doi.org/10.14293/S2199-1006.1.SOR-EDU.AJRG23.v1

Guarino R, Willner W, Pignatti S, Attorre F, Loidi J (2018) Spatio-temporal variations in the application of the Braun-Blanquet approach in Europe. Phytocoenologia 48: 239–250. https://doi.org/10.1127/phyto/2017/0181

Hunter JT, Hunter VH (2020) Montane mire vegetation of the New England Tablelands Bioregion of Eastern Australia. Vegetation Classification and Survey 1: 37–51. https://doi.org/10.3897/VCS/2020/48765

Jansen F, Bergmeier E, Dengler J, Janišová M, Krestov P, Willner W (2016) Vegetation classification: A task of our time. Phytocoenologia 46: 1–4. https://doi.org/10.1127/phyto/2016/0134

Laakso M, Welling P, Bukvova H, Nyman L, Björk BC, Hedlund T (2011) The development of open access journal publishing from 1993 to 2009. PLoS ONE 6: e20961. https://doi.org/10.1371/journal.pone.0020961

McGuigan GS, Russell RD (2008) The business of academic publishing: a strategic analysis of the academic journal publishing industry and its impact on the future of scholarly publishing. Electronic Journal of Academic and Special Librarianship. http://southernlibrarianship.icaap.org/content/v09n03/mcguigan_g01.html [accessed 25 March 2020]

Reichman OJ, Jones MB, Schildhauer MP (2011) Challenges and opportunities of open data in ecology. Science 331: 703–705. https://doi.org/10.1126/science.1197962

Snodgrass R (2006) Single- versus double-blind reviewing: An analysis of the literature. ACM SIGMOD Record 35: 8–21. https://doi.org/10.1145/1168092.1168094

Springer Nature, MPDL Services (2020) Publish and Read Agreement Projekt DEAL and Springer Nature. https://doi.org/10.17617/2.3174351

Tang CQ, Shen LQ, Han PB, Huang DS, Li S, Li YF, Song K, Zhang ZY, Yin LY, … Xu HM (2020) Forest characteristics, population structure and growth trends of *Pinus yunnanensis* in Tianchi National Nature Reserve of Yunnan, southwestern China. Vegetation Classification and Survey 1: 7–20. https://doi.org/10.3897/VCS/2020/37980

Tennant JP, Waldner F, Jacques DC, Masuzzo P, Collister LB, Hartgerink, CHJ (2016) The academic, economic and societal impacts of Open Access: An evidence-based review. F1000Research 5: 1–54. https://doi.org/10.12688/f1000research.8460.3

van der Maarel E (1990) The Journal of Vegetation Science – a journal for all vegetation scientists. Journal of Vegetation Science 1: 1–4. https://doi.org/10.1111/j.1654-1103.1999.tb00576.x

Webb TJ, O'Hara B, Freckleton RP (2008) Does double-blind review benefit female authors? Trends in Ecology & Evolution 23: 351–353. https://doi.org/10.1016/j.tree.2008.03.003

Wiley, MPDL Services (2019) Publish and Access Agreement Projekt DEAL and Wiley. https://www.projekt-deal.de/about-deal [accessed 25 March 2020]

Zeballos S, Giorgis M, Cabido M, Acosta A, Iglesias MR, Cantero J (2020) The southern extreme of seasonally dry subtropical forests in South America: Vegetation types and a call for conservation. Vegetation Classification and Survey 1: 87–102. https://doi.org/10.3897/VCS/2020/38013

Zervas D, Tsiripidis I, Bergmeier E, Tsiaoussi V (2020) A phytosociological survey of aquatic vegetation in the main freshwater lakes of Greece. Vegetation Classification and Survey 1: 53–75. https://doi.org/10.3897/VCS/2020/48377

E-mail and ORCID

Florian Jansen (Corresponding author, florian.jansen@uni-rostock.de), ORCID: https://orcid.org/0000-0002-0331-5185
Idoia Biurrun (idoia.biurrun@ehu.eus), ORCID: https://orcid.org/0000-0002-1454-0433
Jürgen Dengler (juergen.dengler@uni-bayreuth.de), ORCID: https://orcid.org/0000-0003-3221-660X
Wolfgang Willner (wolfgang.willner@univie.ac.at), ORCID: https://orcid.org/0000-0003-1591-8386

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 7–20
doi: 10.3897/VCS/2020/37980

RESEARCH PAPER

Forest characteristics, population structure and growth trends of *Pinus yunnanensis* in Tianchi National Nature Reserve of Yunnan, southwestern China

Cindy Q. Tang[1], Li-Qin Shen[1], Peng-Bin Han[1], Diao-Shun Huang[1], Shuaifeng Li[2], Yun-Fang Li[3], Kun Song[4], Zhi-Ying Zhang[1], Long-Yun Yin[5], Rui-He Yin[5], Hui-Ming Xu[5]

1 *Institute of Ecology and Geobotany, College of Ecology and Environmental Science, Yunnan University, Yunnan, China*
2 *Research Institute of Resource Insects, Chinese Academy of Forestry, Yunnan, China*
3 *Forest Station of Yunlong Forestry Bureau, Yunnan, China*
4 *School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China*
5 *Management Office of Tianchi National Nature Reserve, Yunnan, China*

Corresponding author: Cindy Q. Tang (cindyqtang@aol.com); Shuaifeng Li (12704391@qq.com)

Academic editor: David W. Roberts ♦ **Received** 4 July 2019 ♦ **Accepted** 1 September 2019 ♦ **Published** 4 May 2020

Abstract

Aims: *Pinus yunnanesis* is commercially, culturally and economically important, but there is a lack of ecological data on its role in stand dynamics. Our aims are to clarify the structure, composition, regeneration and growth trends of primary mature *P. yunnanensis* forests. **Study area:** The Tianchi National Nature Reserve in the Xuepan Mountains, Yunlong County, northwestern Yunnan, China. **Methods**: We investigated forests containing *P. yunnanensis*, measured tree ages and analyzed the data. **Results:** Six forest types were identified: (1) coniferous forest: *Pinus yunnanensis* (Type 1); (2) mixed coniferous and evergreen broad-leaved forest: *P. yunnanensis-Lithocarpus variolosus* (Type 2); (3) mixed coniferous and deciduous broad-leaved forest: *P. yunnanensis-Quercus griffithii* (Type 3); (4) mixed evergreen broad-leaved and coniferous forest: *Castanopsis orthacantha-P. yunnanensis-Schima argentea* (Type 4); (5) mixed coniferous, evergreen and deciduous broad-leaved forest: *Pinus yunnanensis-Schima argentea-Quercus griffithii* (Type 5); (6) mixed coniferous and evergreen broad-leaved forest: *Pinus armandii-Quercus rehderiana-Pinus yunnanensis* (Type 6). The size- and age-structure and regeneration patterns of *P. yunnanensis* were highly variable within these six forest types. *P. yunnanensis* regeneration was well balanced in forest Type 1 as compared to the other five types. All six forest types were identified as rare and old-growth with *P. yunnaensis* trees reaching ages of more than 105 years (a maximum age of 165 years with a diameter 116 cm at breast height) except for the Type 4 forest (a 90-year-old stand). Growth rates of *P. yunnanensis*, based upon ring width measurements, were high for the first 10 years, then declined after the 10th year. In contrast, basal area increment (BAI) increased for the first 25 years, plateaued, and only declined as trees became older. Trees in the older age classes grew more quickly than younger trees at the same age, a consequence of either site quality or competitive differences. The BAI of *P. yunnanensis* in all age classes in the Tianchi National Nature Reserve was much higher than those of the secondary and degraded natural *P. yunnanensis* forests of other areas. **Conclusions:** The *P. yunnanensis* forests of the Tianchi area appear to be some of the last remnants of primeval and old-growth forests of this species. These forests are structurally diverse and contain a rich diversity of overstory, mid-story, and understory species.

Taxonomic reference: Editorial Committee of Flora Republicae Popularis Sinicae (1959–2004) for vascular plants.

Abbreviations: BA = basal area; BAI = basal area increment; DBH = diameter at breast height; H = height; RBA = relative basal area.

PENSOFT.

Copyright *Cindy Q. Tang et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Keywords

Age-class, basal area increment, forest stratification, growth rate, old-growth forest, regeneration pattern, species diversity

Introduction

In East Asia, warm-temperate pines (e.g., *Pinus yunnanensis, P. kesiya, P. massoniana, P. taiwanensis, P. roxburghii, P. thunbergii*) grow mainly at low to mid-high elevations on dry or humid mountain slopes, cliffs, rock barrens, or ridges. They also grow in valleys and on disturbed sites in subtropical and warm-temperate areas. Temperate/cold-temperate pines (e.g., *P. densata*, *P. wallichiana*, *P. pumila*) occur at high elevations or in cold locations, being able to withstand cold and snow. Warm-temperate species of *Pinus* often form a mosaic of stand structures across the landscape of subtropical China (Tang 2015). *P. yunnanensis* (Yunnan pine) is native to subtropical southwestern China at 400–3,100 m above sea level (m a.s.l.), but mainly between 1,600–2,900 m ranging 23°–30°N and 96°–108°E (Jin and Peng 2004; Chen et al. 2012; http://www.eFloras.org). The more northern ecological partner, *Pinus tabuliformis,* is widely distributed at 100–2,600 m ranging 31°N–44°N, 101°30'E–124°25'E in temperate areas of China and Korea. The southern ecological partner, *Pinus kesiya,* is found at mainly 700–1,800 m in southeastern Tibet, southern Yunnan, northeastern India, Laos, Myanmar, Philippines, Thailand, Vietnam (Xu 1990; Wen et al. 2010; http://www.eFloras.org). In many localities *P. yunnanensis* occurs in almost pure stands. In the subtropical zone, *P. yunnanensis* is often found in early or intermediate-successional stands after destruction of the evergreen broad-leaved forest by human activities or after forest fires (Tang 2015). In general forest stands of *P. yunnanensis* present a young age structure (Wang et al. 2018). Old-growth or primary mature *P. yunnanensis* forests are now confined to a very few nature reserves in Yunnan and southeastern Tibet.

P. yunnanesis is commercially (resin and timber), culturally and economically important, but there is a lack of ecological data on its role in succession and stand dynamics. There are studies on *P. yunnanensis* community succession after fire (Tang et al. 2013), seed germination following fire (Su et al. 2017), seedling growth under experimental conditions (Cai et al. 2016), regeneration in plantations (Wang et al. 2017), secondary growth forests, degraded and restored forests in central Yunnan (e.g., Chen and An 1993; Peng et al. 2005, 2012; Shi et al. 2009; Yang 2010), as well as its genetics (e.g., Yu et al. 2000; Xu et al. 2011; Wang et al. 2013). However, studies of forest stand characteristics including species diversity, size and age structure, as well as growth rates of the old-growth *P. yunnanensis* forest are not available. Li et al. (2007) identified a *P. yunnanensis* forest in Yongren, central Yunnan as an old-growth forest with trees having a maximum DBH of 48 cm and a corresponding age of 257 years, but they did not provide data on ring width and did not explain how they collected age data. In addition, no information regarding stand characteristics was provided. An understanding of forest features and population structure of old-growth forests is crucial for gene bank and biodiversity conservation.

The Tianchi National Nature Reserve of Yunnan is designated to protect old-growth and primary mature forests dominated by *P. yunnanensis*. The Reserve affords a unique opportunity to study *P. yunnanensis* over a wide range of elevations, forest types, and age classes, including old-growth forest stands. We address the following questions: What are the structural features of forests containing *P. yunnanensis* in the Tianchi National Nature Reserve? What are the population structure and regeneration patterns of this species? What are the growth trends in the study area based upon ring area and width data?

Methods

Study area

The Tianchi National Nature Reserve is located in the subtropical zone of Yunnan between an elevation range of 2,100 to 3,226 m The Reserve includes Tianchi and Longmashan areas in the Xuepan Mountains, Yunlong County, northwestern Yunnan, China (Figures 1a, b).

The mountain slopes of our study area have the red or yellow-reddish soil in 2,100–2,300 m elevation zone, the yellow-brown soil in 2,300–2,700 m zone and the brown soil in 2,700–3,200 m zone (Su et al. 2013). The water content of surface soil is 16.7% on average, ranging from 9.6% to 21.4% at 2,500–2,700 m (Jin and Peng 2004). It is characterized by a subtropical, humid climate that is largely controlled by the summer monsoon of India and the East Asian summer monsoon. The temperature lapse rate with elevation is 0.56 °C /100 m (Su and Wang 2013). The mean annual temperature is 13.8 °C at 2,000 m and 7.1 °C at 3,200 m with a warm month mean of 19.7 °C at 2,000 m and 13.4 °C at 3,200 m in June and a cold month mean of 6.5 °C at 2,000 m and 0.3°C at 3,200 m in January. The mean annual precipitation is 975.1 mm at 2,000 m and 1,313.5 mm at 3,200 m, of which about 80% falls between March and October. The monthly relative humidity is greater than 85%.

Study species

The focal species of this study is *P. yunnanensis* (Figures 2a–e). *P. yunnanensis* is an evergreen coniferous species that can grow to mature heights over 30 m, or assume shrub-like forms in extremely dry habitats. Needles are 2 or 3 per bundle. Seed cones shortly pedunculate, green,

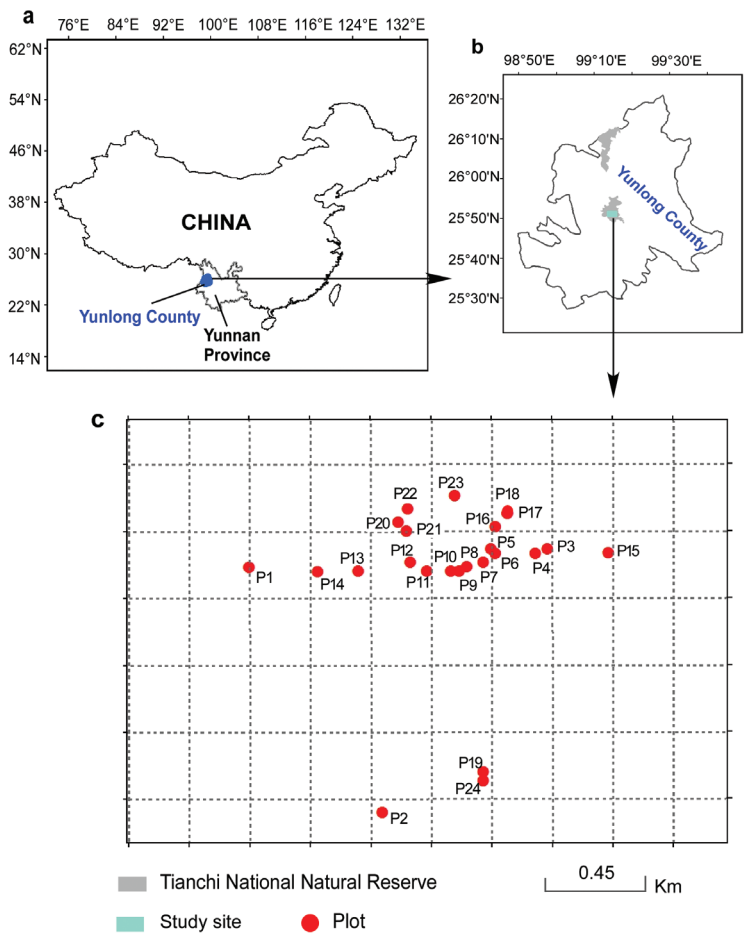

Figure 1. The study area. (a) Yunlong County in northwestern Yunnan. (b) The Tianchi National Nature Reserve in Yunlong County. (c) Plots located in the Tianchi National Nature Reserve.

maturing to brown or chestnut brown. Seeds with membranous wings are anemophilous (wind-dispersed). *P. yunnanensis* is a light-demanding species. It appears to be drought resistant, but requires forest gaps or disturbances to regenerate. Its distribution center is located on the plateau of Yunnan, also extending east into western Guizhou, northeast into western and southwestern Sichuan, south into southern Yunnan, southeast into western Guangxi, and northwest into southeastern Tibet, China.

Data collection and analysis

The forests in the study area are subjected to a range of natural and anthropogenic factors (such as elevations, topography, natural disturbances and human activities) thus, are structurally and floristically heterogeneous and the landscape pattern of vegetation is small mosaic patches. We selected plots in each patch containing *P. yunnanensis* in the study area. During July-August 2017, we established 24 plots containing *P. yunnanensis* between 2,530 and 3,100 m in this specific area of the Reserve (25˚49'48"–25˚57'70"N, 99˚13'14"–99˚20'34"E) (Figure 1c). The plots were established in the locations depending on access. The plot size varied between 20 m × 20 m to 40 m × 30 m where plot size depended on the size of the patch. Patch size was determined by species composition and topographic similarity. General information was noted including slope positions, altitude, slope exposure, slope inclination, and disturbance history.

Tree stems were classified into four classes based on their vertical position, crown position, and height: emergent layer (H ≥ 28 m tall), canopy (20 m ≤ H < 28 m tall), subcanopy (8 m ≤ H < 20 m tall), and shrub layer (1.3 m ≤ H < 8 m tall). For all individuals greater than 1.3 m tall, DBH was used to calculate basal area and then basal area (BA) for each species found in a plot could be determined.

Understory woody species less than 1.3 m tall were divided into two classes: (1) 5 cm ≤ H < 50 cm tall for seedlings and (2) 50 cm ≤ H < 130 cm for saplings. Within these two classes, each individual was identified, counted, and measured for height and percentage foliage cover. For the species in each plot, all individuals at least 1.3 m in height were identified to species level, numbered and tagged, noted whether healthy, unhealthy, or dead.

We obtained 71 increment cores from *P. yunnanensis* trees of varying DBHs in the study area. For each tree trunk, a single increment core was taken from at 1 m above ground level. The length of time from the position at 1 m in height to ground level was estimated to be nine years

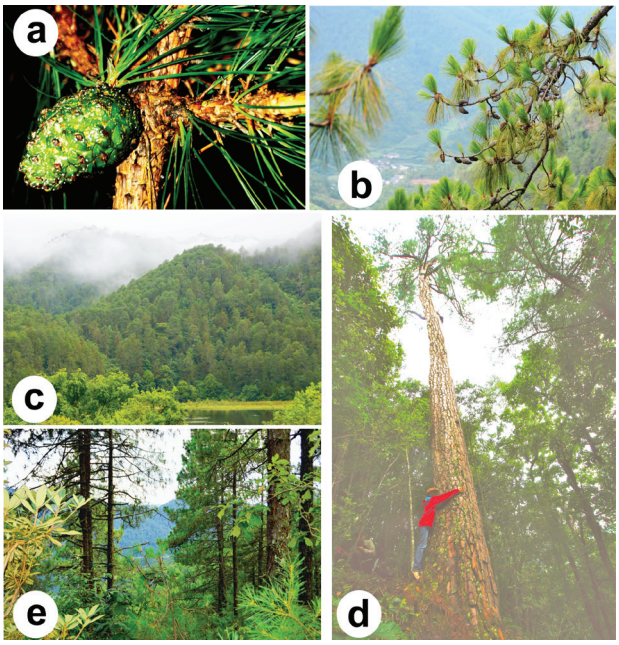

Figure 2. *Pinus yunnanensis* and its forest in the Tianchi National Nature Reserve. (a) Three needles per bundle and a seed cone of *P. yunnanensis*. (b) Branches with foliage and seed cones of *P. yunnanensis*. (c) The *P. yunnanensis* forest. (d) A *P. yunnanensis* tree with 33 m tall and 116 cm DBH. (e) Saplings of *P. yunnanensis* in a canopy gap.

based on field observations. The nine years was added to the data of ages we obtained from each increment core. For comparison, we also obtained 61 increment cores of *P. yunnanensis* from naturally regenerated secondary forests of Kunming and Yongren, central Yunnan. Tree age was determined using the software WinDENRO tree ring analysis system. From this analysis, we were also able to determine ring widths and to calculate basal area increments (BAI). The following formula was used to calculate BAI: X-(X-1) where X is the basal area at year X (last year of growth) and X-1 is the basal area of the tree measured up to the year previous to X. BAI is used in forest growth studies because it accurately quantifies wood production based on the ever-increasing diameter of a growing tree (Rubino and McCarthy 2000).

In each plot, the relative basal area (RBA, %) of each species was used as a measure of abundance of the species. Plant communities were classified using a floristic similarity dendrogram with Relative Sørensen and Group Average clustering [PCORD software (McCune and Mefford 1999)].

Dominance was determined using a dominance analysis according to the RBA of each species (Ohsawa 1984). The communities were named according to dominant species.

Diversity was calculated for each forest stand using species richness (number of species), the Shannon-Wiener's diversity index (Shannon-Wiener index) (Pielou 1969) and Simpson's diversity index (Simpson index) (Lande 1996). The measurement unit bit (logarithm bases 2) for Shannon-Wiener index was used. The proportion of total number of individuals was applied for calculating the diversity indices. Differences in species richness and diversity indices among habitats were analyzed by the non-parametric Kruskal-Wallis all-pairwise comparisons test, using Analyze-it Software (https://analyse-it.com; 2009). In order to examine tree growth in *P. yunnanensis* over time across all age classes both ring width (mm) and BAI (mm^2) were used.

Results

Forest types, stratification and species diversity

From our 2017 vegetation study, six distinct forest communities (at the 62% floristic similarity threshold) were classified according to the floristic similarity dendrogram (Figure 3a). These were: (1) Type 1: coniferous *P. yunnanensis* forest distributed in valley bottoms, slopes and ridges at elevations of 2,570–2,990 m; (2) Type 2: coniferous *P. yunnanensis* and evergreen broad-leaved *Lithocarpus variolosus* mixed forest distributed in mid slopes at elevations 2,680–2,760 m; (3) Type 3: coniferous *P. yunnanensis* and deciduous broad-leaved *Quercus griffithii* mixed forest distributed in lower slope positions at elevations 2,530–2,550 m; (4) Type 4: evergreen broad-leaved and coniferous mixed forest *Castanopsis orthacantha-P. yunnanensis-Schima argentea* distributed in valleys at elevations 2,570–2,600 m; (5) Type 5: coniferous, evergreen and deciduous broad-leaved mixed forest *P. yunnanensis-Schima argentea-Quercus griffithii* distributed in lower and mid slopes at elevations 2,530–2,890 m; (6) Type 6: coniferous and sclerophyllous evergreen broad-leaved mixed forest *P. armandii-Quercus rehderiana-P. yunnanensis* distributed in upper slopes and ridges at elevations 3,040–3,100 m.

The landscape pattern of these six forest types in the Tianchi area was a mosaic determined by elevation and topography as well as various natural and anthropogenic disturbances. *P. yunnanensis* is consistently one of the dominants in each of these six forest types. In forest Type 1 the disturbance histories were diverse and included landslides, cattle and goat browsing, evidence of lightning strike on older trees. In contrast, disturbance histories for the other five forest types mainly consisted of landslides. Additionally, there was evidence of selective cutting and other human activity (such as collecting leaf litter) in the forest understory in Type 2 and Type 3 forests.

Figure 3b depicts the stratification of *P. yunnanensis* with each of the six forest types. In Type 1, *P. yunnanensis* dominated the canopy (20–28 m) and subcanopy (8–20 m) layers. It reached 35 m in height in the emergent layer. In addition, many *P. yunnanensis* individuals were found in the shrub layer. This is a typical primary mature forest of *P. yunnanensis*. A few trees of *Lithocarpus craibianus* and *Schima argentea* were present in the canopy and subcanopy layers. *Alnus nepalensis* and *Quercus griffithii* were found along the forest edge. In the shrub layer, *Lyonia ovalifolia* and *Sorbus folgneri* are the main members.

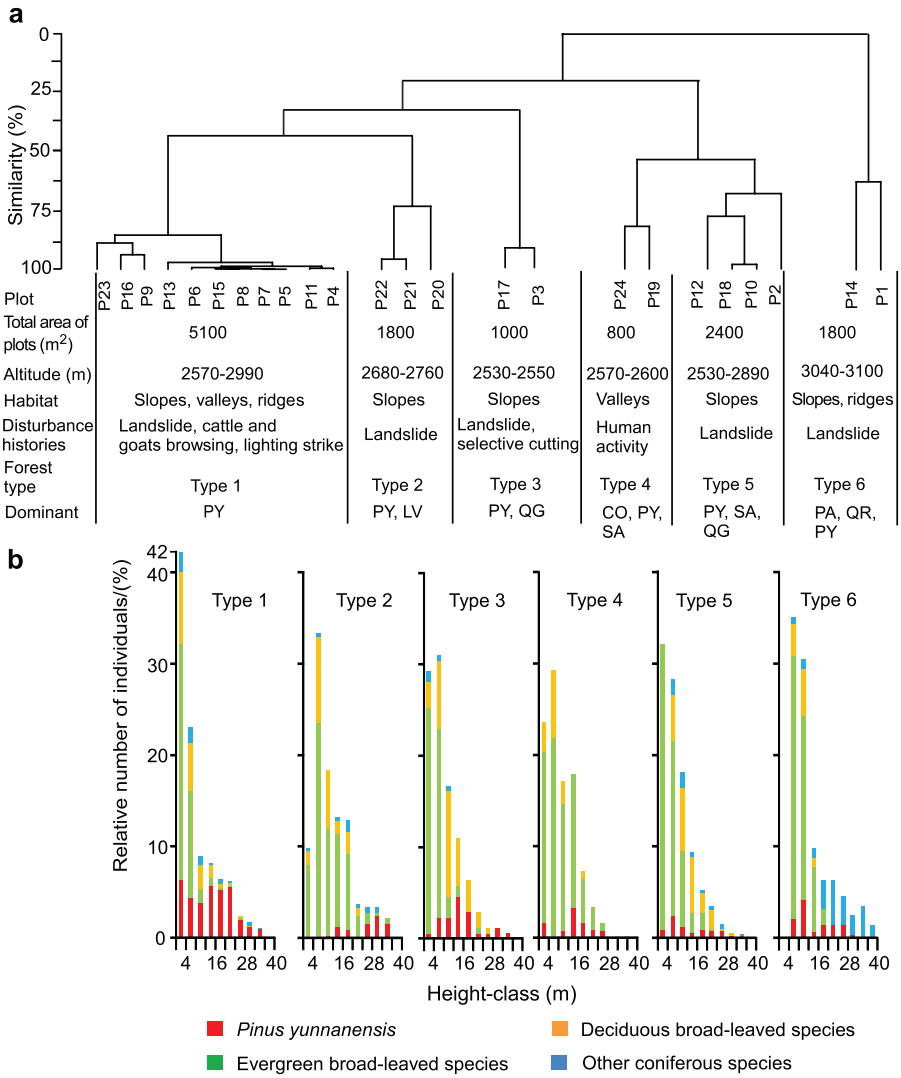

Figure 3. Floristic dendrogram and habitat characteristics, as well as forest stratification. (a) Floristic similarity dendrogram and habitat characteristics. (b) Height-class frequency distribution of species (height ≥ 1.3 m). Abbreviations for (a): PY = *Pinus yunnanensis*; LV = *Lithocarpus variolosus*; QG = *Quercus griffithii*; CO = *Castanopsis orthacantha*; SA = *Schima argentea*; PA = *Pinus armandii*; QR = *Quercus rehderiana*.

In Type 2, *P. yunnaensis* reached both the emergent layer (28–35 m) and the canopy, but only a few were found in the subcanopy and none between 1.3–12 m. *Lithocarpus variolosus* and *Pinus armandii*, *Cyclobalanopsis oxyodon* were found in the subcanopy and shrub layers.

In Types 3 and 4, the maximum height of *P. yunnaensis* also reached 35 m in the emergent layer. In Type 3, *P. yunnaensis* and *Quercus griffithii* shared the canopy and subcanopy. In Type 4, *Castanopsis orthacantha, P. yunnanensis* and *Schima argentea* co-occupied the canopy and subcanopy. In Type 5, *P. yunnanensis, Schima argentea* and *Quercus griffithii* co-dominated the canopy, subcanopy and shrub layers.

Type 6 is found above 3,000 m (3,040–3,100 m). Two pine species, *P. armandii* and *P. yunnanensis*, occupied the canopy layer, while in the emergent layer only *P. armandii* reached 38 m tall. Sclerophyllous evergreen broad-leaved *Quercus rehderiana* shared the subcanopy with the two pine species. In the shrub layer, *Rhododendron delavayi*, *Lyonia ovalifolia*, *Viburnum cylindricum* were common. In forest Types 3, 4, 5 and 6, there were fewer individuals of *P. yunnanensis* in the shrub layer than that of *P. yunnanensis* in the shrub layer of Type 1. The emergent layer of each forest type was made up of light-demanding, long-lived species (i.e. *P. yunnanensis* in the first four forest types, and *P. armandii* in the last two forest types).

The floristic composition of woody species in the six forest types is shown in Table 1. In total, 68 woody species comprised of 3 coniferous, 37 evergreen broad-leaved and 28 deciduous broad-leaved species belonging to 47 genera in 26 families were recorded in the 24 plots (Table 1 and Suppl. material 1). While the plots pooled for each forest type, 48 and 33 woody species were found respectively in Type 1 *P. yunnanensis* forest and Type 5 *P. yunnanensis-Schima argentea-Quercus griffithii* forest. In contrast, fewer than 25 woody species were found in each of the oth-

Table 1. Floristic composition of woody species (height ≥ 1.3 m) in the six forest types. The relative basal area in % is given. Background shading indicates dominant species. PY = *Pinus yunnanensis*; LV = *Lithocarpus variolosus*; QG = *Quercus griffithii*; CO = *Castanopsis orthacantha*; SA = *Schima argentea*; PA = *Pinus armandii*; QR = *Quercus rehderiana*.

Forest type	**Type 1**	**Type 2**	**Type 3**	**Type 4**	**Type 5**	**Type 6**
Dominant species	PY	PY, LV	PY, QG	CO, PY, SA	PY, SA, QG	PA, QR, PY
Range of elevation (m)	2570-2990	2680-2764	2530-2546	2576-2583	2530-2890	3042-3100
Number of plots	11	3	2	2	4	2
Total area of plots (m^2)	5100	1800	1000	800	2400	1800
Coniferous						
Pinus yunnanensis	74.37	43.91	49.88	23.66	34.41	17.05
Pinus armandii	4.58	10.49	0.6		6.63	53.06
Tsuga dumosa	0.03	·	·	·	0.51	0.05
Evergreen broad-leaved						
Lithocarpus variolosus	1.87	23.76	·	·	·	·
Rhododendron irroratum	1.42	·	0.63	0.25	1.61	0.68
Schima argentea	1.06	·	1.93	20.67	30.89	·
Lithocarpus craibianus	0.64	·	·	6.87	2.45	0.94
Rhododendron delavayi	0.53	1.15	1.43	0.22	1.94	2.79
Lyonia ovalifolia	0.32	0.3	1.46	0.12	0.12	0.2
Quercus rehderiana	0.26	·	0.02	·	0.08	20
Rhododendron basilicum	0.23	·	2.23	·	·	·
Viburnum cylindricum	0.18	0.35	0.17	0.01	0.09	0.05
Pieris formosa	0.14	·	·	·	0.09	1.16
Cornus capitata	0.05	0.79	·	·	0.5	·
Eurya nitida	0.05	2.03	·	0.25	·	·
Rhododendron decorum	0.02	1.93	·	·	·	·
Schefflera shweliensis	0.02	·	·	·	0.02	0.02
Cotoneaster franchetii	0.01	·	·	0.001	·	
Gaultheria fragrantissima	0.01	·	·	·	0.01	·
Symplocos lucida	0.01	·	0.05	·	0.001	·
Acanthopanax evodiaefolius var. *gracilis*	0.001	0.23	·	·	0.001	0.05
Daphne papyracea	0.001	·	·	·	·	0.03
Ternstroemia gymnanthera	0.001	·	·	·	·	·
Rhododendron tanastylum	0.001	·	·	·	·	·
Litsea yunnanensis	0.001	·	·	·	·	·
Cyclobalanopsis oxyodon	·	4.4	·	·	·	·
Machilus longipedicellata	·	0.41	·	·	·	·
Quercus guajavifolia	·	0.36	·	·	·	·
Illicium simonsii	·	0.05	·	·	·	·
Ilex dipyrena	·	0.01	·	·	·	·
Castanopsis orthacantha	·	·	·	37.47	·	·
Symplocos sp.	·	·	·	6.19	1.47	·
Ilex cornuta	·	·	·	·	0.01	·
Quercus aquifolioides	·	·	·	·	·	2.89
Deciduous broad-leaved						
Alnus nepalensis	5.78	·	0.22	·	1.89	·
Quercus griffithii	5.47	3.63	38.71	0.07	11.17	0.001
Cerasus clarofolia	1.48	0.18	2.14	1.56	1.89	·
Acer davidii	0.7	·	0.01	0.04	0.77	0.61
Populus davidiana	0.4	0.87	0.07	·	0.93	0.08
Schisandra sphenanthera	0.14	·	0.44	·	·	·
Sorbus folgneri	0.06	0.001	·	0.13	0.03	0.03
Enkianthus quinqueflorus	0.05	·	·	·	0.9	0.16
Litsea pungens	0.02	·	·	0.47	·	·
Elaeagnus umbellata	0.01	·	·	·	·	·
Betula insignis	0.01	·	·	·	·	·
Toxicodendron succedaneum	0.01	·	·	·	·	·
Pyrus xerophila	0.01	·	·	·	·	·
Coriaria nepalensis	0.01	·	·	·	·	·
Hypericum sp.	0.01	·	·	·	·	·
Rosa macrophylla	0.01	·	·	·	·	·
Berberis diaphana	0.001	·	0.001	·	0.01	·
Rosa sp.	0.001	·	·	0.001	·	·
Cotoneaster acuminatus	0.001	·	·	·	·	0.01
Rubus stans	0.001	·	·	·	·	0.001
Rosa multiflora	0.001	·	·	·	·	·
Viburnum betulifolium	0.001	·	·	·	·	·
Betula alnoides	·	2.5	·	·	·	·
Sorbus vilmorinii	·	2.03	·	·	·	0.01
Rhododendron yunnanense	·	0.61	·	·	·	·
Decaisnea insignis	·	0.01	·	·	·	·
Salix matsudana	·	·	·	1.98	0.98	·
Zanthoxylum simulans	·	·	·	0.05	·	·
Rubus hypopitys	·	·	·	·	0.51	·
Symplocos paniculata	·	·	·	·	0.3	·
Hydrangea macrophylla	·	·	·	·	0.08	·
Ligustrum quihoui	·	·	·	·	0.01	·
Padus obtusata	·	·	·	·	0.001	·
Acer oliverianum	·	·	·	·	0.001	0.11

er four forest types (Types 2, 3, 4 and 6) (Figure 4a). However, species richness (average number of species among the plots of each forest type) was not significantly different among all the forest types (Figure 4b). Among the six forest types, diversity indices (ranging from 1.9–2.3 for the Shannon-Wiener index, 0.75–0.86 for the Simpson index) were not significantly different (Figures 4c, d).

Stand structure and regeneration

Diameters of cored trees ranged between 2–116 cm and ages ranged between 11–172 years old. Diameter and age were significantly correlated (Figure 5, $R^2 = 0.86$).

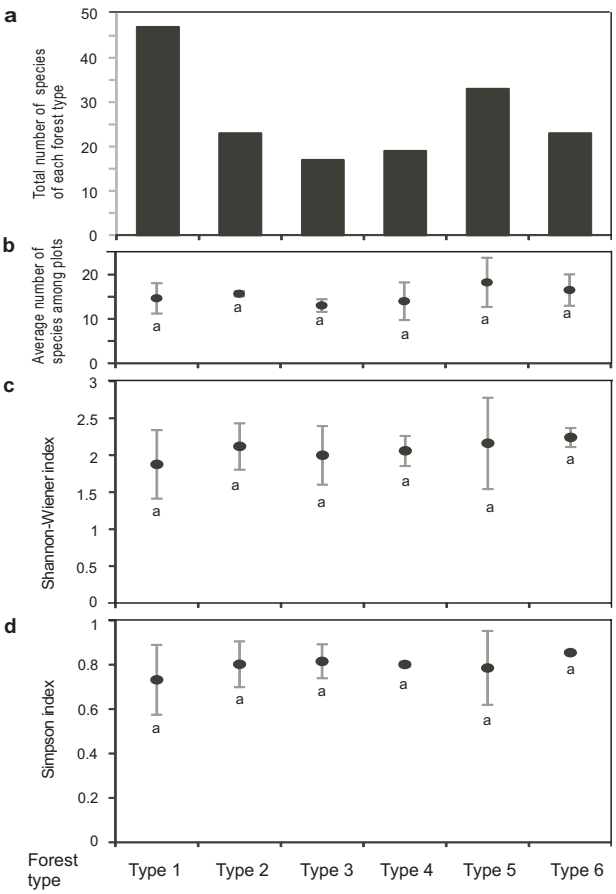

Figure 4. Changes in species richness and diversity among the six forest types. (a) Total number of species of plots of each forest type. (b) Average number of species among plots of each forest type. (c) Shannon-Wiener index. (d) Simpson index. Forests sharing the same letters do not differ significantly by non-parametric Kruskal-Wallis all-pairwise comparisons test, $P < 0.05$. The bar indicates the standard deviation. Forest types: Type 1 = *Pinus yunnanensis* forest; Type 2 = *Pinus yunnanensis-Lithocarpus variolosus* forest; Type 3 = *Pinus yunnanensis-Quercus griffithii* forest; Type 4 = *Castanopsis orthacantha-Pinus yunnanensis-Schima argentea* forest; Type 5 = *Pinus yunnanensis-Schima argentea-Quercus griffithii* forest; Type 6 = *Pinus armandii-Quercus rehderiana-Pinus yunnanensis* forest.

Diameter size-class frequency distributions of *P. yunnanensis* and other co-dominant tree species in all six forest types are shown in Figure 6. In the monodominant *P. yunnanensis* forest (Type 1), five height classes of *P. yunnanensis* corresponded to five peaks in the diameter distribution, indicating sporadic regeneration. But among the peaks, the four highest peaks appeared in the very small DBH classes (0–20 cm), the last peak being in 30–35 cm DBH. The five sub-populations were found in open patches, which provided some direct sunlight to the light demanding *P. yunnanensis* saplings and young trees on the forest floor. A large number, 251, of well-established seedlings/saplings (20–128 cm in height) of *P. yunnanensis* and a very few (5–16) seedlings/saplings of other canopy tree species were found in canopy gaps and forest edges.

In the *P. yunnanensis-Lithocarpus variolosum* forest (Type 2), the two dominants also showed a sporadic pattern of regeneration. There were no young trees (less than 5 cm DBH) of either *P. yunnanensis* or *L. variolosum,* because the evergreen *L. variolosum* crowns in the subcanopy layer allowed very little sunlight to reach the forest floor, resulting in poor regeneration of the two species.

In the *P. yunnanensis-Quercus griffithii* forest (Type 3), the two dominant species showed sporadic regeneration. Two *P. yunnanensis* and five *Quercus griffithii* trees were found between 100–125 cm and 30–75 cm DBH, and trees between 5–25 cm DBH were not abundant. Deciduous *Quercus griffithii* had four peaks within the DBH-classes of 10–40 cm.

In the *Castanopsis orthacantha-P. yunnanensis-Schima argentea* forest (Type 4), all the three dominant species showed sporadic regeneration. The dominants *C. orthacantha*, *P. yunnanensis* and *S. argentea*'s maximum diameters reached only 55, 50 and 45 cm DBH, respectively. In Type 3 and Type 4 forests, which are found at the low elevations (2,530–2,590 m), human impact was evident, as open spaces left after selective tree felling for timber during previous decades.

In the *P. yunnanensis-Quercus griffithii-Schima argentea* forest (Type 5), *P. yunnanensis* and *Q. griffithii* had sporadic regeneration while *S. argentea* showed an inverse-J shaped

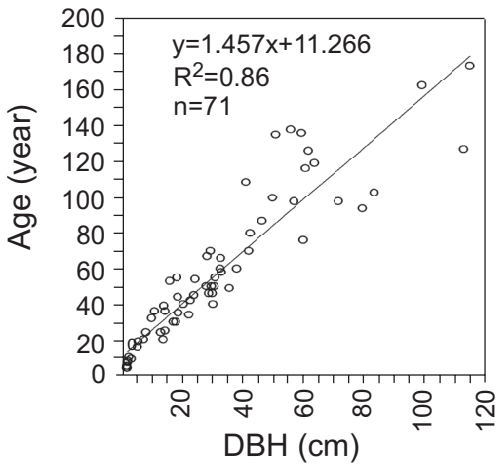

Figure 5. Relationships of age and DBH.

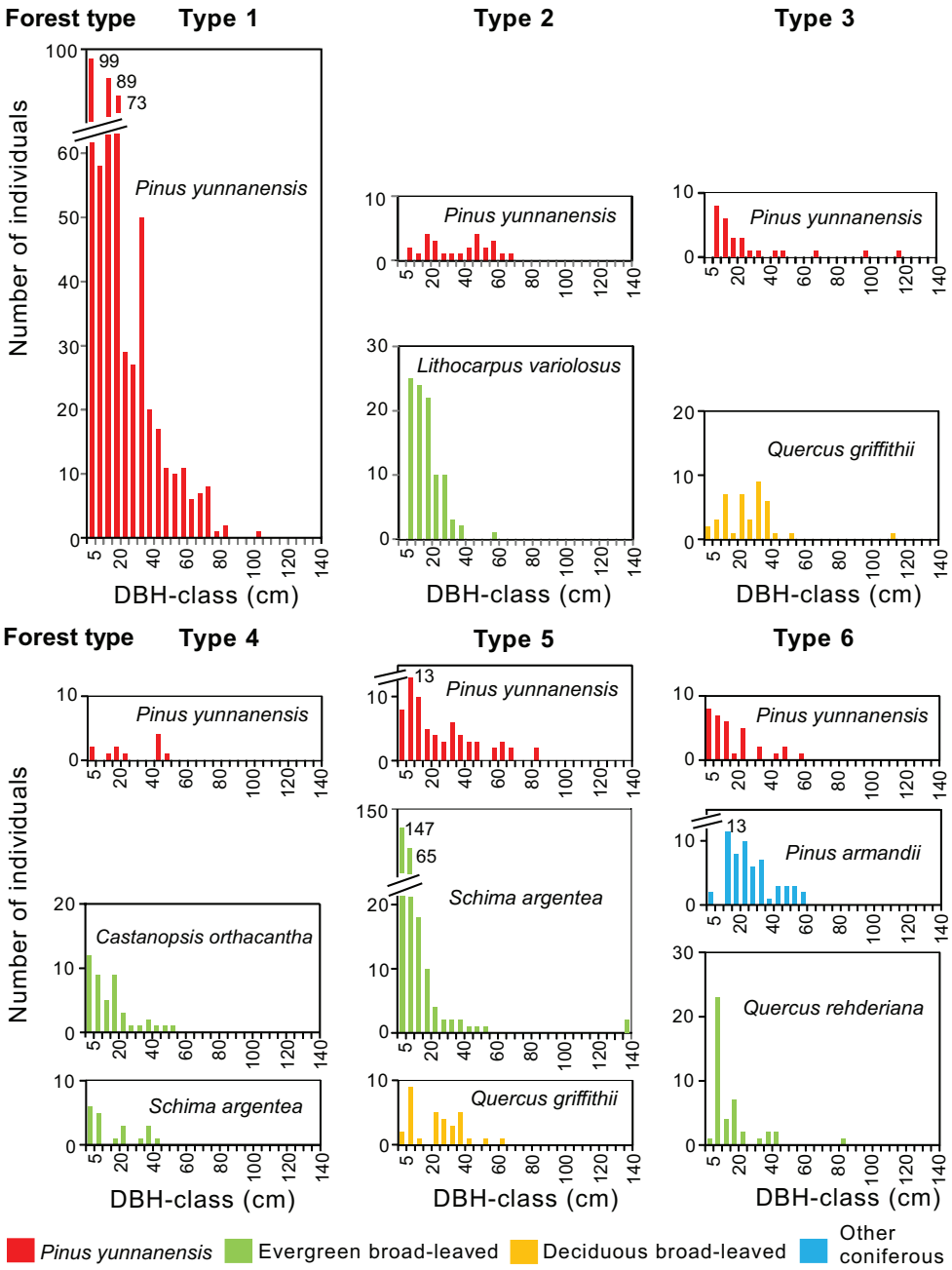

Figure 6. DBH-class frequency distribution of dominant species in various forest types. Type 1 = *Pinus yunnanensis* forest; Type 2 = *Pinus yunnanensis-Lithocarpus variolosus* forest; Type 3 = *Pinus yunnanensis-Quercus griffithii* forest; Type 4 = *Castanopsis orthacantha-Pinus yunnanensis-Schima argentea* forest; Type 5 = *Pinus yunnanensis-Schima argentea-Quercus griffithii* forest; Type 6 = *Pinus armandii-Quercus rehderiana-Pinus yunnanensis* forest.

pattern indicating a very active and recent pattern of regeneration. In this forest type, one tree of *P. yunnanensis* reached 90 cm DBH while two trees of *S. argentea* reached 130–140 cm DBH. *Q. griffithii*'s DBH ranged 0–60 cm.

In the *P. armandii-P. yunnanensis-Quercus rehderiana* forest (Type 6) at the highest elevations (3,040–3,100 m), the three dominant species all showed a sporadic pattern of regeneration. They had peaks at 15–20 (for *P. armandii*), 0–5 (*P. yunnanensis*) and 5–10 (*Q. reheriana*) cm DBH-classes. While the two pine species reached 60 cm DBH, *Q. reheriana* reached 85 cm DBH. Young trees and saplings of *Q. reheriana* appear both under canopy trees and in open spaces suggesting a somewhat shade-tolerant species in contrast to the two shade-intolerant pine species.

A few well-established seedlings/saplings (fewer than 30) of either *P. yunnanensis* or other canopy tree species were found in Types 2–6.

As a whole, there has been a relatively steady recruitment of *P. yunnanensis* trees over time peaking some 15 to 30 years ago. Although for trees taller than 1.3 m, there appears to be fewer trees in the period between 2002 and

2017 (the most recent age class), the seedling data (251 well-established seedlings/saplings) suggest that the regeneration has been good since 2002.

Growth rate and age-structure

Diameter growth of trees can be estimated by ring width and basal area increment. Changes in either may indicate increases or decreases in growth. The growth rate among the 71 samples varied greatly. In general, when the trees were less than 10 years old, the average growth rate of radius (ring width) was relatively high, with 4.04 mm/year, ranging from 5.56 to 2.97 mm/year. Thereafter, the average rate of radial growth fell to 2.50 mm/year between ages 20–30 years, and 1.63 mm/year between 31–60 years, and 1.17 mm/year for trees 61–100 years old. For trees greater than 100 years old, the average growth rate was 0.55 mm/year. At the other extreme, the rate of height growth slowed within the first 10 years (data not shown). It took about nine years on average to reach 1 m tall. Trees in all the four age classes (0–40 years, 40–80 years, 80–120 years, 120–164 years) had a similar pattern to that ring widths started high and decreased in a reverse J-shape (Figure 7a)

P. yunnanensis trees exhibited basal area increments (BAI) that rapidly increased with age for the first 20 years in all trees older than 40 years (Figure 7b). In trees younger than 40 years, BAI gradually increased during the first 10 years, then the level remained roughly the same until age 30 years, and decreased between ages 30–40 years. For trees with an age greater than 80 years, BAI plateaued between age 20 and 30 years and maintained that plateau until between 70 and 80 years old at which point BAI in all trees declined (Figure 7b).

Moreover, *P. yunnanensis* trees in the older age classes grew faster during the first 40 to 80 years than younger trees at the same age. In other words, trees of *P. yunnanensis* generally grew faster during the period 1853–1897 (red line) than 1897–1937 (green line) than 1937–1977 (yellow line) than during 1977–2017 (blue line) in the Tianchi area (Figures 7a, b).

Figure 8 shows the age-structure of *P. yunnanensis* in various forests. The observed maximum age of *P. yunnanensis* was at least 105 years in all the forest types except Type 4. In the Type 1 forest, there were many *P. yunnanensis* presented in the young to middle age-classes. The oldest tree was 135-years; most trees were between 15 and 30 years old. The other two sub-peaks were at 30–60 years. Recruitments were in a sporadic pattern corresponding to their frequency distribution in DBH-classes (Figure 6). In canopy gaps and forest edges, 251 seedlings/saplings over four-years-old but younger than 12 years were found (data are not shown). In the Type 2 forest, tree ages ranged from 16 to 120 years, and no trees less than 15-year-old were found, suggesting that regeneration was not occurring. *P. yunnanensis* in Types 3 and 4 was discontinuously distributed in the age-classes. While *P. yunnanensis* in Type 3 reached 165 years, there were none less than 15 years old. Only eight established seedlings/saplings of *P. yunnanensis* were found in canopy gaps and forest edges. In Types 5 and 6, the forest ages reached 135 and 105 years, respectively. The numbers of *P. yunnanensis* trees in these two forest types show three very small peaks between 15–60 years but poor recruitment in age-classes of less than 15 years. As a whole in the age class data for all the forest types, *P. yunnanensis*' presence of young and old individuals indicates frequent regeneration as well as dominance at maturity in the Tianchi area. The Type 1 forest appeared to have the most frequent episodes of regeneration.

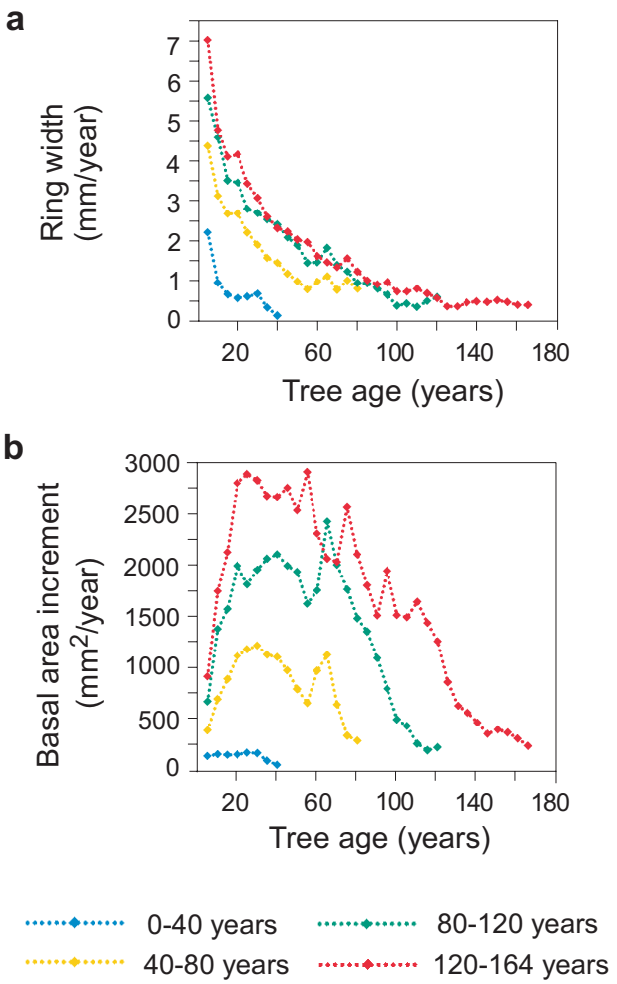

Figure 7. Growth trends of *Pinus yunnanensis* of the Tianchi National Nature Reserve. (a) The basal area increment for trees in the four age classes (i.e., 0–40, 40–80, 80–120, 120–164 years). (b) The ring width for trees in the four age classes.

Discussion

Ecological traits and forest characteristics

P. yunnanensis is a light-demanding species with wind-dispersed seed that depends upon canopy gaps or disturbances for regeneration. It can mono-dominate a forest or co-dominate with diverse species in various mixed

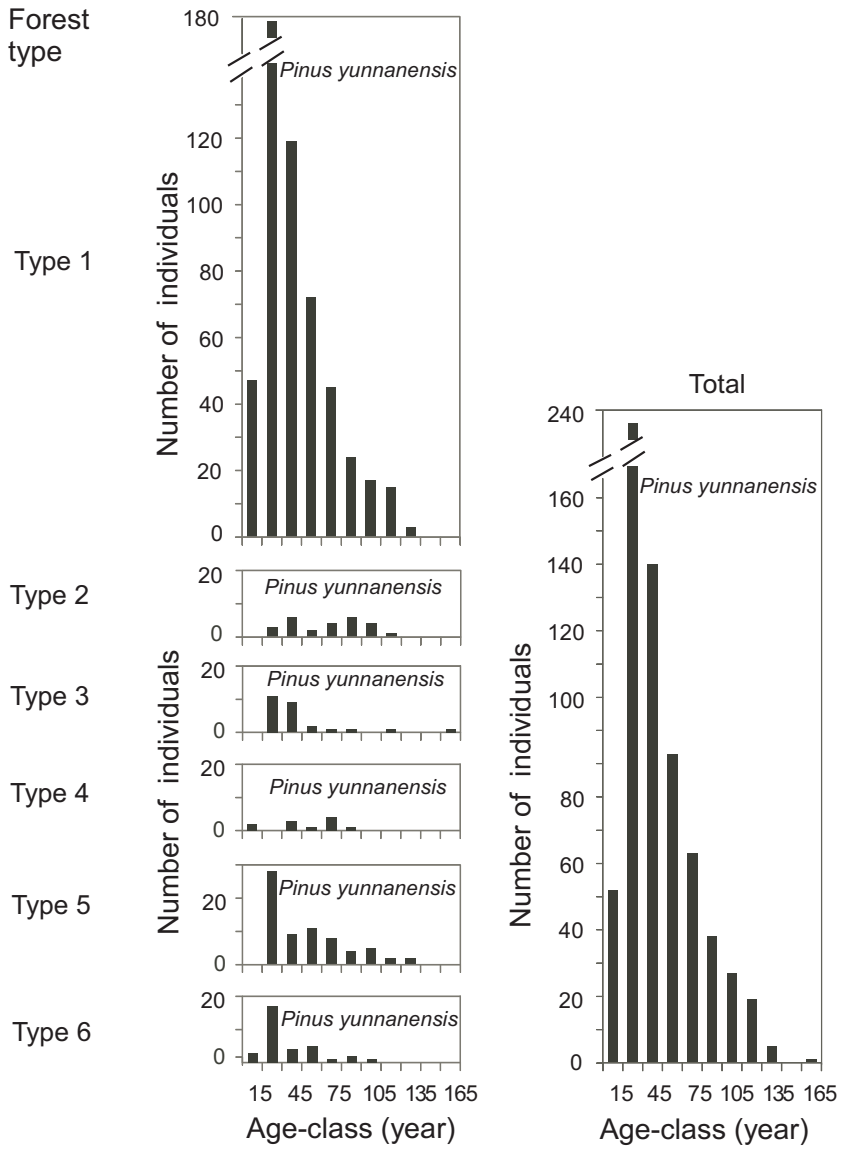

Figure 8. Age frequency distribution of *Pinus yunnanensis* in the six forest types. Forest type 1 = *Pinus yunnanensis* forest; Forest type 2 = *Pinus yunnanensis-Lithocarpus variolosus* forest; Forest type 3 = *Pinus yunnanensis-Quercus griffithii* forest; Forest type 4 = *Castanopsis orthacantha-Pinus yunnanensis-Schima argentea* forest; Forest type 5 = *Pinus yunnanensis-Schima argentea-Quercus griffithii* forest; Forest type 6 = *Pinus armandii-Quercus rehderiana-Pinus yunnanensis* forest.

forests. The overstory dominance of *P. yunnanensis* over a wide range of forest types and elevations suggests that this species plays an important role as an early successional species whose longevity assures presence in later successional stages. Among the evergreen broad-leaved trees (e.g. species of *Schima, Quercus, Castanopsis* and *Lithocarpus*) with which it co-occurs, it survives best on disturbed micro-sites or steep slopes (Figure 3a, Suppl.material 1). These ecological traits are very similar to those of *Pinus roxburghii* found in the Bhutan Himalaya (Wangda and Ohsawa 2006). Moreover, *P. roxburghii* is also associated with evergreen broad-leaved trees of *Quercus* (e.g. *Q. lanata*), the deciduous broad-leaved trees of *Quercus* (e.g. *Q. griffithii*) and shrubs of *Rhododendron* (e.g. *R. arboretum*), *Viburnum* (e.g. *Viburnum cylindricum*), *Lyonia* (e.g. *L. ovalifolia*), etc. In some of our study stands, *P. yunnanensis* co-dominates with deciduous broad-leaved *Q. griffithii* or coniferous *P. armandii*; similarly, its northern ecological partner *Pinus tabuliformis* is associated with deciduous broad-leaved trees of *Quercus aliena* var. *acutiserrata* and coniferous *P. armandii* in the Qinling Mountains, or *Quercus mongolica* (previous *Q. wutaishanica*) and *Betula platyphylla* in the Zhiwuling Mountains; *P. tabuliformis* is also shade-intolerant and its regeneration depends on disturbances (Yang et al. 2007; Wang et al. 2009; Lin 2009; Chai et al. 2012). In other of our study stands, *P. yunnanensis* co-dominates with evergreen broad-leaved *Schima argentea* and *Castanopsis orthacantha*; similarly, its southern ecological partner, also a pioneer and fast-growing pine tree, *P. kensiya* is associated with *Schima wallichii*

and species of *Castanopsis* including *Castanopsis hystrix*, *C. echidnocarpa*, *C. delavayi* and *C. calathiformis* (Li et al. 2013). *Pinus kensiya* occupies northern tropical and southern subtropical areas.

The Shannon-Wiener index of our study *P. yunnanensis* forest (1.9) tends to be higher than the natural mature *P. kensiya* forest (1.7) in the Ailao Mountains of central Yunnan (Song et al. 2011); and it is also higher than the secondary *P. yunnanensis* forests in Luquan (1.5) and Qiongzhusi (1.6), central Yunnan (Tang et al. 2010). All six study forest types had *P. yunnanensis* trees at least 90 years; these old-growth *P. yunnanensis* forests were stratified into multi-layers including emergent, canopy, subcanopy and shrub layers. In contrast, the 15–20 years old secondary *P. yunnanensis* forests of central Yunnan are simply composed of canopy and shrub layers. Often these forests are so dense that even the shrub layer is depauperate.

Recruitment patterns and growth trends

In the Tianchi National Nature Reserve of Yunnan, more seedlings/saplings were found in the Type 1, mono-dominant *P. yunnanensis* forest than in the mixed forest types (Types 2–6), because various disturbances including landslides, browsing, or lightning strike were noted in this forest type (Figure 3a). In the Tianchi area, seedlings/saplings of *P. yunnanensis* appear as uneven clusters. Seedling heights after the first four years following germination averaged only 6–10 cm. It then took another five years on average to reach 1 m in height. The initial height growth is slow as a result of competition for light as well as the allocation of carbon for root development; however, for seedlings growing in more open environments, such as along roadsides, height growth can be much greater taking between four to seven years to reach 1 m. The mortality of young seedlings is high during the first four years. This pattern of seedling growth and survival is similar to that observed with natural regeneration of plantations of *P. yunnanensis* of central Yunnan (Wang et al. 2017).

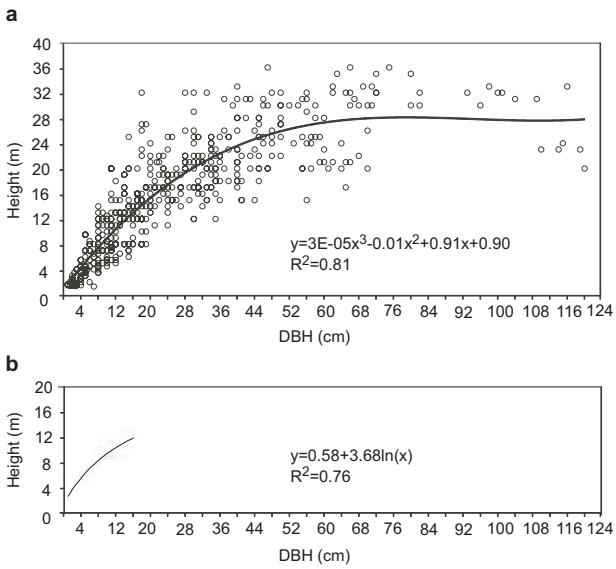

Figure 9. A comparison of relationships of DBH and height of *Pinus yunnanensis* between the old-growth forest of the Tianchi National Nature Reserve (a) and the 14 years-old *P. yunnanensis* plantation of Shiping, central Yunnan (b). Data source: Su et al. (2010) for (b).

After successful establishment, tree height of *P. yunnanensis* increases as DBH increases (Figure 9a). As the height approaches 24 m, the increase slows considerably. When trees of *P. yunnanensis* are smaller than 8 cm DBH, the height increase per year in the Tianchi area is similar to that of the plantation trees in Shiping, central Yunnan (Figure 9b). When both plantation and Tianchi trees are about 12 cm DBH, the Tianchi trees are 2 m taller than the plantation trees. The soil in Shiping is red earth and the climate is drier. Soil type significantly affects *P. yunnanensis* forests' species diversity and growth (Yang 2010). *P. yunnanensis* trees grow best in humid habitats with soils rich in nutrients (Jin and Peng 2004; Hu 2009). The humid habitat with yellow-brownish soil in the Tianchi area is more favorable for the growth of *P. yunnanensis*. Hu (2009) found a *P. yunnanensis* tree with a height of 56 m and a DBH of 86 cm in Baimalinchang of Yongren and it was 137-years-old. In contrast, Li et al. (2007) noted in a *P. yunnanensis* forest in Yongren, central Yunnan that there was a 257-year-old *P. yunnanensis* tree with a DBH of only 48 cm. This species can survive in very dry areas, generally with stunted and a crooked stature. The life span of *P. yunnanensis* growing on moderate to good sites may be around 180–280 years.

P. yunnanensis is a relatively fast-growing species in terms of tree ring width among the conifers of China. It attains a diameter of about 50 cm in 80 to 100 years, depending upon site quality. The patterns of ring width and basal area increment for *P. yunnanensis* trees growing in the Tianchi area where only site and time affected the patterns is shown in Figures 10a, d. In a secondary forest in central Yunnan where tree growth is impacted by site, time and human activity (such as extracting resin), the patterns of ring width and basal area increment are shown in Figures 10b and e. For both trees from the Tianchi forest and the secondary forest, ring widths started between 4 and 6 mm/yr and decreased in a reverse J-shaped pattern. A seemingly small difference in ring widths translates into very large differences in basal area increment (compare Figures 10d, e). For *P. yunnanensis* trees in a highly degraded forest in southwestern Sichuan, ring width showed a wave pattern (Hinckley et al. 2013). This wave pattern resulted from periodic branch removal interspersed by periods of crown recovery. Clearly, as site quality increases and human activity decreases, tree growth increases. The maximum basal area increment approached 1,500 mm^2 per year for trees at Tianchi whereas trees in the secondary forest of Yunnan and southwest Sichuan only approached 750 mm^2/yr.

As noted earlier, trees of the older age classes grew faster than younger trees at the same age in the Tianchi area (Figures 7a, b). This probably resulted from differences in

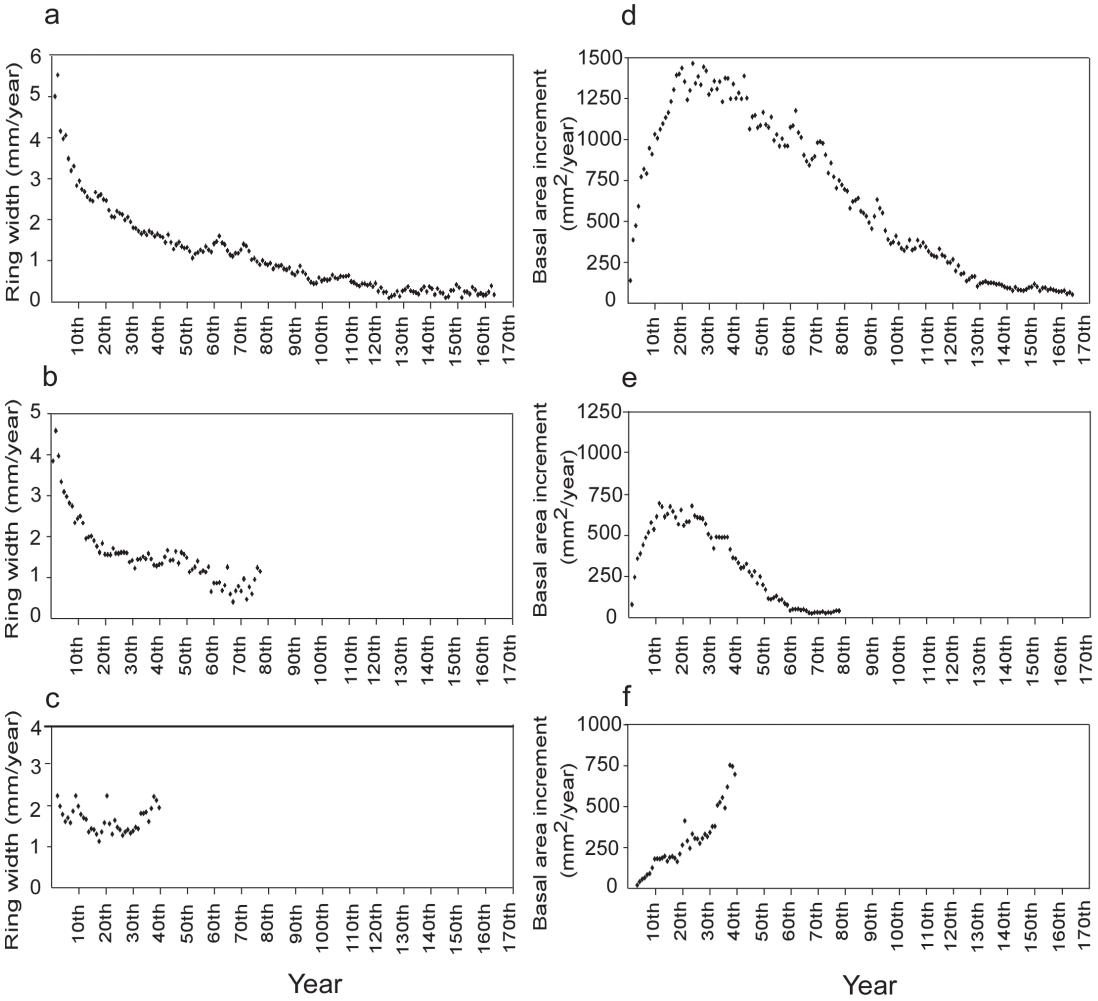

Figure 10. Comparisons of growth trends of *Pinus yunnanensis* among the old growth forest of the Tianchi National Nature Reserve (a & d), the secondary forest of central Yunnan (b & e), and the degraded forest under human pressure of western Sichuan (c & f). Data sources: Our own field work as seen this study for (a), (d), (b) and (e); Hinckley et al. (2013) for (c) and (f).

stand development such as the timing of canopy closure and the growth and development of competing species. It might also be resulted from differences in aspect where *P. yunnanensis*' light-demanding nature would result in better growth on southern versus northern slopes. Differences in disturbance regimes such as landslide frequencies and intensities also might have impacted the growth pattern. Finally, rapid global climate changes over many decades may be an additional important factor influencing growth. All the combined factors may lead to the observed differences.

Old-growth forests

The *P. yunnanensis* forests of the Tianchi area appear to be some of the last remnants of primeval and old-growth forests of this species. These forests are structurally diverse and contain a rich diversity of overstory, mid-story, and understory species. These forests also are valuable as a seed source and can serve as a genetic reservoir.

Author contributions

C.Q.T. designed the study, analyzed the data and wrote the manuscript. L.-Q.S. organized and analyzed the data. S.L. identified the botanical specimens. K.S. read the tree rings and provided the data of ring width. C.Q.T., L.-Q.S., P.-B.H., D.-S.H., Y.-F.L., Z.-Y.Z., L.-Y.Y., R.-H.Y. and H.-M.X. conducted the fieldwork. All the authors contributed discussion to improve the manuscript.

Acknowledgements

We acknowledge funding by the Science and Technology Ministry of China (2015FY210200-15) and the National Natural Science Foundation of China (31500355). We would like to thank all the staff of the management office of the Tianchi National Nature Reserve for allowing us to conduct field research in the reserve. Our sincere thanks go to Dr. Thomas M. Hinckley who provided valuable suggestions and comments to improve our manuscript.

References

Cai N, Xu Y, Chen S, He B, Li G, Li Y, Duan A (2016) Variation in seed and seedling traits and their relations to geo-climatic factors among populations in Yunnan Pine (*Pinus yunnanensis*). Journal of Forest Research 27: 1009–1017. https://doi.org/10.1007/s11676-016-0228-z

Chai ZZ, Wang DX, Zhang LN, Zhang Y, Huang QP, Wu H (2012) Niche characteristics of main plant populations in natural *Pinus tabulaeformis* communities in Qinling Mountains, Northwest China. Chinese Journal of Ecology 31: 1917–1923.

Chen F, Wang, JM, Sun BG, Chen XM, Yang ZX, Duan ZY (2012) Relationship between geographical distribution of *Pinus yunnanensis* and climate. Forest research 25: 163–168.

Chen QC, An BW (1993) Natural regeneration related to altitudes. Sichuan Forestry Science and Technology 14: 77–80.

Editorial Committee of Flora Reipublicae Popularis Sinicae (1959–2004) Flora Republicae Popularis Sinicae. Science Press, Beijing, CN.

Hinckley TM, Chi P, Hagmann K, Harrell S, Schmidt AH, Urgenson L, Zeng ZY (2013) Influence of human pressure on forest resources and productivity at stand and tree scales: The case study of Yunnan pine in SW China. Journal of Mountain Science 10: 824–832. https://doi.org/10.1007/s11629-013-2657-x

Hu XY (2009) An analysis of ring growth of a *Pinus yunnanensis* tree with a maximum height. Forestry Inventory and Planning 34: 23–26.

Jin ZZ, Peng J (2004) Yunnan Pine (*Pinus yunnanensis* Franch). Yunnan Science and Technology Press, Kunming, CN.

Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5–13. https://doi.org/10.2307/3545743

Li S, Su J, Liu W, Lang X, Zhang Z, Su L, Yang H (2013) Quantitative classification of *Pinus kesiya* var. *langbianensis* communities and their species richness in relation to the environmental factors in Yunnan Province of Southwest China. Chinese Journal of Ecology 32: 3152–3159.

Lin Y (2009) Study on the community characteristic of Chinese pine (*Pinus tabulaeformis*) forest and its classification in Qinling Mts. Master Thesis, Northwest Agriculture & Forestry University, Yangling, CN.

Li GX, Shi HJ, Meng GT, Fang XJ, Chai Y, He LP, Zhang ZH, Yang YX (2007) Community structural properties and species diversity in primary *Pinus yunnanensis* forest. Journal of Zhejiang Forestry College 24: 396–400.

McCune B, Mefford MJ (1999) PC-ORD: Multivariate analysis of ecological data. Version 4. MjMSoftware Design, Gleneden Beach, US.

Ohsawa M (1984) Differentiation of vegetation zones and species strategies in the subalpine region of Mt. Fuji. Vegetatio 57: 15–52. https://doi.org/10.1007/BF00031929

Peng C, Li LF, Wang KL, Duan AA, Yin ZY, Zhang J, Wang K, Li WC, Li JH (2012) Analysis on natural regeneration of *Pinus yunnansensis* in Lufengcun Forest Farm of Yiliang County. Journal of Central South University of Forestry & Technology 32: 42–46.

Peng JS, Chai Y, Meng GT, Fang XJ, Li GX, He LP (2005) A study on the gap phase regeneration in the natural forest of *Pinus yunnanensis* along the reaches of Jinshajiang in Yunnan province. Journal of Northwest Forestry University 20: 114–117.

Pielou EC (1969) An introduction to mathematical ecology. Wiley, New York, US.

Rubino DL, McCarthy BC (2000) Dendroclimatological analysis of white oak (*Quercus alba* L., *Fagaceae*) from an old-growth forest of southeastern Ohio, USA. Journal of the Torrey Botanical Society 127: 240–250. https://doi.org/10.2307/3088761

Shi J, Xu YH, Li RB, Lu P (2009) Study on Natural Regeneration of *Pinus yunnanensis* around Songhuaba Reservoir. Forest Inventory and Planning 34: 48–51.

Song L, Liu W, Ma W, Zhao X, Zhou M, Yang G (2011) Community characteristics of monsoon evergreen Broad-leaved and *Pinus kesiya* var. *langbianensis* forests in the west foot of Ailao Mountain, Yunnan. Journal of Mountain Science 29: 164–172.

Su J, Li LF, Zheng W, Yang WB, Han MY, Huang ZM, Xu PB, Feng ZW (2010) Effect of intermediate cutting intensity on growth of *Pinus yunnanensis* plantation. Journal of West China Forestry Science 39: 27–32.

Su H, Wang P (2013) Climate vertical zoning of Tianchi Nature Reserve. Yunnan Geographic Environment Research 25: 90–94.

Su H, Wang P, Ren B (2013) Yunlong Tianchi Nature Reserve of soil distribution features and protection. Journal of Baoshan College 02-026-05: 1674–9340.

Su W, Cui F, Zhao Y, Zhou R, Zhang G, Cao J (2017) Canopy seed bank and serotinous cones of *Pinus yunnanensis* forests. Acta Ecologica Sinica 37: 541–548. https://doi.org/10.5846/stxb201507041414

Tang CQ (2015) The Subtropical Vegetation of Southwestern China. Springer, Dordrecht, NL. https://doi.org/10.1007/978-94-017-9741-2

Tang CQ, He LY, Su WH, Zhang GF, Wang HC, Peng MC, Wu ZL, Wang CY (2013) Regeneration, recovery and succession of a *Pinus yunnanensis* community five years after a mega-fire in central Yunnan, China. Forest Ecology and Management 294: 188–196. https://doi.org/10.1016/j.foreco.2012.07.019

Wang B, Mao JF, Zhao W, Wang XR (2013) Impact of geography and climate on the genetic differentiation of the subtropical Pine *Pinus yunnanensis*. PLoS ONE 8: e67345. https://doi.org/10.1371/journal.pone.0067345

Wang DX, Lin YY, Lei RD, Yang T, Wang Q, Yong XH (2009) Community composition and classification of natural forest of Chinese Pine (*Pinus tabulaeformis* Carr.) in Qinling Mountains. Acta Botanica Boreal.-Occident. Sinica 29: 0867–0873.

Wang L, Zhang JF, Ma JZ, Wei W, Hu Q (2018) Research progress on *Pinus yunnanensis* with degradation status and ecosystem functions of the forest stands. Journal of West China Forestry Science 47: 121–130.

Wang W, Zhang W, Li L, Wang Y, Ou Y, Yang W (2017) Natural regeneration model of the small-scale space under the gap in the *Pinus yunnanensis* forest. Journal of Forest and Environment 37: 336–341.

Wangda P, Ohsawa M (2006) Structure and regeneration dynamics of dominant tree species along altitudinal gradient in a dry valley slopes of the Bhutan Himalaya. Forest Ecology and Management 230: 136–150.https://doi.org/10.1016/j.foreco.2006.04.027

Wen Q, Yang X, Yang Z, Chen X, Lai X, Ding F (2010) Dynamic changes in *Pinus kesiya* var. *langbianensis* forest resources in China. Resources Science 32 : 1621–1626.

Xu HC (1990) *Pinus tabuliformis*. China Forestry Press, Beijing, CN.

Xu YL, Cai NH, Kang XY, Li GQ, He CZ, Duan AA (2011) Progress on genetic diversity of *Pinus yunnanensis* Franch. Journal of Plant Genetic Resources 12: 982–985.

Yang JL (2007) Community characteristics of *Pinus tableaformis* forests in the Ziwuling mountains. Master thesis, Gansu Agriculture University, Lanzhou, CN.

Yang WY (2010) Community structure and natural regeneration of natural Yunnan Pine forest in Middle Yunnan, China. PhD thesis, Chinese Academy of Forestry, Beijing, CN.

Yu H, Ge S, Huang RF, Jiang HQ (2000) A preliminary study on genetic variation and relationships of *Pinus yunnanensis* and its closely related species. Acta Botanica Sinica 42: 107–110.

E-mail and ORCID

Cindy Q. Tang (Corresponding author, cindyqtang@aol.com), ORCID: https://orcid.org/0000-0003-3789-6771
Li-Qin Shen (liyilanbian@foxmail.com)
Peng-Bin Han (baqidehan@qq.com)
Diao-Shun Huang (1351379318@qq.com)
Shuaifeng Li (Corresponding author, 12704391@qq.com), ORCID: https://orcid.org/0000-0002-2555-1808
Yun-Fang Li (974016458@qq.com)
Kun Song (ksong@des.ecnu.edu.cn), ORCID: https://orcid.org/0000-0001-8019-9707
Zhi-Ying Zhang (zhyzhang@ynu.edu.cn)
Long-Yun Yin (409508296@qq.com)
Rui-He Yin (1318765303@qq.com)
Hui-Ming Xu (254134558@qq.com)

Supplementary material

Supplementary material 1
Floristic composition of woody species (height ≥ 1.3 m) in each plot
Link: https://doi.org/10.3897/VCS/2020/37980.suppl1

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 21–36
doi: 10.3897/VCS/2020/38644

RESEARCH PAPER

Plant communities and their environmental drivers on an arid mountain, Gebel Elba, Egypt

Maged M. Abutaha[1,2], Ahmed A. El-Khouly[1], Norbert Jürgens[2], Jens Oldeland[2]

1 *Department of Plant Ecology and Range Management, Desert Research Center, Cairo, Egypt*

2 *Biodiversity, Evolution and Ecology of Plants, Institute of Plant Sciences and Microbiology, Hamburg University, Hamburg, Germany*

Corresponding author: Maged M. Abutaha (maged_abutaha@yahoo.com)

Academic editor: Wolfgang Willner ♦ **Received** 30 July 2019 ♦ **Accepted** 11 November 2019 ♦ **Published** 4 May 2020

Abstract

Aims: Gebel Elba is an arid mountain range supporting biological diversity that is incomparable to any other region of Egypt. This mountain has a vegetation structure and floristic community similar to the highlands of East Africa and the southwestern Arabian Peninsula. We aimed to provide the first classification of the vegetation units on Gebel Elba and identify the environmental factors controlling their distribution. **Study area:** Wadi Yahmib and its tributaries, which drain the north-western slopes of Gebel Elba, south-eastern Egypt. **Methods:** On the basis of 169 relevés, we used TWINSPAN to classify the perennial vegetation. We calculated separate GAMs for the deciduous and evergreen species to describe the patterns for each leaf strategy type with elevation. We used CCA to quantify the relationship between the perennial vegetation and the studied environmental factors. To estimate diversity and our sampling strategy, we used rarefaction curves for species richness. **Results:** We identified seven communities along the elevational gradient of Wadi Yahmib and its tributaries. We found that each community was restricted to a confined habitat depending on its drought resistance ability. Deciduous *Vachellia* woodland was the main vegetation type on Gebel Elba, while evergreen *Olea* woodland appeared in small fragments at higher elevations. We analysed the distribution patterns of deciduous and evergreen trees along the elevational gradient. We found a turnover at 500 m, indicating a potential ecotone between the *Vachellia* and *Olea* woodlands that was occupied by a *Ficus* community. CCA revealed the importance of altitude 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. **Conclusions:** This study identified seven vegetation units in the study area and showed the importance of orographic precipitation, soil quality and the complex topography in determining the habitats.

Taxonomic reference: Boulos (2009); names updated according to POWO (2019).

Abbreviations: CCA = Canonical Correspondence Analysis; GAM = Generalized Additive Model; TWINSPAN = Two Way Indicator Species Analysis.

Keywords

Acacia, Afromontane forest, classification, ecotone, Eritreo-Arabian, soil, vegetation, woodland

Introduction

The Eastern Desert of Egypt is characterized by coastal mountain ranges running parallel to the Red Sea. The most biodiverse mountain range in the region is the Gebel Elba in the south-eastern corner of Egypt, on the border between Egypt and Sudan (Kassas and Zahran 1971; Abd El-Ghani and Abdel-Khalik 2006). The flora of the Gebel Elba range is much richer than those of other coastal mountain ranges. In total, 458 plant species have been collected within the

PENSOFT.

Copyright *Maged M. Abutaha et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

area of Gebel Elba, representing almost 21% of the Egyptian flora (Boulos 2008; Zahran and Willis 2009). The other mountain ranges overlooking the Red Sea are less rich in plant diversity, with less than 130 species recorded in total (Zahran and Willis 2009). The proportion of Afrotropical elements on the Gebel Elba is much higher than those in any other region of Egypt (Abd El-Ghani and Abdel-Khalik 2006; Al-Gohary 2008). This range represents the northern limit of the Eritreo-Arabian province and the Sahel regional transition zone in Africa (Zohary 1973; White 1983), including the Somalia-Masai regional centre of endemism (White 1983; White and Léonard 1991; Boulos 2008). Thus, the Gebel Elba is considered one of the seven main phytogeographical regions of Egypt (Boulos 2009).

The biodiversity of the Gebel Elba region is unique to Egypt, and many globally threatened species are found there (IUCN 2019). In 1986 this area was declared the Gebel Elba National Park, covering nearly 36,000 km^2. Gebel Elba Mountain is the core part of this protected area. The richness of vegetation on Gebel Elba is related to its orographic precipitation. The proximity of Gebel Elba to the sea and its windward position create a unique ecosystem, known as a "mist oasis", that is found nowhere else in Egypt, but is comparable to similar ecosystems in Erkwit, Sudan, and the southern part of the Arabian Peninsula (Kassas 1956; Kürschner et al. 2004; Hegazy and Lovett-Doust 2016). Because of moisture-laden north-eastern winds, the vegetation is much richer on the northern slopes of Gebel Elba than on the southern slopes (Zahran and Willis 2009). Thus, both species richness and abundance are much higher on the mountain than in the exposed open desert (Abutaha et al. 2019). On the foothills of the mountain, *Vachellia tortilis* (synonym: *Acacia tortilis*) forms an extensive natural woodland landscape (Zahran and Willis 2009).

Gebel Elba has a unique phytogeographic position and a floristic composition that is more complex than the total floral composition of the rest of Egypt. This arid granite mountain bears floristic similarities and shares common vegetation with the neighbouring mountains of East Africa and the southwestern Arabian Peninsula (Kassas 1956; Hegazy et al. 1998). Gebel Elba and the southwestern Arabian highlands represent the northern limit of Eritreo-Arabian vegetation (Zohary 1973). The vegetation of the Eritreo-Arabian province is continuous and changes from deciduous *Vachellia-Commiphora* woodland at lower elevations to evergreen Afromontane forest of *Juniperus procera* at elevations above 2000 m (Zohary 1973; Kürschner et al. 2008; Deil 2014; Berhanu et al. 2018). The evergreen woodland dominated by *Olea europaea* subsp. *cuspidata* represents a transition zone between the lower montane *Vachellia-Commiphora* woodland and the upper montane *Juniperus procera* forest (White 1983; Kürschner et al. 2008). Comparably, Zohary (1973) recognized three altitudinal zones of Afrotropical vegetation in Gebel Elba: a lower zone of *Vachellia-Ziziphus* (pseudo-savanna vegetation), a middle zone of *Vachellia-Commiphora* (savanna vegetation), and a montane zone of *Olea-Ficus* forest fragments. Zahran and Willis (2009) found three altitudinal belts of vegetation on the northern slopes of Gebel Elba: a lower zone of *Euphorbia cuneata*, a middle zone of *E. nubica* and a higher zone of moist habitat vegetation. Within this higher zone, many evergreen species were recorded, such as *Euclea racemosa*, *Dodonaea viscosa*, *Carissa spinarum* and *Olea europaea* subsp. *cuspidata* (White 1983). The vegetation of Gebel Elba changes from *Vachellia tortilis* woodland at lower elevations to forested vegetation at middle and higher elevations (Abd El-Ghani and Abdel-Khalik 2006; Zahran and Willis 2009). The elevational gradient of Gebel Elba is known to harbour a relatively large number of tree species. Two prominent leaf strategy types occur (deciduous and evergreen). However, these types do not occur evenly across the elevational gradient; evergreen trees are prominent in the upper altitudes, while deciduous species are more common in the lower, arid parts of the gradient (Abutaha et al. 2019). The ecotone between evergreen woodland at higher elevations and deciduous woodland at lower elevations has not been studied (White 1983; Berhanu et al. 2018).

Most of the previous studies on Gebel Elba have mainly focused on wadis, which are temporary waterways that collect run-off water from the surrounding slopes and contain several microhabitats (Zohary 1973; Gomaa 2014), where vegetation is rich and continuous (Ahmed 1999; Zahran and Willis 2009; Abutaha et al. 2019). While the lower elevations of wadis show recognizable features of zonal communities, the vegetation on the higher slopes is more variable due to minor differences in habitat and recognizing clearly defined zonal communities is difficult (Zahran and Willis 2009). A classification of wadi vegetation is still lacking. Additionally, no agreement has been reached regarding the vegetation zonation of the northern wadis of Gebel Elba (Al-Gohary 2008; Zahran and Willis 2009). The altitudinal range of plant communities and information on environmental drivers are mostly unavailable. Thus, there is a need to identify the vegetation units of Gebel Elba and the environmental drivers controlling their distributions.

In this study, we aimed to describe the altitudinal zonation of the defined plant communities, their compositions and the relations to environmental factors in wadis on the northern slopes of Gebel Elba. This classification was based on 169 relevés which have not been previously sampled on this mountain. We also aimed to analyse the distribution patterns of deciduous and evergreen trees along the elevational gradient to identify a transition zone between the two different leaf strategy types representing different phytoregions. Finally, we also compared our findings on the diversity between the different vegetation communities with previous studies.

Materials and methods

Study area

Gebel Elba Mountain (1435 m) is located at 22.25N and ranges from 36.25 to 36.43E, nearly 15 km west of the Red

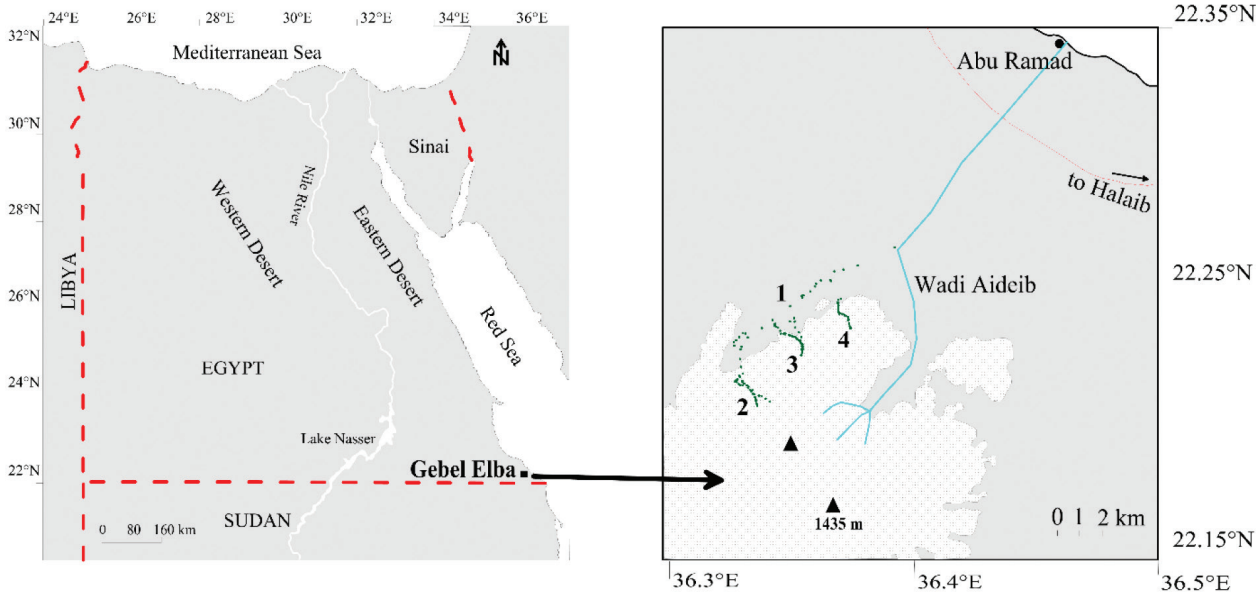

Figure 1. The location of Gebel Elba in Egypt (left) and the distribution of the vegetation relevés (green dots) surveyed for this study in Wadi Yahmib and its tributaries at the northern slopes of Gebel Elba (right); Wadi Yahmib (1), Wadi Marafai (2), Wadi Acow (3) and Wadi Kansisrob (4).

Sea coast, south-eastern Egypt (Figure 1). The mountain itself is formed of a group of granite peaks in the shape of a square with sides of approximately 15 km by 15 km. From the central peak, drainage lines (wadis) radiate in all directions (Ball 1912). The principal wadi on the northern slopes of Gebel Elba is Wadi Yahmib (Zahran and Willis 2009). Yahmib is located at the foothills of the mountain and receives water mainly from three mountainous tributaries: Wadis Marafai, Acow, and Kansisrob, which drain the western-northern flanks of Gebel Elba (Figure 1). The substrates of the wadis vary with an elevation gradient which increases from east to west; the substrate of Wadi Yahmib is fine sand, that of Wadi Kansisrob is coarse gravel, and Wadis Acow and Marafai, at higher elevations, have large granite boulder substrates (Abutaha et al. 2019).

Gebel Elba has a hyper-arid climate (Harris et al. 2014). The climatic aridity of the region is expressed in the climate diagram between 1985–2015 (Figure 2) adopted from Walter and Lieth (1967). The temperature ranges between 15.3 °C and 38.1 °C, with a mean annual temperature of 26.1 °C. The area received less than 40 mm of rainfall per year, mainly from winter rainfall and light summer rainfall (Figure 2). However, Gebel Elba receives up to 400 mm of orographic precipitation per year (Goodman and Meininger 1989; Kamel et al. 2015). Gebel Elba is influenced by winter rain and summer monsoons, dew falls regularly, clouds and mist shrouds the mountain (see Figure 5A–B). Although this mountain is surrounded by an extremely arid desert, orographic precipitation provides a climatic condition that is favourable for rich plant growth (Ball 1912; Hegazy and Lovett-Doust 2016).

Vegetation sampling

We conducted vegetation sampling on five visits; two in 2013, two in 2015 and one in 2016. The visits were made in January or March after the rainy season. We sampled 169 geo-referenced vegetation relevés that were marked with a GPS device (Garmin eTrex 30x). The relevés (10 m × 10 m) were distributed along transects in the four studied wadis, i.e., Yahmib, Marafai, Acow, and Kansisrob (see Abutaha et al. 2019). Locations of the relevés were selected randomly during the field work. For each relevé, we assembled a list of all vascular plant species that were present. We noted the growth forms of the listed species and identified the life forms according to Raunkiaer's system of classification (Raunkiaer 1934). Furthermore, we visually estimated the percentage cover of perennial species in each relevé. Owing to the arid climatic conditions of the study area, annual species were only noted as being present/absent. The nomenclature of the plant species followed Boulos (1999, 2000, 2002, 2005, 2009). We updated the list of taxonomic names according to Plants Of the World Online (POWO 2019) provided by the Royal Botanic Gardens, Kew. Voucher specimens were deposited in the Herbarium of Desert Research Center (CAIH) and the Herbarium Hamburgense (HBG).

Soil sampling and analysis

We took mixed soil samples from the surface layer (0–10 cm) of each relevé. We air-dried and analysed the samples to determine the physical and chemical soil properties. First, we determined soil texture by sieving with succes-

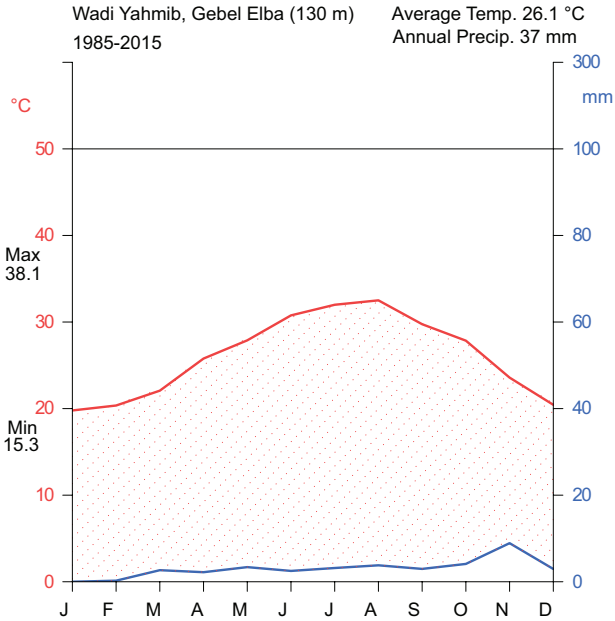

Figure 2. Climate diagram of Wadi Yahmib, Gebel Elba based on CRU datasets TS 4.01. Data is for the period from 1985 to 2015. The upper red line stands for mean monthly temperature of 26.1 °C (left axis); numbers beside the axis are the mean monthly maximum and minimum temperatures. The lower blue line stands for precipitation (right axis). Area shaded with dots (dotted area), above the precipitation line, and below the temperature line, indicates a dry period.

sively finer meshes (Estefan et al. 2013; AG Boden 2005). Second, we prepared soil suspensions by the addition of distilled water in a 1:1 ratio and stirring continuously for 2 hours, then measured the pH and electrical conductivity (EC) of the suspensions with a pH meter (Jenway 3510) and conductivity meter (Jenway 4510), respectively (Hendershot et al. 2008; Miller and Curtin 2008). We then filtered the soil suspensions and used the extracts to determine the soluble mineral contents. The analyses of major constituents in the soil extracts (calcium, magnesium, sodium, potassium, sulfate and chloride) were determined using an ion chromatography system, IC (Dionex, ICS-1100). Carbonate and bicarbonate ions were estimated with the titrimetric method (Jackson 1967; Estefan et al. 2013). Finally, we estimated the organic matter content by the weight loss-on-ignition method (Schulte and Hopkins 1996; Combs and Nathan 1998) and determined $CaCO_3$ volumetrically using a Collin's calcimeter (Piper 1950).

Data analysis

Multivariate analysis procedures

For the floristic classification of the relevés, we imported a vegetation matrix, including the percentage cover values of perennial species, into the software Juice, version 7.0 (Tichý 2002), and used the TWINSPAN classification (Hill 1979). We set the minimum group size to 3, and used percentage cover values of 0, 5 and 50 as cut levels. As a fidelity measure, we used the phi value (De Cáceres and Legendre 2009). The calculations of the phi values were adjusted for equal group sizes. If the phi value exceeded 0.25, a species was considered diagnostic, and if the phi value was > 0.50, the species was considered highly diagnostic; the p-value of Fisher's exact test was 0.05. Species with a frequency higher than 70% were considered as constant. To measure correlations between the perennial species and relevant environmental drivers, we used canonical correspondence analysis (CCA) for the ordination (Ter Braak and Prentice 1988). We selected altitude and edaphic factors after the exclusion of collinear variables (anions and cations were highly correlated with EC). We applied biplot scaling and the species were centred. Only perennials with significant phi values > 0.25 are shown in the ordination. We performed CCA using CANOCO, version 5.0 (Ter Braak and Šmilauer 2012).

To better describe and interpret the results of the classification, we used analysis of variance (ANOVA) and Tukey's post hoc tests for the pairwise comparisons to test for differences in the soil physical and chemical parameters between the identified plant communities. Before the statistical tests, each soil parameter was logarithmically or square root transformed in cases where the data did not follow a normal distribution. The analyses were carried out using R software (R Development Core Team 2018).

Diversity

To evaluate diversity and our sampling strategy, we used rarefaction and extrapolation sampling curves for species richness to estimate the completeness of our vegetation samples (Chao et al. 2014). We performed all calculations for the complete datasets (perennial and annual species) of the four wadis (transects) and for the identified plant communities. We constructed the rarefaction curves with the R-based interactive online programme *iNEXT* (Chao et al. 2016).

Distribution of deciduous and evergreen trees along the elevational gradient

We wanted to determine the altitude at which the change from deciduous to evergreen species occurred. To that end, we first classified each tree species as either deciduous or evergreen and determined the relative percentage of each leaf strategy type (LST) for the estimated plant cover per vegetation relevé along the elevation gradient from 130 to 680 m (14 relevés / 100 m). Then, we calculated separate generalized additive models (GAM) for each LST using the *mgcv* package (Wood 2017) with a binomial distribution and a cubic regression spline for elevation to model the relationship between the percentage of respective LST per relevé and elevation in metres. We plotted the respective models using the *ggplot2* package (Wickham 2016) in R 3.5.0 statistical software (R Development Core Team 2018).

Results

Floristic pattern

We recorded 162 vascular plant species (104 perennials and 58 annuals) belonging to 53 families (Appendix 1). The most common families were Fabaceae (9%), Poaceae (9%), Asteraceae (7%) and Malvaceae (7%). Poaceae is one of the species rich families in the study area. However, the grasses were less abundant (frequent) and were represented by many annual species (Appendix 1; Tables S1–S7 in Suppl. material 1). In total, 84% of the recorded species were found in the mountain tributaries feeding Wadi Yahmib. The number of species varied among the three tributaries: in Marafai, Acow and Kansisrob, there were 131, 99 and 76 species, respectively. The lowest number of plant species (n=26) were recorded in Wadi Yahmib itself, located in the open sandy plain. The dominant life forms were therophytes (36%), phanerophytes (27%) and chamaephytes (24%). Of all perennial species, 63% were woody species, including *Vachellia tortilis*, *Balanites aegyptiaca* and *Dodonaea viscosa*, while 37% were herbs, such as *Forsskaolea tenacissima*, *Cucumis prophetarum* and *Senna italica*. We recorded 21 tree species in Wadi Yahmib and its tributaries (Appendix 1).

Pattern of deciduous-evergreen trees

The response of the two LSTs, i.e., deciduous and evergreen, showed two clear decreasing and increasing patterns along the altitudinal gradient from 130 to 680 m (Figure 3). While there was a slight change below 400 m, the deciduous-evergreen ratio changed from 75/25 to 25/75 between 450 m and 600 m, indicating a potential ecotone; the switch between both LSTs was at 500 m. The smoothness of both GAMs was highly significant, demonstrating a clear pattern in the data. While there were very few evergreen species in the lower parts of the gradient (e.g., *Maerua crassifolia*), deciduous species did occur in low numbers at higher elevations, such as *Vachellia etbaica* (synonym: *Acacia etbaica*) and *V. tortilis*.

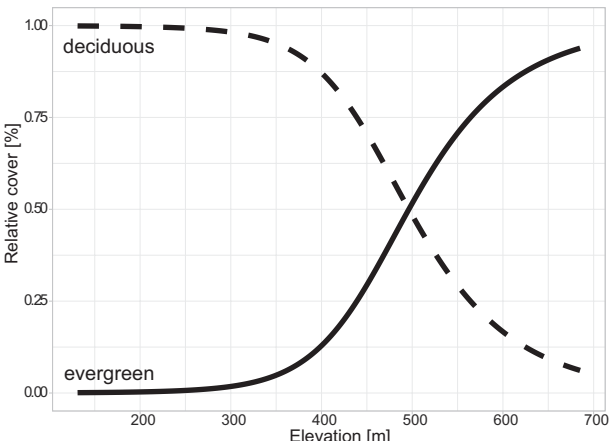

Figure 3. The relative proportions of deciduous and evergreen trees per vegetation relevé along the elevational gradient at the northern slopes of Gebel Elba. The pattern for deciduous tree species is shown as a dashed line while the evergreen tree species are represented by a solid line. The lines are the resulting smoothers of a cubic-regression GAM.

Classification

Seven woodland communities were described on Gebel Elba (Figure 4; Table 1). The first two communities (I-II) contained relevés from middle to higher elevations and were mainly composed of evergreens, while the communities (III-VII) in the lower part of the elevational gradient included relevés from low to middle elevations and were inhabited by deciduous trees (Tables 1, 2; Tables S1–S7 in Suppl. material 1). The observed communities were classified as follows.

I) *Dracaena ombet – Olea europaea* subsp. *cuspidata* community

This evergreen community was confined to the high elevations of Wadi Marafai, from 560 to 680 m. This community supported a high coverage of evergreen species and was characterized by six diagnostic evergreen species in total, including *Olea europaea* subsp. *cuspidata* and *Carissa spinarum* and two deciduous tree species, *Pistacia khinjuk* and *Vachellia etbaica*. The wadi bed was dominated mainly by *O. europaea* subsp. *cuspidata* (Figure 5C). The slopes were characterized by the growth of *V. etbaica* and *Dracaena ombet*. The vegetation in the wadi bed was dense and more vigorous than that occurring at lower elevations. In this community, many liana species, such as *Pergularia daemia*, *Jasminum fluminense* and *J. grandiflorum*, were climbing on olive trees. The soils of this community were often loamy sand on the side slopes and sandy loam in the wadi bed. The presence of large granite boulders increases water run-off to the main channels.

II) *Solanum incanum – Ficus salicifolia* community

This community was located mainly in moist habitats near flowing water or in the water courses of the high-elevation wadis, Wadis Acow and Marafai, at elevations from 346 to 550 m (Figure 5D). The vegetation consisted of two diagnostic fig trees (*Ficus salicifolia* and *F. palmata*) and two small shrubs (*Solanum incanum* and *Diceratella elliptica*). A characteristic species, *Searsia flexicaulis* (synonym: *Rhus flexicaulis*) from the former community, was also recorded in this community. The soil supporting this community was mainly loamy sand, and the organic matter content was the highest (0.41%, Table 3) of all seven communities. The organic matter content was related to the leaf litter of fig trees.

Table 1. Synoptic table of the seven communities showing percentage constancy values of the diagnostic species and non-diagnostic species with high constancy (> 70%). Diagnostic species are highlighted in light grey and highly diagnostic species in dark grey.

Community	I	II	III	IV	V	VI	VII
No. of plots	20	17	36	24	15	23	34
Total no. of species	80	73	84	84	48	68	72
Perennials	50	44	55	53	25	45	40
Annuals	30	29	29	31	23	23	32
No. of diagnostic species	8	4	1	1	2	3	2
***Dracaena ombet* - *Olea europaea* subsp. *cuspidata* community**							
Olea europaea subsp. *cuspidata*	90	12	-	-	-	-	-
Vachellia etbaica	45	-	-	-	-	4	-
Dracaena ombet subsp. *ombet*	40	-	3	-	-	-	-
Carissa spinarum	35	-	-	-	-	-	-
Searsia flexicaulis	55	35	-	-	-	-	-
Jasminum grandiflorum subsp. *floribundum*	30	-	-	-	-	-	-
Pistacia khinjuk var. *glabra*	30	6	-	-	-	-	-
Triumfetta flavescens	75	41	25	29	-	-	6
***Solanum incanum* - *Ficus salicifolia* community**							
Ficus salicifolia	10	47	14	-	-	-	-
Solanum incanum	55	76	17	-	7	-	15
Ficus palmata	-	18	-	-	-	-	-
Diceratella elliptica	-	18	3	-	-	-	-
***Vachellia tortilis* subsp. *tortilis* community**							
Vachellia tortilis subsp. *tortilis*	10	29	100	79	53	70	44
***Euphorbia nubica* community**							
Euphorbia nubica	-	-	17	88	33	57	24
Forsskaolea tenacissima	25	47	19	75	53	65	21
***Aerva javanica* - *Abutilon pannosum* community**							
Abutilon pannosum	-	24	8	8	100	48	9
Aerva javanica	-	18	11	4	67	35	6
Lycium shawii	-	18	50	50	73	39	26
***Euphorbia cuneata* community**							
Euphorbia cuneata	-	6	6	17	7	87	6
Tephrosia purpurea subsp. *apollinea*	-	-	11	67	87	83	26
Delonix elata	-	6	-	-	7	30	-
***Balanites aegyptiaca* – *Vachellia tortilis* subsp. *raddiana* community**							
Balanites aegyptiaca	-	-	11	38	13	-	85
Vachellia tortilis subsp. *raddiana*	-	-	3	8	13	9	44

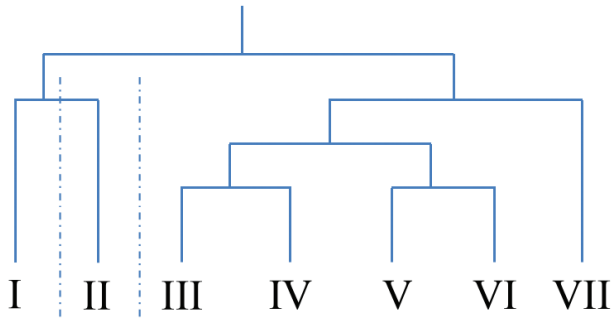

Figure 4. Dendrogram showing the TWINSPAN classification of the seven communities.

III) *Vachellia tortilis* subsp. *tortilis* community

This community was the most widespread one in the study area. The deciduous tree *Vachellia tortilis* subsp. *tortilis* was the only characteristic species (Figure 5E). This community occurred in a variety of habitats from low to middle elevations (130 to 383 m). The most common habitats of *V. tortilis* were the water channels of the wadis and gravelly terraces. This species was also abundant at the foot of Gebel Elba. The soil in this community was always sandy. The substrate deposits varied from fine sand in Wadi Yahmib to coarse sand deposits with gravel and rock detritus in the mountainous tributaries.

IV) *Euphorbia nubica* community

This community usually occurred on run-off slopes and the delta of Wadi Marafai. It was located in rocky habitats at middle elevations from 264 m to 379 m. The succulent shrub *Euphorbia nubica* was the only diagnostic species (Figure 5F). The tree layer was mainly absent on the run-off slopes, and *E. nubica* was the dominant succulent shrub, whereas *Forsskaolea tenacissima* grew on the lower run-off slopes of Wadi Kansisrob. Downward in the delta of Wadi Marafai, *E. nubica* grew in rocky outcrops between trees. We recorded the liana species *Cocculus pendulus* climbing on unhealthy trees of *Vachellia tortilis* and *Balanites aegyptiaca* in shady localities in the delta of Marafai. The soil texture was mainly loamy sand. This community had the highest silt (20.74%) and EC (1.59 mS/m) values.

V) *Aerva javanica* – *Abutilon pannosum* community

This community was located along the main channel of the tributary Wadi Kansisrob and occasionally downstream of

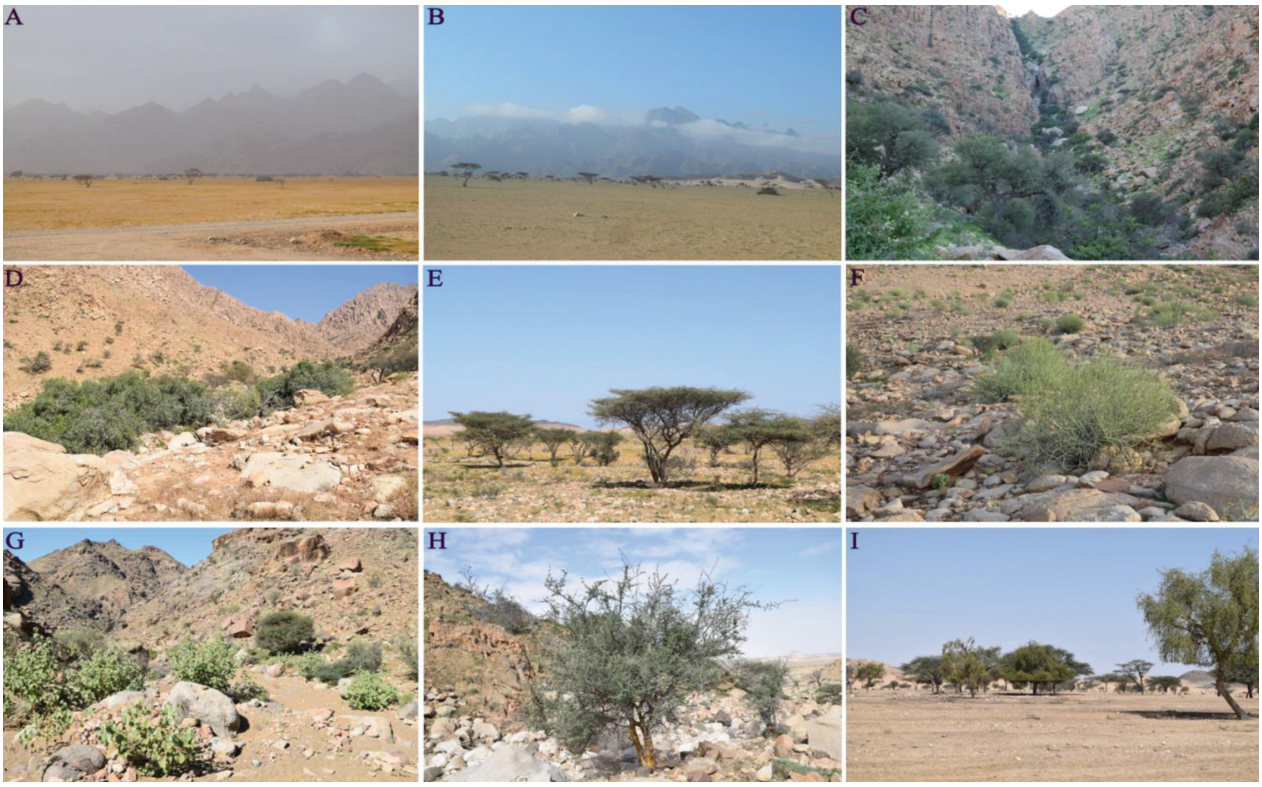

Figure 5. Representative photos showing Gebel Elba shrouded in mist (**A**) and clouds (**B**) accumulation on the Gebel Elba, and the leading species of the seven derived plant communities; *Olea europaea* subsp. *cuspidata* (**C**), *Ficus salicifolia* (**D**), *Vachellia tortilis* subsp. *tortilis* (**E**), *Euphorbia nubica* (**F**), *Abutilon pannosum* (**G**), *Euphorbia cuneata* (**H**), and *Balanites aegyptiaca* (**I**).

Table 2. Distribution of relevés, communities in the studied wadis, and the elevational gradients of the studied wadis and the seven communities (I–VII).

Communities		Localities				relevés per community
	Elevation	Yahmib (130–263 m)	Kansisrob (210–327 m)	Acow (228–410 m)	Marafai (350–680 m)	
I	(560–680 m)	–	–	–	20	20
II	(346–550 m)	–	–	9	8	17
III	(130–383 m)	11	1	16	8	36
IV	(264–379 m)	–	5	10	9	24
V	(237–275 m)	–	10	5	–	15
VI	(241–320 m)	–	17	6	–	23
VII	(196–361 m)	14	1	10	9	34
Total of relevés		**25**	**34**	**56**	**54**	**169**

Wadi Acow. It usually occurred in gravelly habitats near slopes at low elevations, from 237 to 275 m (Figure 5G). The two diagnostic species of this community were *Abutilon pannosum* and *Aerva javanica*. In this community, trees were less common, and the vegetation mainly consisted of shrubs and herbs, such as *Cucumis prophetarum*, *Tephrosia purpurea* and *Lycium shawii*. The soil was shallow, and the ground texture consisted of medium sand mixed with gravel and rock detritus. This community had the highest medium sand and pH values (38.46% and 7.73, respectively).

VI) *Euphorbia cuneata* community

This community occurred in the midstream areas of Wadi Kansisrob and was less frequent in Wadi Acow. It was often located in rocky habitats at elevations from 241 to 320 m (Figure 5H). Three diagnostic species characterized this community: two trees, *Euphorbia cuneata* and *Delonix elata*, and one herb, *Tephrosia purpurea*. The soil of this community had a high pH (7.63) and was similar to the soil of community V.

Table 3. Means and standard deviations for elevation and soil properties of the seven communities (I–VII). ANOVA test is for original, sqrt, or log data values, where values are not normally distributed. F-value and P-value refer to the ANOVA. Small letters denote the statistically different groups as identified by ANOVA post-hoc test.

	Parameter	I	II	III	IV	V	VI	VII	F-value	P-value
	Altitude.$_{log}$	^{a} 617.45 (57.72)	^{b} 450.49 (104.09)	^{c} 285.92 (96.63)	^{c} 321.51 (57.33)	^{c} 255.13 (19.43)	^{c} 280.51 (39.37)	^{c} 278.39 (82.94)	42.33	<0.001
Soil separates	**Coarse sand.$_{sqrt}$**	^{a} 22.88 (15.63)	^{ab} 14.25 (4.81)	^{b} 10.00 (7.09)	^{ab} 12.84 (4.94)	^{b} 11.13 (8.35)	^{ab} 15.48 (7.83)	^{ab} 14.39 (8.72)	5.073	<0.001
	Medium sand.$_{sqrt}$	^{bc} 27.75 (9.71)	^{abc} 32.80 (9.02)	^{ab} 36.10 (12.59)	^{c} 27.47 (8.06)	^{a} 38.46 (9.36)	^{a} 37.73 (8.64)	^{a} 37.92 (12.37)	4.997	<0.001
	Fine sand	^{b} 26.36 (10.58)	^{ab} 33.09 (5.46)	^{a} 37.76 (6.80)	^{a} 37.69 (6.12)	^{a} 36.78 (8.81)	^{ab} 32.82 (8.54)	^{ab} 32.88 (8.05)	5.997	<0.001
	Sand.$_{sqrt}$	^{b} 76.99 (15.41)	^{ab} 80.14 (9.33)	^{ab} 83.87 (9.39)	^{ab} 78.00 (7.80)	^{a} 86.37 (7.69)	^{a} 86.03 (7.49)	^{a} 85.19 (8.16)	3.823	<0.01
	Silt.$_{sqrt}$	^{ab} 20.06 (12.63)	^{ab} 18.75 (8.32)	^{ab} 15.28 (8.62)	^{a} 20.74 (6.86)	^{ab} 13.07 (7.31)	^{ab} 13.47 (7.18)	^{b} 14.04 (7.70)	2.968	<0.01
	Clay.$_{sqrt}$	^{a} 2.62 (3.27)	^{ab} 0.95 (1.20)	^{b} 0.77 (1.00)	^{ab} 1.21 (1.29)	^{b} 0.47 (0.57)	^{b} 0.36 (0.50)	^{b} 0.57 (0.91)	4.145	<0.001
Soil chemistry	**pH**	^{b} 7.26 (0.24)	^{b} 7.36 (0.24)	^{b} 7.35 (0.23)	^{b} 7.30 (0.20)	^{a} 7.73 (0.24)	^{a} 7.63 (0.26)	^{b} 7.26 (0.26)	12.41	<0.001
	EC$_{.log}$	^{c} 0.74 (0.35)	^{abc} 0.80 (0.20)	^{abc} 1.19 (0.98)	^{a} 1.59 (1.54)	^{bc} 0.84 (0.66)	^{abc} 1.12 (1.00)	^{ab} 1.20 (0.56)	4.199	<0.001
	$CaCO_{3.log}$	^{a} 1.05 (1.06)	^{ab} 1.21 (1.56)	^{c} 0.55 (0.39)	^{abc} 0.61 (0.31)	^{c} 0.54 (0.58)	^{abc} 0.71 (0.50)	^{bc} 0.57 (0.35)	4.096	<0.001
	$CO_{3.sqrt}$	^{a} 0.03 (0.02)	^{a} 0.04 (0.03)	^{a} 0.03 (0.01)	^{a} 0.04 (0.02)	^{a} 0.03 (0.02)	^{a} 0.03 (0.02)	^{a} 0.04 (0.04)	1.541	0.168
	$HCO_{3.log}$	^{b} 0.29 (0.17)	^{a} 0.63 (0.62)	^{ab} 0.35 (0.16)	^{a} 0.47 (0.20)	^{b} 0.24 (0.10)	^{b} 0.29 (0.14)	^{ab} 0.39 (0.19)	5.045	<0.001
	Organic matter.$_{sqrt}$	^{c} 0.11 (0.08)	^{a} 0.41 (0.30)	^{c} 0.20 (0.17)	^{ab} 0.35 (0.27)	^{c} 0.15 (0.12)	^{abc} 0.23 (0.16)	^{bc} 0.21 (0.19)	6.113	<0.001
	Ca.$_{log}$	^{b} 0.05 (0.02)	^{a} 0.09 (0.05)	^{a} 0.10 (0.08)	^{a} 0.14 (0.21)	^{ab} 0.07 (0.05)	^{ab} 0.08 (0.08)	^{a} 0.09 (0.05)	5.154	<0.001
	Mg.$_{log}$	^{b} 0.03 (0.02)	^{ab} 0.07 (0.07)	^{ab} 0.04 (0.02)	^{a} 0.06 (0.04)	^{b} 0.02 (0.01)	^{ab} 0.03 (0.02)	^{ab} 0.05 (0.03)	4.038	<0.001
	Na.$_{log}$	^{b} 0.04 (0.03)	^{ab} 0.04 (0.03)	^{a} 0.07 (0.05)	^{ab} 0.06 (0.06)	^{ab} 0.04 (0.04)	^{ab} 0.05 (0.05)	^{a} 0.06 (0.03)	3.652	<0.01
	K.$_{log}$	^{c} 0.04 (0.03)	^{ab} 0.09 (0.06)	^{ab} 0.09 (0.11)	^{a} 0.12 (0.11)	^{bc} 0.05 (0.05)	^{bc} 0.07 (0.10)	^{a} 0.09 (0.07)	7.485	<0.001
	SO_4	^{a} 0.02 (0.05)	^{a} 0.02 (0.02)	^{a} 0.08 (0.12)	^{a} 0.17 (0.55)	^{a} 0.08 (0.12)	^{a} 0.08 (0.14)	^{a} 0.07 (0.07)	1.06	0.389
	Cl.$_{log}$	^{c} 0.04 (0.04)	^{bc} 0.05 (0.05)	^{ab} 0.15 (0.20)	^{ab} 0.22 (0.43)	^{abc} 0.08 (0.13)	0.13 (0.20)	0.13 (0.10)	5.194	<0.001

VII) *Balanites aegyptiaca* – *Vachellia tortilis* subsp. *raddiana* community

This community was located in Wadi Yahmib and in the deltas of its tributaries at elevations ranging from 196 to 361 m. It was represented mainly by patches in Wadi Yahmib (Figure 5I) and some patches in the midstream areas of its tributaries. *Balanites aegyptiaca* and *Vachellia tortilis* subsp. *raddiana* were the two diagnostic species of this community. Unlike the *V. tortilis* subsp. *tortilis* community, which occurred in several habitats, this community was usually restricted to water channels. The soil supporting this community was usually pure sand with fine soil deposits.

Environmental drivers

The soils of the study area were characterized as neutral to slightly alkaline, with the mean pH value ranging from 7.26 to 7.73 (Table 3). The soil texture was pure sand on the desert plain and changed to sandy loam at higher elevations. The EC (0.74–1.59 mS/m) and mineral contents were low. The $CaCO_3$ content was less than 3% (0.54–1.21%), and the organic matter content ranged from 0.11 to 0.41% (Table 3), which is considered very low but typical for arid ecosystems.

The CCA results revealed that the edaphic factors changed with the elevational gradient (Figure 6). At the foot of Gebel Elba, the soil texture was defined primarily by fine and medium sands. High proportion of sands at low elevations led to poor water holding capacity, and thus, the EC of the surface layer increased. The vegetation in the sandy part of the gradient consisted mainly of deep-rooted tree species, e.g., *Vachellia tortilis* and *Balanites aegyptiaca*. At higher elevations on Gebel Elba, the silt and clay contents increased, thus supporting the growth of less drought-resistant species, such as *Ficus salicifolia*, *Olea europaea* subsp. *cuspidata*, *Carissa spinarum* and *Pistacia khinjuk* (Figure 6). Mountain communities at lower elevations, mainly in Wadi Kansisrob, contained plant species suited to higher soil pH values i.e., *Abutilon pannosum* and *Euphorbia cuneata*. Overall, Wadi Kansisrob was the driest and the least diverse among the studied mountainous wadis.

Plant diversity (species richness)

The plant diversity in the study area clearly differed between the four sampled wadis and the seven observed communities. Generally, Wadi Marafai was the most diverse wadi, with 131 species, while W. Yahmib was the least diverse, with only 26 species. When the sampling size was fixed at 24 relevés (Figure 7; Table 4), we expected the wadis to be ranked as Marafai > Acow > Kansisrob > Yahmib, which reflected the same order as the altitude gradient. The lower and upper bounds of the extrapolated species richness curve did not overlap, although there was some overlap between Acow and Kansisrob, yet there was still a significant difference in the lower bound of species richness (Figure 7; Table 4). Interestingly, these two wadis showed greater differences when the sampling rate was lower (Figure 7). When we compared the upper vs the lower bounds of species richness for the communities (Table 4), we recognized two main groups. The first group contained the communities with high species richness (I, II, and IV) from the higher wadis, i.e., Acow and Marafai. The communities located in the lower wadis, i.e., Kansisrob and Yahmib (III, V, VI, and VII) belonged to the second group, with significantly reduced species rich-

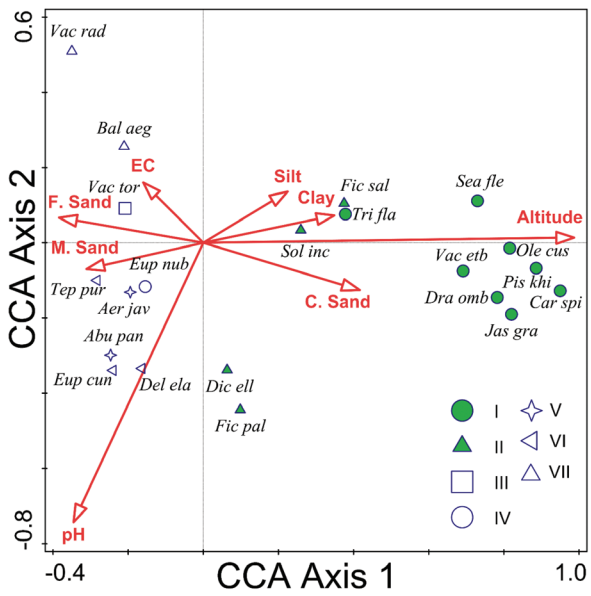

Figure 6. CCA ordination showing the relation between perennial species with phi coefficient > 0.25 and environmental factors represented by altitude and seven soil parameters. Variation is mostly explained by elevation (Alt), soil texture and pH. The lower left part contains species from Wadi Kansisrob. The upper part contains species of the open sandy plain, Wadi Yahmib. The right part contains evergreen species from mid to higher elevations. Eigenvalues for biplot scaling are 0.60 for axis 1 and 0.16 for axis 2 and the adjusted explained variation is 11.54%. The legend is placed at the lower right part of the figure. The diagnostic species for each community are represented by different symbols; solid symbols for communities of higher elevations and hollow symbols for communities from low to middle elevations. For species and sand fractions abbreviations see Tables 1, 3.

ness (significant because the upper confidence value did not overlap with the lower value of the other group).

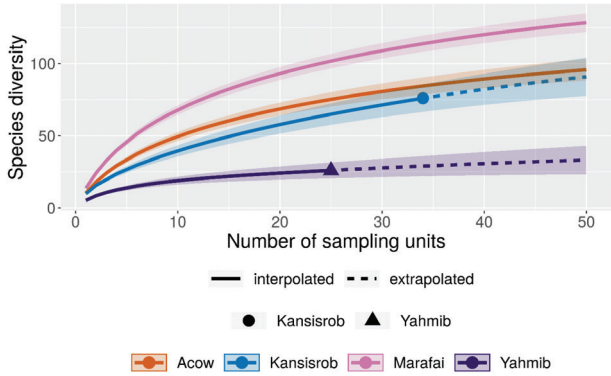

Figure 7. Sample-size-based rarefaction and extrapolation sampling curve for the four studied wadis.

Table 4. Sample based rarified richness for the four studied wadis and the seven studied communities at sample size equal 24 relevés for wadis and 13 for communities.

		t	Richness	Lower	upper
Wadi	**Marafai**	24	100.15	94.30	106.00
	Acow	24	74.02	69.65	78.38
	Kansisrob	24	63.62	56.94	70.30
	Yahmib	24	25.64	20.11	31.17
Community	**I**	13	68.11	62.97	73.25
	II	13	65.15	58.88	71.43
	III	13	52.35	47.51	57.20
	IV	13	63.73	57.82	69.64
	V	13	44.07	37.58	50.56
	VI	13	51.54	45.51	57.57
	VII	13	46.26	41.87	50.65

Discussion

Floristic pattern

The location of Gebel Elba offers a lush "mist oasis" ecosystem where the sea-facing slopes are blanketed by moisture-laden clouds (Hegazy and Lovett-Doust 2016). Gebel Elba Mountain acts as a refuge for tropical flora in an otherwise arid regional climate. While the flora of Gebel Elba is found across south Egypt, the floristic composition is similar to that of neighbouring mountains, such as Jebel Marra, Sudan, and the Asir Mountains, Saudi Arabia (Wickens 1976; Hegazy et al. 1998). Fabaceae, Poaceae and Asteraceae have previously been reported as the most common families on Gebel Elba and in the arid mountains of East Africa and the southern Arabian Peninsula (Abd El-Ghani and Abdel-Khalik 2006). We found that therophytes, phanerophytes and chamaephytes were the dominant life forms in Gebel Elba. Similar results for life forms were observed in the Eastern desert of Egypt and in south-western Saudi Arabia (Abd El-Ghani and Abdel-Khalik 2006). The flora of East Africa and southwest Asia is influenced by Somalia-Masai elements. The Somalia-Masai regional centre of endemism is covered by deciduous and evergreen bushlands, while grasses are represented by a few annual and short-lived perennial species (White 1983; White and Léonard 1991). According to Zohary (1973), Gebel Elba and southwestern Arabia harbour Sudanian floras and represent the northern boundaries of the Eritreo-Arabian province. This area comprises a belt of savanna vegetation in East Africa and extends through tropical Arabia (Zohary 1973; Zahran and Willis 2009). The Sudanian flora of Gebel Elba is characterized by a large proportion of tropical shrub and tree species (Zohary 1973; Abd El-Ghani and Abdel-Khalik 2006; Al-Gohary 2008). The number of tree species we recorded (n=21) was greater than other studies found in similar regions in Egypt (e.g. Boulos 2008). The most abundant species were deciduous trees at lower elevations, e.g., *Vachellia tortilis* subsp. *tortilis*, *V. tortilis* subsp. *raddiana* and *Balanites aegyptiaca*, while evergreen trees characterized the higher elevations, such as *Searsia flexicaulis* and *Olea europaea* subsp. *cuspidata*. It is misleading to describe the vegetation as savanna depending on the floristic list only, because Gebel Elba is characterized by deciduous bushland and grasses contribute little to the plant biomass (White 1983).

Classification

Many Saharo-Arabian vegetation types grow in Egypt, and Sudanian vegetation is represented only in the southern part of Egypt. The Sudanian vegetation is divided into Nubo-Sindian vegetation, mainly in desert wadis and depressions, and Eritreo-Arabian vegetation, which is restricted to the Gebel Elba region (Zohary 1973). According to White and Léonard (1991) and Boulos (2008), vegetation of the Gebel Elba represents a satellite of the Somalia-Masai region, and the southern part of the Arabian Peninsula is an extension of this region into southwest Asia. However, Gebel Elba is lower than the tropical mountain ranges in the area (Ghazanfar 1991; Hegazy et al. 1998). The vegetation showed altitudinal zonation that was comparable to the patterns in East Africa and tropical Arabia. Two main climatic zones were observed, both of which are typical for East Africa and tropical Arabia. Palaeotropical *Vachellia-Commiphora* woodland was present from the foothills of Gebel Elba to the middle elevations, and the mist zone showed fragments of Afromontane forest dominated by *O. europaea* subsp. *cuspidata* (Zohary 1973; Zahran and Willis 2009).

Our classification results for the northern slopes of Gebel Elba accorded with the observation of Zahran and Willis (2009). According to Zohary (1973), the lower elevations of Gebel Elba were classified as Acacietea sudano-arabica. This class comprises the bulk of the xerotropical vegetation on Gebel Elba from low to middle elevations. In this study, we described six communities within deciduous *Vachellia-Commiphora* woodland and one community within evergreen *Olea* woodland. However, the fine resolution of this study allowed us to characterize specific habitats within each community, thereby providing a more exact zonation of the plant communities along the altitudinal gradients.

Only two communities represented the desert plains and foothills to the mid elevations of Gebel Elba, forming an open woodland; *Balanites aegyptiaca - Vachellia tortilis* subsp. *raddiana* and *Vachellia tortilis* subsp. *tortilis*, although the former was restricted to the main water channels. The *V. tortilis* subsp. *tortilis* community is more drought resistant and occurred in several habitats, e.g., channels, terraces and gentle slopes. *V. tortilis* subsp. *raddiana* is much more widespread in the Eastern Desert and Sinai Peninsula (Zohary 1973; Abutaha 2010; Morsy et al. 2010), whereas *V. tortilis* subsp. *tortilis* communities are mostly confined to the southern part of Egypt, Sudan and tropical Arabia (Kassas 1957; Ghazanfar 1991; Zahran and Willis 2009).

In the mountain wadis, the lower part of the elevation gradient (210–350 m) was more arid than the higher part (350–680 m). Three communities were recorded in rocky habitats (stony, rocky outcrops and run-off slopes) from low to middle elevations. Stony habitats near run-off slopes were occupied by *Aerva javanica – Abutilon pannosum* community. This community was characterized by frutescent vegetation. The characteristic species were shrubs and herbs, whereas the tree layer was less established. *Aerva* communities are more common in stony wadis and the southern slopes of Gebel Elba (Ahmed 1999; Zahran and Willis 2009). Additionally, *Aerva javanica* and *Abutilon pannosum* are frequent in the frutescent communities of the Hijaz Mountains, Saudi Arabia (Abd El-Ghani 1996). Rocky outcrop habitats are more favourable for plants than habitats with shallow soil containing stones in the upper layer, because rainwater can accumulate in rock crevices, leading to well-developed soil. In addition, rocks offer shade for herbs (Zohary 1973). We found that the *Euphorbia cuneata* community dominated this habitat in the lower parts of the northern slopes of Gebel Elba. While this community is found on the northern slopes of Gebel Elba and is common in the arid zones of Erkwit, the species *Euphorbia cuneata* has occasionally been recorded in the runnels of the southern slopes of Gebel Elba (Kassas 1956; Zahran and Willis 2009). At middle elevations, the succulent species, *Euphorbia nubica*, grows on run-off slopes and rocky outcrops. *Euphorbia cuneata* community is replaced by *Euphorbia nubica* community on rocky outcrops as the elevation increases. This distribution pattern of the two *Euphorbia* communities on Gebel Elba was comparable to that of the coastal mountains of Sudan (Kassas 1960; Zahran and Willis 2009). While rainwater is well preserved between boulders in wadi beds, run-off slopes are dry habitats, and rainfall is less available for plants (Deil 2014). Thus, the succulent *E. nubica* community is the pedoclimax community on the run-off slopes of Gebel Elba, whereas *Vachellia-Commiphora* woodland is the climax community on wadi beds. This distribution pattern is comparable to the pattern of succulent vegetation in Yemen; however, we did not record any similar communities (Deil 2014).

The higher elevations of Gebel Elba are influenced relatively by monsoon clouds more than the lowlands. The vegetation in this moist zone is less resistant to drought and is represented by fragments of *Ficus* and *Olea* forest (Zohary 1973). Similarly to Zohary, we identified two communities, *Solanum incanum - Ficus salicifolia* which is found lower down than *Dracaena ombet - Olea europaea* subsp. *cuspidata*; the former represents the *Ficus* community, whereas the latter represents the *Olea* community. *Ficus* is a typical wadi species that grows on water run-on habitats in *Vachellia-Commiphora* woodlands (Zohary 1973; Ghazanfar 1991). *Vachellia tortilis* subsp. *tortilis* is frequent in this community, which also contains characteristic species of *Olea* communities. In our view, this community represents an ecotone (transitional plant community) between the *Vachellia* and *Olea* woodlands.

Dracaena ombet - Olea europaea subsp. *cuspidata* was found in the mist zone of Gebel Elba. Many characteristic species from the evergreen *Olea* woodland can be observed here, such as *Dodonaea viscosa*, *Euclea racemosa* and *Maytenus senegalensis*. The wadi bed was dominated mainly by evergreen trees, such as *O. europaea* subsp. *cuspidata* and *Searsia flexicaulis*, which may form forest-like growth (Abd El-Ghani and Abdel-Khalik 2006). Plant individuals

were crowded in patches (Zahran and Willis 2009) due to the presence of many liana species on olive trees, such as *Pergularia daemia*, *Jasminum fluminense* and *J. grandiflorum*. The olive community contained many vascular species that are the least resistant to drought and are thus confined to the highest elevations of the northern slopes of Gebel Elba (Zahran and Willis 2009). The mountain slopes were characterized by rich *Vachellia etbaica* growth, which was also recorded on the northern slopes of three coastal mountains in the Elba range but not on the inland mountains (Zahran and Willis 2009). Most of these species were also very abundant in the wettest zone of the Erkwit mist oasis, Sudan (Kassas 1956). Additionally, healthy populations of *Dracaena ombet* were observed at higher elevations on the northern slopes of Gebel Elba (Kamel et al. 2015; Elnoby and Moustafa 2017). *Dracaena ombet* is usually associated with *O. europaea* subsp. *cuspidata* on Gebel Elba, and scattered populations extend southward from Sudan to Somalia along the African hills that face the Red Sea (Marrero et al. 1998; Kamel et al. 2015).

According to White (1983) and Kürschner et al. (2008) the evergreen '*Olea* woodland' is in close association with the *Vachellia-Commiphora* woodland sensu Zohary (1973), which characterize the lower slopes and also to the montane forest communities of *Juniperus procera* forest. Because of the lower topography of Gebel Elba (1435 m), we encountered the *Olea* woodland but not the upper montane *Juniperus procera* woodland which occured above ca. 2000 m in the Asir mountains, Saudi Arabia and the Yemen highlands (Kürschner et al. 2008). Also, the *Dracaena ombet - Olea europaea* subsp. *cuspidata* community here is found at lower elevations (560–680 m) than the community of *Tarchonanthus camphoratus - Olea europaea* subsp. *cuspidata* (1600–2000 m) in the Arabian Peninsula (Kürschner et al. 2008).

Environmental drivers

The water supply for plants strongly depends on soil structure, rainfall, and plant cover. The capacity of soil to store moisture, in turn, depends on the depth and quality of soil supporting plant growth (Körner 2012). Sandy soils at low elevations exhibited poor water storage capacities in our study. The sandy plain mainly supported the growth of drought-tolerant trees, e.g., *Vachellia tortilis* subsp. *tortilis*, *V. tortilis* subsp. *raddiana* and *Balanites aegyptiaca* (Zahran and Willis 2009). However, soils in rocky habitats at higher elevations often have higher water holding capacities. Fine soil material accumulates in rock crevices, and rainwater is well protected against evaporation (Zohary 1973; Deil 2014). The sandy loamy soils support a dense growth of *Olea* trees (Ahmed et al. 2016). Furthermore, water droplets from mist and clouds increase the moisture content of soils and reduce plant transpiration rates (Hegazy and Lovett-Doust 2016). The drought stress has a stronger effect on species richness than physiological stress associated with extreme soil pH values (Palpurina et al. 2017). The elevational gradient of the studied wadis could mirror an inversed stress gradient (Abutaha et al. 2019). In arid climates, water evaporates quickly, leading to an increase in the alkalinity and EC of soil (Knapp 1973; Abutaha 2010). At higher elevations, orographic precipitation decreases the pH and EC. This negative relationship between precipitation and soil pH results in favourable soil conditions for plant growth at higher wadis. Although we did not determine the soil moisture content, orographic precipitation and the soil quality at higher elevations seem to support the growth of moist vegetation.

Plant diversity (species richness)

In the wadi systems of Gebel Elba, the species richness increased from low to mid elevation, followed by a plateau pattern from mid to high elevation (Abutaha et al. 2019). This pattern represented the transition from desert to mountain wadi systems. The increase in species richness was the result of reduced climatic stress and increased water availability. The high species richness from mid to higher elevations was related to more climatically suitable conditions for plant growth and diversity (Ghazanfar 1991; El-Keblawy et al. 2016; Hoppe et al. 2018). However, there are many other factors that may affect plant species richness, particularly mountain topography. A complex topography results in relatively greater habitat diversity. Cliffs, crevices and large boulders offer more favourable conditions to plants (Zohary 1973; Hegazy and Lovett-Doust 2016). For example, rocky habitats collect water run-off, supporting dense tree populations. Furthermore, the topography offers more shade for herbs and shrub species. Plant growth is commonly less constrained by soil moisture shortages at high elevations than at low elevations. Precipitation often increases with increasing elevation, and the evaporation/precipitation ratio decreases (Körner 2007). The increase in richness on Gebel Elba could thus be the result of reduced stress and an increase in water availability due to orographic precipitation at higher elevations (Abutaha et al. 2019).

Deciduous / evergreen trees pattern with elevation

The tree limit in arid mountains is mainly determined by drought resistance (Gieger and Leuschner 2004; Karger et al. 2019). The natural vegetation of Gebel Elba includes deciduous and evergreen woodlands (Zohary 1973). The studied elevational gradient (130–680 m) seems to be a major stress gradient in terms of water availability and temperature. The lower elevations are more arid and thus support the growth of scattered drought-deciduous species such as *Vachellia* trees. However, the orographic precipitation at higher elevations exhibit a trend of increasing evergreen species richness that are less resistant to drought (Zahran and Willis 2009). Hence, we can confirm that deciduous species prevail in the more arid parts of the total elevational gradient and occur

in the upper parts as they also can cope with the humid conditions. Nevertheless, drought-resistant deciduous trees appear to be outcompeted by evergreen species with continuous increasing elevation. Above 500 m, evergreen species continuously dominate the vegetation relevés. This confirms our findings from the vegetation classification, i.e. evergreen *Olea* and *Ficus* communities compared with identified deciduous vegetation units *Vachellia* and *Balanites*. Local tree limits can also be greatly altered by fine-scale topography (Case and Duncan 2014; Karger et al. 2019). Up to 400 m, the slopes of Gebel Elba mainly comprise of open sandy plain or stony habitats. From 500 m upward, the mountain slopes of Wadi Marafai become steeper and narrower, thus providing more shadow, and the rockier slopes increase water runoff to wadi beds (Abutaha et al. 2019).

Conclusion

In this study, we identified seven communities along the elevational gradients of four wadis in the northern slopes of Gebel Elba. These communities show an altitudinal zonation and represent the core of the Eritreo-Arabian (tropical) vegetation in the Gebel Elba National Park, Egypt. Two main woodland types are observed in Gebel Elba; first, a deciduous *Vachellia* woodland, appearing in the desert plain and foothills to the mid-elevations of Gebel Elba (communities III–VII). Second, an evergreen *Olea* woodland, at the upper moisture altitudes (community I). The lower limit of the evergreen vegetation in Gebel Elba is found to be lower than in the higher mountains of East Africa and tropical Arabia. The studied elevational gradient mirrors a typical stress gradient. We found that each plant community within the *Vachellia* woodland is restricted to a definite habitat depending on its ability to adapt to drought stress, while the climatically more favourable habitats are occupied by the *Olea* community. The *Ficus* community (II) represents a transition zone between deciduous and evergreen communities. In sum, orographic precipitation, soil quality and complex topography are the main factors that affect the vegetation structure and species richness of Gebel Elba.

Author contributions

M.M.A. carried out fieldwork and soil analysis, M.M.A. and J.O. performed the statistical analyses and wrote the first draft of the manuscript, while all authors contributed to the final version.

Acknowledgements

This research was partially funded by the Egyptian government, Ministry of Higher Education and the Academy of Scientific Research & Technology, Egypt.

References

Abd El-Ghani MM (1996) Vegetation along a transect in the Hijaz mountains (Saudi Arabia). Journal of Arid Environments 32: 289–304. https://doi.org/10.1006/jare.1996.0024

Abd El-Ghani MM, Abdel-Khalik KN (2006) Floristic diversity and phytogeography of the Gebel Elba National Park, south-east Egypt. Turkish Journal of Botany 30: 121–136.

Abutaha MM (2010) Habitat and species diversity in some wadis in Sinai Peninsula. Master Thesis, University of Ain Shams, Cairo, EG, 147 pp.

Abutaha MM, El-Khouly AA, Jürgens N, Morsy AA, Oldeland J (2019) Elevation-richness pattern of vascular plants in wadis of the arid mountain Gebel Elba, Egypt. African Journal of Ecology 57: 238–246. https://doi.org/10.1111/aje.12593

Boden AG (2005) Bodenkundliche Kartieranleitung, 5. verbesserte und erweiterte Auflage. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, DE, 438 pp.

Ahmed AM (1999) Phytosociological analysis of natural plant cover of fourteen wadis dissecting the Red Sea mountainous chains including Gebel Elba. In: Ahmed AM (Ed.) Ecological studies and biodiversity of Shalateen–Halaib area, Red Sea coast, Egypt. Project Report, Desert Research Center, Cairo, EG, 88–111.

Ahmed MI, Ashraf MI, Malik S.U, Hussain Q (2016) Influence of soil based growing media on vegetative propagation of selected cultivars of *Olea europaea* L. Pakistan Journal of Botany 48: 1489–1493.

Al-Gohary IH (2008) Floristic composition of eleven wadis in Gebel Elba, Egypt. International Journal of Agriculture and Biology 10: 151–160.

Ball J (1912) The geography and geology of south-eastern Egypt. Government press, Cairo, EG, 394 pp.

Berhanu A, Demsew S, Woldu Z, Friis I, van Breugel P (2018) Intermediate evergreen Afromontane forest (IAF) in northwestern Ethiopia: observations, description and modelling its potential distribution. Phytocoenologia 48: 351–367. https://doi.org/10.1127/phyto/2018/0207

Boulos L (1999) Flora of Egypt, Vol. 1 (*Azollaceae-Oxalidaceae*). Al-Hadara Publishing, Cairo, EG, 419 pp.

Boulos L (2000) Flora of Egypt, Vol. 2 (*Geraniaceae-Boraginaceae*). Al-Hadara Publishing, Cairo, EG, 352 pp.

Boulos L (2002) Flora of Egypt, Vol. 3 (*Verbenaceae-Compositae*). Al-Hadara Publishing, Cairo, EG, 373 pp.

Boulos L (2005) Flora of Egypt, Vol. 4 (*Monocotyledons*). Al-Hadara Publishing, Cairo, EG, 617 pp.

Boulos L (2008) Flora and Vegetation of the Deserts of Egypt. Flora Mediterranea 18: 341–359.

Boulos L (2009) Flora of Egypt checklist, revised annotated edition. Al-Hadara Publishing, Cairo, EG, 410 pp.

Case BS, Duncan RP (2014) A novel framework for disentangling the scale-dependent influences of abiotic factors on alpine treeline position. Ecography 37: 838–851. https://doi.org/10.1111/ecog.00280

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84: 45–67. https://doi.org/10.1890/13-0133.1

Chao A, Ma KH, Hsieh TC (2016) iNEXT (iNterpolation and EXTrapolation): Online program and user's guide. http://chao.stat.nthu.edu.tw/wordpress/software_download/ [accessed on 11.02.2019]

Combs SM, Nathan MV (1998) Soil organic matter. In: Brown JR (Ed.) Recommended Chemical Soil Test Procedure for the North Central Region. Missouri Agricultural Experiment Station, Columbia, US, 53–58.

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90: 3566–3574. https://doi.org/10.1890/08-1823.1

Deil U (2014) Rock communities and succulent vegetation in Northern Yemen (SW Arabia) –ecological, phytochorological and evolutionary aspects. Phytocoenologia 44: 193–234. https://doi.org/10.1127/0340-269X/2014/0044-0590

El-Keblawy AA, Khedr AA, Khafaga TA (2016) Mountainous landscape vegetation and species composition at Wadi Helo: a protected area in Hajar Mountains, UAE. Arid Land Research and Management 30: 389–399. https://doi.org/10.1080/15324982.2015.1136970

Elnoby SK, Moustafa AA (2017) Impact of climate change on the endangered Nubian dragon tree (Dracaena ombet) in the South Eastern of Egypt. Catrina 16: 25–31.

Estefan G, Sommer R, Ryan J (2013) Methods of soil, plant, and water analysis: A manual for the West Asia and North Africa region (3rd ed.). International Center for Agricultural Research in the Dray Areas (ICARDA), Beirut, LB, 243 pp.

Ghazanfar SA (1991) Vegetation structure and phytogeography of Jabal Shams, an arid mountain in Oman. Journal of Biogeography 18: 299–309. https://doi.org/10.2307/2845400

Gieger T, Leuschner C (2004) Altitudinal change in needle water relations of *Pinus canariensis* and possible evidence of a drought-induced alpine timberline on Mt. Teide, Tenerife. Flora 199: 100–109. https://doi.org/10.1078/0367-2530-00139

Gomaa HN (2014) Microhabitat variations and seed bank-vegetation relationships in a desert wadi ecosystem. Flora 209: 725–732. https://doi.org/10.1016/j.flora.2014.09.004

Goodman SM, Meininger PL (1989) The birds of Egypt. Oxford University Press, Oxford, GB, 551 pp.

Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. International Journal of Climatology 34: 623–642. https://doi.org/10.1002/joc.3711

Hegazy AK, Lovett-Doust J (2016) Plant ecology in the Middle East. Oxford University Press, Oxford, GB, 339 pp. https://doi.org/10.1093/acprof:oso/9780199660810.001.0001

Hegazy AK, El-Demerdash MA, Hosni HA (1998) Vegetation, species diversity and floristic relations along an altitudinal gradient in southwest Saudi Arabia. Journal of Arid Environments 38: 3–13. https://doi.org/10.1006/jare.1997.0311

Hendershot WH, Lalande H, Duquette M (2008) Soil reaction and exchangeable acidity. In: Carter MR, Gregorich EG (2nd ed.) Soil Sampling and Methods of Analysis. CRC Press, Boca Raton, Florida, US, 173–178. https://doi.org/10.1201/9781420005271.ch16

Hill MO (1979) TWINSPAN - a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University, New York, US, 90 pp.

Hoppe F, Schickhoff U, Oldeland J (2018) Plant species diversity of pastures in the Naryn Oblast (Kyrgyzstan). Die Erde 149: 214–226. https://www.die-erde.org/index.php/die-erde/article/view/384

IUCN (2019) The IUCN Red List of Threatened Species v. 2018-2. http://www.iucnredlist.org/ [accessed on 07.03.2019]

Jackson ML (1967) Soil chemical analysis. Prentice Hall of India Private limited, New Delhi, IN, 498 pp.

Kamel M, Ghazaly UM, Callmander MW (2015) Conservation status of the Endangered Nubian dragon tree in Gebel Elba National Park, Egypt. Oryx 49: 704–709. https://doi.org/10.1017/S0030605313001385

Karger DN, Kessler M, Conrad O, Weigelt P, Kreft H, König C, Zimmermann NE (2019) Why tree lines are lower on islands—Climatic and biogeographic effects hold the answer. Global Ecology and Biogeography 28: 839–850. https://doi.org/10.1111/geb.12897

Kassas M (1956) The mist oasis of Erkwit, Sudan. Journal of Ecology 44: 180–194. https://doi.org/10.2307/2257161

Kassas M (1957) On the ecology of the Red Sea coastal land. Journal of Ecology 45: 187–203. https://doi.org/10.2307/2257084

Kassas M (1960) Certain aspects of landform effects on plant-water resources. Bulletin de la Société de Géographie d'Égypte 33: 45–52.

Kassas M, Zahran MA (1971) Plant life on the coastal mountains of the Red Sea, Egypt. The Journal of the Indian Botanical Society, Golden Jubilee Volume 50A: 571–589.

Knapp R (1973) Die Vegetation von Afrika. Fischer, Stuttgart, DE, 626 pp.

Körner C (2007) The use of 'altitude' in ecological research. Trends in Ecology & Evolution 22: 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Körner C (2012) Alpine treelines: Functional ecology of the global high elevation tree limits. Springer, Basel, CH, 220 pp. https://doi.org/10.1007/978-3-0348-0396-0

Kürschner H, Hein P, Kilian N, Hubaishan AM (2004) The Hybantho durae-Anogeissetum dhofaricae ass. nova - phytosociology, structure and ecology of an endemic South Arabian forest community. Phytocoenologia 34: 569–612. https://doi.org/10.1127/0340-269X/2004/0034-0569

Kürschner H, Kilian N, Hein P (2008) The Tarchonantho camphoratae-Oleetum cuspidatae ass. nov. - an Afromontane evergreen sclerophyllous community of the Arabian Peninsula with strong relationships to E Africa. Phytocoenologia 38: 85–106. https://doi.org/10.1127/0340-269X/2008/0038-0085

Marrero A, Almeida RS, Gonzalez-Martin M (1998) A new species of the wild dragon tree, *Dracaena* (Dracaenaceae) from Gran Canaria and its taxonomic and biogeographic implications. Botanical Journal of Linnean Society 128: 291–314. https://doi.org/10.1006/bojl.1998.0193

Miller JJ, Curtin D (2008) Electrical conductivity and soluble ions. In: Carter MR, Gregorich EG (2nd ed.) Soil Sampling and Methods of Analysis. CRC Press, Boca Raton, Florida, US, 161–171. https://doi.org/10.1201/9781420005271.ch15

Morsy AA, Hassanein AA, Keilani SS, Abutaha MM (2010) A comparative study on the vegetation of two wadis, Sinai Peninsula. Taeckholmia 30: 29–57.

Palpurina S, Wagner V, von Wehrden H, Hájek M, Horsák M, Brinkert A, Hölzel N, Wesche K, Kamp J., ... Chytrý M (2017) The relationship between plant species richness and soil pH vanishes with increasing aridity across Eurasian dry grasslands. Global Ecology and Biogeography 26: 425–434. https://doi.org/10.1111/geb.12549

Piper CS (1950) Soil and plant analysis: a laboratory manual of methods for the examinations of soils and the determination of the inorganic constituents of plants. University of Adelaide, Adelaide, AU, 368 pp.

POWO (2019) plants of the world online, facilitated by the Royal Botanic Gardens, Kew. http://powo.science.kew.org/ [accessed on 28.08.2019]

R Development Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raunkiaer C (1934) The life forms of Plants and statistical plant geography, being the collected papers of C. Raunkiaer. Clarendon Press, Oxford, GB, 632 pp.

Schulte EE, Hopkins BG (1996) Estimation of soil organic matter by weight loss-on-ignition. In: Magdoff FR, Tabatabai MA, Hanlon Jr EA (Eds) Soil Organic Matter: Analysis and Interpretation. Soil Science Society of America, Wisconsin, US, 21–31. https://doi.org/10.2136/sssaspecpub46.c3

Ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. Advances in Ecological Research 18: 271–317. https://doi.org/10.1016/S0065-2504(08)60183-X

Ter Braak CJF, Šmilauer P (2012) Canoco reference manual and user's guide: software for ordination (version 5.0). Microcomputer Power, New York, US, 496 pp.

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Walter H, Lieth H (1967) Klimadiagramm-Weltatlas. Gustav Fischer Verlag, Jena, DE, 256 pp.

White F (1983) The vegetation of Africa: a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. UNESCO, Paris, FR, 356 pp.

White F, Léonard J (1991) Phytogeographical links between Africa and southwest Asia. Flora et Vegetatio Mundi 9: 229–246.

Wickens GE (1976) The flora of Jebel Marra (Sudan Republic) and its geographical affinities. Her Majesty's Stationery Office, London, GB, 368 pp.

Wickham H (2016) ggplot2: elegant graphics for data analysis. 2nd ed. Springer, Cham, CH, 260 pp.

Wood SN (2017) Generalized Additive Models, an introduction with R. 2nd ed. Chapman and Hall/CRC, New York, US, 496 pp. https://doi.org/10.1201/9781315370279

Zahran MA, Willis AJ (2009) The Vegetation of Egypt. 2nd ed. Springer, Dordrecht, NL, 437 pp.

Zohary M (1973) Geobotanical foundations of the Middle East (2 vols). Gustav Fischer, Stuttgart, DE, 738 pp.

E-mail and ORCID

Maged M. Abutaha (Corresponding author, maged_abutaha@yahoo.com), ORCID: https://orcid.org/0000-0001-5959-7719
Ahmed A. El-Khouly (elkhouly3000@hotmail.com)
Norbert Jürgens (norbert.juergens@t-online.de), ORCID: https://orcid.org/0000-0003-3211-0549
Jens Oldeland (jens.oldeland@uni-hamburg.de), ORCID: https://orcid.org/0000-0002-7833-4903

Appendix 1

Species list including information on growth form and the distribution of species in the studied Wadis (M = Marafai, A = Acow, K = Kansisrob, and Y = Yahmib).

	Family	Species incl. author	Life cycle	Life form	Growth form	Wadi			
						M	A	K	Y
1	*Acanthaceae*	***Barleria hochstetteri*** Nees	P	Ch	shrub	*			
2		***Blepharis edulis*** (Forssk.) Pers.	P	Ch	herb	*	*	*	
3		***Dicliptera paniculata*** (Forssk.) I. Darbysh.	A	Th	herb	*	*	*	
4	*Aizoaceae*	***Aizoon canariense*** L.	A	Th	herb	*	*	*	*
5	*Amaranthaceae*	***Achyranthes aspera*** L. var. ***sicula*** L.	P	H	herb	*		*	
6		***Aerva javanica*** (Burm. f.) Juss. ex Schult. in Roem. & Schult. var ***javanica***	P	Ch	herb	*	*	*	
7		***Aerva lanata*** (L.) Juss. ex Schult.	P	Ch	herb	*	*		
8		***Amaranthus graecizans*** L. subsp. ***aschersonianus*** (Thell.) Costea, D. M. Brenner & Tardif	A	Th	herb	*	*	*	
9		***Chenopodiastrum murale*** (L.) S. Fuentes, Uotila & Borsch	A	Th	herb	*	*	*	*
10		***Psilotrichum gnaphalobryum*** (Hochst.) Schinz	P	Ch	herb	*			
11		***Pupalia lappacea*** (L.) Juss.	P	Ch	herb	*			
12	*Amaryllidaceae*	***Pancratium tortuosum*** Herb.	P	G	herb	*	*	*	
13	*Anacardiaceae*	***Pistacia khinjuk*** Stocks var. ***glabra*** Schweinf. ex Engl.	P	Ph	tree	*			
14		***Searsia flexicaulis*** (Baker) Moffett	P	Ph	tree	*			
15		***Searsia glutinosa*** subsp. ***abyssinica*** (Hochst. ex Oliv.) Moffett	P	Ph	tree	*			
16		***Searsia tripartita*** (Ucria) Moffett	P	Ph	tree	*			
17	*Apiaceae*	***Pimpinella etbaica*** Schweinf.	A	Th	herb	*	*		
18	*Apocynaceae*	***Calotropis procera*** (Aiton) W. T. Aiton	P	Ph	tree		*		*
19		***Carissa spinarum*** L.	P	Ph	shrub/liana	*			
20		***Leptadenia pyrotechnica*** (Forssk.) Decne.	P	Ph	shrub		*		*
21		***Pergularia daemia*** (Forssk.) Chiov.	P	Ch	liana	*			
22		***Periploca aphylla*** Decne. subsp. ***laxiflora*** (Bornm. ex Drar) Browicz	P	Ph	shrub	*	*		
23	*Asparagaceae*	***Dracaena ombet*** Heuglin ex Kotschy & Peyr. subsp. ***ombet***	P	Ph	tree	*			
24	*Asphodelaceae*	***Asphodelus tenuifolius*** Cav.	A	Th	herb	*	*	*	*
25	*Asteraceae*	***Bidens bipinnata*** L.	A	Th	herb	*			
26		***Bidens schimperi*** Sch. Bip. ex Walp.	A	Th	herb	*	*		

	Family	Species incl. author	Life cycle	Life form	Growth form	Wadi			
						M	A	K	Y
27	*Asteraceae*	***Echinops hussonii*** Boiss.	P	H	herb	*	*	*	
28		***Launaea nudicaulis*** (L.) Hook. f.	P	H	herb		*		
29		***Osteospermum vaillantii*** (Decne.) Norl.	P	H	herb	*		*	
30		***Pegolettia senegalensis*** Cass.	A	Th	herb	*	*		
31		***Phagnalon schweinfurthii*** Sch. Bip. ex Schweinf.	P	Ch	herb	*			
32		***Pulicaria petiolaris*** Jaub. & Spach	P	H	herb	*			
33		***Pulicaria undulata*** (L.) C. A. Mey.	P	Ch	shrub	*	*	*	
34		***Reichardia tingitana*** (L.) Roth subsp. ***tingitana***	A	Th	herb	*	*		
35		***Senecio flavus*** (Decne.) Sch. Bip.	A	Th	herb	*			
36		***Urospermum picroides*** (L.) Scop. ex. F. W. Schmidt	A	Th	herb	*	*	*	
37	*Boraginaceae*	***Arnebia hispidissima*** (Sieber ex Lehm.) A. DC.	A	Th	herb		*		
38		***Heliotropium bacciferum*** Forssk.	P	Ch	herb				*
39		***Heliotropium supinum*** L.	A	Th	herb				*
40		***Heliotropium zeylanicum*** (Burm. f.) Lam.	P	Ch	herb	*		*	
41		***Trichodesma africanum*** (L.) R. Br. var. ***africanum***	A	Th	herb	*	*		
42		***Trichodesma ehrenbergii*** Schweinf.	P	H	herb	*	*	*	
43	*Brassicaceae*	***Diceratella elliptica*** (DC.) Jonsell	P	H	herb	*	*		
44		***Farsetia longisiliqua*** Decne.	P	Ch	shrub	*	*	*	
45		***Sisymbrium erysimoides*** Desf.	A	Th	herb	*	*	*	
46	*Burseraceae*	***Commiphora gileadensis*** (L.) C. Chr.	P	Ph	shrub			*	
47	*Capparaceae*	***Boscia senegalensis*** (Pers.) Lam. ex Poir.	P	Ph	shrub	*			
48		***Capparis decidua*** (Forssk.) Edgew.	P	Ph	tree	*		*	
49		***Maerua crassifolia*** Forssk.	P	Ph	tree	*	*	*	*
50		***Maerua oblongifolia*** (Forssk.) A. Rich.	P	Ch	liana			*	
51	*Caryophyllaceae*	***Cometes abyssinica*** R. Br. ex Wall.	A	Th	herb	*	*	*	
52		***Paronychia argentea*** Lam.	A	Th	herb			*	
53		***Spergularia flaccida*** (Madden) I. M. Turner	A	Th	herb	*		*	*
54	*Celastraceae*	**Gymnosporia senegalensis** (Lam.) Loes.	P	Ph	shrub	*			
55	*Cleomaceae*	***Cleome amblyocarpa*** Barratte & Murb.	A	Th	herb		*		*
56	*Commelinaceae*	***Commelina benghalensis*** L.	A	Th	herb	*	*		
57		***Commelina forskaolii*** Vahl	A	Th	herb	*	*	*	
58	*Convolvulaceae*	***Convolvulus hystrix*** Vahl subsp. ***hystrix***	P	Ch	shrub	*		*	
59		***Cuscuta chinensis*** Lam.	A	Th	liana	*	*	*	
60		***Cuscuta pedicellata*** Ledeb.	A	Th	liana		*		
61		***Ipomoea biflora*** (L.) Pers.	A	Th	herb	*	*	*	
62	*Cucurbitaceae*	***Citrullus colocynthis*** (L.) Schrad.	P	H	herb	*	*	*	
63		***Cucumis prophetarum*** L. subsp. ***dissectus*** (Naudin) C. Jeffrey	P	H	herb	*			
64		***Cucumis prophetarum*** L. subsp. ***prophetarum***	P	H	herb	*	*	*	*
65		***Kedrostis gijef*** (Forssk. ex. J. F. Gmel.) C. Jeffrey	P	Ch	liana	*	*		
66	*Cyperaceae*	***Cyperus laevigatus*** L. subsp. ***laevigatus***	P	H	sedge	*			
67	*Ebenaceae*	***Euclea racemosa*** Murray subsp. ***schimperi*** (A. DC.) F. White	P	Ph	tree	*			
68	*Ephedraceae*	***Ephedra foliata*** Boiss. ex C. A. Mey.	P	Ph	shrub	*	*	*	
69	*Euphorbiaceae*	***Chrozophora oblongifolia*** (Delile) A. Juss. ex Spreng.	P	Ch	herb	*		*	
70		***Chrozophora tinctoria*** (L.) Raf.	A	Th	herb	*	*		
71		***Euphorbia cuneata*** Vahl subsp. ***cuneata***	P	Ph	tree	*	*	*	
72		***Euphorbia nubica*** N. E. Br.	P	Ch	shrub	*	*	*	
73		***Euphorbia granulata*** Forssk.	A	Th	herb	*		*	
74		***Euphorbia*** sp. L.	A	Th	herb			*	
75	*Fabaceae*	***Crotalaria impressa*** Nees ex Walp.	A	Th	herb			*	
76		***Crotalaria senegalensis*** (Pers.) Bacle ex DC.	A	Th	herb			*	
77		***Delonix elata*** (L.) Gamble	P	Ph	tree		*	*	
78		***Indigofera spinosa*** Forssk.	P	Ch	shrub	*	*	*	*
79		***Rhynchosia minima*** (L.) DC. var. ***memnonia*** (Delile) T. Cooke	P	Ch	liana	*			
80		***Senegalia laeta*** (R. Br. ex Benth.) Seigler & Ebinger	P	Ph	tree	*			
81		***Senegalia mellifera*** (Benth.) Seigler & Ebinger	P	Ph	shrub	*	*	*	
82		***Senna italica*** Mill.	P	Ch	herb	*	*	*	*
83		***Tephrosia purpurea*** (L.) Pers. subsp. ***apollinea*** (Delile) Hosni & El-Karemy	P	Ch	herb	*	*	*	*
84		***Vachellia etbaica*** (Schweinf.) Kyal. & Boatwr.	P	Ph	tree	*	*		
85		***Vachellia oerfota*** (Forssk.) Kyal. & Boatwr. var. ***oerfota***	P	Ph	shrub			*	
86		***Vachellia*** sp. Wight & Arn.	P	Ph	tree		*		
87		***Vachellia tortilis*** (Forssk.) Galasso & Banfi subsp. ***raddiana*** (Savi) Kyal. & Boatwr.	P	Ph	tree	*	*	*	*
88		***Vachellia tortilis*** (Forssk.) Galasso & Banfi subsp. ***tortilis***	P	Ph	tree	*	*	*	*
89	*Geraniaceae*	***Erodium neuradifolium*** Delile ex Godr.	A	Th	herb	*	*		
90		***Geranium trilophum*** Boiss.	A	Th	herb	*	*	*	
91	*Lamiaceae*	***Lavandula coronopifolia*** Poir.	P	Ch	shrub	*	*	*	
92		***Leucas neuflizeana*** Courbon	A	Th	herb	*			
93		***Ocimum forskoelei*** Benth.	P	Ch	shrub	*	*		
94		***Otostegia fruticosa*** (Forssk.) Schweinf. ex Penzig subsp. ***fruticosa***	P	Ch	shrub	*	*		
95		***Salvia aegyptiaca*** L.	P	Ch	shrub	*	*		
96	*Loranthaceae*	***Plicosepalus acaciae*** (Zucc.) Wiens & Polhill	P	Ph	shrub	*	*		
97		***Plicosepalus curviflorus*** (Benth. ex Oliv.) Tiegh.	P	Ph	shrub	*	*		
98	*Malvaceae*	***Abutilon bidentatum*** Hochst. ex A. Rich.	P	Ch	shrub	*			
99		***Abutilon fruticosum*** Guill. & Perr.	P	Ch	shrub	*	*	*	
100		***Abutilon pannosum*** (G. Forst.) Schltdl.	P	Ph	shrub	*	*	*	
101		***Grewia tenax*** (Forssk.) Fiori	P	Ph	shrub	*			
102		***Grewia tembensis*** Fresen.	P	Ph	shrub	*			

	Family	Species incl. author	Life cycle	Life form	Growth form	Wadi			
						M	A	K	Y
103	*Malvaceae*	***Grewia villosa*** Willd.	P	Ph	shrub	*			
104		***Hibiscus micranthus*** L. f.	P	Ch	shrub	*	*	*	
105		***Hibiscus vitifolius*** L.	P	Ch	shrub	*	*		
106		***Malva parviflora*** L.	A	Th	herb		*		
107		***Pavonia triloba*** Guill. & Perr.	P	Ch	herb	*			
108		***Triumfetta flavescens*** Hochst. ex A. Rich.	P	Ch	shrub	*	*	*	*
109		***Triumfetta rhomboidea*** Jacq.	P	Ch	shrub	*			
110	*Menispermaceae*	***Cocculus pendulus*** (J. R. & G. Forst.) Diels	P	Ch	liana	*	*	*	*
111	*Moraceae*	***Ficus palmata*** Forssk.	P	Ph	tree		*		
112		***Ficus salicifolia*** Vahl	P	Ph	tree	*	*		
113	*Moringaceae*	***Moringa peregrina*** (Forssk.) Fiori	P	Ph	tree	*	*		
114	*Nyctaginaceae*	***Commicarpus helenae*** (Roem. & Schult.) Meikle	P	Ph	shrub	*		*	
115	*Oleaceae*	***Jasminum fluminense*** Vell. subsp. ***gratissimum*** (Deflers) P. S. Green	P	Ph	liana	*			
116		***Jasminum grandiflorum*** L. subsp. ***floribundum*** (R. Br. ex Fresen.) P. S. Green	P	Ph	liana/shrub	*			
117		***Olea europaea*** L. subsp. ***cuspidata*** (Wall. ex G. Don) Ciferri	P	Ph	tree	*			
118	*Orobanchaceae*	***Lindenbergia indica*** (L.) Vatke	P	Ch	shrub	*	*		
119	*Oxalidaceae*	***Oxalis anthelmintica*** A. Rich.	P	G	herb	*	*		
120	*Phyllanthaceae*	***Andrachne aspera*** Spreng.	P	Ch	herb	*			
121	*Plantaginaceae*	***Nanorrhinum hastatum*** (R. Br. ex Benth.) Ghebr.	A	Th	herb	*	*	*	
122		***Plantago afra*** L.	A	Th	herb	*		*	*
123		***Plantago ciliata*** Desf.	A	Th	herb		*		
124	*Poaceae*	***Brachypodium distachyon*** (L.) P. Beauv.	A	Th	grass		*		*
125		***Bromus fasciculatus*** C. Presl	A	Th	grass	*			
126		***Cenchrus ciliaris*** L.	P	H	grass	*	*	*	*
127		***Cenchrus pennisetiformis*** Hochst. & Steud.	A	Th	grass	*	*	*	*
128		***Cenchrus setiger*** Vahl	P	G	grass			*	
129		***Centropodia forskalii*** (Vahl) Cope	P	H	grass		*		
130		***Cynodon dactylon*** (L.) Pers.	P	G	grass		*	*	
131		***Digitaria nodosa*** Parl.	P	H	grass			*	
132		***Eragrostis cilianensis*** (All.) Vignolo ex Janch.	A	Th	grass	*	*		
133		***Melanocenchris abyssinica*** (R. Br. ex Fresen.) Hochst.	A	Th	grass	*	*		
134		***Panicum turgidum*** Forssk.	P	G	grass	*	*		
135		***Stipagrostis ciliata*** (Desf.) De Winter	P	H	grass			*	
136		***Tragus racemosus*** (L.) All.	A	Th	grass		*		
137		***Urochloa deflexa*** (Schumach.) H. Scholz	A	Th	grass		*	*	
138	*Polygonaceae*	***Rumex simpliciflorus*** Murb.	A	Th	herb	*			
139		***Rumex vesicarius*** L.	A	Th	herb	*	*	*	
140	*Portulacaceae*	***Portulaca oleracea*** L. subsp. ***oleracea***	A	Th	herb	*	*		
141	*Primulaceae*	***Lysimachia arvensis*** (L.) U. Manns & Anderb.	A	Th	herb		*		
142	*Pteridaceae*	***Onychium divaricatum*** (Poir.) Alston	P	H	herb	*			
143	*Resedaceae*	***Caylusea hexagyna*** (Forssk.) M. L. Green	A	Th	herb		*	*	
144		***Ochradenus baccatus*** Delile	P	Ph	shrub	*	*	*	
145	*Rubiaceae*	***Galium spurium*** L.	A	Th	herb	*			
146	*Salvadoraceae*	***Salvadora persica*** L.	P	Ph	shrub	*		*	
147	*Sapindaceae*	***Dodonaea viscosa*** Jacq.	P	Ph	shrub	*			
148	*Scrophulariaceae*	***Scrophularia arguta*** Sol. ex Aiton	A	Th	herb	*	*		
149	*Solanaceae*	***Lycium shawii*** Roem. & Schult.	P	Ph	shrub	*	*	*	*
150		***Solanum forskaolii*** Dunal	P	Ch	shrub	*	*	*	
151		***Solanum incanum*** L.	P	Ch	shrub	*	*		
152		***Solanum nigrum*** L. var. ***elbaensis*** Täckh. & Boulos	A	Th	herb	*	*		
153		***Solanum villosum*** Mill. subsp. ***villosum***	A	Th	herb	*	*		
154		***Withania somnifera*** (L.) Dunal	P	Ch	shrub			*	
155	*Urticaceae*	***Forsskaolea tenacissima*** L.	P	H	herb	*	*	*	*
156		***Forsskaolea viridis*** Webb	A	Th	herb	*	*	*	
157		***Parietaria debilis*** G. Forst.	A	Th	herb	*	*	*	
158	*Verbenaceae*	***Lantana viburnoides*** (Forssk.) Vahl	P	Ch	shrub	*			
159	*Violaceae*	***Viola cinerea*** Boiss. var. ***stocksii*** (Boiss.) Becker	A	Th	herb	*			
160	*Zygophyllaceae*	***Balanites aegyptiaca*** (L.) Delile	P	Ph	tree	*	*	*	*
161		***Tribulus terrestris*** L.	A	Th	herb	*	*	*	
162		***Zygophyllum simplex*** L.	A	Th	herb	*	*	*	*

Supplementary material

Supplementary material 1

Supplementary tables showing the percentage cover and the distribution of perennial species in the studied relevés for each community. Wadi Marafai (M), W. Acow (A), W. Kansisrob (K), and W. Yahmib (Y).

Link: https://doi.org/10.3897/VCS/2020/38644.suppl1

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 37–51
doi: 10.3897/VCS/2020/48765

RESEARCH PAPER

Montane mire vegetation of the New England Tablelands Bioregion of Eastern Australia

John T. Hunter[1], Vanessa H. Hunter[2]

1 *School of Environmental and Rural Science, University of New England, Armidale, New South Wales, Australia*
2 *Hewlett Hunter Pty Ltd, Armidale, New South Wales, Australia*

Corresponding author: John T. Hunter (jhunter8@bigpond.com)

Academic editor: Jürgen Dengler ♦ **Received** 28 August 2018 ♦ **Accepted** 18 November 2018 ♦ **Published** 4 May 2020

Abstract

Aims: To use unsupervised techniques to produce a hierarchical classification of montane mires of the study region. **Study area:** New England Tablelands Bioregion (NETB) of eastern Australia. **Methods:** A dataset of 280 vascular floristic survey plots placed across the variation in montane mires of the NETB was collated. Vegetation types were identified with the aid of a clustering method based on group averaging and tested using similarity profile analysis (SIMPROF) and through ordinations using Bray-Curtis similarity and non-metric multidimensional scaling (NMDS). A hierarchical schema was developed based on EcoVeg hierarchy and was circumscribed using positive and negative diagnostic taxa via similarity percentage analysis (SIMPER) and importance based on summed cover scores and frequency. **Results:** We defined one macrogroup to include all montane mire vegetation of the NETB and within these two groups and twelve alliances. **Conclusions:** Our study re-enforced the separation of bogs from other montane mire systems and confirmed the separation of fens and wet meadows, a distinction that previously had not been independently tested. Based on our results many existing montane mire communities of the NETB have been ill-defined at multiple hierarchical levels, leading to confusion in threat status and mapping. Additionally, nearly half of the alliances we recognise were found to have no correlates within current classification systems, which necessarily has implications for the effectiveness of current conservation planning.

Taxonomic reference: PlantNET (http://plantnet.rbgsyd.nsw.gov.au/, accessed June 2016).

Abbreviations: BC Act = Biodiversity Conservation Act; EPBC Act = Environmental Protection and Biodiversity Act; NETB = New England Tablelands Bioregion; NMDS = non-metric multidimensional scaling; PCT = plant community type; RE = regional ecosystem; SIMPER = similarity percentage analysis; SIMPROF = similarity profile analysis.

Keywords

Australia, bog, EcoVeg, fen, marsh, New England Tableland Bioregion, similarity percentage analysis (SIMPER), wet meadow, unsupervised classification

Introduction

The first step in understanding the distribution, rarity and interrelationships of vegetated systems is description and classification (Franklin et al. 2016; Jensen et al. 2016). This is particularly true for systems that are under greatest threat and impact from human activities and which provide significant ecosystem services. Unfortunately, vegetation within many areas of the globe have poor survey coverage and/or inconsistent survey protocols, leading to insufficient or poor data hampering classification (Gellie et al. 2017; De Cáceres et al. 2018). Even within areas considered relatively well surveyed, many highly restricted and/or ephemeral systems are likely to be poorly sampled and incompletely treated within current classification systems, leading to misunderstandings of their

PENSOFT.

Copyright *John T. Hunter, Vanessa H. Hunter.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

placement, function, importance and rarity (Hunter and Hunter 2017; Hunter and Lechner 2017). Not all classification systems are hierarchical in nature, and many have no clear analytical proof of conceptual links (De Cáceres et al. 2018; Gellie et al. 2017). Ideally, hierarchical classification systems facilitate integrated understanding of relationships between vegetation assemblages and also allow conceptualisations at different ranks to match scales at which management and investigations may be applied, from local to global (Faber-Langendoen et al. 2018).

Australia is a dry continent, and thus, the more common and widely distributed wetlands are those that are impermanent in nature; that is, they may 'wet-up' once a year, multiple times a year or once within several decades, often not associated with seasonal patterns, but are dry more often than they are wet (Paijmans et al. 1985; Bell et al. 2008; Bell et al. 2012; Hunter and Lechner 2017). Such wetlands may contain shallow water less than 2 m depth, but more commonly only have saturated soils or seasonally standing water a few centimetres depth. Montane areas within Australia are limited and thus montane wetlands, in particular, are sparsely distributed and rare within the continent and poorly sampled across their range (Wahren et al. 1999; Whinam and Hope 2005).

The montane region bordering northern New South Wales and south east Queensland has been defined as the New England Tableland Bioregion (NETB) based on its unique biological and environmental elements (Thackwell and Creswell 1995). The Hunter Valley to the south of the NETB creates a break in the Great Dividing Range and separates the NETB from more southern montane environments in south eastern Australia. Within the NETB a number of semi-permanent and ephemeral mire systems locally known as bogs, fens, lagoons (marshes) and sod tussock grasslands (wet meadows) occur (Hunter and Bell 2007; 2009; Bell et al. 2008; Hunter and Hunter 2016a). Whinam and Chilcott (2002) showed through unsupervised analyses of floristic plots that the NETB bogs were dissimilar floristically from other montane bogs further south in eastern Australia. Hunter and Hunter (2016) also highlighted the distinct floristic differences between montane sod tussock grasslands (wet meadows) and those of other south eastern Australian montane districts. Lechner et al. (2016), in an analysis of environmental data associated with montane wetlands, found the NETB was largely encompassed by a unique montane wetland ecoregion.

Bogs of the NETB are characterised by altitudes above 850 m a.s.l, commonly on nutrient poor sites with low pH, saturation occurring seasonally or sporadically, and shallow standing water infrequent (Hunter and Bell 2007) (Suppl. material 1: Plate 1). Peat often forms but is largely created by sedge debris and at times *Sphagnum* (Hunter and Bell 2007; Hunter and Bell 2013; Hunter 2016a). Due to frequent fires, peat accumulation is often thin but can develop to depth where fires are excluded for long periods of time (Hunter and Bell 2007). These systems are largely dominated by cyperaceous taxa with a distinct component of woody shrubs species usually 0.5–1.5 m in height (*Myrtaceae*, *Fabaceae*, *Proteaceae* and *Ericaceae*) (Hunter and Bell 2007).

Fens within the NETB are found along watercourses and flat to concave valley floors generally associated with mineral rich substrates (Hunter and Bell 2009) (Suppl. material 1: Plate 1). Fens are dominated by softer leaved sedges, grasses and herbs and do not have a woody shrub component within the NETB (Hunter and Bell 2009). Peat accumulation can occur but is largely based on cyperaceous materials and soil pH is slightly acidic to neutral. Overall fens are far more common within the NETB but are much less common within the national reserve system (Hunter 2013).

Lagoons within the NETB may be best described as semi-permanent or ephemeral marshes (Bell et al. 2008) (Suppl. material 1: Plate 1). Unlike the other wetlands they are generally oval in shape and are distinguished by having a well-defined bank with a sandy lunette on their downwind shores formed under previous climatic conditions (Bell et al. 2008). Only 58 of these ephemeral marshes are known within the NETB and these are restricted to the top of the Great Dividing Range almost exclusively on basalt soils (Bell et al. 2008). Ephemeral marshes differ in depth and duration of inundation but water, when present, is less than 1.5 m deep and never persistent. The lagoons have very localised catchments often only a few hundred hectares in size or less and thus inundation is often unpredictable and reliant on very localised rainfall often unrelated to regional rainfall averages or season. Due to longer and deeper inundation, the ephemeral marshes, unlike the other wetland systems on the NETB, can support free floating and aquatic vegetation usually >20% vegetation cover (Bell et al. 2008; Hunter 2016a).

The sod tussock grasslands would likely be classed as spring fed and floodplain wet meadows within the mire classification (van Diggelen et al. 2006; Hunter and Hunter 2016) (Suppl. material 1: Plate 1). Wet meadows of the NETB occur within lower physiographic positions and frost hollows generally on higher nutrient soils which are seasonally damp or inundated with a few centimetres of water (Hunter and Hunter 2016).

Within the state of New South Wales, vegetation has been described into units called plant community types (PCTs), which are considered an equivalent to an association level of nomenclature (Benson et al. 2010) and used to assign conservation significance and threat. PCTs are based on a mixture of supervised and semi-supervised techniques (Gellie et al. 2017), and they have been subsequently placed within an independently derived hierarchical system of classes and formations (Keith 2004). As these classes and formations are circumscribed largely by supervised methods, and independently from PCTs, the interrelationships between the two systems and thus the placement of PCTs within formations and classes has been achieved by expert opinion without independent statistical testing (Gellie et al. 2017). The circumscription of associations within mires of the NETB have been either poor, misinterpreted, inconsistent or missed entirely

within state-based vegetation classifications (Hunter and Bell 2007; 2009; Hunter and Hunter 2016). For instance, though Groves (1981) described a *Glyceria australis* wet grassland, no such PCT has been formally included in summaries of vegetation types for the NETB by Benson et al. (2010), nor wet meadows been included within state wide classes and formations (Keith 2004). Only four PCTs currently circumscribe the range of fens, bogs and lagoons found within the NETB (Benson et al. 2010).

Currently within certain Australian jurisdictions the development of vegetation community types is based almost solely on floristic classification techniques with little or no influence of environmental factors, although types may contain environmental terms as descriptors secondarily to floristics (Sivertsen 2009; Environmental Protection Authority 2016; Gillie et al. 2018). Although this has not always been the case due to poor plot data coverage within New South Wales, any new proposed associations need proof of floristic distinctiveness via unsupervised analyses. Floristic distinctiveness via unsupervised analysis is now a requirement that also applies for listings of threatened ecological communities on both the Federal *Environmental Protection and Biodiversity Act* and the New South Wales *Biodiversity Conservation Act*. Thus, currently for both general classification purposes and for endangered community listings floristic distinctiveness by analysis is removed from ecological distinctiveness and is generally the only method of recognition of types.

A concerted and comprehensive effort has been placed on plot-based sampling of the montane wetlands of the NETB in order to describe phytosociological units through unsupervised means (Bell et al. 2008; Hunter and Bell 2007; 2009; Hunter and Hunter 2016). Using the plot-based data and unsupervised floristic analyses, these studies describe 28 phytosociological assemblages equivalent to associations (Hunter and Bell 2007; Bell et al. 2008; Hunter and Bell 2009; Hunter and Hunter 2016). The majority of these associations are not encompassed within formal PCTs (Benson et al. 2010) and many are difficult to place within current published classes and formations (Keith 2004). However, these recent investigations into NETB mires have been conducted in isolation of each other and there is a need to provide an understanding of their interrelationships and to formally place them within an unsupervised hierarchy. Here we provide a plot-based analysis of mire assemblages within the NETB, to provide a formal understanding of the floristic relationships between the types and derive from analysis a hierarchical classification above that of association for the mires within the NETB.

Methods

Study area

The study region encompasses the New England Tablelands Bioregion (NETB; 30,000 km^2; Figure 1) which lie on the Great Dividing Range in eastern Australia. The NETB is largely restricted to north-east New South Wales but extends into south eastern Queensland with altitudes ranging from 700 to 1500 m a.s.l. The region has a strong west-east rainfall gradient (600–2500 mm) with easterly airflows from the Pacific Ocean causing orographic influences in the east (Resource and Conservation Assessment Council 1996).

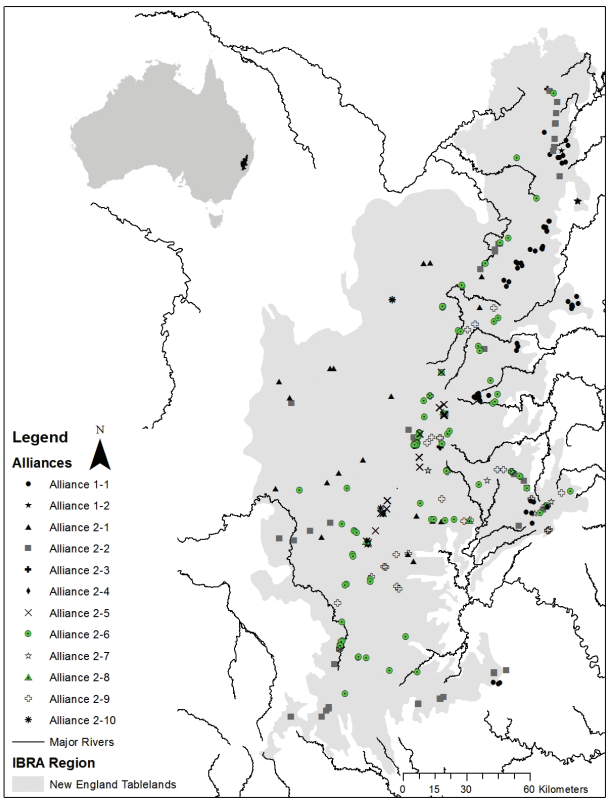

Figure 1. Location of the New England Tablelands Bioregion within Australia and location of 280 full vascular floristic survey plots.

Field sampling

Data from 280 full vascular floristic survey plots were collated from wetlands within the NETB. The plots were sampled on public lands, where possible first preference was to occurrences within state conservation reserves and secondarily within private reserves or travelling stock reserves. Conservation reserves are un-grazed by non-native animals while travelling stock reserves are only periodically grazed by non-native animals with grazing regulated by state government authorities. Thus non-native animal grazing was absent or minimal and tightly controlled. Standard plot sizes were 20 m × 20 m. Species were scored using a six-point modified Braun-Blanquet system based on percentage foliage cover (Westhoff and van der Maarel 1980): 1= 1–5% cover, uncommon; 2 = 1–5% cover, common; 3 = 6–25%; 4 = 26–50%; 5 = 51–75% and 6 = >75%. Plots where placed across the study area over a ten-year period between 2008 and 2018 within spring and summer. All plots were scored

for general wetland type (bog, fen, sod grassland, lagoon), and location and altitude were based on global positioning system (GPS). All plot data has been submitted for hosting in version 3 of sPlot (Bruelheide et al. 2019; https://www.idiv.de/?id=176&L=0) and is listed on GIVD as AU-AU-003 (https://www.givd.info/databases.xhtml). No new data has been collected for this research with only existing data collected by the authors and previously published separately being used (see Hunter and Bell 2007; Bell et al. 2008; Hunter and Bell 2009; Hunter and Hunter 2016; Hunter 2018). Further details of the wetland types investigated, stratification and how data was collected for each survey is contained within these previous publications including information on species richness, elevation, vegetation cover and height, synoptic tables and photographs for each defined association.

Statistical analysis

Primer E (ver. 7.0.11; Quest Research Limited; Ivybridge, Devon, UK) was used for data exploration, whereby an initial triangular resemblance matrix using Bray-Curtis similarity co-efficient was created without transformation, as the Braun-Blanquet scoring was considered a pre-treatment. Non-metric multidimensional scaling (NMDS) in two and three dimensions was also created. Clustering was achieved through group averaging and the similarity profile tested using similarity profile analysis (SIMPROF) permutation tests (999 iterations). SIMPROF tests the statistical significance of every node within a dendrogram starting from the top of the dendrogram and (all points within a single group) and highlighting only those groups which show within group multivariate structure. The EcoVeg approach (Faber-Langendoen et al. 2014) was used to define hierarchical levels and guide the nomenclatural of the types. The type and density of data available allowed for the circumscription of vegetation types at the medial scales of group and alliance with associations derived from previous published analyses of the same data.

Similarity percentage analysis (SIMPER) identifies the species driving differences between selected types. SIMPER uses the Bray–Curtis similarity measure (Primer E ver. 7.0.11; Quest Research Limited; Ivybridge, Devon, UK) to identify positively and negatively diagnostic taxa across vegetation types. Taxa with combined high fidelity and cover were also identified and listed for diagnostic purposes and type delineation. Attempts to place current eastern Australian state based noncultural units was derived by comparing diagnostic and non-diagnostic taxa from SIMPER results.

The results of our analyses were used to define mid to lower level classification levels (macrogroup, group and alliance) based on EcoVeg terminology. It should be noted that although EcoVeg uses the alliance and association as does the Braun-Blanquet approach, the nomenclatural and procedural roles are distinct. Previous unsupervised cluster analyses using Kulzynski similarity measure have been performed and published on subsets of these datasets defining vegetation units at approximately the association level (see Hunter and Bell 2007; Bell et al. 2008; Hunter and Bell 2009; Hunter and Hunter 2016; Hunter 2018). It is the intention of this analysis to define hierarchical levels above association using the combined datasets from these previous investigations.

Results

Collectively, all mires within the NETB were defined as NETB montane mires (Level 5 – macrogroup) (Table 1). Our analyses support the separation of bogs, fens and wet meadows as broadly distinct units (Figures 2–4). Plots sampled within ephemeral marshes did not form a consistent group in either 2 or 3 axis results and were distributed throughout the non-bog plots (Figures 2–4). Both SIMPROF cluster analysis and NMDS ordination highlight a clear separation of bogs from that of the other types of mires within the NETB (Figures 2, 3). Bogs are floristically and often structurally distinct, being the only mire type on the NETB with a prominent shrub layer (Figure 5, Table 1). This high-level separation is considered appropriate for delineating at Level 6 – Group and thus two groups have been delineated; *Baeckea omissa – Lepidosperma limicola* NETB montane bog mires and *Glyceria australis – Carex gaudichaudiana* NETB fen, wet meadow and ephemeral marsh mires (Table 1).

Splicing the dendrogram at a similarity of 16, we further defined 12 alliances all of which are delineated at a level which shows statistical evidence of multivariate structure via SIMPROF (Figure 2; Suppl. material 1), two within the *Baeckea omissa – Lepidosperma limicola* NETB montane bogs and 10 within the *Glyceria australis – Carex gaudichaudiana* NETB fen, wet meadow and ephemeral marsh mires (Table 2). General environmental data and average species richness is given in Table 3 while the percent frequency of occurrence synoptic results of the most frequent taxa are presented in Table 4 (full table in Suppl. material 2).

A comparison of the placement of NETB montane mires with the currently published classification systems (PCT, class, formation, RE) shows only some congruence with our results (Table 2). The NETB montane mires would be placed within two formations and at least three class categories with some types unable to be clearly assigned. Seven of our 12 Alliances are not adequately circumscribed by current PCTs within New South Wales. Only one Queensland Regional Ecosystem (RE) describes montane mires within the NETB and this unit may cover three of our alliances, leaving three that are known to occur in this jurisdiction but uncategorized.

Discussion

We have successfully applied a consistent classification section to montane mire vegetation within the NETB using unsupervised techniques which have highlighted a number of differences with the current classifications used within eastern Australia. Although the EcoVeg approach

Table 1. Circumscription of mires of the New England Tableland Bioregion (NETB) of eastern Australia. Descriptions 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. Common taxa are listed in decreasing order of cumulative frequency and cover within each identified group.

Hierarchy	Positive diagnostic (SIMPER)	Negative diagnostic (SIMPER)	Common taxa	Notes and distribution
Macrogroup: Scientific Name: *Baeckea – Carex - Glyceria* mires. Colloquial: New England Tableland montane mires	*Baeckea omissa, Glyceria australis, Leptospermum gregarium, Carex gaudichaudiana*	NA	NA	Restricted to the NETB commonly at altitudes above 800 m and rainfall above 700 mm per annum
Group 1: Scientific Name: *Baeckea omissa – Lepidosperma limicola* New England Tableland montane bog mires	*Baeckea omissa, Epacris microphylla, Leptospermum gregarium, Gonocarpus micranthus, Goodenia bellidifolia, Baloskion stenocoleum, Lepidosperma limicola, Callistemon pityoides, Hakea microcarpa, Entolasia stricta*	*Glyceria australis, Carex gaudichaudiana, Carex appressa, Poa sieberiana, Pennisetum alopecuroides, Epilobium billardierianum, Stellaria angustifolia*	*Baeckea omissa, Epacris microphylla, Baloskion stenocoleum, Lepidosperma limicola, Goodenia bellidifolia, Leptospermum gregarium, Gonocarpus micranthus, Lepyrodia scariosa, Leptospermum arachnoides, Callistemon pityoides*	Commonly found on nutrient poor sites with low pH. Often with a prominent shrub layer and forming a peat layer. Often on granite, acid volcanic and metasedimentary rock types
Alliance 1-1: Scientific Name: *Baeckea omissa – Epacris microphylla* shrubby bog	*Baeckea omissa, Epacris microphylla, Leptospermum gregarium, Gonocarpus micranthus, Goodenia bellidifolia, Baloskion stenocoleum, Lepidosperma limicola, Callistemon pityoides, Hakea microcarpa, Entolasia stricta*	*Aristida jerichoensis, Comesperma retusum, Schoenus brevifolius, Caustis flexuosa, Tricostularia pauciflora, Eragrostis elongata, Melichrus procumbens*	*Lepidosperma limicola, Baeckea omissa, Thelionema caespitosa, Drosera binata, Caustis flexuosa, Tricostularia pauciflora, Schoenus brevifolius, Geranium solanderi*	Commonly found along the entire eastern half of NETB in higher rainfall areas. Structurally a shrubby sedgeland or sedgeland
Alliance 1-2: Scientific Name: *Lepidosperma gunnii – Lepidosperma limicola* herbaceous bog	*Lepidosperma gunnii, Comesperma retusum, Aristida jerichoensis, Caustis flexuosa, Dampiera stricta, Thelionema caespitosa, Austrostipa pubescens*	*Callistemon pityoides, Baloskion stenocoleum, Hakea microcarpa*	*Lepidosperma limicola, Xyris operculata, Lepyrodia scariosa, Drosera binata, Drosera spatulata, Baloskion fimbriatum, Amphibpogon strictus, Thelionema caespitosum, Caustis flexuosa*	Generally restricted to the higher rainfall extreme north east of the NETB. Sometimes with a dominant shrub layer. Structurally a sedgeland or shrubby sedgeland
Group 2: Scientific Name: *Glyceria australis – Carex gaudichaudiana* New England Tableland fen, wet meadow and ephemeral marsh mires	*Glyceria australis, Carex gaudichaudiana, Juncus australis, Carex appressa, Poa sieberiana, Geranium solanderi, Pennisetum alopecuroides*	*Baeckea omissa, Lepidosperma limicola, Leptospermum gregarium, Gonocarpus micranthus, Goodenia bellidifolia, Lepyrodia scariosa, Callistemon pityoides, Entolasia stricta, Xyris complanata, Banksia spinuolsa, Epacris obtusifolia, Xyris operculata*	*Glyceria australis, Carex gaudichaudiana, Carex appressa, Poa sieberiana, Geranium solanderi, Pennisetum alopecuroides, Juncus australis, Carex disticha, Epilobium billardiarianum, Isachne globosa, Stellaria angustifolia, Themeda triandra*	Commonly found nutrient rich sites with moderate to high pH. Shrubs rarely present and dominated by sedges, grasses and forbs. Usually restricted to basalt or higher nutrient metasediment rock types. Often forming a peat layer
Alliance 2-1: Scientific Name: *Carex appressa* herbaceous fen	*Carex appressa*	*Myriophyllum variifolium, Lachnagrostis filiformis, Eleocharis acuta, Paspalum distichum, Amphibromus sinuatus, Ottelia ovalifolia, Potamogeton tricarinatus, Amphibromus pithogastrus, Isolepis fluitans*	*Carex appressa, Carex gaudichaudiana, Eleocharis acuta, Geranium solanderi, Stellaria angustifolia, Pennisetum alopecuroides, Juncus australis, Haloragis heterophylla, Epilobium billardiarianum*	Commonly found on medial to lower rainfall areas of the NETB within central and western areas. A sedgeland
Alliance 2-2: Scientific Name: *Carex gaudichaudiana – Isachne globosa* herbaceous fen	*Carex gaudichaudiana, Isachne globosa, Epilobium billardierianum, Stellaria angustifolia, Geranium solanderi, Cyperus sphaeroideus*	*Isachne globosa, Scrirpus polystachyus, Viola caleyana, Lycopus australis, Baloskion stenocoleum, Lythrum salicaria*	*Carex gaudichaudiana, Isachne globosa, Epilobium billardiarianum, Stellaria angustifolia, Geranium solanderi, Carex appressa, Scripus polystachyus, Carex disticha, Lythrum salicaria, Cyperus sphaeroideus, Baumea planifolia*	More commonly found within higher rainfall areas of the NETB, particularly in the eastern half. A sedgeland

Hierarchy	Positive diagnostic (SIMPER)	Negative diagnostic (SIMPER)	Common taxa	Notes and distribution
Alliance 2-3: Scientific Name: *Philydrum lanuginosum – Potamogeton tricarinatus* herbaceous ephemeral marsh and fen	*Philydrum lanuginosum – Potamogeton tricarinatus, Cynodon dactylon, Cardamine paucijuga, Persicaria elatior, Lythrum salicaria*	*Lachnagrostis filiformis, Eleocharis acuta, Eleocharis gracilis, Paspalum distichum, Hydrocotyle tripartita, Glyceria australis.*	*Eleocharis pusilla, Cynodon dactylon, Myriophyllum variifolium, Philydrum lanuginosum, Potamogeton tricarinatus, Lythrum salicaria.*	Found often on wet mud and retreating lagoon margins and around the margins of more permanent sedgeland on the edge of lagoons.
Alliance 2-4: Scientific Name: *Lachnagrostis filiformis* herbaceous wet meadow or marsh	*Lachnagrostis filiformis*	*Myriophyllum variifolium, Eleocharis acuta, Eleocharis gracilis, Paspalum distichum, Hydrocotyle tripartita, Glyceria australis, Ranunculus inundatus*	*Lachnagrostis filiformis, Cyperus gunnii, Geranium solanderi, Rumex brownii*	Found on wet mud associated with retreating lagoon margins. Often very weedy. A sedgeland or herbfield
Alliance 2-5: Scientific Name: *Myriophyllum variifolium – Eleocharis acuta* herbaceous ephemeral marsh	*Myriophyllum variifolium, Eleocharis acuta, Lachnagrostis filiformis, Hydrocotyle tripartita, Eleocharis gracilis, Ranunculus inundatus, Paspalum distichum, Glyceria australis, Juncus australis, Eleocharis sphacelata, Isotoma fluviatilis*	*Carex appressa, Isachne globosa, Carex gaudichaudiana, Carex disticha, Lythrum salicaria*	*Myriophyllum variifolium, Glyceria australis, Eleocharis dietrichiana, Eleocharis sphacelata, Eleocharis acuta, Eleocharis gracilis, Potamogeton tricarinatus, Panicum obseptum, Nymphoides geminata, Eleocharis pusilla, Lachnagrostis filiformis, Amphibromus nervosus, Ranunculus inundatus, Nymphoides montana*	Almost exclusively found on basalt substrates at the top of the Great Dividing Range within the central areas of the NETB. Primarily restricted to ephemeral lagoons. A herbfield or sedgeland
Alliance 2-6: Scientific Name: *Glyceria australis* grassy wet meadow	*Glyceria australis*	*Gonocarpus micranthus, Hypericum japonicum, Themeda triandra*	*Glyceria australis, Pennisetum alopecuroides, Geranium solanderi, Carex disticha, Carex gaudichaudiana, Poa sieberiana, Lachnagrostis filiformis*	Found throughout but more common within central areas of the NETB. A wet tussock grassland
Alliance 2-7: Scientific Name: *Juncus australis – Cenchrus purpurascens* herbaceous wet meadow	*Juncus australis*	*Carex tereticaulis, Dianella longifolia, Veronica gracilis, Hydrocotyle laxiflora*	*Juncus australis, Carex disticha, Pennisetum alopecuroides, Ranunculus lappaceus, Lotus uliginosus, Gonocarpus micranthus, Carex gaudichaudiana, Glyceria australis, Poa sieberiana*	Found in open cold air drainage areas often on the margins of damper wet meadows and on the upper margins of lagoons. A rushland, herbfield or wet tussock grassland
Alliance 2-8: Scientific Name: *Carex tereticaulis – Asperula conferta* herbaceous wet meadow and fen	*Asperula conferta, Carex tereticaulis, Hydrocotyle laxiflora*	*Themeda triandra, Schoenus apogon, Glyceria australis, Haloragis heterophylla, Carex appressa*	*Carex tereticaulis, Asperula conferta, Hydrocotyle laxiflora, Geranium solanderi, Dianella longifolia, Veronica gracilis, Ranunculus lappaceus, Poa sieberiana, Pennisetum alopecuroides, Carex gaudichaudiana*	Found on sandy soils sometimes associated with the drier margins of lagoons or around drier margins of wetter meadows. A wet tussock grassland or fen
Alliance 2-9: Scientific Name: *Poa sieberiana – Themeda triandra* grassy wet meadow	*Poa sieberiana, Themeda triandra, Pennisetum alopecuroides, Schoenus apogon, Haloragis heterophylla*	*Carex gaudichaudiana, Cyperus gunnii, Glyceria australis, Carex tereticaulis, Daucus glochidiatus, Viola hederacea, Caesia calliantha*	*Eleocharis atricha, Leptorhynchos squamatus, Juncus subsecundus, Hydrocotyle tripartita, Sporobolus creber, Calotis scapigera, Pennisetum alopecuroides, Schoenus apogon, Dichelachne macrantha, Carex inversa*	Found in cold frost drainage valley floors that are periodically damp and around the margins of wetter meadows such as Alliance 2-6 and lagoon margins. A wet tussock grassland
Alliance 2-10: Scientific Name: *Leptorhynchos squamatus – Schoenus apogon* herbfield	*Leptorhynchos squamatus, Schoenus apogon*	*Carex tereticaulis, Asperula conferta, Hydrocotyle laxiflora, Dianella longifolia, Geranium solanderi, Carex gaudichaudii. Veronica gracilis*	*Eleocharis atricha, Leptorhynchos squamatus, Juncus subsecundus, Hydrocotyle tripartita, Sporobolus creber, Calotis scapigera, Pennisetum alopecuroides, Schoenus apogon, Dichelachne macrantha, Carex inversa*	Found restricted to lagoons that are largely dry for extended periods and often only become damp rather than inundated. A herbfield or wet tussock grassland

Table 2. Comparison with existing hierarchical classifications within eastern Australia. Plant Community Types (PCT), class and formation are part of the current New South Wales vegetation classification schema and Regional Ecosystems are what are the Queensland equivalent of association.

Hierarchy	PCT (Benson et al. 2010)	Class (Keith 2004)	Formation (Keith 2004)	Regional Ecosystem (Sattler and Williams (1999)
Macrogroup: New England Tableland montane mires	NA	Temperate Montane Grasslands; Montane Bogs and Fens; Montane Lakes	Grasslands; Freshwater Wetlands	NA
Group 1: *Baeckea omissa – Lepidosperma limicola* New England Tableland montane bog mires	NA	Montane Bogs & Fens	Freshwater Wetlands	Regional ecosystem 13.12.7 – Sedgeland along small drainage lines and soaks at high altitude
Alliance 1-1: *Baeckea omissa – Epacris microphylla* shrubby bog	PCT 607: Montane bogs (in part); 518: Heath swamps wetland on leucogranite and granite (not in Benson et al. 2010)	Montane Bogs & Fens	Freshwater Wetlands	Regional ecosystem 13.12.7 – Sedgeland along small drainage lines and soaks at high altitude
Alliance 1-2: *Lepidosperma gunnii – Lepidosperma limicola* herbaceous bog	PCT 582: Sedgeland fens wetland of impeded drainage	Montane Bogs and Fens	Freshwater Wetlands	NA
Group 2: *Glyceria australis – Carex gaudichaudiana* NETB fen, wet meadow and ephemeral marsh mires	No equivalent	Temperate Montane Grasslands	Grasslands	No equivalent
Alliance 2-1: *Carex appressa* herbaceous fen	PCT: 574 Tea-tree riparian shrubland/heathland wetland	Montane Bogs and Fens	Freshwater Wetlands	Regional ecosystem 13.12.7 Sedgeland along small drainage lines and soaks at high altitude
Alliance 2-2: *Carex gaudichaudiana – Isachne globosa* herbaceous fen	PCT 582: Sedgeland fens wetland of impeded drainage	Montane Bogs and Fens	Freshwater Wetlands	NA
Alliance 2-3: *Philydrum lanuginosum – Potamogeton tricarinatus* herbaceous ephemeral marsh and fen	No equivalent	Montane Lakes	Freshwater Wetlands	NA
Alliance 2-4: *Lachnagrostis filiformis* herbaceous wet meadow or marsh	No equivalent	Montane Lakes	Freshwater Wetlands	NA
Alliance 2-5: *Myriophyllum variifolium – Eleocharis acuta* herbaceous ephemeral marsh.	PCT 500: Upland wetlands	Montane Lakes	Freshwater Wetlands	NA
Alliance 2-6: *Glyceria australis* grassy wet meadow	No equivalent	Temperate Montane Grassland	Grassland	No equivalent
Alliance 2-7: *Juncus australis – Cenchrus purpurascens* herbacous wet meadow	No equivalent	No equivalent	?Grassland	NA
Alliance 2-8: *Carex tereticaulis – Asperula conferta* fen and wet meadow	No equivalent	No equivalent	No equivalent	NA
Alliance 2-9: *Poa sieberiana – Themeda triandra* grassy wet meadow	PCT 586: Snow Grass – Swamp Foxtail tussock grassland sedgeland	Temperate Montane Grassland	Grassland	No equivalent
Alliance 2-10: *Leptorhynchos squamatus – Schoenus apogon* herbfield	No equivalent	No equivalent	No equivalent	NA

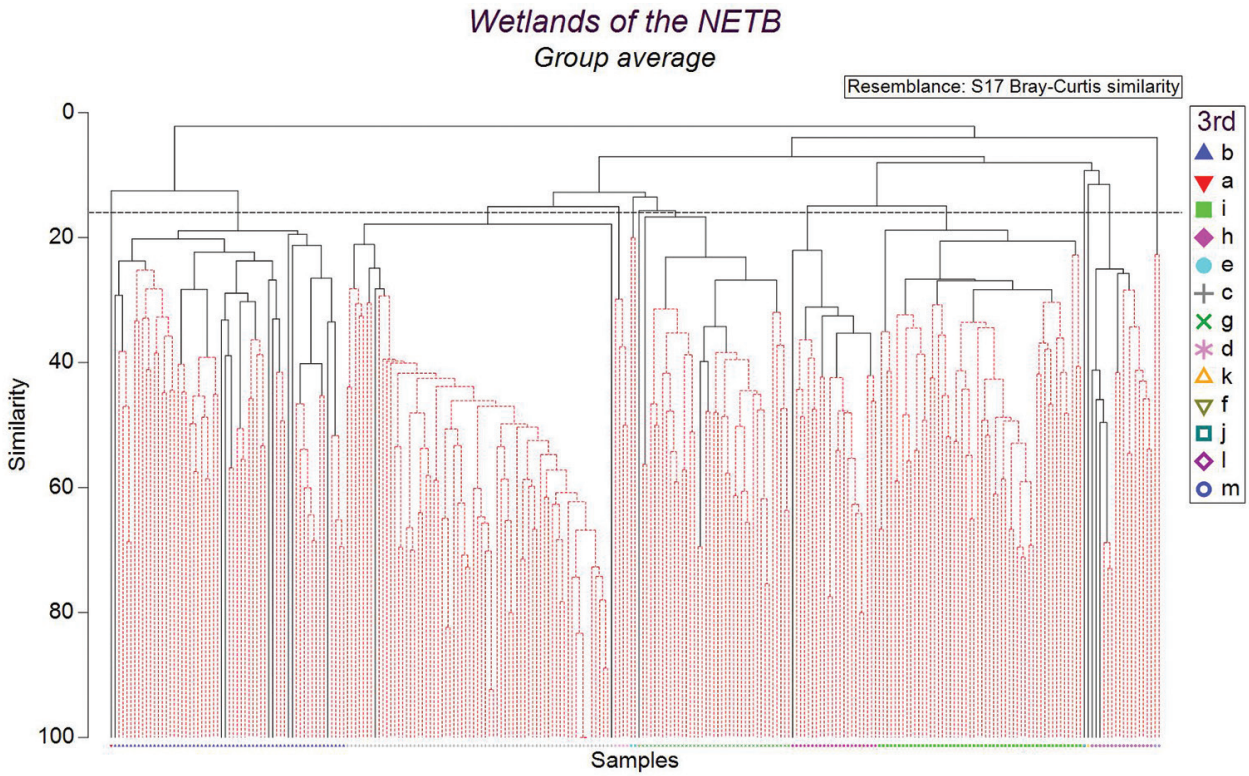

Figure 2. SIMPROF cluster analysis of the full dataset from mires of the New England Tablelands Bioregion of eastern Australia showing alliances recognised at similarity of 16.

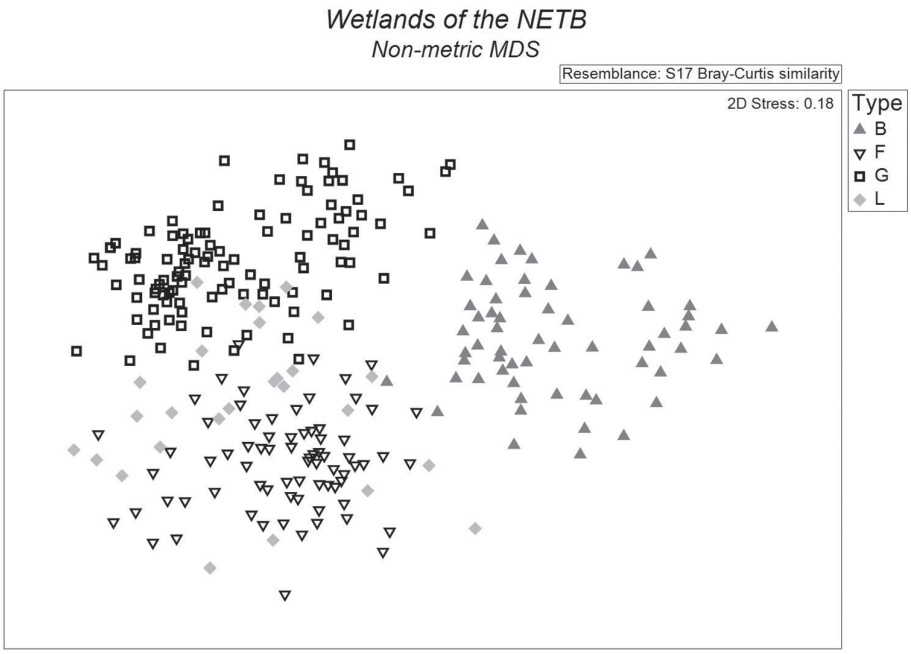

Figure 3. Ordination of full dataset of plots placed within mires of the New England Tablelands Bioregion of eastern Australia. Bogs (B), Fens (F), Sod Tussock Grasslands (G) and Lagoons (L).

typically considers ecological criteria, this is currently not the accepted general practice used in defining vegetation types within New South Wales or for state and federal listings of threatened communities. We believe our classification allows a better and more consistent understanding of the floristic relationships between these montane wetland types that co-occur within the NETB. The current New South Wales classification schema includes bogs and fens within the same class separate from wet meadows (Keith 2004). Our results and those of Hunter (2016a) show

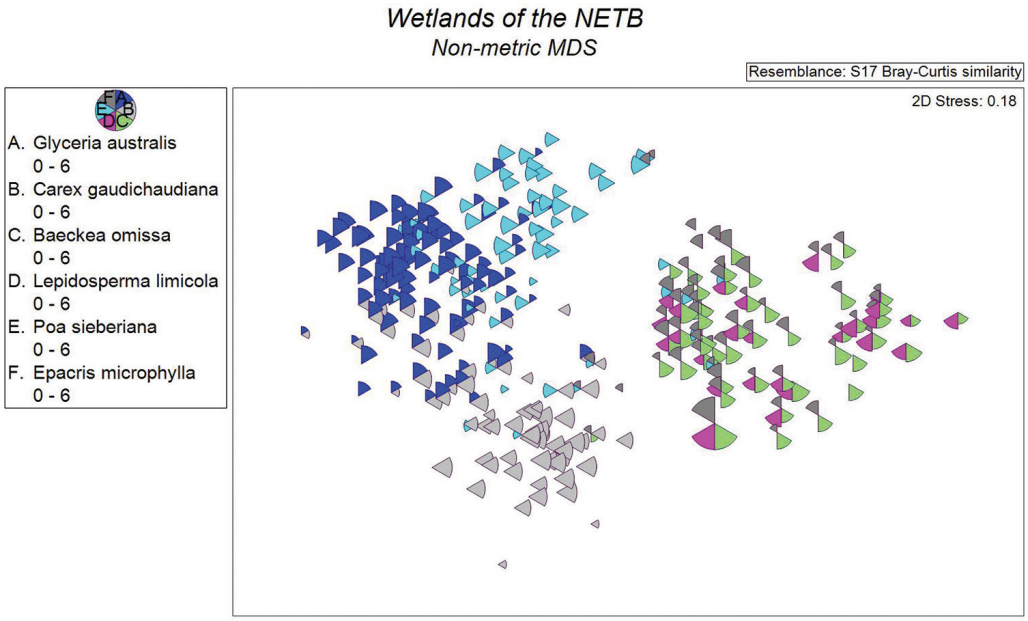

Figure 4. NMDS ordination Segmented bubble plot of the six species with a Pearson correlation greater than 0.5. Segment sizes are proportional to the Braun-Blanquet score given to each species within plots (0–6).

Figure 5. Broad wetland types found within the New England Tablelands Bioregion. A) Bog, B) Fen, C) Lagoon in its more common dry phase, D) Sod Tussock Grasslands.

a clear differentiation between bogs and other wetland types within the NETB.

Previous research has shown that bogs within the NETB are ecologically and functionally distinct dominated by taxa with traits dissimilar to those of the sympatric other wetland types such as fens and wet meadows (Hunter 2016a). Bogs form generally on low nutrient and acid soils with fire as a more frequent disturbance due to the dominance of oil-bearing resprouting shrub species. Bogs are the only wetland types to more consistently allow de-

Table 3. Comparison of species density and general environmental data for each alliance.

Hierarchy	Mean species density per 400 m²	Elevation (m a.s.l.)	Mean vegetation height (m)	Water depth (m)	Rock type
Alliance 1-1: Scientific Name: *Baeckea omissa – Epacris microphylla* shrubby bog	27	940–1372	0.2–6	0–0.2	Granite, acid volcanic, basalt
Alliance 1-2: Scientific Name: *Lepidosperma gunnii – Lepidosperma limicola* herbaceous bog	22	920–1040	0.2–3	0–0.2	Granite
Alliance 2-1: Scientific Name: *Carex appressa* herbaceous fen	18	446–1120	0.3–1.2	0–0.2	Granite, metasediment, acid volcanic, basalt
Alliance 2-2: Scientific Name: *Carex gaudichaudiana – Isachne globosa* herbaceous fen	18	780–1400	0.3–1	0–0.2	Granite, metasediment, basalt, sediment
Alliance 2-3: Scientific Name: *Philydrum lanuginosum – Potamogeton tricarinatus* herbaceous ephemeral marsh and fen	14	800–1000	0.1–1	0–0.5	Granite
Alliance 2-4: Scientific Name: *Lachnagrostis filiformis* herbaceous wet meadow or marsh	10	800–1300	0.1–1	0	Basalt, granite
Alliance 2-5: Scientific Name: *Myriophyllum variifolium – Eleocharis acuta* herbaceous ephemeral marsh	13	1040–1400	0.1–1	0–1.5	Basalt, granite
Alliance 2-6: Scientific Name: *Glyceria australis* grassy wet meadow	11	700–1400	0.2–1.2	0–0.2	Granite, metasediment, acid volcanic, basalt, shale, sediment
Alliance 2-7: Scientific Name: *Juncus australis – Cenchrus purpurascens* herbaceous wet meadow	8	1200–1350	0.2–1	0–0.1	Basalt, Metasediment
Alliance 2-8: Scientific Name: *Carex tereticaulis – Asperula conferta* herbaceous wet meadow and fen	22	1000–1350	0.5–1.5	0	Metasediment, sediment
Alliance 2-9: Scientific Name: *Poa sieberiana – Themeda triandra* grassy wet meadow	17	980–1350	0.15–1.2	0	Granite, metasediment, basalt, mudstone, acid volcanic
Alliance 2-10: Scientific Name: *Leptorhynchos squamatus – Schoenus apogon* herbfield	11	930–1100	0.15–0.3	0	Basalt

velopment of *Sphagnum* and it forms a major component of peat in patches less frequently burnt or more generally by restionaceous materials. The other mire types identified all predominantly occur on higher nutrient soils, do not generally burn and almost never contain *Sphagnum* as a component, with peat largely derived from cyperaceous and grass root and above ground materials.

Our numerical analysis approach has highlighted a deficiency in previous supervised or semi-supervised techniques to describe the variation within mires within the NETB. Nearly half of the alliances we have circumscribed are not represented within published state PCTs and even less of the 28 previously published associations are currently recognised as accepted PCTs (Hunter and Bell 2007; Hunter and Bell 2009; Hunter and Hunter 2016). A similar result was also found when comparing an unsupervised analysis of arid and semi-arid ephemeral wetlands within New South Wales to accepted PCTs, classes and formations (Hunter and Lechner 2017). More concerning is the Regional Ecosystem (RE) approach of Queensland, in which half of our circumscribed assemblages do not have an equivalent type and the remainder would all be placed within a single RE in spite of this classification being attributed to the association level (Addicott et al. 2018). This RE appears to be more aligned with our macrogroup level rather than association or alliance (Table 2) and thus we would suggest that the RE system may be operating at a different thematic scale and may not be closely aligned to association as the authors suggest.

What we consider as a single macrogroup is distributed across three classes and two formations within the New South Wales system which calls for the need to review the clarity and consistency of those accepted higher hierarchical levels (Hunter and Lechner 2017). We consider a more appropriate conceptualisation is that all the wetlands within our analysis be considered as types of mires and contained within a single hierarchical level. Thus, our macrogroup is floristically and biogeographically distinct, i.e. a New England Tableland Montane Mires (Table 1). This conceptualisation is supported both floristically and geographically. Floristically, Whinam and Chilcott (2002), Hunter and Bell (2013) and Hunter and Hunter (2016) have shown this region is floristically distinctive in terms of bog and wet meadow floristics. Lechner et al.

Table 4. Synoptic table of the most important species (≥ 5% mean constancy or ≥ 50% constancy in at least one alliance) of mire alliances of the New England Tableland Bioregion. Values in the columns are percentage constancies. Species with 50% or more in at least one alliance are listed under the alliance where they reach the highest constancy. Those species that did not reach 50% constancy in any of the alliances are listed under "Companion species" according to decreasing mean constancy. See Suppl. material 2 for full synoptic table. 1-1 *Baeckea omissa – Epacris microphylla* shrubby bog, 1-2 *Lepidosperma gunnii – Lepidosperma limicola* herbaceous bog, 2-1 *Carex appressa* herbaceous fen, 2-2 *Carex gaudichaudiana – Isachne globosa* herbaceous fen, 2-3 *Philydrum lanuginosum – Potamogeton tricarinatus* herbaceous ephemeral marsh and fen, 2-4 *Lachnagrostis filiformis* herbaceous wet meadow or marsh, 2-5 *Myriophyllum variifolium – Eleocharis acuta* herbaceous ephemeral marsh, 2-6 *Glyceria australis* grassy wet meadow, 2-7 *Juncus australis – Cenchrus purpurascens* herbaceous wet meadow, 2-8 *Carex tereticaulis – Asperula conferta* herbaceous wet meadow and fen, 2-9 *Poa sieberiana – Themeda triandra* grassy wet meadow, 2-10 *Leptorhynchos squamatus – Schoenus apogon* herbfield.

Alliance	**Mean**	1-1	1-2	2-1	2-2	2-3	2-4	2-5	2-6	2-7	2-8	2-9	2-10
Number of plots		59	5	22	77	4	14	57	87	5	7	36	4
Alliance 1-1													
Baeckea omissa	13.5	100	60	–	2	–	–	–	–	–	–	–	–
Epacris microphylla	16.1	100	80	–	7	–	–	–	–	–	–	6	–
Gonocarpus micranthus	11.3	76	40	5	4	–	–	–	–	2	–	9	–
Leptospermum gregarium	5.9	71	–	–	–	–	–	–	–	–	–	–	–
Baloskion stenocoleum	11.9	63	60	–	20	–	–	–	–	–	–	–	–
Callistemon pityoides	4.9	59	–	–	–	–	–	–	–	–	–	–	–
Hakea microcarpa	6.0	55	–	–	11	–	–	–	–	–	–	6	–
Alliance 1-2													
Austrostipa pubescens	8.3	–	100	–	–	–	–	–	–	–	–	–	–
Dampiera stricta	9.0	8	100	–	–	–	–	–	–	–	–	–	–
Goodenia bellidifolia	14.7	73	100	–	–	–	–	–	–	–	–	3	–
Persoonia oleoides	8.7	4	100	–	–	–	–	–	–	–	–	–	–
Pteridium esculentum	9.8	10	100	–	2	–	–	–	–	–	–	6	–
Dillwynia phylicoides	7.0	4	80	–	–	–	–	–	–	–	–	–	–
Entolasia stricta	11.1	53	80	–	–	–	–	–	–	–	–	–	–
Hovea heterophylla	6.7	–	80	–	–	–	–	–	–	–	–	–	–
Leptospermum arachnoides	10.6	47	80	–	–	–	–	–	–	–	–	–	–
Petrophile canescens	7.3	8	80	–	–	–	–	–	–	–	–	–	–
Aristida jerichoensis	5.0	–	60	–	–	–	–	–	–	–	–	–	–
Banksia spinulosa	7.6	31	60	–	–	–	–	–	–	–	–	–	–
Dianella caerulea	5.5	6	60	–	–	–	–	–	–	–	–	–	–
Lepidosperma gunnii	5.8	10	60	–	–	–	–	–	–	–	–	–	–
Lepidosperma limicola	9.3	51	60	–	–	–	–	–	–	–	–	–	–
Lepidosperma tortuosum	5.5	6	60	–	–	–	–	–	–	–	–	–	–
Leptospermum minutifolium	6.3	10	60	5	–	–	–	–	–	–	–	–	–
Lepyrodia scariosa	7.9	35	60	–	–	–	–	–	–	–	–	–	–
Lindsaea linearis	6.5	18	60	–	–	–	–	–	–	–	–	–	–
Lomandra multiflora	7.0	14	60	–	–	–	–	–	4	–	–	6	–
Melichrus procumbens	5.2	2	60	–	–	–	–	–	–	–	–	–	–
Pimelea linifolia	6.2	14	60	–	–	–	–	–	–	–	–	–	–
Rytidosperma indutum	5.0	–	60	–	–	–	–	–	–	–	–	–	–
Selaginella uliginosa	5.3	4	60	–	–	–	–	–	–	–	–	–	–
Stylidium graminifolium	6.0	12	60	–	–	–	–	–	–	–	–	–	–
Alliance 2-1													
Carex appressa	14.9	2	–	100	37	–	–	4	10	–	–	26	–
Rubus anglocandicans	17.4	2	–	64	37	–	–	6	27	20	50	3	–
Rumex crispus	15.6	–	–	64	46	–	31	21	8	–	17	–	–
Verbena bonariensis	19.0	–	–	64	26	33	31	6	26	–	33	9	–
Alliance 2-2													
Holcus lanatus	41.8	4	–	41	100	33	8	45	64	80	67	59	–
Carex gaudichaudiana	19.9	2	–	23	98	33	–	26	17	20	17	3	–
Epilobium billardierianum	15.1	6	–	41	78	–	–	28	16	–	–	12	–
Stellaria angustifolia	14.3	2	–	27	76	–	–	17	9	–	–	15	25
Isachne globosa	7.7	24	–	–	65	–	–	2	1	–	–	–	–
Geranium solanderi	24.7	37	40	45	63	–	8	6	32	20	33	12	–
Cyperus sphaeroideus	7.3	2	–	27	50	–	–	9	–	–	–	–	–
Alliance 2-3													
Philydrum lanuginosum	8.8	2	–	–	4	100	–	–	–	–	–	–	–
Asperula conferta	14.0	–	–	9	–	67	–	4	14	–	33	41	–
Brachyscome tenuiscapa	8.4	2	–	–	–	67	–	–	8	–	–	24	–
Carex breviculmis	10.2	–	–	–	–	67	–	–	9	–	17	29	–

Alliance	**Mean**	1-1	1-2	2-1	2-2	2-3	2-4	2-5	2-6	2-7	2-8	2-9	2-10
Number of plots		59	5	22	77	4	14	57	87	5	7	36	4
Plantago lanceolata	24.8	2	–	41	7	67	–	6	30	40	33	47	25
Alliance 2-4													
Lachnagrostis filiformis	25.5	4	–	23	17	–	100	74	18	–	17	3	50
Conyza bonariensis	17.0	–	–	27	11	–	77	17	26	40	–	6	–
Trifolium repens	24.3	–	–	32	26	33	54	17	42	40	–	47	–
Alliance 2-5													
Myriophyllum variifolium	12.1	2	–	–	7	33	–	100	3	–	–	–	–
Alliance 2-6													
Glyceria australis	22.8	–	–	9	11	67	–	26	100	20	–	41	–
Cirsium vulgare	32.8	6	–	50	52	–	31	23	79	60	33	35	25
Alliance 2-7													
Juncus australis	29.3	–	–	41	26	33	–	38	49	100	17	47	–
Cenchrus purpurascens	26.8	10	–	36	17	33	–	19	31	80	17	53	25
Carex disticha	10.8	–	–	5	35	–	–	–	18	60	–	12	–
Alliance 2-8													
Carex tereticaulis	8.5	–	–	–	–	–	–	2	–	–	100	–	–
Anthoxanthum odoratum	23.5	2	–	9	43	33	15	15	32	–	83	50	–
Carex inversa	11.0	2	–	14	28	–	–	4	3	–	50	6	25
Alliance 2-9													
Poa sieberiana	23.3	14	–	9	4	67	–	2	30	20	33	100	–
Hypochaeris radicata	31.9	22	–	50	30	–	69	17	26	40	33	71	25
Themeda triandra	14.6	35	–	–	–	67	–	–	5	–	–	68	–
Schoenus apogon	14.3	29	–	9	4	–	–	15	12	–	–	53	50
Haloragis heterophylla	14.3	8	–	36	28	33	–	9	8	–	–	50	–
Alliance 2-10													
Leptorhynchos squamatus	8.8	–	–	–	–	–	–	2	3	–	–	–	100
Paspalum dilatatum	35.3	–	–	73	20	33	31	34	25	60	33	15	100
Eleocharis atricha	6.3	–	–	–	–	–	–	–	–	–	–	–	75
Hydrocotyle tripartita	15.6	–	–	23	22	–	8	47	6	–	–	6	75
Juncus subsecundus	8.7	16	–	5	4	–	–	4	–	–	–	–	75
Eragrostis curvula	5.5	–	–	5	–	–	–	2	9	–	–	–	50
Phleum pratense	4.5	–	–	–	–	–	–	4	–	–	–	–	50
Sporobolus creber	5.6	2	–	–	–	–	–	–	–	–	–	15	50
Companion species													
Ranunculus lappaceus	15.3	18	–	14	39	33	–	4	12	20	17	26	–
Taraxacum officinale	15.3	2	–	14	22	33	8	13	43	–	33	15	–
Euchiton sphaericus	11.2	14	–	9	–	33	15	6	13	20	–	24	–
Ammi majus	10.5	–	–	–	–	–	46	–	26	–	33	21	–
Rumex brownii	10.3	–	–	18	2	33	8	2	16	20	–	24	–
Ranunculus inundatus	9.5	–	–	9	24	33	–	36	6	–	–	6	–
Persicaria prostrata	8.5	–	–	18	–	–	38	4	–	–	17	–	25
Eleocharis acuta	8.4	–	–	36	9	–	–	47	6	–	0	3	–
Festuca elatior	8.4	–	–	32	48	–	–	–	4	–	17	–	–
Persicaria hydropiper	8.3	–	–	23	30	–	–	19	8	20	–	–	–
Hypericum gramineum	8.1	29	20	5	7	–	–	2	3	–	–	6	25
Lythrum salicaria	8.0	4	–	5	48	33	–	–	3	–	–	3	–
Lomandra longifolia	7.9	29	20	–	4	33	–	–	–	–	–	9	–
Hemarthria uncinata	7.3	2	–	9	9	–	8	28	6	–	17	9	–
Poa labillardieri	7.3	–	40	5	9	33	–	–	1	–	–	–	–
Juncus usitatus	7.3	2	–	18	9	33	–	0	4	–	–	21	–
Phalaris aquatica	6.8	12	–	14	–	–	–	–	27	–	17	12	–
Rumex conglomeratus	6.8	–	–	23	13	–	–	–	23	20	–	3	–
Hypericum japonicum	6.7	16	–	5	20	–	–	6	1	20	–	12	–
Cynodon dactylon	6.6	–	–	9	–	33	–	11	3	20	–	3	–
Eleocharis sphacelata	6.2	4	–	5	24	–	–	38	3	–	–	–	–
Setaria pumila	6.0	6	–	–	7	–	–	4	4	–	17	9	25
Eleocharis pusilla	5.9	–	–	–	11	33	–	15	6	–	–	6	–
Prunella vulgaris	5.8	6	–	14	17	–	–	2	4	20	–	6	–
Viola hederacea	5.8	22	20	–	4	–	–	–	–	–	17	6	–
Geranium neglectum	5.7	–	–	–	2	–	38	2	3	–	17	6	–
Eleocharis gracilis	5.4	–	–	5	17	–	–	40	3	–	–	–	–
Juncus fockei	5.4	–	–	5	11	–	8	34	1	–	–	6	–
Oxalis perennans	5.3	4	–	5	–	–	–	–	3	–	17	35	–
Rorippa palustris	5.2	–	–	–	–	–	38	6	1	–	17	–	–
Sorghum leiocladum	5.2	4	–	–	–	33	–	–	1	–	–	24	–

(2016) showed the New England Region formed distinct ecoregions in terms of the occurrence of mapped mires of all types. Furthermore, the highland region of the New England Tablelands Bioregion is disconnected from more southern highland areas by the Hunter Valley.

Most of the NETB mires are currently listed as endangered communities on state and national acts (Hunter and Bell 2007; Bell et al. 2008; Hunter and Bell 2009; Hunter and Hunter 2016) and thus an understanding of the natural variation and interrelationships between these systems is important. Clear distinction of vegetation units is a necessity for conservation and management. Indistinct or ill-defined systems can lead to inappropriate management actions (Hunter and Hunter 2016; Hunter 2018). For example, semi-permanent or ephemeral marshes of the NETB are considered a distinct floristic association, class and formation within current New South Wales classification schema (Keith 2004; Benson et al. 2010). In addition, semi-permanent or ephemeral marshes are currently listed as an endangered ecological community both under the state *Biodiversity Conservation* (BC) *Act* 2017 (*Upland Wetlands of the Drainage Divide of the New England Tableland Bioregion*), and the federal *Environment Protection and Biodiversity Conservation* (EPBC) *Act* 1999 (*Upland wetlands of the New England Tablelands and the Monaro Plateau*).

Upland wetlands (lagoons) are a geomorphologically defined landscape element that contains a number of vegetation types within it (Bell et al. 2008; Hunter and Bell 2009; Hunter and Hunter 2016; Hunter 2018). However, only the floristics and not the geomorphological features are the dominant criteria used to distinguish this threatened community legislatively, but the system contains a number of distinct floristic types (fens, marshes, wet meadows). In practice this means that 'lagoons' are classed as an endangered vegetation community but this same community may also contain within it other endangered vegetation communities including *Carex* fens dominated by *Carex appressa*, which has its own listing, and bogs dominated by *Carex gaudichaudiana*, which also has its own listing and wet meadows which is under threat and may warrant listing in the near future (Hunter and Hunter 2016). Thus, within the one location two endangered communities can occur within another yet they are all supposed to be based on distinct floristic composition. This is further exacerbated by the fact that most of these 'lagoons' may only wet a few times a century and thus cannot be defined easily by floristics alone. The confusion of listing a geomorphological feature as an endangered system but defining it based on floristics has led to a distortion in understanding. We believe defining clear and distinct floristic units clarifies the relationships between wetland types and would avoid this nestedness of endangered community listings.

The most distinctive alliance, largely restricted to lagoons (2-5 *Myriophyllum variifolium – Eleocharis acuta* ephemeral marsh), is the least likely to be temporally present and often within only a proportion of the lagoon area and yet it is used to define the wetland. A more detail temporal understanding of the dynamics of this system is required (Bell et al. 2008; Hunter 2016a; Hunter 2018). As the majority of lagoons within the NETB cycle sporadically between mainly drier and often rare wet phases, that may or may not include inundation but almost always include zonation, samples taken within them were found to occur within various alliances within our analyses. We believe that by creating and defining vegetation types based on floristic analysis allows a better understanding of temporal changes and the effects of these wetting and drying cycles. Lumping several distinct floristic assemblages into a single geomorphic unit obscures our ability to conceptualise and study plant competition, establishment and changes due to fluctuating resources (Hunter 2016a, 2018). Based on our analysis, lagoons are likely to contain two formations, three classes and four PCTs rather than a single PCT, class and formation based on the works of Keith (2004) and Benson et al. (2010).

Supervised techniques have also led to the confusion in the determination of other state listed threatened montane mires within the NETB. Threatened community listings within state and federal acts are meant to be based on floristic distinctiveness. Fens dominated by either *Carex gaudichaudiana* or *Carex appressa* are peat forming and, closely aligned within our analyses but they are distinct from bogs, and do not occur within the same threatened community listings. Montane bogs are listed as endangered on the state BC Act as "*Montane peatlands and swamps of the New England Tableland*, *New South Wales North Coast*, *Sydney Basin. South East Corner*, *South Eastern Highlands and the Australian Alps bioregions*". This determination includes what we have circumscribed as bogs and fens, including fens that are dominated by *Carex gaudichaudiana* but not other fen types (Hunter and Bell 2007). Our analyses clearly indicate bogs and fens are very distinct systems (Figures 2–4). Fens dominated by *Carex appressa* (but excluding those dominated by *Carex gaudichaudiana*) are also listed as a separate endangered ecological community on the state BC Act as "*Carex sedgelands of the New England Tableland*, *Nandewar*, *Brigalow Belt South and New South Wales North Coast bioregions*". Thus, the same fen type is listed under two different ecological community listings and is also separated from other closer related fen types (Hunter and Bell 2009). This is in spite of the fact that such determinations are meant to be based on floristic uniqueness and determined by largely by species composition.

Classification within Australia has largely been driven by the need to manage natural resources from both conservation and production perspectives and is linked to mapping outputs with a recent emphasis on unsupervised modelling techniques such as segmentation (Hunter 2016b; Gellie et al. 2017). However, undescribed vegetation types cannot be modelled and poorly circumscribed entities are likely to be inaccurately modelled and mapped (Hunter 2016b; Hunter and Lechner 2017). This is particularly a problem with wetland types, especially semi-permanent or ephemeral wetlands. Recent vegetation modelling within part of the NETB provided only a 10% accuracy of wetland extent

and types (Hunter 2013; Hunter 2018). Similar inaccuracy rates for modelled wetlands have been found with other recent state mapping programs (Hunter and Hawes 2013; Hunter 2016b). The lack of clear delineation of wetland vegetation types and the poor accuracy of modelled maps severely hampers our ability to understand and conserve these highly threatened systems.

Our results and those of other recent work (Hunter and Lechner 2017) has highlighted that wetlands within eastern Australia have been generally poorly sampled, at times ill-defined and often contain significant undescribed variation whose interrelationships have not been properly understood. This has led to poor circumscription of listed threatened ecological communities and difficulty in modelling for mapping and conservation purposes. While we have attempted to provide some clarity within a new proposed hierarchical classification schema for the NETB, there is a need to better circumscribe all Australian terrestrial wetland systems. There is significant utility in the creation of a well-defined hierarchical schema of vegetation types that is non-jurisdiction based and scalable to enable better understanding and management, and increase our ability to protect and conserve them.

Author contributions

J.T.H. and V.H.H. conceived and undertook all field work. J.T.H. completed all analyses and J.T.H. wrote the majority of the manuscript with V.H.H. providing comment and additional text.

Acknowledgements

We wish to thank the late Dr. Dorothy Bell for her assistance in collecting data and the many discussions that help our understanding of the wetland systems of the NETB.

References

Addicott E, Newton M, Laurance S, Neldner J, Laidlaw M, Butler D (2018) A new classification of savanna plant communities on the igneous rock lowlands and Tertiary sandy plan landscapes of Cape York Peninsula bioregion. Cunninghamia 18: 29–72.

Bell DM, Hunter JT, Haworth RJ (2008) Montane lakes (lagoons) of the New England Tablelands Bioregion. Cunninghamia 10: 475–492.

Bell DM, Hunter JT, Montgomery L (2012) Ephemeral wetlands of the Pilliga Outwash, northwest NSW. Cunninghamia 12: 181–190. https://doi.org/10.7751/cunninghamia.2012.12.015

Benson JS, Richards P, Waller S, Allen C (2010) New South Wales vegetation classification and assessment: Part 3. Plant communities of the NSW Brigalow Belt South, Nandewar and west New England Bioregions and update of NSW Western Plains and South-western Slopes plant communities. Version 3 of the NSWVCA database. Cunninghamia 11: 457–579.

Bruelheide H, Dengler J, Jiménez-Alfaro B, Purschke O, Hennekens SM, Chytrý M, Pillar VD, Jansen F, Kattge J, … Zverev A (2019) sPlot – a new tool for global vegetation analysis. Journal of Vegetation Science 30: 161–186. https://doi.org/10.1111/jvs.12710

Clarke PJ, Copeland LM, Hunter JT, Nano CE, Williams JB, Wills KE (1999) The vegetation and plant species of Torrington State Recreation Area. Division of Botany, University of New England, Armidale, AU.

De Cáceres M, Franklin SB, Hunter JT, Landucci F, Dengler J, Roberts DW (2018) Global overview of plot-based vegetation classification approaches. Phytocoenologia 48: 101–112. https://doi.org/10.1127/phyto/2018/0256

De Cáceres M, Chytrý M, Agrillo E, Attorre F, Botta-Dukát Z, Capelo J, Czúz B, Dengler J, Ewald J, Faber-Langendoen D, ... Wiser SK (2015) A comparative framework for broad-scale plot-based vegetation classification. Applied Vegetation Science 18: 543–560. https://doi.org/10.1111/avsc.12179

Environmental Protection Authority (2016) Technical guidance – Flora and vegetation surveys for environmental impact assessment. EPA, Western Australia. http://www.epa.wa.gov.au/sites/default/files/Policies_and_Guidance/EPA%20Technical%20Guidance%20-%20Flora%20and%20Vegetation%20survey_Dec13.pdf

Faber-Langendoen D, Baldwin K, Peet RK, Meidinger D, Muldavin E, Keeler-Wolf T, Josse C (2018) The EcoVeg approach in the Americas: U.S., Canadian and international vegetation classifications. Phytocoenologia 48: 215–237. https://doi.org/10.1127/phyto/2017/0165

Faber-Langendoen D, Keeler-Wolf T, Meidinger D, Tart D, Hoagland B, Josse C, Navarro G, Ponomarenko S, Saucier J-P, … Comer P (2014) EcoVeg: a new approach to vegetation description and classification. Ecological Monographs 84: 533–561. https://doi.org/10.1890/13-2334.1

Franklin SB, Hunter JT, De Cáceres M, Dengler J, Landucci F, Krestov P (2016) Introducing the IAVS Vegetation Classification Working Group. Phytocoenologia 46: 5–8. https://doi.org/10.1127/phyto/2016/0116

Gellie NJH, Hunter JT, Benson JS, Kirkpatrick JB, Cheal DC, McCreery K, Brocklehurst P (2017) Overview of plot-based vegetation classification approaches within Australia. Phytoceonologia 48: 251–272. https://doi.org/10.1127/phyto/2017/0173

Hunter JT (2013) Upland wetlands in the Namoi Catchment: mapping, distribution and disturbance classes of fens, bogs and lagoons. Cunninghamia 13: 331–335. https://doi.org/10.7751/cunninghamia2013.009

Hunter JT (2016a) Differences in disturbance type and nutrient availability favour different functional traits across three co-occurring wetland systems in eastern Australia. Australian Journal of Botany 64: 526–529. https://doi.org/10.1071/BT16021

Hunter JT (2016b) Validation of the Greater Hunter Native Vegetation Mapping as it pertains to the Upper Hunter Region of New South Wales. Ecological Management and Restoration 17: 1–7. https://doi.org/10.1111/emr.12195

Hunter JT (2018) Survey and monitoring of upland lagoons on the Northern Tablelands. Report for the Local Land Services NSW.

Hunter JT, Bell DM (2007) Vegetation of montane bogs in east-flowing catchments of northern New England, New South Wales. Cunninghamia 10: 77–92.

Hunter JT, Bell DM (2009) The *Carex* Fen vegetation of northern New South Wales. Cunninghamia 11: 49–64.

Hunter JT, Bell DM (2013) Season and timing of moisture availability predict composition of montane shrub-dominated wetlands at distri-

butional limits in eastern Australia. Australian Journal of Botany 61: 243–253. https://doi.org/10.1071/BT13017

Hunter JT, Hawes W (2013) Review of the Greater Namoi Native Vegetation Map. Report to the Namoi Catchment Management Committee.

Hunter JT, Hunter VH (2016) Tussock and sod tussock grasslands of the New England Tablelands Bioregion of eastern Australia. Pacific Conservation Biology 22: 12–19. https://doi.org/10.1071/PC15037

Hunter JT, Hunter VH (2017) Floristics, dominance and diversity within the threatened *Themeda* grassy headlands of the North Coast Bioregion of New South Wales. Pacific Conservation Biology 23: 71–80. https://doi.org/10.1071/PC16013

Hunter JT, Lechner AM (2017) A multiscale, hierarchical, ecoregional and floristic classification of arid and semi-arid ephemeral wetlands in New South Wales, Australia. Marine and Freshwater Research 68: 1–14.

Jensen F, Bergmeier E, Dengler J, Janišová M, Krestov P, Willner W (2016) Vegetation classification: a task for our time. Phytocoenologia 46: 1–4. https://doi.org/10.1127/phyto/2016/0134

Lechner AM, McCaffrey N, McKenna P, Venables W, Hunter JT (2016) Ecoregionalisation classification of wetlands based on a cluster analysis of environmental data. Applied Vegetation Science 19: 724–735. https://doi.org/10.1111/avsc.12248

Paijmans K, Galloway RW, Faith DP, Fleming PM, Haantjens HA, Heyligers PC, Kalma JD, Loffler E (1985) Aspects of Australian wetlands. CSIRO Division, Canberra, AU.

Resource and Conservation Assessment Council (1996) Regional report of Upper North East. New South Wales Vol. 2: Physical attributes. Resource and Conservation Assessment Council, Sydney, AU.

Sivertsen D (2009) Native Vegetation Interim Type Standard. Department of Environment, Climate Chante and Water NSW, Sydney, AU. https://www.environment.nsw.gov.au/resources/nativeveg/10060nvinttypestand.pdf

Thackwell R, Creswell ID (1995) An interim biogeographic regionalisation for Australia: a framework for setting priorities in the national reserve system. Version 4.0. Australian Nature Conservation Agency, Canberra, AU.

van Diggelen R, Middleton B, Bakker J, Grootjans A, Wassen M (2006) Fens and floodplains of the temperate zone: present status, threats, conservation and restoration. Applied Vegetation Science 9: 157–162. https://doi.org/10.1111/j.1654-109X.2006.tb00664.x

Wahren CH, Williams RJ, Papsi WA (1999) Alpine and subalpine wetland vegetation on the Bogong High Plains, south eastern Australia. Australian Journal of Botany 47: 165–188. https://doi.org/10.1071/BT97106

Westhoff V, van der Maarel E (1980) The Braun-Blanquet approach. In: Whittaker RH (Ed.) Classification of plant communities, 2nd ed. W. Junk, the Hague, NL, 289–329.

Whinam J, Chilcott N (2002) Floristic description and environmental relationships of *Sphagnum* communities in NSW and the ACT and their conservation management. Cunninghamia 7: 463–500.

Whinam J, Hope G (2005) The peatlands of the Australasian region. Stapfia 85: 397–400.

E-mail and ORCID

John T. Hunter (Corresponding author, jhunter8@bigpond.com), ORCID: https://orcid.org/0000-0001-5112-0465
Vanessa H. Hunter (vhhunter@bigpond.com)

Supplementary material

Supplementary material 1
Images of the circumscribed NETB montane mire alliances
Link: https://doi.org/10.3897/VCS/2020/48765.suppl1

Supplementary material 2
Full synoptic table of the 12 distinguished alliances
Link: https://doi.org/10.3897/VCS/2020/48765.suppl2

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 53–75
doi: 10.3897/VCS/2020/48377

RESEARCH PAPER

A phytosociological survey of aquatic vegetation in the main freshwater lakes of Greece

Dimitrios Zervas[1,2], Ioannis Tsiripidis[1], Erwin Bergmeier[3], Vasiliki Tsiaoussi[2]

1 *Department of Botany School of Biology, Aristotle University of Thessaloniki, Greece*
2 *Greek Biotope/Wetland Centre (EKBY), The Goulandris Natural History Museum, Thessaloniki, Greece*
3 *Department of Vegetation and Phytodiversity Analysis, University of Göttingen, Germany*

Corresponding author: Dimitrios Zervas (dzervas@ekby.gr)

Academic editor: Flavia Landucci ♦ **Received** 11 November 2019 ♦ **Accepted** 21 December 2019 ♦ **Published** 4 May 2020

Abstract

Aims: This study aims to contribute to the knowledge of European freshwater lake ecosystems with updated and new information on aquatic plant communities, by conducting national-scale phytosociological research of freshwater lake vegetation in Greece. Moreover, it investigates the relationship between aquatic plant communities and lake environmental parameters, including eutrophication levels and hydro-morphological conditions. **Study area:** Lakes in Greece, SE Europe. **Methods:** 5,690 phytosociological relevés of aquatic vegetation were sampled in 18 freshwater lake ecosystems during 2013–2016. The relevés were subjected to hierarchical cluster and indicator species analyses in order to identify associations and communities of aquatic vegetation, as well as to describe their syntaxonomy. Multiple regression analysis was applied to investigate the relationship between vegetation syntaxa and environmental parameters of lakes, i.e. physico-chemical parameters and water level fluctuation. **Results:** Ninety-nine plant taxa belonging to 30 different families were recorded. Forty-six vegetation types were identified and described by their ecological characteristics, diagnostic taxa and syntaxonomical status. Thirteen vegetation types, the largest number belonging to the vegetation class *Charetea*, are considered to be new records for Greece. The distribution of the vegetation types recorded in the 18 freshwater lakes was found to depend on environmental parameters and levels of eutrophication. **Conclusions:** An updated aquatic vegetation inventory was produced for Greek lakes, and primary results showed that the presence/absence of aquatic plant communities and the community composition in freshwater lakes can be utilized to assess the pressure of eutrophication on lake ecosystems.

Taxonomic reference: Euro+Med (2006–).

Abbreviations: MNT = Mean number of taxa; WFD = Water Framework Directive.

Keywords

aquatic plant, charophyte, ecological status, eutrophication, Greece, lake, macrophyte, phytosociology, plant community, vegetation

Introduction

Freshwater ecosystems are among the most threatened ecosystems around the world (Sala et al. 2000; Foley et al. 2005; Dudgeon et al. 2006). Overexploitation, water pollution, flow modification, destruction or degradation of habitats, and exotic species invasions are the five main drivers of biodiversity loss in freshwater ecosystems (Dudgeon et al. 2006). The European Union addressed the vulnerability of freshwater ecosystems with the adoption of the European Water Framework Directive (WFD, European Commission 2000). In this frame-

PENSOFT.

Copyright *Dimitrios Zervas et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

work, the monitoring of aquatic plant communities was proposed as a key element in order to assess the ecological status of freshwater ecosystems, as macrophytes play a significant role in determining the structure and functions of lake ecosystems by influencing environmental conditions, nutrient cycling, and biotic assemblages and interactions (Carpenter and Lodge 1986; Jeppesen et al. 1997; Engelhardt and Ritchie 2001). As a result, most of the monitoring and assessment systems developed by European countries utilise rankings in the tolerance and sensitivity of macrophyte taxa to eutrophication (Kolada et al. 2014; Poikane et al. 2018). The monitoring of aquatic macrophytes in Greek freshwater ecosystems, in the context of the Greek National Water Monitoring Network (GNWMN) under the WFD, began in 2013 (Zervas et al. 2018).

The number of floristic and phytosociological investigations in freshwater ecosystems within Greece has increased during the past three to four decades (Sarika-Hatzinikolaou et al. 2003; Sarika et al. 2005). Also publications containing phytosociological data for lacustrine aquatic plant communities have accumulated over time, but remain scarce and not evenly distributed across the country: Gradstein and Smittenberg (1977: western Crete), Lavrentiades and Pavlidis (1985: Lake Mikri Prespa), Papastergiadou (1990: various lakes in Northern Greece), Bergmeier (2001: seasonal pools in the island of Gavdos), Sarika-Hatzinikolaou et al. (2003: seven lakes in Epirus), Grigoriadis et al. (2005: Agras wetland), Dimopoulos et al. (2005: Kalodiki marsh); Zotos (2006: Lakes Trichonida and Lysimachia), Fotiadis et al. (2008: Lake Chimaditida), and Pirini (2011: Lakes Vegoritida and Petres). These studies provide important information about aquatic vegetation in Greece, but the older ones do need to be revised and updated. Furthermore, research gaps remain in the country, i.e. a number of important lakes remain unsurveyed.

Taking into consideration all of the above information, the main objectives of this study are (i) to contribute to the knowledge of European freshwater lake ecosystems with new and updated country-wide information on the aquatic plant communities found in the main Greek freshwater lakes, and (ii) to investigate the relationship between the distribution patterns of macrophyte communities and environmental parameters indicating increased levels of eutrophication and altered hydro-morphological conditions.

Study area

The study covers 18 lakes (Table 1; Figure 1) selected for GNWMN monitoring of aquatic macrophytes (Mavromati et al. 2017; Zervas et al. 2018). While the studied lakes are scattered over the Greek mainland, most of them are clustered in the west and north-central part of the country, differing in altitude, size, water depth, and local climatic conditions within their catchment area (Table 1). Of the three transboundary lakes (Doirani, Megali Prespa, Mikri Prespa) only their Greek areas were studied.

Methods

Vegetation and environmental data

Each lake was surveyed once in 2013–2016 during the main growing season (May to September) (Table 1). In all lakes, the belt transect-mapping method was applied

Table 1. Overview of the geographical, geometric and climatic characteristics of the studied lakes. Asterisks mark transboundary lakes, for which the characteristics refer to their part in Greece. Climatic characteristics have been collected by the European Climate Assessment & Dataset (Klein Tank et al. 2002). Average annual temperature and annual precipitation values have been calculated on the basis of available data during the period 1995-2005. Survey period and number of transects and relevés surveyed per lake is also given.

No	Lake	Centroid Latitude (°N)	Centroid Longitude (°E)	Mean Altitude (masl)	Area (km²)	Mean-Max depth (m)	Aver. Annual Temp. (°C)	Annual Precipitation (mm)	Climate zone (Köppen & Geiger)	Survey period	No of transects/ relevés recorded
1	Volvi	40.67740	23.47368	37	75.5	13-28	15.6	458	Csa	Aug 2016	20 / 317
2	Doirani*	41.23853	22.76487	146	30.7	4-8	14.3	453	Cfa	Aug 2016	10 / 173
3	Vegoritida	40.74464	21.78442	517	46.5	25-52	11.5	530	Cfb	June 2016	20 / 509
4	Petres	40.72604	21.69612	573	12	3-6	11.5	562	Cfb	June 2016	16 / 227
5	Zazari	40.62507	21.54690	600	3	5-8	11.5	595	Cfb	July 2016	12 / 124
6	Chimaditida	40.59258	21.56585	592	9.1	1-5	11.5	595	Cfb	July 2016	16 / 239
7	Kastoria	40.52269	21.30080	627	31.2	4-9	11.4	697	Cfb	Aug 2014	20 / 312
8	Megali Prespa*	40.85057	20.98875	845	39.4	~16-26	10.2	750	Cfb	Aug 2015	12 / 206
9	Mikri Prespa*	40.77031	21.10128	850	46.7	4-10	10.2	728	Cfb	Aug 2015	15 / 294
10	Pamvotida	39.66270	20.88518	469	22.6	5-12	13.2	1081	Csa	Sept 2013	20 / 74
11	Amvrakia	38.75113	21.17941	20	13.5	22-54	17.3	930	Csa	June 2014	20 / 331
12	Ozeros	38.65358	21.22294	24	10.5	4-7	17.2	931	Csa	June 2014	20 / 178
13	Lysimachia	38.56234	21.37665	15	13	4-8	17.1	909	Csa	June 2014	20 / 215
14	Trichonida	38.57309	21.54813	16	93.4	30-56	17.1	902	Csa	July 2015	20 / 792
15	Paralimni	38.45862	23.35285	37	10.6	5-8	17.5	527	Csa	July 2014	20 / 503
16	Yliki	38.39764	23.27973	75	22.5	22-34	17.5	527	Csa	July 2014	20 / 29
17	Feneos	37.92861	22.28513	872	0.5	10-29	11.5	862	Csb	Aug 2014	10 / 373
18	Kourna	35.33180	24.27776	16	0.6	~15-22	18.2	831	Csa	May 2014	14 / 794

Figure 1. Map of the surveyed Greek freshwater lakes. See Table 1 for lake names.

(Zervas et al. 2018), the most commonly used method for aquatic vegetation surveys in Europe, due to the fact that it provides abundance, frequency and depth distribution data for the different taxa found within the vegetation of a lake (Kolada et al. 2009). Ten to 20 transects per lake were established from the shoreline perpendicular to the maximum depth of plant growth. Sampling was conducted in relevés of 4 m^2, evenly distributed along the belt transects following a gradient of increasing depth. Sampling was undertaken using a double-headed rake with a scaled handle or attached to a rope, a bathyscope, and a geo-bathymetric device. In this way, a total of 5,690 relevés were sampled, in which all angiosperms (helophytes, hydrophytes, amphiphytes and aquatic forms of land species), pteridophytes, bryophytes, charophytes and green filamentous macroalgae (e.g. *Cladophora* spp.) were recorded and determined to species or subspecies level (except filamentous macroalgae), and their abundance was estimated with the use of the semi-quantitative five-point DAFOR scale (Palmer et al. 1992). Vascular plant taxonomy follows Euro+Med (2006), while algae taxonomy follows Guiry and Guiry (2019). Chorological information was collected from Dimopoulos et al. (2013, 2016), Guiry and Guiry (2019), and Julve (1998).

A number of environmental data (e.g. total phosphorus concentrations in the water column, Secchi depth, water electric conductivity, water level fluctuation measurements) were collected periodically from each lake in the context of GNWMN (for details see Zervas et al. 2018). These data were used to assess the relationships between the distribution patterns of aquatic syntaxa and eutrophication and hydro-morphological factors.

Statistical analysis

In order to define the vegetation types in the most objective manner possible, the relevés were subjected to a number of hierarchical cluster analyses. Extremely rare taxa, i.e. recorded in one to three out of 5690 plots, were excluded from the analyses in order to reduce "noise" in the data. DAFOR abundance classes were translated to their average percentage abundance values as follows: Dominant = 87.5%, Abundant = 50%, Frequent = 17.5%, Occasional = 5.5% and Rare = 0.5% (CEN 2007). Species abundances were chord distance-based transformed (Legendre and Galacher 2001). The transformed dataset was then subjected to cluster analysis with the use of flexible beta linkage method with b = -0.25 (Lance and Williams 1967) and Bray-Curtis dissimilarity (Bray and Curtis 1957). Elbow and Average Silhouette methods (Kaufman and Rousseeuw 1990), and NbClust statistic (Charrad et al. 2014) were used to assist in the determination of the optimal number of clusters for the dataset. Finally, diagnostic taxa were determined by indicator species analysis (Dufrene and Legendre 1997; De Cáceres et al. 2012), using the indicators function, in order to finalize the number of clusters corresponding to distinct vegetation types, and describe the best combination of indicator species for each vegetation type.

Due to the overall low number of common taxa among the resulting clusters, the hierarchic dendrogram that was produced was not able to successfully group all vegetation types into meaningful syntaxa, thus we proceeded with an additional cluster analysis. The synoptic table, which contained the clusters representing our dataset, was integrated into a dataset of clusters representing the types of Greek aquatic vegetation published in the past (bibliography in Suppl. material 1) and was processed again using the flexible beta linkage method and Bray-Curtis dissimilarity. The aim of including these vegetation types from the literature within our dataset was to support the present syntaxonomical decisions. The syntaxonomy of higher syntaxa (alliances, orders and classes) in the current study follows, with few exceptions, Mucina et al. (2016).

Depth distribution for each vegetation type was calculated and presented. The distribution of higher-rank syntaxa for each lake was also computed on the basis of the number of relevés per syntaxon in proportion to the total number of relevés in each lake. Calculations were summarized at the level of class for most of the vegetation types, except the ones belonging to the *Potamogetonetea* which were divided at the level of alliance, owing to the high variation in this class with different life forms. Finally, a multiple linear regression model was applied to assess the relation between aquatic vegetation patterns, as expressed by the abundance of higher-rank syntaxa, and environmental parameters in each lake. Pearson's correlation coefficient (R) and p-value (p) of the model were assessed.

All analyses were performed with the use of vegan (Oksanen et al. 2018), cluster (Maechler et al. 2018), factoextra (Kassambara and Mundt 2017), NbClust (Charrad et al. 2014), indicspecies (De Cáceres and Legendre 2009), and tidyverse (Wickam 2017) R packages in R environment version 3.5.2 (R Core Team 2018).

Results and discussion

Species composition

The total number of taxa (vascular plants and macroalgae species) recorded in the studied lakes was 99. The most species-rich among the 30 different plant families were Characeae (12%), Cyperaceae (12%) and Potamogetonaceae (10%), followed by Hydrocharitaceae (7%), Lamiaceae (6%) and Poaceae (6%). Hydrophytes were the dominant life form (55% of total species) followed by hemicryptophytes (25%) and geophytes (19%). The most prominent chorological element was the Cosmopolitans (26%), followed by Paleotemperates (15%), European-SW Asians (15%) and Circumtemperates (14%). Most of the taxa (80 out of 99) were recorded with frequencies of less than 1%, i.e. they were found in fewer than 57 plots out of all 5,690. The most frequent taxa (found in more than 500 plots) were *Myriophyllum spicatum* (29.3%), *Phragmites australis* (27.2%), *Ceratophyllum demersum* (25.1%), *Vallisneria spiralis* (23%), *Stuckenia pectinata* (22.5%) and *Najas marina* (14.3%). Twenty-six out of 99 taxa were recorded in three or fewer plots (taxon frequencies for each lake are summarized in Suppl. material 2).

Vegetation classification

Cluster analysis and subsequent tests resulted in 46 different vegetation types for interpretation (see Suppl. material 3 for Elbow, Average Silhouette and NbClust results, and Suppl. material 4 for produced dendrogram). Due to the survey methodology used, i.e. consecutive relevés distributed along a depth gradient at equal depth intervals, a number of the resulting vegetation types correspond to transitional ecotonal stands. These vegetation types were retained in the synoptic tables and are described in the text so as to present a more comprehensive picture of the spatial and ecological patterns of vegetation differentiation within the studied lakes. For syntaxonomic purposes, they may well be merged with an adjacent vegetation type. The diagnostic species for each vegetation type were selected from the results of the indicator species analysis as those combinations that reached a higher Indicator Value, while maintaining high prediction power and sensitivity (De Cáceres et al. 2012) (see Suppl. material 5 for all diagnostic taxa parameters). Diagnostic and accompanying species for each vegetation type are given in Tables 2–4. Short descriptions of the ecology (structure, water-depth preference etc.), the floristic composition and the distribution for each vegetation type are presented at the following paragraphs (see Suppl. material 6 for summary of vegetation types in all lakes). Syntaxonomic remarks that led to their final syntaxonomic assignment (Table 5) are also presented.

Class 1. Plantaginetea majoris

Syntaxon 1.1. *Phyla nodiflora* community (Code PhN, Table 2, Mean number of taxa MNT = 2.4)

Appearance and habitat: Sparse temporarily submerged carpets, dominated by *Phyla nodiflora*, a perennial herb of prostrate growth, covering periodically flooded shores. *Phyla nodiflora* is a cosmopolitan pioneer herb that grows prolifically in floodplain wetlands with periodical flooding of short duration (Sharma and Singh 2013). Other aquatic macrophytes rapidly colonizing flooded areas, such as *Myriophyllum spicatum* and *Vallisneria spiralis*, can also be found in this community.

Diagnostic taxa (% constancy): *Phyla nodiflora* (100%).

Distribution: Amvrakia, Yliki.

Syntaxonomic remarks: No association dominated by *Phyla nodiflora* was found in the European literature. An association of *Phyla nodiflora* growing together with *Kyllinga peruviana* (*Kyllingo-Phyletum nodiflorae* Vanden Berghen 1990) (De Foucault et al. 2013) was described in West African temporarily inundated coastal dune slacks, another with *Paspalum vaginatum* (*Lippio nodiflorae-Paspaletum vaginati* Galán de Mera, Linares, Campos and Vicente 2009) in South American saltwater influenced grasslands on the Pacific coast (Galán de Mera et al. 2009). In publications from the western Mediterranean basin (e.g. Brullo and Sciandrello 2006; Ninot et al. 2011) an association of *Phyla nodiflora* growing in littoral grassy plains together with *Panicum repens* (*Lippio nodiflorae-Panicetum repentis* O. Bolòs 1957) has been described, but our community differs as *Panicum repens* is absent. Our material is insufficient to provide a firm basis for describing a new association. We do not follow Mucina et al. (2016) who treat the perennial *Phyla nodiflora* as a diagnostic species of the class *Isoëto-Nanojuncetea*, defined as pioneer ephemeral vegetation in periodically flooded freshwater habitats. We assign the *Phyla nodiflora* community described here to the order *Paspalo-Heleochloetalia* and to the alliance *Paspalo-Agrostion semiverticillati* instead, which comprises Mediterranean-subtropical temporarily inundated, disturbed, perennial grass-herblands rich in stoloniferous plants of tropical and subtropical distribution.

Syntaxon 1.2. *Paspalo distichi-Agrostietum verticillatae* (Code PD, Table 2, MNT = 3.1)

Appearance and habitat: Emerged and floating mats of *Paspalum distichum* colonizing exposed areas of wet ground that may be temporarily shallowly inundated. *Paspalum distichum* is a perennial grass, originating from tropical America, which is widely established in riparian habitats of the Mediterranean basin, often forming monotypic stands (Aguiar et al. 2005).

Diagnostic taxa (% constancy): *Paspalum distichum* (100%).

Distribution: Doirani, Lysimachia, Paralimni, Trichonida and Vegoritida.

Table 2. Synoptic table of the identified associations and communities belonging to Classes *Plantaginetea majoris*, *Phragmito-Magnocaricetea* and *Lemnetea*. Taxa constancy in percentage and their average abundance class (r = 0-1%, + = 2-5%, 1 = 6-20%, 2 = 21-40, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%) superscripted are shown. Companion taxa with less than 20% constancy are shown at the end of the Table. Diagnostic taxa for each vegetation type are marked in bold (see relevant text and Table 5 for vegetation type codes).

Vegetation type code	PhN	PD	PA	PAE	SL	TD	TL	TA	BU	LM	UV	CD	CDE	CDMS
Number of relevés	5	22	1065	29	18	18	18	14	17	11	10	735	55	62
Mean number of species	2.4	3.1	1.2	3.4	5.6	3.1	2.3	2.1	4.5	5.8	5.2	1.5	3.5	2.6
PLANTAGINETEA														
Phyla nodiflora	**100^{1}**	5^{1}	1^{r}	.	6^{r}	.	.	.	.	.	.	.	.	.
Paspalum distichum	.	**100^{1}**	.	.	17^{1}	.	.	.	.	55^{1}	.	1^{1}	.	.
PHRAGMITO-MAGNOCARICETEA														
Phragmites australis	.	14^{+}	**100^{4}**	**97^{2}**	78^{1}	84^{2}	6^{r}	8^{1}	30^{1}	28^{1}	20^{+}	11^{1}	**64^{2}**	7^{1}
Schoenoplectus lacustris	.	5^{r}	1^{+}	.	**100^{2}**	.	.	.	.	.	20^{+}	1^{1}	.	.
Typha domingensis	.	10^{+}	2^{1}	7^{1}	50^{2}	**100^{3}**	.	.	.	19^{1}	10^{1}	6^{1}	11^{+}	.
Typha latifolia	.	10^{1}	1^{+}	21^{1}	6^{r}	.	**100^{1}**	8^{r}	.	19^{1}	20^{4}	.	4^{1}	.
Typha angustifolia	.	.	1^{1}	.	6^{1}	.	6^{1}	**100^{1}**	.	.	.	.	.	.
Butomus umbellatus	.	.	.	.	.	.	.	.	**100^{2}**	.	.	.	.	.
Schoenoplectus litoralis	.	.	.	.	.	.	.	.	36^{1}	.	.	.	.	.
Alisma plantago-aquatica	.	.	.	.	.	12^{1}	.	.	.	19^{r}	30^{2}	.	2^{1}	.
Carex pseudocyperus	.	.	1^{1}	.	.	.	.	.	.	.	30^{2}	.	.	.
Juncus subnodulosus	.	.	.	.	.	.	.	.	.	.	30^{1}	.	.	.
Mentha aquatica	.	5^{r}	.	4^{1}	6^{1}	.	.	.	.	.	40^{1}	1^{+}	.	.
Lycopus europaeus	.	5^{r}	1^{1}	.	6^{r}	.	4^{1}	.	.	19^{+}	20^{1}	1^{1}	.	.
Eleocharis palustris	.	.	1^{1}	4^{1}	.	.	6^{r}	.	.	.	.	.	.	.
Stachys palustris	.	.	.	4^{1}	.	6^{1}	.	.	.	.	20^{1}	.	2^{1}	.
Lythrum salicaria	.	.	.	.	.	.	.	.	.	.	.	.	4^{1}	.
Rorippa amphibia	.	.	.	7^{+}	.	.	.	.	.	.	.	.	4^{1}	.
Oenanthe aquatica	.	.	.	4^{r}	.	.	.	.	.	28^{r}	.	.	2^{r}	.
Sparganium erectum	.	5^{1}	.	.	12^{1}	.	.	.	.	.	.	.	.	.
LEMNETEA														
Lemna minor	.	5^{1}	1^{1}	11^{2}	.	.	.	.	.	**100^{3}**	30^{2}	.	17^{2}	.
Lemna gibba	.	.	.	.	.	.	.	.	.	46^{1}	.	.	4^{1}	.
Azolla filiculoides	.	.	1^{r}	4^{r}	.	.	.	.	.	**73^{1}**	.		.	.
Spirodela polyrhiza	.	.	1^{+}	4^{1}	.	.	.	.	.	37^{1}	.	1^{+}	15^{1}	.
Salvinia natans	.	.	1^{1}	4^{r}	.	.	.	.	.	19^{2}	.	.	15^{1}	.
Utricularia vulgaris + australis	.	.	1^{1}	4^{1}	.	.	.	.	.	.	**100^{2}**	.	.	.
Ceratophyllum demersum	.	.	6^{1}	11^{1}	23^{1}	39^{3}	.	.	.	28^{1}	.	**100^{3}**	**100^{2}**	**100^{2}**
Ceratophyllum submersum	.	.	1^{1}	.	.	6^{1}	.	.	.	.	.	1^{1}	.	.
Hydrocharis morsus-ranae	.	.	1^{+}	4^{1}	.	12^{1}	.	.	.	10^{1}	40^{1}	.	17^{1}	.
Other taxa														
Myriophyllum spicatum	60^{1}	10^{1}	3^{1}	14^{+}	39^{1}	.	78^{1}	43^{+}	**100^{1}**	10^{1}	.	8^{+}	19^{+}	**100^{1}**
Stuckenia pectinata	.	.	3^{1}	71	28^{+}	.	.	.	.	.	.	3^{1}	19^{1}	9^{+}
Vallisneria spiralis	60^{2}	10^{+}	2^{1}	7^{+}	39^{+}	34^{1}	.	.	83^{1}	.	.	7^{1}	13^{+}	12^{1}
Potamogeton lucens	.	5^{1}	1^{1}	.	.	.	.	.	59^{1}	.	.	3^{1}	.	10^{1}
Rumex palustris	.	10^{r}	1^{1}	4^{1}	12^{+}	.	.	.	.	37^{2}	20^{1}	.	.	.
Potamogeton nodosus	20^{1}	10^{r}	.	.	17^{1}	.	.	.	.	.	.	1^{1}	.	5^{1}
Najas marina	.	5^{1}	3^{1}	**18^{1}**	23^{1}	.	.	.	6^{1}	.	10^{r}	.	10^{+}	10^{+}
Zannichellia palustris	.	.	1^{1}	4^{r}	.	.	.	.	.	.	20^{1}	.	.	.
Ludwigia peploides	.	23^{1}	2^{1}	.	.	.	.	.	.	.	.	1^{1}	.	.
Chara globularis	.	5^{1}	.	.	.	23^{1}	.	22^{1}	.	.	.	.	.	.
Cladophora glomerata	.	37^{+}	1^{+}	**49^{1}**	17^{1}	17^{1}	.	.	30^{+}	37^{+}	.	5^{+}	13^{2}	2^{r}
Nitellopsis obtusa	.	.	.	**14^{3}**	.	.	.	.	.	.	.	1^{1}	.	.

Taxa with less than 20% constancy: *Juncus articulatus*, SL:17^{1}; *Mentha pulegium*, TA:8^{1}; *Eleocharis mitracarpa*, UV:10^{1}; *Potamogeton perfoliatus*, PD:5^{1}, PA:1^{1}, PAE:7^{1}, BU:6^{r}, SL:6^{1}, CD:1^{+}, CDE:13^{1}, CDMS:4^{1}; *Potamogeton crispus*, PD:5^{r}, PAE:4^{r}, CD:1^{1}; *Potamogeton compressus*, CD:1^{1}; *Potamogeton trichoides*, PD:10^{1}, CD:1^{1}, CDMS:2^{1}; *Najas minor*, PD:5^{1}, PA:1^{1}, PAE:4^{1}, CD:1^{1}, CDE:4^{1}; *Myriophyllum verticillatum*, TL:12^{r}, CD:1^{1}; *Potamogeton berchtoldii*, CD:1^{+}; *Trapa natans*, PA:1^{1}, CD:2^{1}, CDE:6^{1}; *Nymphaea alba*, PD:5^{r}, 2=1^{1}, SL:17^{+}, 13=2^{1}; *Nymphoides peltata*, PA:1^{r}, PAE:4^{1}; *Persicaria amphibia*, PA:1^{r}, PAE:14^{1}, SL:6^{r}; *Chara tomentosa*, PA:1^{1}, LM:10^{1}; *Nitella mucronata*, PAE:7^{1}, CD:1^{+}, CDE:2^{r}, CDMS:2^{r}; *Nitella hyalina*, PD:5^{r}, TA:8^{1}; *Agrostis stolonifera*, SL:17^{2}, CDMS:2^{1}; *Juncus inflexus*, SL:6^{1}, TA:8^{1}, CDMS:2^{1}; *Ranunculus trichophyllus*, PA:1^{+}.

Syntaxonomic remarks: Of the four different associations with *Paspalum distichum* described in the western Mediterranean (*Paspalo distichi-Agrostietum verticillatae* Braun-Blanq. 1936; *Ranunculo scelerati-Paspaletum paspalodis* Rivas Goday 1964 corr. Peinado, Bartolomé, Martínez-Parras and Ollala 1988; *Heliotropio supini-Paspaletum paspalodis* Martínez-Parras, Peinado, Bartolomé and Molero 1988; *Paspaletum dilatato-distichi* Herrera and F. Prieto in T.E. Díaz and F. Prieto 1994) (José et al. 1988; Rivas-Martinez et al. 2001; Neto et al. 2009), we choose to assign our vegetation type as a variant of the first one, which is first in priority order if *P. distichum* dominance stands are treated as a single association. Zotos (2006) identified two communities with *Paspalum distichum* in his study of wet meadows around lakes Trichonida and Lysimachia, including one dominated by *Paspalum distichum*. All the above-mentioned associations and communities have been grouped in the alliance

Paspalo-Agrostion semiverticillati and order *Paspalo-Heleochloetalia*. We do not follow Mucina et al. (2016) who grouped this order of perennial herb-grasslands in the annual-dominated class *Bidentetea* and we prefer the class of perennial plant communities on damp or temporarily flooded, often trampled, disturbed ground, *Plantaginetea majoris*, which Mucina et al. (2016) lumped together with the *Molinio-Arrhenatheretea*.

Class 2. Phragmito-Magnocaricetea

Syntaxon 2.1. *Phragmitetum communis* (Code PA, Table 2, MNT = 1.2)

Appearance and habitat: Extensive and dense (>50% cover) reed beds of *Phragmites australis*, the most commonly noticed and recorded association in most lakes. They cover major parts of the littoral zone, reaching down to 6m depth.

Diagnostic taxa (% constancy): *Phragmites australis* (100%).

Distribution: Pamvotida, Amvrakia, Kastoria, Lysimachia, Ozeros, Paralimni, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Vegoritida, Zazari, Petres, Doirani and Chimaditida.

Syntaxonomic remarks: This association, widespread across all bioclimatic zones of Eurasia, matches with what has been identified as *Phragmitetum communis* (*australis*) or *Scirpo-Phragmitetum* in numerous publications in Greece (Drosos et al. 1996; Sarika-Hatzinikolaou et al. 2003; Grigoriadis et al. 2005; Zotos 2006) and Europe (Preising et al. 1990; Šumberová et al. 2011a; Landucci et al. 2013; Kamberović et al. 2014; Jenačković 2017; Lastrucci et al. 2017).

Syntaxon 2.2. Transitional stands of *Phragmites australis* (Code PAE, Table 2, MNT = 3.4)

Appearance and habitat: Stands of *Phragmites australis* with floristic composition similar to the preceding cluster but with lower *Phragmites* cover (<50%). They are found at the edges of dense reed beds, down to 6m depth, where the *Phragmitetum communis* progressively gives way to, or is interconnected with, aquatic communities such as *Cladophoretum glomeratae, Najadetum marinae, Lemnetum minoris, Ceratophylletum demersi, Potamogetono pectinati-Myriophylletum spicati* etc. Due to their sparse cover, other riparian and aquatic plants of the above-mentioned or other plant communities colonize the open areas among and beneath the reeds.

Diagnostic taxa (% constancy): *Phragmites australis* (97%), *Cladophora glomerata* (48.3%), *Najas marina* (17.3%), *Nitellopsis obtusa* (13.8%).

Distribution: Pamvotida, Feneos, Kastoria, Megali Prespa, Volvi, Vegoritida, Zazari, Petres and Chimaditida.

Syntaxonomic remarks: This cluster falls within the range of variation of the *Phragmitetum communis*.

Syntaxon 2.3. *Scirpetum lacustris* (Code SL, Table 2, MNT = 5.6)

Appearance and habitat: Dense stands of club-rush *Schoenoplectus lacustris* (>25% cover) and low presence of other helophytes (*Phragmites*, *Sparganium* and *Typha* spp.). In lacustrine ecosystems, it often forms a zone in mostly shallow waters down to 1m deep, sensitive to wave action, between the open water and the dense reed-bed areas dominated by other species, like *Phragmites australis*.

Diagnostic taxa (% constancy): *Schoenoplectus lacustris* (100%), *Phragmites australis* (78%).

Distribution: Volvi, Paralimni, Trichonida, Mikri Prespa, Petres and Chimaditida.

Syntaxonomic remarks: Matches the descriptions of this association (sometimes under the name *Schoenoplectetum lacustris*) from publications in Greece (Sarika-Hatzinikolaou et al. 2003; Dimopoulos et al. 2005; Zotos 2006; Fotiadis et al. 2008) and in Europe (Preising et al. 1990; Lukács et al. 2009; Šumberová et al. 2011a; Landucci et al. 2013; Jenačković 2017).

Syntaxon 2.4. *Typhetum domingensis* (Code TD, Table 2, MNT = 3.1)

Appearance and habitat: Dense stands of the Mediterranean cattail *Typha domingensis* (>25% cover) and low presence of other helophytes (*Phragmites*, *Sparganium*, other *Typha* spp.). *Typha domingensis* stands, like other *Typha* communities, are usually colonizing next to the extensive *Phragmites australis* reed zone, in waters down to 4m deep, under low water fluctuation regime.

Diagnostic taxa (% constancy): *Typha domingensis* (100%).

Distribution: Trichonida and Chimaditida.

Syntaxonomic remarks: Matches the descriptions of this association in European publications (Biondi and Bagella 2005; Landucci et al. 2013; Jenačković 2017). In Greece, Zotos (2006) recorded two vegetation types in lake Trichonida, one with *Typha domingensis* alone and another with co-dominance of *Phragmites australis*. These are variants of the *Typhetum domingensis*.

Syntaxon 2.5. *Typhetum latifoliae* (Code TL, Table 2, MNT = 2.3)

Appearance and habitat: Dense stands of the cattail *Typha latifolia* (>25% cover) and low presence of other helophytes (*Phragmites*, *Sparganium* and other *Typha* spp.). *Typha latifolia*, like other *Typha* spp., colonizes openings next to the extensive *Phragmites australis* reed zone, in waters down to 2m deep, under low water fluctuation regime.

Diagnostic taxa (% constancy): *Typha latifolia* (100%), *Myriophyllum spicatum* (78%).

Distribution: Pamvotida, Feneos, Vegoritida and Doirani.

Syntaxonomic remarks: Matches the descriptions of Greek (Sarika-Hatzinikolaou et al. 2003; Fotiadis et al. 2008) and European publications (Preising et al. 1990; Šumberová et al. 2011a; Landucci et al. 2013; Jenačković 2017). Lower cover of *Typha latifolia* (<25% cover) was recorded in some plots, possibly due to sub-optimal water fluctuation conditions often prevailing in Mediterranean lakes (Coops et al. 2003; Flores and Barone 2005).

Syntaxon 2.6. *Typhetum angustifoliae* (Code TA, Table 2, MNT = 2.1)

Appearance and habitat: Dense stands of the cattail *Typha angustifolia* (>25% cover) and low presence of other helophytes (*Phragmites*, *Sparganium* and other *Typha* spp.). *Typha angustifolia*, like *Typha. latifolia* and *T. domingensis*, forms clonal rhizomatous stands next to *Phragmites australis* reed-beds, in waters to 2m deep, under low water fluctuation regime.

Diagnostic taxa (% constancy): *Typha angustifolia* (100%).

Distribution: Feneos and Mikri Prespa.

Syntaxonomic remarks: Matches the descriptions from Greek (Sarika-Hatzinikolaou et al. 2003; Dimopoulos et al. 2005, as *Typho-Phragmitetum typhetosum angustifoliae*; Fotiadis et al. 2008) and other European publications (Preising et al. 1990; Šumberová et al. 2011a; Landucci et al. 2013; Jenačković 2017). Lower cover of *Typha angustifolia* (<25% cover) was recorded in some plots which, as in the *Typhetum latifoliae*, may be due to higher than optimal water fluctuation in Mediterranean lakes (Coops et al. 2003; Flores and Barone 2005).

Syntaxon 2.7. *Butometum umbellati* (Code BU, Table 2, MNT = 4.5)

Appearance and habitat: Stands of partly submerged *Butomus umbellatus*, in open water littoral areas, down to 3m deep and with high water-transparency. It is characterized by the helophyte *Butomus umbellatus* (>25% cover) while other helophytes (*Phragmites*, *Sparganium*, *Typha*) occur with very low presence. A number of hydrophytes such as *Myriophyllum spicatum* and *Vallisneria spiralis* are constantly filling the gaps between these stands.

Diagnostic taxa (% constancy): *Butomus umbellatus* (100%), *Myriophyllum spicatum* (100%).

Distribution: Trichonida.

Syntaxonomic remarks: This association has been identified in various parts of Europe (Preising et al. 1990; Nagy et al. 2009; Šumberová et al. 2011a; Stępień et al. 2015), mostly described from shallower waters than in our study, accompanied by helophytes and lemnids. To our knowledge, a distinct *Butomus umbellatus* community had not been identified before in Greece.

Class 3. Lemnetea

Syntaxon 3.1. *Lemnetum minoris* (Code LM, Table 2, MNT = 5.8)

Appearance and habitat: Mats of the free-floating duckweed *Lemna minor* (>50% cover), accompanied by less abundant lemnids, such as *Spirodela polyrhiza*, *Azolla filiculoides* and other *Lemna* spp., can be found in the littoral zone of still and relatively nutrient-rich freshwater bodies, in very shallow waters 0–1m deep, in spots protected against wave action.

Diagnostic taxa (% constancy): *Lemna minor* (100%), *Azolla filiculoides* (73%).

Distribution: Doirani, Vegoritida and Chimaditida.

Syntaxonomic remarks: Matches the descriptions of this widespread association from Greece (Lavrentiades and Pavlidis 1985; Papastergiadou 1990; Zotos 2006) and elsewhere in Europe (Goldyn et al. 2005; Kłosowski and Jabłońska 2009; Šumberová 2011b; Felzines 2012).

Syntaxon 3.2. *Lemno-Utricularietum* and *Utricularietum australis* (Code UV, Table 2, MNT = 5.2)

Appearance and habitat: Open to fully closed submerged carpets of the free-floating carnivorous bladderworts *Utricularia vulgaris* or *Utricularia australis* (>25% cover), with other taxa found in low numbers. As the bladderworts cannot be identified with certainty if not in flower, both species are likely to be included. Frequently present at the surface of the water occur *Hydrocharis morsus-ranae* and lemnids, like *Lemna minor*, *Lemna gibba*, *Spirodela polyrhiza* etc., while *Ceratophyllum demersum* may occur in lower strata of the water column. Vegetation of free-floating bladderworts can be found in very shallow, down to 1m deep, mesotrophic to eutrophic waters protected against wave action.

Diagnostic taxa (% constancy): *Utricularia vulgaris* + *U. australis* (100%).

Distribution: Doirani, Pamvotida, Petres and Chimaditida.

Syntaxonomic remarks: Matches the descriptions of this widespread association from Greece (Sarika-Hatzinikolaou et al. 2003; Pirini 2011, with *Utricularia vulgaris* and *Chara vulgaris*) and elsewhere in Europe (Šumberová 2011b; Felzines 2012; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 3.3. *Ceratophylletum demersi* (Code CD, Table 2, MNT = 1.5)

Appearance and habitat: Extensive (>50% cover) carpets of *Ceratophyllum demersum*, a free-floating aquatic macrophyte in variable habitat conditions. Due to its ability to grow well in turbid water, under poor light conditions, it spreads rapidly and may cover the whole water column, possibly limiting the growth of other hydrophytes. While it thrives mostly in shallow waters, it may colonize the full depth range of aquatic macrophytes (in Greece 0–13m).

Diagnostic taxa (% constancy): *Ceratophyllum demersum* (100%).

Distribution: Amvrakia, Kastoria, Lysimachia, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Vegoritida, Petres, Doirani and Chimaditida.

Syntaxonomic remarks: Matches the descriptions in European publications (Goldyn et al. 2005; Šumberová 2011b; Felzines 2012; Lastrucci et al. 2014, 2015; Džigurski et al. 2016; Cvijanović et al. 2018). In Greece, Papastergiadou (1990) and Dimopoulos et al. (2005) identified this association with similar floristic composition, while Sarika-Hatzinikolaou et al. (2003) described a more variable and perhaps composite association, with higher constancies of other *Lemnetea* and *Potamogetonetea* diagnostic taxa (*Lemna minor*, *Spirodela polyrhiza*, *Hydrocharis morsus-ranae*, *Myriophyllum spicatum* and *Potamogeton*

crispus). Gradstein and Smittenberg (1977) recorded a community in which *Ceratophyllum demersum* co-occurs with *Potamogeton trichoides*.

Syntaxon 3.4. Transitional stands of *Ceratophyllum demersum* (Code CDE, Table 2, MNT = 3.5)

Appearance and habitat: Similar to the *Ceratophylletum demersi* but with less cover (<50%) of *Ceratophyllum*, are found at the edges of the dense *Ceratophyllum* stands, in waters down to 13m deep, where the *Ceratophylletum demersi* progressively transitions into other macrophytic communities (*Phragmitetum communis*, *Lemnetum minoris*, *Potamogetono pectinati-Myriophylletum spicati*, *Potametum pectinati* etc.). Other macrophytes like *Phragmites australis*, *Lemna minor*, *Salvinia natans*, *Spirodela polyrhiza*, *Myriophyllum spicatum* and *Stuckenia pectinata* colonize the openings.

Diagnostic taxa (% constancy): *Ceratophyllum demersum* (100%), *Phragmites australis* (64%)

Distribution: Volvi, Doirani, Kastoria, Lysimachia, Ozeros, Mikri Prespa, Vegoritida and Chimaditida.

Syntaxonomic remarks: This cluster is a variant of the *Ceratophylletum demersi*.

Syntaxon 3.5. *Ceratophyllum demersum-Myriophyllum spicatum* community (Code CDMS, Table 2, MNT = 2.6)

Appearance and habitat: This cluster represents a transition between *Ceratophylletum demersi* and *Potamogetono pectinati-Myriophylletum spicati* found at the edges of these communities, in waters down to 6m deep, where *Ceratophyllum demersum* becomes sparse and *Myriophyllum spicatum* stands are able to colonize the open spots.

Diagnostic taxa (% constancy): *Ceratophyllum demersum* (100%), *Myriophyllum spicatum* (100%).

Distribution: Amvrakia, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Vegoritida and Doirani.

Syntaxonomic remarks: These complex stands may be assigned to any of the two associations depending on species' prevalence.

Class 4. Potamogetonetea*: *Alliance 1. Potamogetonion

Syntaxon 4.(1.)1. *Potamogetono pectinati-Myriophylletum spicati* (Code MS, Table 3, MNT = 2.4)

Appearance and habitat: Dense stands (mostly >50% cover) of the water-milfoil *Myriophyllum spicatum*, a submerged macrophyte with a broad ecological range, common even in disturbed sites. It roots at the lake bottom and reaches the water surface to emerge its inflorescence. These stands colonize waters down to 6m deep, provided water transparency is sufficiently high (chiefly mesotrophic conditions).

Diagnostic taxa (% constancy): *Myriophyllum spicatum* (100%).

Distribution: Amvrakia, Feneos, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Vegoritida, Petres and Doirani.

Syntaxonomic remarks: Matches the descriptions of this association, mostly under the name of *Myriophylletum spicati*, in publications from Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Dimopoulos et al. 2005; Fotiadis et al. 2008; Pirini 2011) and throughout Europe (Goldyn et al. 2005; Klosowski 2006; Šumberová 2011a; Džigurski et al. 2016). One possible reason for occasional lower cover of *Myriophyllum* (<50% cover) may be light limitations in deeper plots (Middelboe and Markager 1997; Klosowski 2006).

Syntaxon 4.(1.)2. *Potamogetonetum pectinati* (Code SP, Table 3, MNT = 1.3)

Appearance and habitat: Dense stands (>50% cover) of *Stuckenia pectinata* (=*Potamogeton pectinatus*), a submerged aquatic plant quite tolerant of brackish and turbid fresh water, found in open water of various depth down to 14m if water transparency permits.

Diagnostic taxa (% constancy): *Stuckenia pectinata* (100%).

Distribution: Kastoria, Kourna, Trichonida, Volvi, Vegoritida, Petres and Doirani.

Syntaxonomic remarks: Matches the descriptions of this association from Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Pirini 2011) and elsewhere in Europe (Solińska-Górnicka and Symonides 2001; Hrivnák 2002; Melendo et al. 2003; Goldyn et al. 2005; Šumberová 2011a; Lastrucci et al. 2014; Cvijanović et al. 2018).

Syntaxon 4.(1.)3. Transitional stands of *Stuckenia pectinata* (Code SPE, Table 3, MNT = 3.6)

Appearance and habitat: Stands of *Stuckenia pectinata*, similar in composition with the preceding cluster, but with lower cover of *Stuckenia* (<50%), were found at the edges of the dense *Stuckenia* stands, in waters down to 4m deep, in contact with other macrophyte communities such as the *Phragmitetum communis*, *Potamogetono pectinati-Myriophylletum spicati* etc., in openings with macrophytes such as *Phragmites australis*, *Myriophyllum spicatum* and *Chara tomentosa*.

Diagnostic taxa (% constancy): *Stuckenia pectinata* (96%), *Phragmites australis* (74%).

Distribution: Volvi, Doirani, Kastoria, Kourna, Vegoritida and Petres.

Syntaxonomic remarks: This cluster is a variant of the *Potamogetonetum pectinati*.

Syntaxon 4.(1.)4. *Stuckenia pectinata-Myriophyllum spicatum* community (Code SPMS, Table 3, MNT = 3.3)

Appearance and habitat: This cluster is transitional between *Potamogetonetum pectinati* and *Potamogetono pectinati-Myriophylletum spicati*, often found at the edges of the two asssociations, in waters down to 6m.

Diagnostic taxa (% constancy): *Stuckenia pectinata* (100%), *Myriophyllum spicatum* (92%).

Distribution: Kastoria, Paralimni, Trichonida, Volvi, Vegoritida and Doirani.

Syntaxonomic remarks: Relevés of this cluster are assignable to any of the two associations depending on species' dominance.

Table 3. Synoptic table of the identified associations and communities belonging to Class *Potamogetonetea*. Taxa constancy in percentage and their average abundance class (r = 0-1%, + = 2-5%, 1 = 6-20%, 2 = 21-40, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%) superscripted are shown. Companion taxa with less than 20% constancy are shown at the end of the Table. Diagnostic taxa for each vegetation type are marked in bold (see relevant text and Table 5 for vegetation type codes).

Vegetation type code	MS	SP	SPE	SPMS	PP	PCr	PV	PVMS	PL	PLMS	PoN	PCo	PT	NMa	NMaE	NMi	TN	NA	NL	NP	LP
Number of relevés	472	866	41	56	39	5	772	167	116	43	21	6	9	334	80	20	6	7	5	10	34
Mean number of species	2.4	1.3	3.6	3.3	2.2	2.4	2.0	2.8	2.4	3.3	4.7	3.3	6.1	1.8	3.4	6.7	4.3	5.4	1.2	4.8	2.0
POTAMOGETONETEA																					
Potamogetonion																					
Myriophyllum spicatum	**100^{2}**	4^{+}	32^{1}	**92^{1}**	47^{+}	20^{1}	54^{1}	**74^{1}**	67^{1}	**98^{1}**	86^{1}	.	**45^{+}**	24^{+}	53^{1}	65^{1}	50^{+}	43^{1}	.	.	.
Stuckenia pectinata	10^{+}	**100^{3}**	**96^{1}**	**100^{2}**	24^{1}	.	5^{1}	7^{+}	1^{1}	3^{1}	5^{1}	67^{+}	12^{1}	13^{1}	32^{1}	30^{1}	34^{r}	.	.	.	.
Potamogeton perfoliatus	4^{+}	3^{+}	22^{+}	20^{1}	**100^{2}**	.	2^{1}	5^{1}	.	.	.	17^{1}	23^{r}	9^{1}	20^{1}	20^{+}	34^{1}	.	.	.	.
Potamogeton crispus	1^{+}	.	.	.	.	**100^{1}**	1^{1}	2^{1}	2^{+}	3 (r)	5^{1}	.	.	.	3^{1}	15^{+}	.	.	.	.	.
Vallisneria spiralis	20^{1}	3^{1}	8^{1}	47^{1}	3^{1}	20^{1}	**100^{3}**	**100^{1}**	15^{1}	14^{+}	20^{+}	50^{1}	23^{r}	5^{1}	20^{+}	**85^{1}**	.	43^{1}	.	.	.
Potamogeton lucens	27^{1}	.	.	4^{1}	.	.	6^{1}	2^{+}	**100^{2}**	**87^{1}**	72^{+}	.	.	1^{r}	8^{1})	10^{r}	17^{1}	15^{1}	.	.	.
Potamogeton nodosus	10^{1}	.	.	.	.	.	1^{+}	2^{+}	19^{1}	24^{+}	**96^{2}**	.	.	1^{+}	10^{1}	20^{1}	.	15^{r}	.	.	.
Potamogeton compressus	.	1^{1}	.	2^{1}	.	.	1^{1}	2^{1}	.	.	.	**100^{3}**	.	.	2^{1}	.	.	.	.	.	.
Potamogeton trichoides	1^{1}	.	.	.	.	.	.	.	2^{1}	5^{1}	10^{1}	.	**67^{1}**	1^{1}	2^{1}	5^{1}	.	.	.	.	.
Najas marina	9^{1}	12^{1}	25^{+}	15^{1}	24^{+}	40^{1}	10^{1}	22^{1}	3^{1}	7^{+}	39^{+}	34^{1}	12^{1}	**100^{3}**	**100^{1}**	70^{1}	17^{r}	**58^{+}**	.	.	.
Najas minor	3^{1}	1^{r}	3^{r}	6^{r}	.	40^{+}	1^{1}	2^{r}	3^{+}	5^{+}	20^{+}	.	12^{1}	2^{1}	12^{1}	**100^{2}**	.	.	.	.	.
Trapa natans	.	.	.	2^{1}	.	.	1^{+}	2^{1}	.	3^{r}	.	34^{1}	.	.	.	5^{1}	**100^{3}**	.	.	20^{+}	.
Nymphaeion albae																					
Nymphaea alba	2^{+}	.	.	.	.	.	1^{1}	1^{1}	1^{1}	3^{r}	.	.	.	.	2^{1}	.	.	**100^{3}**	.	.	.
Nuphar lutea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**100^{3}**	.	.
Nymphoides peltata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**100^{2}**	.
Ludwigia peploides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**100^{3}**
Persicaria amphibia	.	.	3^{1}	4^{1}	3^{r}	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20^{1}	.
Other taxa																					
Phragmites australis	10^{1}	2^{1}	**74^{1}**	4^{+}	6^{1}	.	5^{1}	11^{1}	10^{1}	**31^{1}**	24^{1}	.	23^{1}	7^{1}	**28^{2}**	20^{1}	.	**86^{+}**	.	30^{1}	71^{1}
Butomus umbellatus	1^{1}	.	.	.	.	.	3^{1}	1^{1}	.	.	.	.	.	.	.	5^{r}	.	.	.	30^{1}	.
Schoenoplectus lacustris	1^{1}	.	15^{1}	.	.	.	.	1^{1}	.	.	5^{r}	.	12^{1}	.	2^{1}	10^{r}	.	43^{+}	.	30^{+}	.
Typha latifolia	.	1^{+}	.	.	.	.	.	1^{1}	.	3^{r}	5^{r}	.	**45^{1}**	.	2^{1}	5^{r}	.	.	.	.	.
Typha angustifolia	2^{+}	.	.	.	.	.	.	.	.	.	10^{1}	.	.	.	.	.	.	43^{1}	.	.	.
Eleocharis mitracarpa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30^{1}	.
Rorippa amphibia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30^{r}	.
Lemna minor	.	1^{r}	.	.	.	.	.	.	.	.	.	.	34^{+}	.	2^{1}	10^{+}	.	.	.	.	3^{1}
Lemna gibba	.	.	.	.	.	.	.	.	.	.	.	.	34^{r}	.	.	.	.	.	.	.	.
Azolla filiculoides	.	.	.	.	.	.	.	.	.	.	.	.	23^{r}	.	.	.	.	.	.	30^{+}	.
Spirodela polyrhiza	.	1^{r}	.	.	.	.	.	.	.	.	.	.	34^{+}	.	2^{1}	10^{+}	17^{r}	.	.	30^{r}	.
Ceratophyllum demersum	30^{1}	3^{1}	18^{+}	8^{1}	8^{+}	20^{1}	12^{1}	35^{1}	17^{+}	40^{1}	24^{+}	34^{+}	**56^{+}**	14^{1}	29^{1}	70^{1}	**100^{2}**	**100^{2}**	20^{r}	30^{1}	3^{1}
Cladophora glomerata	7^{1}	3^{1}	.	15^{1}	.	.	7^{+}	8^{+}	.	.	10^{+}	.	**56^{1}**	2^{1}	3^{+}	.	.	.	.	.	3^{1}
Rumex palustris	.	.	3^{r}	.	.	.	.	.	.	.	.	.	45^{+}	.	.	.	.	.	.	.	.
Paspalum distichum	1^{r}	1^{1}	3^{1}	2^{1}	.	.	.	.	3^{1}	3^{r}	20^{1}	.	23^{+}	.	.	30^{1}	.	.	.	.	9^{1}
Chara tomentosa	.	1^{1}	32^{1}	.	.	.	.	.	.	.	.	.	.	1^{1}	.	5^{r}	.	.	.	.	.

Taxa with less than 20% constancy: *Mentha pulegium*, SPMS:2^{r}; *Samolus valerandi*, SP:1^{r}, SPE:3^{r}; *Eleocharis caduca*, SP:1^{+}; *Juncus articulatus*, MS:1^{+}; *Phyla nodiflora*, PV:1^{1}, PVMS:1^{r}; *Typha domingensis*, SPE:5^{1}, LP:3^{r}; *Alisma plantago-aquatica*, NP:20^{+}; *Lycopus europaeus*, PT:12^{1}, NP:20^{r}; *Sparganium erectum*, MNi:5^{r}, NP:20^{+}; *Lythrum salicaria*, NMi:10^{r}; *Mentha aquatica*, NP:10^{r}; *Juncus subnodulosus*, PoN:5^{1}; *Schoenoplectus litoralis*, MS:1^{1}, SPE:5^{1}, PV:2^{1}, PVMS:2^{+}, PLMS:3^{1}; *Salvinia natans*, NMaE:2^{1}, NMi:15^{+}, TN:17^{1}; *Ceratophyllum submersum*, MS:1^{1}, SP:1^{r}, SPE:3^{1}, SPMS:2^{r}, PVMS:2^{1}, NMaE:2^{r}; *Hydrocharis morsus-ranae*, SP:1^{1}, NMa:1^{r}, NMi:15^{+}, TN:17^{1}, NP:10^{r}; *Utricularia vulgaris*, SP:1^{r}, PVMS:1^{r}; *Myriophyllum verticillatum*, PV:1^{r}; *Potamogeton berchtoldii*, PVMS:3^{1}, NMi:5^{1}; *Ranunculus trichophyllus*, MS:1^{+}, SP:1^{+}, SPMS:2^{1}, PVMS:2^{1}, PLMS:3^{r}, PoN:5^{r}, TN:17^{1}, NP:10^{1}; *Fontinalis antipyretica*, SP:1^{+}; *Chara aspera*, SP:1^{r}, NMa:2^{1}; *Chara globularis*, PV:1^{1}; *Chara corfuensis*, SP:4^{+}, NMa:1^{r}, NMaE:5^{1}; *Nitellopsis obtusa*, MS:1^{1}, SP:1^{1}, SPE:5^{1}, PV:2^{1}, PVMS:3^{+}, NMa:1^{1}, NMaE:3^{1}, NMi:10^{1}; *Chara vulgaris*, MS:1^{1}, PP:3^{1}, SPE:8^{+}, SPMS:8^{+}, PV:1^{+}, PVMS:2^{2}, NMa:1^{1}, NMaE:2^{1}; *Nitella mucronata*, MS:4^{+}, SP:1^{1}, PV:1^{+}, PVMS:2^{1}; *Nitella hyalina*, PoN:5^{1}, NMi:5^{1}; *Agrostis stolonifera*, MS:1^{1}; *Juncus inflexus*, MS:1^{+}, PoN:10^{1}, NMaE:2^{r}; *Scirpoides holoschoenus*, SPMS:2^{1}, PVMS:1^{1}, PL:1^{r}, PLMS:3^{r}, PoN:5^{r}, NMa:1^{1}; *Zannichellia pedunculata*, SPE:8^{2}, NMa:1^{+}.

Syntaxon 4.(1.)5. *Potamogetonetum perfoliati* (Code PP, Table 3, MNT = 2.2)

Appearance and habitat: Submerged stands dominated (>25% cover) by the pondweed *Potamogeton perfoliatus*, accompanied with a lower abundance of *Myriophyllum spicatum*, *Stuckenia pectinata* and *Najas marina*. *Potamogeton perfoliatus* roots at lake bottom and produces emergent inflorescences. It forms extensive stands in waters down to 5m, provided water transparency is high (mostly under mesotrophic conditions).

Diagnostic taxa (% constancy): *Potamogeton perfoliatus* (100%).

Distribution: Kastoria, Megali Prespa, Volvi, Vegoritida, Zazari and Doirani.

Syntaxonomic remarks: Matches the descriptions from Greek (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003) and European publications (Solińska-Górnicka and Symonides 2001; Klosowski 2006; Šumberová 2011a).

Syntaxon 4.(1.)6. *Potamogetonetum crispi* (Code PCr, Table 3, MNT = 2.4)

Appearance and habitat: Submerged stands dominated (>25% cover) by *Potamogeton crispus*, accompanied at lower abundance by *Myriophyllum spicatum*, *Vallisneria spiralis* and *Najas marina*. Like *Potamogeton perfoliatus*, *P. crispus* forms extensive stands rooting at lake bottom down to 4m depth under usually meso- to eutrophic conditions.

Diagnostic taxa (% constancy): *Potamogeton crispus* (100%).

Distribution: Yliki and Megali Prespa.

Syntaxonomic remarks: Matches the descriptions throughout Europe (Hrivnák 2002; Melendo et al. 2003; Goldyn et al. 2005; Šumberová 2011a; Lastrucci et al. 2014, 2015) and Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Grigoriadis et al. 2005).

Syntaxon 4.(1.)7. *Potamogetono-Vallisnerietum spiralis* (Code PV, Table 3, MNT = 2.0)

Appearance and habitat: Dense carpets (>25% cover) of the submerged eel-grass *Vallisneria spiralis* covering the lake-bottom in areas with favourable light and nutrient conditions down to a depth of 10m. Sporadic *Myriophyllum spicatum* and other *Potamogetonetea* taxa root in small openings within the *Vallisneria spiralis* carpet, exploiting the water column above.

Diagnostic taxa (% constancy): *Vallisneria spiralis* (100%).

Distribution: Amvrakia, Feneos, Kastoria, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Volvi, Vegoritida and Doirani.

Syntaxonomic remarks: Matches the descriptions of this apparently uncommon association scattered in Europe (Gabka 2002; Hutorowicz et al. 2006; Lastrucci et al. 2014) and Greece (Papastergiadou 1990; Grigoriadis et al. 2005; Pirini 2011). A similar association (*Ceratophyllo demersi-Vallisnerietum spiralis*) with higher constancy of *Ceratophyllum demersum* was identified in Serbia (Cvijanović et al. 2018).

Syntaxon 4.(1.)8. *Vallisneria spiralis-Myriophyllum spicatum* community (Code PVMS, Table 3, MNT = 2.8).

Appearance and habitat: This cluster is transitional between the *Potamogetono-Vallisnerietum* and the *Potamogetono pectinati-Myriophylletum spicati*. If water transparency permits (mostly oligotrophic to mesotrophic conditions) such stands can be found in waters 10m deep.

Diagnostic taxa (% constancy): *Vallisneria spiralis* (100%), *Myriophyllum spicatum* (74%).

Distribution: Amvrakia, Feneos, Kastoria, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Volvi, Vegoritida and Doirani.

Syntaxonomic remarks: The relevés can be assigned to either of the two associations depending on species' dominance.

Syntaxon 4.(1.)9. *Potamogetonetum lucentis* (Code PL, Table 3, MNT = 2.4)

Appearance and habitat: Dense stands (>25% cover) of the submerged pondweed *Potamogeton lucens* accompanied at lower abundance by *Myriophyllum spicatum, Vallisneria spiralis* and *Potamogeton nodosus*, colonizing waters down to a 6m depth when water transparency permits (usually under oligotrophic to mesotrophic conditions).

Diagnostic taxa (% constancy): *Potamogeton lucens* (100%).

Distribution: Paralimni and Yliki.

Syntaxonomic remarks: Matches the descriptions in Greece (Gradstein and Smittenberg 1977; Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Dimopoulos et al. 2005) and throughout most of Europe (Preising et al. 1990; Hrivnák 2002; Melendo et al. 2003; Goldyn et al. 2005; Klosowski 2006; Šumberová 2011a).

Syntaxon 4.(1.)10. *Potamogeton lucens-Myriophyllum spicatum* community (Code PLMS, Table 3, MNT = 3.3)

Appearance and habitat: This cluster is transitional between *Potamogetono pectinati-Myriophylletum spicati* and *Potamogetonetum lucentis*, characterized by a more or less equivalent constancy and abundance of the two characteristic species (*Myriophyllum spicatum*, *Potamogeton lucens*). It grows in waters down to 6m deep, where *Myriophyllum spicatum* stands become quite sparse and other hydrophytes, mostly *Potamogeton lucens*, occur in openings.

Diagnostic taxa (% constancy): *Myriophyllum spicatum* (98%), *Potamogeton lucens* (87%), *Phragmites australis* (30.3%).

Distribution: Paralimni, Megali Prespa and Mikri Prespa.

Syntaxonomic remarks: Relevés of this cluster can be assigned to either of the two associations according to the species' dominance.

Syntaxon 4.(1.)11. *Potamogetonetum denso-nodosi* (Code PoN, Table 3, MNT = 4.7)

Appearance and habitat: Open to fully closed (>25% cover) *Potamogeton nodosus* stands with floating leaves, accompanied at lower abundance by taxa such as *Myriophyllum spicatum, Potamogeton lucens* and *Najas marina*. *Potamogeton nodosus* forms extensive mats in still freshwater bodies down to 3m deep.

Diagnostic taxa (% constancy): *Potamogeton nodosus* (96%).

Distribution: Amvrakia, Feneos and Paralimni.

Syntaxonomic remarks: Matches the descriptions of this widespread but infrequent association (Melendo et al. 2003; Šumberová 2011a; Lastrucci et al. 2014; Džigurski et al. 2016; Cvijanović et al. 2018), which in Greece, so far only Papastergiadou (1990, as *Ranunculetum fluitantis* but with similar floristic composition) described in slow-flowing waters.

Syntaxon 4.(1.)12. *Potamogetonetum compressi* (Code PCo, Table 3, MNT = 3.3)

Appearance and habitat: Dense stands (>25% cover) of the submerged pondweed *Potamogeton compressus* accompanied at lower abundance by taxa such as *Vallisneria spiralis*, *Stuckenia pectinata* and *Najas marina*. Its shallow root system is vulnerable to wave action, thus *Potamogeton compressus* forms limited stands in shallow (down to 2m deep) water near lake shorelines.

Diagnostic taxa (% constancy): *Potamogeton compressus* (100%).

Distribution: Kastoria.

Syntaxonomic remarks: Only a few publications described this association from Eurasia (Kuzmichev et al. 2008;

Borsukevych 2013; Chepinoga et al. 2013), which is rare and/or declining in Europe (Birkinshaw et al. 2013). There are no previous records of this association from Greece.

Syntaxon 4.(1.)13. *Potamogetonetum trichoidis* (Code PT, Table 3, MNT = 6.1)

Appearance and habitat: Dense stands (>25% cover) of the submerged narrow-leaved pondweed *Potamogeton trichoides*, accompanied at lower abundance by taxa such as *Myriophyllum spicatum, Ceratophyllum demersum* and *Lemna minor*. Being quite variable, this vegetation type was found in meso-eutrophic waters down to 4m deep, where *Potamogeton trichoides* leaves spaces for a mix of other elodeid and lemnid aquatic macrophytes as well as helophytes.

Diagnostic taxa (% constancy): *Potamogeton trichoides* (67%), *Ceratophyllum demersum* (56%), *Cladophora glomerata* (56%), *Myriophyllum spicatum* (44.5%), *Typha latifolia* (44.5%).

Distribution: Kastoria, Lysimachia, Vegoritida, Doirani and Chimaditida.

Syntaxonomic remarks: Similar to the descriptions of Greek (Dimopoulos et al. 2005; Gradstein and Smittenberg 1977; Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003) and European publications (Preising et al. 1990; Hrivnák 2002; Melendo et al. 2003; Šumberová 2011a).

Syntaxon 4.(1.)14. *Najadetum marinae* (Code NMa, Table 3, MNT = 1.8)

Appearance and habitat: Dense submerged carpets (>25% cover) of the naiad *Najas marina* accompanied at lower abundance by *Potamogetonetea* species such as *Potamogeton perfoliatus*, *Myriophyllum spicatum* and *Vallisneria spiralis*. *Najas marina* forms dense carpets on the bottom of still water bodies, down to 5m deep, under mesotrophic to eutrophic and even slightly brackish conditions.

Diagnostic taxa (% constancy): *Najas marina* (100%).

Distribution: Amvrakia, Kastoria, Kourna, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Petres and Doirani.

Syntaxonomic remarks: Described from Europe (Melendo et al. 2003; Šumberová 2011a; Lastrucci et al. 2014; Džigurski et al. 2016; Cvijanović et al. 2018) and Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Pirini 2011).

Syntaxon 4.(1.)15. Transitional stands of *Najas marina* (Code NMaE, Table 3, MNT = 3.4)

Appearance and habitat: Submerged carpets with lower cover (<25%) of *Najas marina* than in the preceding cluster. Found at the edges of dense *Najas marina* stands in waters down to 5m deep where the *Najadetum marinae* progressively gives way to other macrophyte communities such as *Potamogetono pectinati-Myriophylletum spicati*, *Phragmitetum communis*, *Potamogetonetum pectinati* or *Ceratophylletum demersi* etc.). Other macrophytes like *Myriophyllum spicatum*, *Phragmites australis*, *Stuckenia pectinata* and *Ceratophyllum demersum* colonize open *Najas* stands.

Diagnostic taxa (% constancy): *Najas marina* (100%), *Phragmites australis* (27.5%).

Distribution: Amvrakia, Kastoria, Kourna, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Petres and Doirani.

Syntaxonomic remarks: This cluster is a variant of the *Najadetum marinae*.

Syntaxon 4.(1.)16. *Najadetum minoris* (Code NMi, Table 3, MNT = 6.7)

Appearance and habitat: Dense submerged carpets (>25% cover) of the naiad *Najas minor* sometimes accompanied by *Myriophyllum spicatum*, *Vallisneria spiralis* and *Najas marina*. Both *Najas* species form dense carpets on the bottom of still water bodies, with *N. minor* occurring in more shallow waters down to 3.5m deep, under mesotrophic to eutrophic but not brackish conditions.

Diagnostic taxa (% constancy): *Najas minor* (100%), *Vallisneria spiralis* (85%).

Distribution: Kastoria, Paralimni, Megali Prespa and Doirani.

Syntaxonomic remarks: Matches the descriptions throughout Europe (Gabka and Dolata 2010; Šumberová 2011a; Lastrucci et al. 2014). In Greece, only Papastergiadou (1990) gathered a relevé dominated by *Najas minor*, accompanied by *Zannichellia palustris*, which was assigned to the *Zannichellietum palustris*.

Class 4. Potamogetonetea*: *Alliance 2. Nymphaeion albae

Syntaxon 4.(2.)17. *Trapetum natantis* (Code TN, Table 3, MNT = 4.3)

Appearance and habitat: Open to closed (>25% cover) floating mats of the annual water caltrop *Trapa natans*, most often accompanied by *Ceratophyllum demersum* which tolerates poor light conditions. Nymphaeids such as *Trapa natans* are macrophytes that root at the bottom of still freshwater bodies, but most of their biomass, in particular most of the leaves, is floating on the water surface. *Trapa* occurs in waters down to 3m deep, limiting light levels for other submerged macrophytes underneath.

Diagnostic taxa (% constancy): *Trapa natans* (100%), *Ceratophyllum demersum* (100%).

Distribution: Kastoria and Megali Prespa.

Syntaxonomic remarks: The *Trapetum natantis* has been described in Greece, (Lavrentiades and Pavlidis 1985; Papastergiadou 1990) and Europe (Šumberová 2011a; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 4.(2.)18. *Nymphaeetum albae* (Code NA, Table 3, MNT = 5.4)

Appearance and habitat: Open to closed (>25% cover) floating vegetation mats of the water lily *Nymphaea alba*, most often accompanied by *Ceratophyllum demersum* which is undemanding in terms of light. Like other nymphaeids, *Nymphaea alba* is bottom-rooted and forms dense floating leaf mats, occurring in waters down to 4m deep.

Diagnostic taxa (% constancy): *Nymphaea alba* (100%), *Ceratophyllum demersum* (100%), *Phragmites australis* (86%), *Najas marina* (57.2%).

Distribution: Paralimni, Trichonida and Mikri Prespa.

Syntaxonomic remarks: Similar to the descriptions in Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Zotos 2006) and Europe (Goldyn et al. 2005; Šumberová 2011a; Lastrucci et al. 2014, 2015; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 4.(2.)19. *Nymphaeo albae-Nupharetum luteae* (Code NL, Table 3, MNT = 1.2)

Appearance and habitat: Open to closed (>25% cover) floating leaf mats of *Nuphar lutea*, rooting at the lake bottom down to 3m deep.

Diagnostic taxa (% constancy): *Nuphar lutea* (100%).

Distribution: Pamvotida and Lysimachia.

Syntaxonomic remarks: Matches the descriptions of this association (often under the name of *Myriophyllo-Nupharetum luteae*) from Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003) and from throughout Europe (Preising et al. 1990; Solińska-Górnicka and Symonides 2001; Hrivnák 2002; Melendo et al. 2003; Goldyn et al. 2005; Gabka and Dolata 2010; Šumberová 2011a; Lastrucci et al. 2015; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 4.(2.)20. *Nymphoidetum peltatae* (Code NP, Table 3, MNT = 4.8)

Appearance and habitat: Open to closed (>25% cover) floating mats of *Nymphoides peltata* accompanied by low-abundant lemnids and helophytes. Like all other nymphaeids, *Nymphoides peltata* forms a dense floating leaf canopy, bottom-rooted in shallow waters down to 2m deep, sharing its space with other floating or emerged macrophytes.

Diagnostic taxa (% constancy): *Nymphoides peltata* (100%).

Distribution: Pamvotida and Megali Prespa.

Syntaxonomic remarks: Similar to the descriptions in Greece (Lavrentiades and Pavlidis 1985, co-dominating with *Trapa natans*; Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003) and Europe (Preising et al. 1990; Gabka and Dolata 2010; Šumberová 2011a; Lastrucci et al. 2014; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 4.(2.)21. *Ludwigia peploides* community (Code LP, Table 3, MNT = 2.0)

Appearance and habitat: Open to closed (>25% cover) mats of *Ludwigia peploides* subsp. *montevidensis*, an amphibious perennial macrophyte forming creeping mats on the wet mud and flooded shores of freshwater bodies or floating mats on the muddy surface of the riparian zone. The floating mats, often found within the gaps of *Phragmites australis* reedbeds, reach down to 2m deep, leaving no room for other aquatic macrophytes.

Diagnostic taxa (% constancy): *Ludwigia peploides* ssp. *montevidensis* (100%).

Distribution: Lysimachia.

Syntaxonomic remarks: *Ludwigia peploides* subsp. *montevidensis*, native to South America, is locally naturalized in South Europe, SW Asia and other continents where it is often invasive (Dutartre 1986; Zotos et al. 2006). In South America the association *Polygono-Ludwigietum peploidis* has been described (Padovani et al. 1993; Hauenstein et al. 2002), where *Ludwigia peploides* is often (but not always) accompanied by *Persicaria hydropiperoides* which does not occur in Europe. We did not find *Ludwigia peploides* relevés from Europe other than those published by Zotos (2006) and Zotos et al. (2006), together with *Paspalum distichum* or dominated by *Phragmites australis*. We found *Ludwigia peploides* as the dominant species associated with *Phragmites*. Taking into consideration the ecological similarities between *Ludwigia peploides* and *Ludwigia grandiflora* (Zotos et al. 2006), a diagnostic taxon of the *Nymphaeion*, we assign with some reservations the *Ludwigia peploides* community to that alliance.

Class 5. Platyhypnidio-Fontinalietea antipyreticae

Syntaxon 5.1. *Fontinalietum antipyreticae* (Code FA, Table 4, MNT = 4.0)

Appearance and habitat: Patchy carpets dominated by the water moss *Fontinalis antipyretica* usually developing under shady conditions, on rocks in very shallow water (down to 0.5m deep), often in very clear (oligo-mesotrophic) streams, sometimes in lacustrine littoral zones.

Diagnostic taxa (% constancy): *Fontinalis antipyretica* (100%).

Distribution: Kourna and Feneos.

Syntaxonomic remarks: Matches the descriptions from Europe (Dawson and Szoszkiewicz 1999; *Pedrotti* 2008; Ceschin et al. 2010; Grzybowski et al. 2010). In Greece, only Gradstein and Smittenberg (1977) published a relevé of *Fontinalis antipyretica* together with *Stuckenia pectinata*.

Class 6. Charetea intermediae

Syntaxon 6.1. *Charetum globularis* (Code ChG, Table 4, MNT = 1.4)

Appearance and habitat: Dense (>25% cover) underwater stonewort meadows of *Chara globularis* tolerating a broad range of ecological conditions but thriving in oligo-mesotrophic calcareous freshwater lakes to a depth of 8m.

Diagnostic taxa (% constancy): *Chara globularis* (100%).

Distribution: Feneos.

Syntaxonomic remarks: Matches the descriptions of this association from publications in Europe (Šumberová et al. 2011b; Iakushenko and Borysova 2012; Azzella et al. 2013). In Greece, to our knowledge, no distinct *Chara globularis* community has been hitherto identified.

Syntaxon 6.2. *Magno-Charetum hispidae* (Code CH, Table 4, MNT = 2.1)

Appearance and habitat: Sparse underwater stonewort meadows dominated by *Chara corfuensis* (= *Chara hispida*

Table 4. Synoptic table of the identified associations and communities belonging to Classes *Platyhypnidio-Fontinalietea antipyreticae*, *Charetea intermediae* and *Stigeoclonietea tenuis*. Taxa constancy in percentage and their average abundance class (r = 0-1%, + = 2-5%, 1 = 6-20%, 2 = 21-40, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%) superscripted are shown. Companion taxa with less than 20% constancy are shown at the end of the Table. Diagnostic taxa for each vegetation type are marked in bold (see relevant text and Table 5 for vegetation type codes).

Vegetation type code	FA	ChG	CH	CHE	NO	CV	CA	NMu	NHy	ClGL	ClGM
Number of relevés	4	105	32	10	51	139	11	26	6	83	35
Mean number of species	4.0	1.4	2.1	4.9	1.8	1.1	1.1	2.1	5.3	2.3	3.3
PLATYHYPNIDIO-FONTINALIETEA ANTIPYRETICAE											
Fontinalis antipyretica	**100^{1}**	.	7^{+}	10^{r}	.	.	.	.	.	.	.
CHARETEA INTERMEDIAE											
Chara globularis	50^{1}	**100^{3}**	.	.	.	3^{1}	.	.	50^{+}	.	.
Chara corfuensis	.	.	**100^{1}**	**100^{1}**	.	.	.	.	.	.	.
Nitellopsis obtusa	.	.	.	.	**100^{3}**	.	.	.	.	.	.
Chara tomentosa	.	.	.	.	20^{1}	.	.	.	.	.	6^{1}
Chara vulgaris	.	1^{1}	.	.	4^{1}	**100^{2}**	.	.	17^{1}	.	.
Chara aspera	25^{r}	.	.	.	.	2^{+}	**100^{++}**	.	.	.	.
Nitella mucronata	.	.	.	.	.	.	.	**100^{2}**	.	4^{+}	.
Nitella hyalina	.	2^{1}	.	.	.	1^{1}	.	.	**100^{4}**	.	.
STIGEOCLONIETEA TENUIS											
Cladophora glomerata	.	.	4^{1}	20^{r}	.	.	.	12^{+}	.	**100^{2}**	**100^{2}**
Other taxa											
Eleocharis caduca	.	.	10^{+}	**90^{2}**	.	.	.	.	.	.	.
Paspalum dilatatum	25^{1}	.	4^{r}	**70^{1}**	.	2^{2}	.	.	.	.	.
Elatine alsinastrum	25^{r}	.	4^{r}	70^{1}	.	1^{r}	.	.	.	.	.
Samolus valerandi	25^{r}	.	.	20^{r}	.	2^{r}	.	.	.	.	.
Phragmites australis	.	.	.	.	6^{1}	.	.	8^{+}	50^{1}	16^{1}	40^{1}
Typha latifolia	25^{1}	4^{1}	.	.	.	.	.	.	84^{1}	5^{1}	.
Typha angustifolia	50^{+}	6^{1}	.	.	.	.	.	.	84^{1}	.	.
Eleocharis palustris	50^{1}	1^{1}	.	.	.	.	.	.	.	.	.
Myriophyllum spicatum	25^{1}	12^{1}	.	.	2^{1}	1^{r}	.	24^{1}	34^{r}	17^{1}	**83^{2}**
Stuckenia pectinata	.	1^{1}	75^{1}	70^{+}	20^{1}	1^{1}	10^{r}	27^{1}	.	19^{+}	46^{1}
Vallisneria spiralis	.	6^{+}	.	.	.	.	.	8^{+}	50^{+}	21^{1}	6^{+}
Ceratophyllum demersum	.	1^{r}	.	.	6^{1}	.	.	31^{+}	.	16^{1}	32^{1}

Taxa with less than 20% constancy: *Rumex palustris*, CGl:4^{+}; *Paspalum distichum*, CGl:8^{+}; *Typha domingensis*, NO:4^{2}; *Mentha aquatica*, CGm:6^{1}; *Mentha pulegium*, CG:1^{1}, NHy:17^{r}; *Schoenoplectus lacustris*, NHy:17^{r}, CGm:3^{1}; *Juncus inflexus*, NHy:17^{r}; *Lemna minor*, CGl:4^{+}; *Azolla filiculoides*, CGl:3^{+}; *Ceratophyllum submersum*, NMu:4^{1}, CGl:2^{r}; *Potamogeton perfoliatus*, NO:2^{1}, CGl:4^{1}, CGm:3^{1}; *Potamogeton lucens*, CGl:2^{1}; *Potamogeton nodosus*, CGl:2^{r}; *Najas marina*, CG:7^{+}, NO:14^{1}, CGl:8^{1}, CGm:3^{1}; *Najas minor*, CGl:2^{r}; *Trapa natans*, NO:2^{1}; *Zannichellia pedunculata*, CH:4^{r}, CV:2^{1}; *Ranunculus trichophyllus*, CGl:3^{+}; *Nitella gracilis*, CG:4^{1}.

f. *corfuensis*, Wood 1962) in oligo-mesotrophic calcareous waters, down to 3m deep.

Diagnostic taxa (% constancy): *Chara corfuensis* (100%).

Distribution: Kourna (found also by Langangen 2012).

Syntaxonomic remarks: Matches the descriptions of this association (often under the name *Charetum hispidae*) from Europe (Preising et al. 1990; Hrivnák et al. 2005; Pelechaty and Pukacz 2006; Šumberová et al. 2011b). Pirini (2011) lumped relevés from lake Vegoritida containing *Bolboschoenus maritimus* and *Chara hispida* in a complex community.

Syntaxon 6.3. Transitional stands of *Chara corfuensis* (Code CHE, Table 4, MNT = 4.9)

Appearance and habitat: *Chara corfuensis* stands similar in composition to the previous (CH), but with lower stonewort cover (<10%), were found at the shallow edges of the littoral zone, in 0–0.5m deep waters, where the *Magno-Charetum hispidae* merges into a community dominated by *Eleocharis caduca* and other helophytes.

Diagnostic taxa (% constancy): *Chara corfuensis* (100%), *Eleocharis caduca* (70%), *Paspalum dilatatum* (70%).

Distribution: Kourna.

Syntaxonomic remarks: This cluster is a variant of the *Magno-Charetum hispidae*.

Syntaxon 6.4. *Nitellopsidetum obtusae* (Code NO, Table 4, MNT = 1.8)

Appearance and habitat: Sparse to dense (25% cover) underwater stonewort meadows dominated by *Nitellopsis obtusa* occurring from oligotrophic to meso-eutrophic calcareous deep standing waters down to 12m deep with muddy deposits.

Diagnostic taxa (% constancy): *Nitellopsis obtusa* (100%).

Distribution: Feneos, Kastoria and Petres.

Syntaxonomic remarks: Matches the descriptions in publications of this association scattered in Europe (Solińska-Górnicka and Symonides 2001; Iakushenko and Borysova 2012; Kipriyanova 2013). In Greece, a distinct *Nitellopsis obtusa* community has not yet been identified.

Syntaxon 6.5. *Charetum vulgaris* (Code CV, Table 4, MNT = 1.1)

Appearance and habitat: Sparse to dense (>25% cover) underwater stonewort meadows dominated by *Chara vulgaris* in oligo-mesotrophic neutral to slightly alkaline standing fresh water, down to 6m deep.

Diagnostic taxa (% constancy): *Chara vulgaris* (100%).

Distribution: Feneos and Kourna.

Table 5. Syntaxonomic overview of the plant associations and communities found in the current study.

***Plantaginetea majoris* Tx. et Preising ex von Rochow 1951**
***Paspalo-Heleochloetalia* Br.-Bl. ex Rivas Goday 1956**
***Paspalo-Agrostion semiverticillati* Br.-Bl. in Br.-Bl. et al. 1952**
(PhN) *Phyla nodiflora* community
(PD) *Paspalo distichi-Agrostietum verticillatae* Br.-Bl. in Br.-Bl et al. 1936
***Phragmito-Magnocaricetea* Klika in Klika et Novák 1941**
***Phragmitetalia* Koch 1926**
***Phragmition communis* Koch 1926**
(PA) *Phragmitetum communis* Savič 1926
(PAE) *Phragmites australis* transitional community
(SL) *Scirpetum lacustris* Chouard 1924
(TD) *Typhetum domingensis* Brullo et al. 1994
(TL) *Typhetum latifoliae* Nowiński 1930
(TA) *Typhetum angustifoliae* Pignatti 1953
***Oenanthetalia aquaticae* Hejný ex Balátová-Tuláčková et al. 1993**
***Eleocharito palustris-Sagittarion sagittifoliae* Passarge 1964**
(BU) *Butometum umbellati* Philippi 1973
***Lemnetea* O. de Bolòs et Masclans 1955**
***Lemnetalia minoris* O. de Bolòs et Masclans 1955**
***Lemnion minoris* O. de Bolòs et Masclans 1955**
(LM) *Lemnetum minoris* von Soó 1927
***Utricularion vulgaris* Passarge 1964**
(UV) *Lemno-Utricularietum vulgaris* Soó 1947 + *Utricularietum australis* Müller et Görs 1960
***Stratiotion* Den Hartog et Segal 1964**
(CD) *Ceratophylletum demersi* Corillion 1957
(CDE) *Ceratophyllum demersum* transitional community
(CDMS) *Ceratophyllum demersum – Myriophyllum spicatum* mixed community
***Potamogetonetea* Klika in Klika et Novák 1941**
***Potamogetonetalia* Koch 1926**
***Potamogetonion* Libbert 1931**
(MS) *Potamogetono pectinati-Myriophylletum spicati* Rivas-Goday 1964
(SP) *Potamogetonetum pectinati* Carstensen ex Hilbig 1971
(SPE) *Stuckenia pectinata* transitional community
(SPMS) *Stuckenia pectinata – Myriophyllum spicatum* mixed community
(PP) *Potamogetonetum perfoliati* Miljan 1933
(PCr) *Potamogetonetum crispi* von Soó 1927
(PV) *Potamogetono-Vallisnerietum spiralis* Braun-Blanquet 1931
(PVMS) *Vallisneria spiralis – Myriophyllum spicatum* mixed community
(PL) *Potamogetonetum lucentis* Hueck 1931
(PLMS) *Potamogeton lucens – Myriophyllum spicatum* mixed community
(PoN) *Potamogetonetum denso-nodosi* de Bolós 1957
(PCo) *Potamogetonetum compressi* Tomaszewicz 1979
(PT) *Potamogetonetum trichoidis* Tüxen 1974
(Nma) *Najadetum marinae* Fukarek 1961
(NMaE) *Najas marina* transitional community
(NMi) *Najadetum minoris* Ubrizsy 1961
***Nymphaeion albae* Oberd. 1957**
(TN) *Trapetum natantis* Kárpáti 1963
(NA) *Nymphaeetum albae* Vollmar 1947
(NL) *Nymphaeo albae-Nupharetum luteae* Nowiński 1927
(NP) *Nymphoidetum peltatae* Bellot 1951
(LP) *Ludwigia peploides* community
***Platyhypnidio-Fontinalietea antipyreticae* Philippi 1956**
***Leptodictyetalia riparii* Philippi 1956**
***Fontinalion antipyreticae* W. Koch 1936**
(FA) *Fontinalietum antipyreticae* Kaiser 1926
***Charetea intermediae* F. Fukarek 1961**
***Charetalia intermediae* Sauer 1937**
***Charion intermediae* Sauer 1937**
(CG) *Charetum globularis* Corillion 1949
(CH) *Magno-Charetum hispidae* Corillion 1957
(CHE) *Chara corfuensis* transitional community
(NO) *Nitellopsidetum obtusae* Dambska 1961
***Charion vulgaris*(W. Krause et Lang 1977) W. Krause 1981**
(CV) *Charetum vulgaris* Corillion 1949
(CA) *Charetum asperae* Corillion 1957
***Nitelletalia* W. Krause 1969**
***Nitellion syncarpo-tenuissimae* W. Krause 1969**
(NMu) *Nitelletum mucronatae* Tomaszewicz ex Hrivnák et al. 2001
(NHy) *Nitelletum hyalinae* Corillion 1949
***Stigeoclonietea tenuis* Arendt 1982**
***Stigeoclonietalia tenuis* Arendt 1982**
***Cladophorion fractae* Margalef 1951**
(CGl) *Cladophoretum glomeratae* Sauer 1937, lake substratum variant
(CGm) *Cladophoretum glomeratae* Sauer 1937, macrophyte-substratum variant

Syntaxonomic remarks: Matches the descriptions of this widespread association from Greece (Grigoriadis et al. 2005; Pirini 2011, with *Utricularia vulgaris*) and elsewhere in Europe (Preising et al. 1990; Goldyn et al. 2005; Hrivnák et al. 2005; Pelechaty and Pukacz 2006; Šumberová et al. 2011b; Iakushenko and Borysova 2012; Kipriyanova 2013).

Syntaxon 6.6. *Charetum asperae* (Code CA, Table 4, MNT = 1.1)

Appearance and habitat: Patchy and monospecific underwater stonewort meadows of *Chara aspera*, growing in calcareous oligo-mesotrophic still water, on substrate with gravel or sand near the shoreline, down to 2m deep.

Diagnostic taxa (% constancy): *Chara aspera* (100%).

Distribution: Kourna.

Syntaxonomic remarks: Matches the descriptions of this association from elsewhere in Europe (Heuff 1984; Preising et al. 1990; Solińska-Górnicka and Symonides 2001; Pelechaty and Pukacz 2006; Iakushenko and Borysova 2012; Azzella et al. 2013; Kipriyanova 2013). In Greece, no distinct *Chara aspera* community has yet been identified.

Syntaxon 6.7. *Nitelletum mucronatae* (Code NMu, Table 4, MNT = 2.1)

Appearance and habitat: Sparse to dense (>25% cover) underwater stonewort meadows of *Nitella mucronata* found in water depths between 3 and 7m, in meso-eutrophic more or less alkaline freshwater.

Diagnostic taxa (% constancy): *Nitella mucronata* (100%).

Distribution: Vegoritida.

Syntaxonomic remarks: Matches the descriptions of this association in Europe (Hrivnák 2002; Iakushenko and Borysova 2012; Täuscher and van de Weyer 2015). In Greece, a community dominated by *Nitella mucronata* has not yet been identified.

Syntaxon 6.8. *Nitelletum hyalinae* (Code NHy, Table 4, MNT = 5.3)

Appearance and habitat: Sparse to dense (>25% cover) underwater stonewort meadows of *Nitella hyalina* in very shallow clear oligotrophic alkaline waters, 0–1m deep.

Diagnostic taxa (% constancy): *Nitella hyalina* (100%).

Distribution: Feneos.

Syntaxonomic remarks: Matches the descriptions of this association from Europe (Golub et al. 1991; Landucci et al. 2011; Csiky et al. 2014). In Greece, no community dominated by *Nitella hyalina* has been identified yet.

Class 7. Stigeoclonietea tenuis

Syntaxon 7.1. *Cladophoretum glomeratae*, lake-substratum variant (Code ClGL, Table 4, MNT = 2.3)

Appearance and habitat: Open to closed (>25% cover) submerged carpets of the filamentous macroalgae *Clado-*

phora glomerata, found in stagnant eutrophic lowland waters. It is a quite light-demanding taxon which is often entangled with other macrophytes (subsequent cluster), or attached to the rocky substrate. These relevés, with a low cover of other aquatic macrophytes, were found in waters down to 5m deep.

Diagnostic taxa (% constancy): *Cladophora glomerata* (100%).

Distribution: Amvrakia, Paralimni, Trichonida, Megali Prespa and Vegoritida.

Syntaxonomic remarks: Matches the descriptions of this association from Europe (Margalef 1949; Den Hartog 1959; Carretero 1986). In Greece, *Cladophoretum glomeratae* has not yet been identified.

Syntaxon 7.2. *Cladophoretum glomeratae*, macrophyte-substratum variant (Code ClGM, Table 4, MNT = 3.3)

Appearance and habitat: This cluster is also assigned to the *Cladophoretum glomeratae* defined by the dominance of the benthic filamentous macroalgae *Cladophora glomerata*, but in this cluster it is accompanied by other aquatic macrophytes, especially *Myriophyllum spicatum* and *Stuckenia pectinata*, serving as the algae's substrate. The relevés within this cluster have been recorded in waters down to 4m deep.

Diagnostic taxa (% constancy): *Cladophora glomerata* (100%), *Myriophyllum spicatum* (82.9%).

Distribution: Kourna, Vegoritida and Petres.

Syntaxonomic remarks: See preceding unit.

Relation of phytosociological units to environmental parameters

Water depth is widely known to be an important environmental parameter which affects the distribution of aquatic plants, by regulating prevailing light conditions, temperature, water chemistry, wave action and substrate granulometry (Spence and Chrystal 1970; Chambers and Kaiff 1985; Middelboe and Markager 1997). Each macrophyte species has its own water depth tolerance limits, which depend on its morphological and physiological characteristics. However, due to the competition for space, light and nutrients from other macrophyte species they are not free to colonize the water volume that falls within their tolerance limits (McCreary 1991; Gopal and Goel 1993; Gross 2003). These mechanisms produce distinct zonation patterns in aquatic vegetation along water depth gradients (Spence 1982; Shipley et al. 1991). Figure 2 summarizes the depth distribution of the 46 described vegetation types, as recorded in the lakes that were surveyed in the current study. Among the helophytic vegetation types (*Plantaginetea majoris*; *Phragmito-Magnocaricetea*) the *Phyla nodiflora* community, and the *Paspalo distichi-Agrostietum verticillatae*, *Scirpetum lacustris*, and *Typhetum angustifoliae* were recorded colonizing the littoral zones to a depth of 1.5m. The *Typhetum domingensis*, *Typhetum latifoliae*, and *Butometum umbellati* were able to reach a bit deeper down to a depth of 2m, while the *Phragmitetum communis* which dominates the littoral zone of Greek lakes, quite often reach-

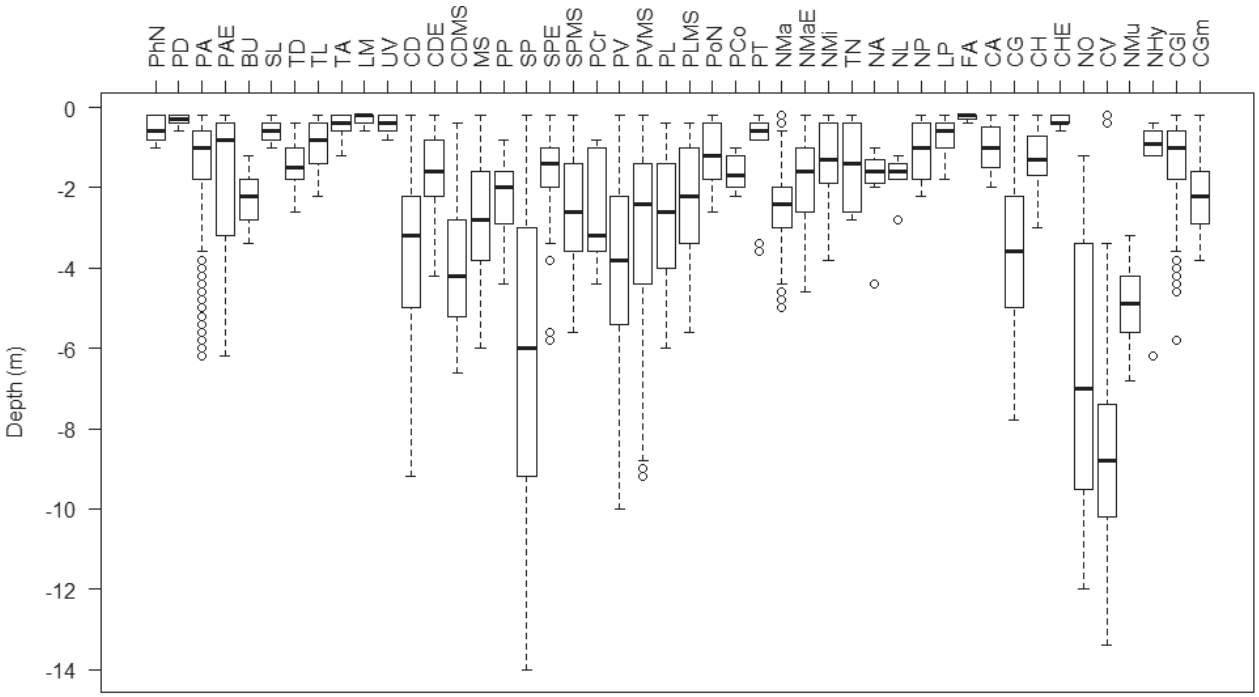

Figure 2. Depth distribution of the 46 described associations and communities (see related text and Table 5 for vegetation type abbreviations). Bold lines represent median values and boxplots represent the interquartile range (IQR) between first and third quartiles (25% and 75%). Whiskers represent minimum and maximum values excluding outlier values (symbolized by an empty circle), which are calculated as values beyond the range of 1.5xIQR.

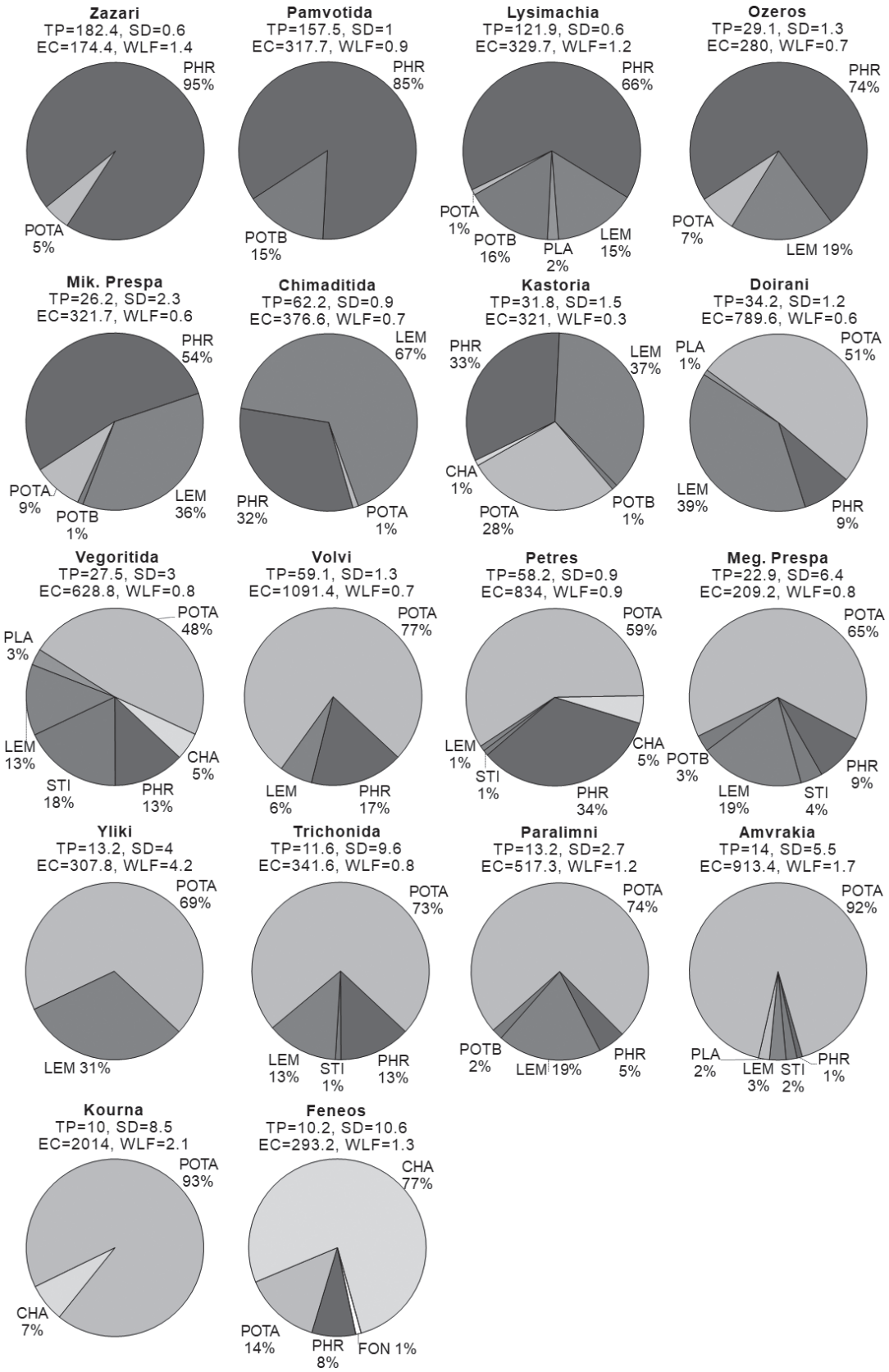

Figure 3. Distribution of higher-rank syntaxa (classes to alliances) in the lakes of the current study (number of relevés per syntaxon to total number or relevés in each lake). PLA: *Plantaginetea majoris*; PHR: *Phragmito-Magnocaricetea*; LEM: *Lemnetea*; POTA: *Potamogetonion*; POTB *Nymphaeion albae*; FON: *Platyhypnidio-Fontinalietea antipyreticae*; CHA: *Charetea intermediae*; STI: *Stigeoclonietea tenuis*. Environmental data [TP: Annual mean total phosphorus (μg/L); SD: Secchi depth transparency in meters; EC: Electrical conductivity (μS/cm); WLF: Annual water level fluctuation in meters] are also presented.

Table 6. Overview of the relationships between the abundance of higher-rank syntaxa (classes to alliances) for each lake within the current study and its environmental variables. Pearson's correlation coefficient (*R*) and the p-value of significance are given for each linear regression. Significant relationships ($p < 0.05$) are marked in bold. The two final rows of the table contain part of the results of the multiple linear regression analysis with the involvement of more than one higher-rank syntaxa (one with all the higher-rank syntaxa and one with those giving the best solution for all the environmental parameters). PLA: *Plantaginetea majoris*; PHR: *Phragmito-Magnocaricetea*; LEM: *Lemnetea*; POTA: *Potamogetonion*; POTB *Nymphaeion albae*; FON: *Platyhypnidio-Fontinalietea antipyreticae*; CHA: *Charetea intermediae*; STI: *Stigeoclonietea tenuis*; TP: Annual mean total phosphorus (µg/L); SD: Secchi depth transparency in meters; EC: Electrical conductivity (µS/cm); WLF: Annual water level fluctuation in meters.

Syntaxa in regression	TP		SD		EC		WLF	
	R	p	R	p	R	p	R	p
PHR	**0.821**	**<0.001**	**-0.585**	**0.011**	-0.444	0.065	-0.296	0.233
STI	-0.158	0.532	0.049	0.846	0.019	0.940	-0.118	0.641
LEM	-0.221	0.379	-0.321	0.194	-0.299	0.228	-0.131	0.604
PLA	-0.006	0.981	-0.099	0.695	0.098	0.699	-0.036	0.888
POTA	**-0.584**	**0.011**	0.441	0.067	**0.630**	**0.005**	0.341	0.166
POTB	**0.594**	**0.009**	-0.282	0.258	-0.235	0.348	-0.078	0.759
CHA	-0.210	0.402	**0.567**	**0.014**	-0.064	0.802	0.050	0.845
FON	-0.187	0.458	**0.545**	**0.019**	-0.147	0.560	0.040	0.876
PHR+STI+LEM+PLA+POTA+POTB+CHA+FON	**0.860**	**0.026**	0.802	0.091	**0.893**	**0.009**	0.410	0.953
PHR+POTA+POTB+CHA+FON	**0.858**	**0.003**	**0.788**	**0.024**	**0.813**	**0.013**	0.375	0.844

es down to a depth of 4m. Freely floating macrophytes (*Lemnetea*) and anchored floating macrophytes (*Nymphaeion albae*) are also restricted to shallow waters down to 1m and 3m deep respectively, with the exception of the *Ceratophylletum demersi* which can be found commonly down to 6m deep. Submerged hydrophytes (*Potamogetonion*; *Charetea intermediae*) predominantly colonize the deeper part of the euphotic zone of lacustrine littoral areas, between the zone colonized by emergent vegetation and the aphotic zone. Therefore, the majority of vegetation types belonging to *Potamogetonion* or *Charetea intermediae* are usually located in a depth zone starting at 1–2m and reaching 4–6m deep (in Greek waters), depending on the variability of light penetration and the specific lake physico-chemical characteristics. In cases where the euphotic zone reaches more than 6–8m deep, the *Potamogetonetum pectinati*, *Nitellopsidetum obtusae*, and *Charetum vulgaris* are the most commonly found vegetation types.

An equally important environmental parameter to water depth, that influences the distribution of aquatic plants, is prevailing light conditions. Light penetration in lacustrine ecosystems is highly dependent upon their water quality status (Phillips et al. 1978; Canfield et al. 1985; Middelboe and Markager 1997). Nutrient loading and eutrophication lead to the growth of phytoplankton, epiphytes and filamentous algae, which leads to increased shading and light attenuation. As a result, macrophyte dominance is reduced due to their biomass decline, plant cover reduction and loss of species richness (Phillips et al. 1978; 2016; Sand-Jensen 2000). Figure 3 and Table 6 summarize the relationships we found between the distribution and abundance of higher-rank syntaxa for each lake and the prevailing physico-chemical and hydrological conditions. Positive and significant correlations were found between the distribution of *Phragmito-Magnocaricetea* and *Nymphaeion albae* with total phosphorus concentrations, while *Potamogetonion* was negatively correlated. In addition, positive and significant correlations were found between *Charetea intermediae* and *Platyhypnidio-Fontinalietea antipyreticae* with Secchi depth transparency, while *Phragmito-Magnocaricetea* was negatively correlated. Only *Potamogetonion* was positively correlated with electrical conductivity. No syntaxon was correlated significantly with water level fluctuation. Multiple linear regression analysis produced the best solution for the above-mentioned environmental parameters (TP, SD and EC) using the combination of distribution values for five syntaxa: *Phragmito-Magnocaricetea*, *Potamogetonion*, *Nymphaeion albae*, *Charetea intermediae*, and *Platyhypnidio-Fontinalietea*. The distribution patterns of these five higher-rank syntaxa appear to act as good indicators of lake eutrophication. Raised total phosphorus concentrations in lake water and lowered water transparency led to the dominance of *Phragmito-Magnocaricetea*, and *Nymphaeion albae* syntaxa in aquatic vegetation. The expansion of *Potamogetonion*, *Charetea intermediae*, and *Platyhypnidio-Fontinalietea* syntaxa in aquatic vegetation is associated with lower total phosphorus concentrations and higher values of water transparency.

These results are of relevance for WFD assessment purposes and are similar to those presented in Poikane et al. (2018) that reviewed national macrophyte-based approaches for assessing ecological status according to the WFD. Poikane et al. (2018) reported that a marked decline in submerged vegetation, especially Charophyta (characterizing 'good' status according to WFD), and an increase in abundance of floating and emerged plants (characterizing 'less than good' status) were the most significant changes along the ecological status gradient. Similar results have also been reported from other areas within Europe, where the indicator value of different groups of taxa belonging to these syntaxa were tested against eutrophication levels in the context of WFD assessement systems (e.g. Penning et al. 2008a, 2008b; Søndergaard et al. 2010; Kolada 2016).

Conclusions

The current study is a national-scale phytosociological survey of freshwater lake vegetation, based on the most recent data available (years 2013–2016). Forty-six vegetation types were identified and interpreted for eighteen major Greek freshwater lakes. Among these vegetation types, the following are new records for Greece: *Phyla nodiflora* community, *Butometum umbellati*, *Potamogetonetum denso-nodosi*, *Potamogetonetum compressi*, *Najadetum minoris*, *Fontinaletum antipyreticae*, *Charetum globularis*, *Magno-Charetum hispidae*, *Nitellopsidetum obtusae*, *Charetum asperae*, *Nitelletum mucronatae*, *Nitelletum hyalinae*, *Cladophoretum glomeratae*. A primary analysis on the distribution of higher-rank syntaxa of the 46 vegetation types showed that the majority of these types are significantly affected by physico-chemical parameters indicative of higher levels of eutrophication. Aquatic plant communities could be utilized in eutrophication indices to broaden the assessment of the ecological status of freshwater lakes. Additional research on this topic is needed.

Data availability

The data that support the findings of this study were used under license from The Goulandris Natural History Museum, Greek Biotope/Wetland Centre (EKBY). They are available from the lead author upon reasonable request and with permission of The Goulandris Natural History Museum, Greek Biotope/Wetland Centre (EKBY).

Author contributions

D.Z. and I.T. conceived of the research idea; D.Z. collected vegetation data; V.T. supervised environmental parameters samplings and analyses; D.Z. and I.T. performed statistical analyses; E.B. supervised vegetation type descriptions and syntaxonomical decisions; D.Z., with contributions from I.T. and E.B., wrote the paper; all authors discussed the results and commented on the manuscript.

Acknowledgements

Executed in the frame of the Greek National Water Monitoring Network, according to the JMD 140384/2011, implemented by The Goulandris Natural History Museum, Greek Biotope/Wetland Centre (EKBY). The Network is supervised by the Directorate for the Protection and Management of Water Resources of the Ministry of Environment and Energy. The data used in this report come from Acts MIS 5001204 financed by the European Union Cohesion Fund (Partneship Agreement 2014–2020), MIS 371010, 371138, 371140, 371144, 371145 of the Operational Program "Environment and Sustainable Development" financed by the European Regional Development Fund. Special thanks must be given to G. Poulis, for his contribution to aquatic macrophyte samplings and identification and to E. Tsakiri for the identification of bryophytes. EKBY's personnel conducted monitoring samplings and analysis of environmental parameters.

References

Aguiar FC, Ferreira MT, Albuquerque A, Bernez I (2005) Invasibility patterns of knotgrass (*Paspalum distichum*) in Portuguese riparian habitats. Weed Technology 19: 509–516. https://doi.org/10.1614/WT-04-080R.1

Azzella MM, Rosati L, Blasi C (2013) Phytosociological survey as a baseline for environmental status assessment: the case of hydrophytic vegetation of a deep volcanic lake. Plant Sociology 50: 33–46.

Bergmeier E (2001) Seasonal pools in the vegetation of Gavdos (Greece) – in situ conservation required. Bocconea 13: 511–516.

Biondi E, Bagella S. (2005) Vegetazione e paesaggio vegetale dell'arcipelago di La Maddalena (Sardegna nord-orientale). Fitosociologia 42: 3–99.

Birkinshaw N, Kemp E, Clarke S (2013) The ecology of grass-wrack pondweed *Potamogeton compressus*. Natural England Commissioned Reports: Number 130.

Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. Ecological Monographs 27: 325–349. https://doi.org/10.2307/1942268

Borsukevych L (2013) The distribution, ecology and phytosociology of rare *Potamogeton* species in central part of western Ukraine. In: Dyguś KH (Ed.) Natural human environment: Dangers, protection, education: Monograph. Oficyna Wydawnicza Wyższej Szkoły Ekologii i Zarządzania, Warsaw, PL.

Brullo S, Sciandrello S (2006) La vegetazione del bacino lacustre "Biviere di Gela" (Sicilia meridionale). Fitosociologia 43: 1–20.

Canfield DE, Langeland KA, Linda SB, Haller, WT (1985) Relations between water transparency and maximum depth of macrophyte colonization in lakes. Journal of Aquatic Plant Management 23: 25–28.

Carpenter SR, Lodge DM (1986) Effects of submersed macrophytes on ecosystem processes. Aquatic Botany 26: 341–370. https://doi.org/10.1016/0304-3770(86)90031-8

Carretero JL (1986) Ricefield flora and vegetation in provinces of the Valencia and Tarragona (Spain). Collectanea Botanica 17: 113–124. https://doi.org/10.3989/collectbot.1988.v17.163

CEN – European Committee for Standardization (2007) IS EN 15460 – Water quality – Guidance Standard for the surveying of macrophytes in lakes, CEN, Brussels, BE.

Ceschin S, Zuccarello V, Caneva G (2010) Role of macrophyte communities as bioindicators of water quality: Application on the Tiber River basin (Italy). Plant Biosystems 144: 528–536. https://doi.org/10.1080/11263500903429221

Chambers PA, Kaiff J (1985) Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. Canadian Journal of Fisheries and Aquatic Sciences 42: 701–709. https://doi.org/10.1139/f85-090

Charrad M, Ghazzali N, Boiteau V, Niknafs A (2014) NbClust: An R package for determining the relevant number of clusters in a data set. Journal of Statistical Software 61: 1–36. https://doi.org/10.18637/jss.v061.i06

Chepinoga V, Bergmeier E, Rosbakh S, Fleckenstein K (2013) Classification of aquatic vegetation (Potametea) in Baikal Siberia, Russia, and its diversity in a northern Eurasian context. Phytocoenologia 43: 127–167. https://doi.org/10.1127/0340-269X/2013/0043-0541

Coops H, Beklioglu M, Crisman TL (2003) The role of water-level fluctuations in shallow lake ecosystems – workshop conclusions. Hydrobiologia 506–509: 23–27. https://doi.org/10.1023/B:HYDR.0000008595.14393.77

Csiky J, Purger D, Blaženčić J (2014) New occurrence and distribution of *Nitella hyalina* (DC.) Agardh (Characeae) and the first report on *Nitelletum hyalinae* Corrilion 1957, in Croatia. Archives of Biological Science Belgrade 66: 203–208. https://doi.org/10.2298/ABS1401203C

Cvijanović DL, Lakušić DV, Živković MM, Novković MZ, Anđelković AA, Pavlović DM, Vukov DM, Radulović SB (2018) An overview of aquatic vegetation in Serbia. Tuexenia 38: 269–286.

Dawson FH, Szoszkiewicz K (1999) Relationships of some ecological factors with the associations of vegetation in British rivers. Hydrobiologia 415: 117–122. https://doi.org/10.1023/A:1003820308436

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90: 3566–3574. https://doi.org/10.1890/08-1823.1

De Cáceres M, Legendre P, Wiser SK, Brotons L (2012) Using species combinations in indicator analyses. Methods in Ecology and Evolution 3: 973–982. https://doi.org/10.1111/j.2041-210X.2012.00246.x

De Foucault B, Koffi A, Batawila K, Bouchet P (2013) Contribution à une étude phytosociologique du littoral sableux du Togo. Acta botanica Gallica 147: 333–344. https://doi.org/10.1080/12538078.2000.10515865

Den Hartog C (1959) The Batrachospermeto-Chaetophoretum, a remarkable algal association in the Netherlands. Acta Botanica Neerlandica 8: 247–256. https://doi.org/10.1111/j.1438-8677.1959.tb00535.x

Dimopoulos P, Raus Th, Bergmeier E, Constantinidis Th, Iatrou G, Kokkini S, Strid A, Tzanoudakis D (2013) Vascular plants of Greece: An annotated checklist. Berlin: Botanischer Garten und Botanisches Museum Berlin-Dahlem; Athens: Hellenic Botanical Society. Englera 31.

Dimopoulos P, Raus Th, Bergmeier E, Constantinidis Th, Iatrou G, Kokkini S, Strid A, Tzanoudakis D (2016) Vascular plants of Greece: An annotated checklist. Supplement. Willdenowia 46: 301–347. https://doi.org/10.3372/wi.46.46303

Dimopoulos P, Sykora K, Cilissen C, Wiecherink D, Georgiadis T (2005) Vegetation ecology of Kalodiki Fen (NW Greece). Biologia 60: 69–82.

Drosos E, Athanasiadis N, Thedoropoulos K, Eleftheriadou E (1996) Ammophilous, halophilous and hydrophilous plant communities of delta of Thessalian Pinios river (Thessalia, Hellas). Scientific annals of the Department of Forestry and Natural environment of Thessaloniki 39: 329–365. [in Greek]

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Leveque C, Naiman RJ, Prieur-Richard AH, Soto D, … Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163–182. https://doi.org/10.1017/S1464793105006950

Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366. https://doi.org/10.2307/2963459

Dutartre A (1986) Aquatic plants introduced in freshwater lakes and ponds of Aquitaine (France): dispersion and ecology of *Lagerosiphon major* and *Ludwigia peploides*. Proceedings of 7th International Symposium on aquatic weeds: 93–98.

Džigurski D, Nikolić LJ, Ljevnaić-Mašić B (2016) Vegetation of the Hydrochari-Lemnetea and Potametea classes in the Danube-Tisza-Danube hydrosystem (Serbia). Contemporary Problems of Ecology 9: 329–341. https://doi.org/10.1134/S1995425516030033

Engelhardt KAM, Ritchie ME (2001) Effects of macrophyte species richness on wetland ecosystem functioning and services. Nature 411: 687–689. https://doi.org/10.1038/35079573

Euro+Med (2006-) Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed. [accessed 4 Jan 2019]

European Commission (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23rd October 2000. Establishing a Framework for Community Action in the Field of Water Policy. Official Journal of the European Communities, L327/1. European Commission, Brussels, BE.

Felzines JC (2012) Contribution to the prodrome of the vegetations of France: *Lemnetea minoris* Tüxen ex O. Bolòs & Masclans 1955. Journal de Botanique de la Société Botanique de France 59: 189–240.

Flores LN, Barone R (2005) Water-level fluctuations in Mediterranean reservoirs: Setting a dewatering threshold as a management tool to improve water quality. Hydrobiologia 548: 85–99. https://doi.org/10.1007/s10750-005-1149-6

Foley JA, DeFries R, Asner GP, Badford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, … Snyder PK (2005) Global consequences of land use. Science 309: 550–574. https://doi.org/10.1126/science.1111772

Fotiadis G, Kazoglou Y, Bousbouras D (2008) Vegetation types of Lake Chimaditis before the artificial increase of its water level. Proceedings of the 6th Panhellenic Rangeland Congress in Leonidio Arcadia Peloponnesus 2008: 101–107. [in Greek]

Galán de Mera A, Linares-Perea E, De la Cruz JC, Orellana JAV (2009) Nuevas observaciones sobre la vegetación del sur del Perú. Del Desierto Pacífico al Altiplano. Acta Botanica Malacitana 34: 107–144. https://doi.org/10.24310/abm.v34i0.6904

Gabka M (2002) Vallisneria spiralis (Hydrocharitaceae) – nowy gatunek we florze Polski. Fragmenta Floristica et Geobotanica Polonica 9: 67–73.

Gabka M, Dolata PT (2010) Rare and endangered associations of vegetation within the fish ponds from the south Wielkopolska region. Badania Fizjograficzne Seria B – Botanika B59: 75–96.

Goldyn R, Goldyn H, Kaniewski W (2005) Water plant associations in the valley of the Cybina river. Roczniki Akademii Rolniczej w Poznaniu 373: 69–87.

Golub VB, Losev GA, Mirkin, BM (1991) Aquatic and hygrophytic vegetation of the Lower Volga valley. Phytocoenologia 20: 1–63. https://doi.org/10.1127/phyto/20/1991/1

Gopal B, Goel U (1993) Competition and allelopathy in aquatic plant communities. The Botanical Review 59: 155–210. https://doi.org/10.1007/BF02856599

Gradstein SR, Smittenberg JH (1977) The hydrophilous vegetation of western Crete. Vegetatio 34: 65–86. https://doi.org/10.1007/BF00054476

Grigoriadis N, Donth S, Theodoropoulos K, Eleftheriadou E (2005) Establishment of a habitat monitoring system in Agra wetland (Pella, Greece). Annali di Botanica (nuova serie) 5: 21–36.

Gross EM (2003) Allelopathy of aquatic autotrophs. Critical Reviews in Plant Sciences 22: 313–339. https://doi.org/10.1080/713610859

Grzybowski M, Szarek J, Skibniewska KA, Guziur J (2010) Evaluation of diversity of submerged and emergent flora of lake Szelag Wielki as threatened by a pesticide tomb. Polish Journal of Natural Science 25: 154–172. https://doi.org/10.2478/v10020-010-0013-y

Guiry MD, Guiry GM (2019) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org. [accessed 4 Jan 2019]

Hauenstein E, González M, Peña-Cortés F, Muñoz-Pedreros A (2002) Flora and vegetation of coastal wetlands near Tolten, Chile. Gayana Botánica 59: 87–100. https://doi.org/10.4067/S0717-66432002000200006

Heuff H (1984) The vegetation of Irish Lakes. Wildlife Service, Office of Public Works, Dublin, IE.

Hrivnák R (2002) Aquatic plant communities in the catchment area of the Ipel' river in Slovakia and Hungary. Thaiszia – Journal of Botany 12: 137–160.

Hrivnák R, Oťaheľová H, Kochjarová J, Blanár D, Husák S (2005) Plant communities of the class Charetea fragilis FUKAREK ex KRAUSCH 1964 in Slovakia: new information on their distribution and ecology. Thaiszia – Journal of Botany 15: 117–128.

Hutorowicz A, Dziedzic J, Kapusta A (2006) *Vallisneria spiralis* (Hydrocharitaceae) localities in Konin Lakes (Kujawy Lakeland). Fragmenta Floristica et Geobotanica Polonica 13: 89–94.

Iakushenko D, Borysova O (2012) Plant communities of the class Charetea Fukarek ex Krausch 1964 in Ukraine: an overview. Biodiversity Research and Conservation 25: 75–82. https://doi.org/10.2478/v10119-012-0014-5

Jenačković DD (2017) A phytosociological-ecological study of marshland vegetation (*Phragmitetea communis* R. Tx. et Preising 1942) in the central Balkans. PhD Thesis, University of Belgrade, RS.

Jeppesen E, Sondergaard M, Sondergaard M, Christoffersen K [Eds] (1997) The structuring role of submerged macrophytes in lakes [Ecological Studies 131]. Springer, New York, US, 423 pp. https://doi.org/10.1007/978-1-4612-0695-8

Julve P (1998) Baseflor. Index botanique, écologique et chorologique de la Flore de France. Version 2016. Programme Catminat. http://perso.wanadoo.fr/philippe.julve/catminat.htm. [accessed 18 Sept 2017]

Kamberović J, Barudanovic S, Mašić E, Dedic A (2014) Marshland vegetation of the order Phragmitetalia on shores of mine pit lakes in north-eastern Bosnia and Herzegovina. Biologica Nyssana 5: 1–10.

Kassambara A, Mundt F (2017) factoextra: Extract and visualize the results of multivariate data analyses. R package version 1.0.5. https://CRAN.R-project.org/package=factoextra.

Kaufman L, Rousseeuw PJ (1990) Finding groups in data: An introduction to cluster analysis. Wiley, New York, US. https://doi.org/10.1002/9780470316801

Kipriyanova LM, Romanov RE (2013) Communities of charophytes in water bodies and water courses in the North of the endorheic basin of the Ob-Irtysh Interfluve (Western Siberia). Inland Water Biology 6: 184–193. https://doi.org/10.1134/S1995082913020053

Klein Tank AMG, Wijngaard JB, Können GB, Böhm R, Demarée G, Gocheva A, Mileta M, Pashiardis S, Hejkrlik L, … Petrovic P (2002) Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. International Journal of Climatology 22: 1441–1453. https://doi.org/10.1002/joc.773

Data and metadata available at http://www.ecad.eu.

Kłosowski S (2006) The relationships between environmental factors and the submerged Potametea associations in lakes of north-eastern Poland. Hydrobiologia 560: 15–29. https://doi.org/10.1007/s10750-005-1141-1

Kłosowski S, Jabłońska E (2009) Aquatic and swamp plant communities as indicators of habitat properties of astatic water bodies in north-eastern Poland. Limnologica 39: 115–127. https://doi.org/10.1016/j.limno.2008.01.003

Kolada A (2016) The use of helophytes in assessing eutrophication of temperate lowland lakes: Added value? Aquatic Botany 129: 44–54. https://doi.org/10.1016/j.aquabot.2015.12.002

Kolada A, Hellsten S, Kanninen A, Søndergaard M, Dudley B, Nõges P, Ott I, Ecke F, Mjelde M, … Duel H (2009) Overview and comparison of macrophyte survey methods used in European countries and a proposal of harmonized common sampling protocol to be used for WISER uncertainty exercise including a relevant common species list. Wiser Deliverable D3.2–1. http://www.wiser.eu/results/deliverables/ [accessed 4 Jan 2019]

Kolada A, Willby N, Dudley B, Noges P, Sondergaard M, Hellsten S, Mjelde M, Penning E, van Geest G, … Karus K (2014) The applicability of macrophyte compositional metrics for assessing eutrophication in European lakes. Ecological Indicators 45: 407–415. https://doi.org/10.1016/j.ecolind.2014.04.049

Kuzmichev AI, Krasnova AN, Kuznetsova LV (2008) The typological structure of hydrophilic flora and vegetation of technologically transformed lakes of Vologda Poozerye. Inland Water Biology 1: 362–370. https://doi.org/10.1134/S1995082908040081

Lance GN, Williams WT (1967) A general theory of classification sorting strategies: I. Hierarchical systems. Computer Journal 9: 373–380. https://doi.org/10.1093/comjnl/9.4.373

Landucci F, Gigante G, Venanzoni R (2011) An application of the Cocktail method for the classification of the hydrophytic vegetation at Lake Trasimeno (Central Italy). Fitosociologia 48: 3–22.

Landucci F, Gigante G, Venanzoni R, Chytrý M (2013) Wetland vegetation of the class Phragmito-Magno-Caricetea in central Italy. Phytocoenologia 43: 67–100. https://doi.org/10.1127/0340-269X/2013/0043-0545

Langangen A (2012) Charophytes (Charales) from Crete (Greece) collected in 2010. Flora Mediterranea 22: 25–32. https://doi.org/10.7320/FlMedit22.025

Lastrucci L, Bonari G, Angiolini C, Casini F, Giallonardo T, Gigante D, Landi M, Landucci F, Venanzoni R, Viciani D (2014) Vegetation of Lakes Chiusi and Montepulciano (Siena, central Italy): updated knowledge and new discoveries. Plant Sociology 51: 29–55.

Lastrucci L, Cerri M, Coppi A, Ferranti F, Ferri V, Foggi B, Lazzaro L, Reale L, Venanzoni R, … Gigante D (2017) Understanding common reed die-back: a phytocoenotic approach to explore the decline of palustrine ecosystems. Plant Sociology 54: 15–28.

Lastrucci L, Valentini E, Dell'Olmo L, Vietina B, Foggi B (2015) Hygrophilous vegetation and habitats of conservation interest in the area of the lake Porta (Tuscany, Central Italy). Atti della Società toscana di scienze naturali Memorie Serie B 122: 131–146.

Lavrentiades G, Pavlidis G (1985) Contribution to research of hydrophytic and helophytic communities of Mikri Prespa. Praktika 4ou Epistimonikou Synedriou Ellinikis Votanikis Eterias 1985: 145–155. [in Greek]

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271–280. https://doi.org/10.1007/s004420100716

Lukács BA, Dévai G, Tóthmérész B (2009) Aquatic macrophytes as bioindicators of water chemistry in nutrient rich backwaters along the Upper-Tisza river (in Hungary). Phytocoenologia 39: 287–293. https://doi.org/10.1127/0340-269X/2009/0039-0287

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K (2018) cluster: Cluster Analysis Basics and Extensions. R package version 2.0.7-1. https://CRAN.R-project.org/package=cluster.

Margalef R (1949). Las asociaciones de algas en las aguas dulces de pequeño volumen del Noreste de España. Vegetatio 1: 258–284. https://doi.org/10.1007/BF00184535

Mavromati E, Kagalou I, Kemitzoglou D, Apostolakis A, Tsiaoussi V (2017) Linkages between physicochemical status and hydromorphology in Greek lakes under WFD policy. European Water 58: 273–279.

McCreary NJ (1991) Competition as a mechanism of submersed macrophyte community structure. Aquatic Botany 41: 177–193. https://doi.org/10.1016/0304-3770(91)90043-5

Middelboe AL, Markager S (1997) Depth limits and minimum light requirements of freshwater macrophytes. Freshwater Biology 37: 553–568. https://doi.org/10.1046/j.1365-2427.1997.00183.x

Melendo M, Cano E, Valle F (2003) Synopsis of aquatic plant-communities of the class Potametea in the southern Iberian Peninsula. Acta Botanica Gallica 150: 429–444. https://doi.org/10.1080/12538078.2003.10516011

Mucina L, Bültmann H, Dierssen K, Theurillat JP, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, … Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen and algal communities. Applied Vegetation Science 19: 3–264. https://doi.org/10.1111/avsc.12257

Nagy J, Gál B, Tuba Z, Szerdahelyi T, Czóbel, S, Szirmai O, Cserhalmi D, Ürmös Z (2009) Monodominant plant associations in the Bodrogköz (NE Hungary) new for science and for Hungary. Thaiszia – Journal of Botany 19: 299–314.

Ninot JM, Font X, Masalles RM, Vigo J (2011) Syntaxonomic conspectus of the vegetation of Catalonia and Andorra. II: Ruderal communities. Acta Botanica Barcinonensia 53: 113–189.

Oksanen J, Blanchet FG, Friendly M, Kindt M, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, … Wagner H (2018). vegan: Community Ecology Package. R package version 2.4-6. https://CRAN.R-project.org/package=vegan

Padovani CSM, Jaramillo RM, Nempu PO, García CR (1993) La biodiversidad vegetacional del santuario de la naturaleza «Rio Cruces» (Valdivia, Chile). Acta Botanica Malacitana 18: 259–279.

Palmer MA, Bell SL, Butterfield IA (1992) A botanical classification of standing waters in Britain: application for conservation and monitoring. Aquatic Conservation: Marine and Freshwater Ecosystems 2: 125–143. https://doi.org/10.1002/aqc.3270020202

Papastergiadou E (1990) Phytosociological and ecological studies of aquatic macrophytes (Hydrophytes), in Northern Greece. PhD Thesis. Aristotle University of Thessaloniki, GR. [in Greek]

Pedrotti F (2008) La vegetazione delle marcite di Norcia (Italia Centrale). Braun-Blanquetia 44: 1–32.

Pelechaty M, Pukacz A (2006) Charophyte species and communities of different types of water ecosystems of the Ziemia Lubuska region (Western Poland). Biodiversity Research and Conservation 1–2: 138–142.

Penning WE, Dudley B, Mjelde M, Hellsten S, Hanganu J, Kolada A, van den Berg M, Poikane S, Phillips G, … Ecke F (2008a) Using aquatic macrophyte community indices to define the ecological status of European lakes. Aquatic Ecology 42: 253–264. https://doi.org/10.1007/s10452-008-9183-x

Penning WE, Mjelde M, Dudley B, Hellsten S, Hanganu J, Kolada A, van den Berg M, Poikane S, Phillips G, … Ecke F (2008b) Classifying aquatic macrophytes as indicators of eutrophication in European lakes. Aquatic Ecology 42: 237–251. https://doi.org/10.1007/s10452-008-9182-y

Phillips GL, Eminson D, Moss B (1978) A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. Aquatic Botany 4: 103–126. https://doi.org/10.1016/0304-3770(78)90012-8

Phillips GL, Willby N, Moss B (2016) Submerged macrophyte decline in shallow lakes: what have we learned in the last forty years? Aquatic Botany 135: 37–45. https://doi.org/10.1016/j.aquabot.2016.04.004

Pirini BC (2011) The ecosystem of Lakes Vegoritida and Petron: flora, vegetation and plant geography. PhD Thesis, Aristotle University of Thessaloniki, GR. [in Greek]

Poikane S, Portielje R, Denys L, Elferts D, Kelly M, Kolada A, Mäemets H, Phillips G, Søndergaard M, … van den Berg MS (2018) Macrophyte assessment in European lakes: Diverse approaches but convergent views of 'good' ecological status. Ecological Indicators 94: 185–197. https://doi.org/10.1016/j.ecolind.2018.06.056

Preising E, Vahle –, Brandes D, Hofmeister H, Tüxen J, Weber HE (1990) Die Pflanzengesellschaften Niedersachsens. Bestandsentwicklung, Gefährdung und Schutzprobleme. Wasser- und Sumpfpflanzengesellschaften des Süßwassers. Naturschutz und Landschaftspflege in Niedersachsen 20: 47–161.

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, … Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287: 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sand-Jensen K, Riis T, Vestergaard O, Larsen SE (2000) Macrophyte decline in Danish lakes and streams over the past 100 years. Journal of Ecology 88: 1030–1040. https://doi.org/10.1046/j.1365-2745.2000.00519.x

Sarika M, Dimopoulos P, Yannitsaros A (2005) Contribution to the knowledge of the wetland flora and vegetation of Amvrakikos Gulf, W Greece. Willdenowia 35: 69–85. https://doi.org/10.3372/wi.35.35105

Sarika-Hatzinikolaou M, Yannitsaros A, Babalonas D (2003) The macrophytic vegetation of seven aquatic ecosystems of Epirus (NW Greece). Phytocoenologia 33: 93–151. https://doi.org/10.1127/0340-269X/2003/0033-0093

Sharma RA, Singh R (2013) A review on *Phyla nodiflora* Linn.: A wild wetland medicinal herb. International Journal of Pharmaceutical Sciences Review and Research 20: 57–63.

Shipley B, Keddy PA, Lefkovitch LP (1991) Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient. Canadian Journal of Botany 69: 1420–1424. https://doi.org/10.1139/b91-184

Solińska-Górnicka B, Symonides E (2001) Long-term changes in the flora and vegetation of lake Mikolajskie (Poland) as a result of its eutrophication. Acta Societatis Botanicorum Poloniae 70: 323–334. https://doi.org/10.5586/asbp.2001.040

Søndergaard M, Johansson LS, Lauridsen TL, Jorgensen TB, Liboriussen L, Jeppesen E (2010) Submerged macrophytes as indicators of the

ecological quality of lakes. Freshwater Biology 55: 893–908. https://doi.org/10.1111/j.1365-2427.2009.02331.x

Spence DHN (1982) The zonation of plants in freshwater lakes. Advances in Ecological Research 12: 37–125. https://doi.org/10.1016/S0065-2504(08)60077-X

Spence DHN, Chrystal J (1970) Photosynthesis and zonation of freshwater macrophytes: I. Depth distribution and shade tolerance. New Phytologist 69: 205–215. https://doi.org/10.1111/j.1469-8137.1970.tb04064.x

Stępień E, Zawal A, Buczyński P, Buczyńska E (2015) Changes in the vegetation of a small lowland river valley (Krąpiel, NW Poland) after dredging. Acta Biologica 22: 167–196. https://doi.org/10.18276/ab.2015.22-13

Šumberová K (2011a) Vegetace vodních rostlin zakořeněných ve dně (Potametea). Vegetation of aquatic plants rooted in the bottom. In: Chytrý M (Ed.) Vegetace České republiky, 3, Vodní a mokřadní vegetace. Vegetation of the Czech Republic, 3, Aquatic and wetland vegetation. Academia, Prague, CZ, 100–247.

Šumberová K (2011b) Vegetace volně plovoucích vodních rostlin (Lemnetea). Vegetation of free floating aquatic plants. In: Chytrý M (Ed.) Vegetace České republiky, 3, Vodní a mokřadní vegetace. Vegetation of the Czech Republic, 3, Aquatic and wetland vegetation. Academia, Prague, CZ, 43–99.

Šumberová K, Hájková P, Chytrý M, Hroudová Z, Sádo J, Hájek M, Hrivnák R, Navrátilová J, Hanáková P, Ekrt L, Ekrtová E (2011a) Vegetace rákosin a vysokých ostřic (Phragmito-Magno-Caricetea). Marsh vegetation. In: Chytrý M (Ed.) Vegetace České republiky, 3, Vodní a mokřadní vegetace. Vegetation of the Czech Republic, 3, Aquatic and wetland vegetation. Academia, Prague, CZ, 385–579.

Šumberová K, Hrivnák R, Rydlo J, Oťaheľová H (2011b) Vegetace parožnatek (Charetea). Vegetation of stoneworts. In: Chytrý M (Ed.) Vegetace České republiky, 3, Vodní a mokřadní vegetace. Vegetation of the Czech Republic, 3, Aquatic and wetland vegetation. Academia, Prague, CZ, 248–267.

Täuscher L, van de Weyer K (2015) Die Armleuchteralgen-Gesellschaften Deutschlands. In: Arbeitsgruppe Characeen Deutschlands (Ed.) Armleuchteralgen. Die Characeen Deutschlands. Springer Spektrum, Berlin, Heidelberg, DE, 139–147. https://doi.org/10.1007/978-3-662-47797-7_9

Wickam H, (2017) tidyverse: Easily install and load the 'Tidyverse'. R package version 1.2.1. https://CRAN.R-project.org/package=tidyverse.

Wood RD (1962) New combinations and taxa in the revision of Characeae. Taxon 11: 7–25. https://doi.org/10.2307/1216853

Zervas D, Tsiaoussi V, Tsiripidis I (2018) HeLM: a macrophyte-based method for monitoring and assessment of Greek lakes. Environmental Monitoring and Assessment 190: 1–326. https://doi.org/10.1007/s10661-018-6708-1

Zotos AG (2006) Flora, vegetation ecology and management proposals for the wet meadows and reed thickets of the lakes Trichonida and Lysimachia (W. Greece). PhD Thesis, University of Ioannina, GR. [in Greek]

Zotos A, Sarika M, Lucas E, Dimopoulos P (2006) *Ludwigia peploides* subsp. *montevidensis*, a new alien taxon for the flora of Greece and the Balkans. Journal of Biological Research 5: 71–78.

E-mail and ORCID

Dimitrios Zervas (Corresponding author, dzervas@ekby.gr), ORCID: https://orcid.org/0000-0002-2892-6046
Ioannis Tsiripidis (tsiripid@bio.auth.gr)
Erwin Bergmeier (erwin.bergmeier@bio.uni-goettingen.de)
Vasiliki Tsiaoussi (vasso@ekby.gr)

Supplementary material

Supplementary material 1
Bibliographic data sources of Greek aquatic plant communities.
Link: https://10.3897/VCS/2020/48377.suppl1

Supplementary material 2
Summary of the recorded taxa in the studied lakes.
Link: https://doi.org/10.3897/VCS/2020/48377.suppl2

Supplementary material 3
Resulting graphs of cluster statistics.
Link: https://doi.org/10.3897/VCS/2020/48377.suppl3

Supplementary material 4
Classification dendrogram of the current study.
Link: https://doi.org/10.3897/VCS/2020/48377.suppl4

Supplementary material 5
Selected taxa combinations of diagnostic taxa.
Link: https://doi.org/10.3897/VCS/2020/48377.suppl5

Supplementary material 6
Distribution of the recorded vegetation types.
Link: https://doi.org/10.3897/VCS/2020/48377.suppl6

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 77–86
doi: 10.3897/VCS/2020/48518

RESEARCH PAPER ECOINFORMATICS

Finite Mixture Model-based classification of a complex vegetation system

Fabio Attorre[1], Vito E. Cambria[2], Emiliano Agrillo[3], Nicola Alessi[4], Marco Alfò[5], Michele De Sanctis[1], Luca Malatesta[1], Tommaso Sitzia[2], Riccardo Guarino[6], Corrado Marcenò[7], Marco Massimi[1], Francesco Spada[1], Giuliano Fanelli[1]

1 *Department of Environmental Biology, Sapienza University of Rome, Italy*
2 *Department of Land, Environment, Agriculture and Forestry, University of Padova, Legnaro, Italy*
3 *Institute for Environmental Protection and Research (ISPRA), Rome, Italy*
4 *Faculty of Science and Technology, Free University of Bozen-Bolzano, Italy*
5 *Department of Statistical Sciences, Sapienza University of Rome, Italy*
6 *Department of Environmental Biology and Biodiversity, University of Palermo, Italy*
7 *Department of Plant Biology and Ecology, University of the Basque Country, Bilbao, Spain*

Corresponding author: Vito E. Cambria (vitoemanuele.cambria@phd.unipd.it)

Academic editor: Florian Jansen ♦ **Received** 15 November 2019 ♦ **Accepted** 31 January 2020 ♦ **Published** 4 May 2020

Abstract

Aim: To propose a Finite Mixture Model (FMM) as an additional approach for classifying large datasets of georeferenced vegetation plots from complex vegetation systems. **Study area**: The Italian peninsula including the two main islands (Sicily and Sardinia), but excluding the Alps and the Po plain. **Methods**: We used a database of 5,593 georeferenced plots and 1,586 vascular species of forest vegetation, created in TURBOVEG by storing published and unpublished phytosociological plots collected over the last 30 years. The plots were classified according to species composition and environmental variables using a FMM. Classification results were compared with those obtained by TWINSPAN algorithm. Groups were characterized in terms of ecological parameters, dominant and diagnostic species using the fidelity coefficient. Interpretation of resulting forest vegetation types was supported by a predictive map, produced using discriminant functions on environmental predictors, and by a non-metric multidimensional scaling ordination. **Results**: FMM clustering obtained 24 groups that were compared with those from TWINSPAN, and similarities were found only at a higher classification level corresponding to the main orders of the Italian broadleaf forest vegetation: *Fagetalia sylvaticae, Carpinetalia betuli, Quercetalia pubescenti-petraeae* and *Quercetalia ilicis*. At lower syntaxonomic level, these 24 groups were referred to alliances and sub-alliances. **Conclusions**: Despite a greater computational complexity, FMM appears to be an effective alternative to the traditional classification methods through the incorporation of modelling in the classificatory process. This allows classification of both the co-occurrence of species and environmental factors so that groups are identified not only on their species composition, as in the case of TWINSPAN, but also on their specific environmental niche.

Taxonomic reference: Conti et al. (2005).

Abbreviations: CLM = Community-level models; FMM = Finite Mixture Model; NMDS = non-metric multidimensional scaling.

Keywords

cluster analysis, finite mixture model, forest vegetation, Italian peninsula, vegetation plots

PENSOFT.

Copyright *Fabio Attorre et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The analysis of the spatial distribution of assemblages of communities is receiving increasing attention by ecologists (Nieto-Lugilde et al. 2017). To this purpose community-level models (CLM) are being used more and more, based on an "assemble-and-predict-together" strategy to simultaneously model multiple co-occurring species within a single process (Ferrier and Guisan 2006). They include methods that model the distribution of multiple species using a common set of environmental variables (De'ath 2002; Yee 2004, 2006; Leathwick et al. 2006). This feature makes CLM particularly promising for the classification of vegetation since the identification of one type is based on both its species composition and the environmental space it occupies (De Cáceres et al. 2015; Guarino et al. 2018).

Approaches to CLM clustering can be either based on minimizing a given loss function (for instance, the sum of within-group deviance), or can be based on associating each group to a specific joint density, which is parametrically specified. In this last case, CLM based clustering arises. While in standard (either hard or fuzzy) partitioning groups are summarized or represented by prototypes, in CLM clustering groups are represented by specific shapes of the corresponding probability density. Using such an approach, vegetation plots can be classified using the posterior probability that each belongs to a given component of the mixture, each component describing a group. Moreover, when the dataset is large, hierarchical approaches, based on the calculation of the pairwise (between plots) distances, rapidly become unfeasible. In this case, partitioning around prototypes, either means, medians or other, in a hard or a fuzzy perspective are usually adopted. However, much of these are based on simple Euclidean distances between each plot and the group prototypes that do not consider the dependence, the association and the covariance between the variables (plant species abundance values) characterizing the plots. In this respect, finite mixtures of multivariate Gaussian densities provide a simple, model-based, extension to the K-means method, allowing for overlapping clusters oriented according to the group-specific covariances and providing, *a posteriori*, for the classification of each plot to one of the groups. For this reason, among CLMs, Finite Mixture Modelling (FMM) is an emerging method and has already been used to identify marine bioregions on the Western Australian continental margin (Woolley et al. 2013) and forest physiognomic types in Italy (Attorre et al. 2014). In this latter paper, data from a National Forest Inventory were used, while here we test the applicability of FMM as a classification method for the forest vegetation of the Italian peninsula (including the major islands but excluding the Alps and the Po Plain). This area is characterized by great biogeographical and environmental variability and hosts a number of forest vegetation types, for which several classification schemes have been proposed (Pedrotti 1995; Pignatti 1998; Ubaldi 2003; Biondi et al. 2014; Mucina et al. 2016). The Italian peninsula is a broad ecotone between the Temperate and the Mediterranean regions (Attorre et al. 2014; Pesaresi et al. 2014). Boundaries between communities are not clearly defined having many species with overlapping ranges. Geo-pedological diversity, a variety of microclimates (Attorre et al. 2007), and a long history of disturbance that dates thousands of years and includes logging, fire, grazing, and plantation activities (Médail and Quézel 1999; Scarascia-Mugnozza et al. 2000; Vallejo et al. 2005), make the identification and classification of vegetation types difficult.

Within this framework, this paper aims to verify the applicability of FMM as classification method of vegetation plots using a complex case study and a large dataset, comparing the classification results with (1) those obtained by the TWINSPAN algorithm and (2) with current syntaxonomic classification schemes.

Methods

Data set

Observation data include 5,593 georeferenced vegetation plots of between 100 and 300 m^2 and 1,586 vascular species of forests in the Italian peninsula and major islands (Landucci et al. 2012; Agrillo et al. 2017). The database was created in TURBOVEG 3 (Hennekens and Schaminée 2001) by digitalizing and georeferencing published plots collected over the last 30 years (http://www.givd.info/ID/EU-IT-011).

Environmental covariates to be used in the statistical model were derived from a database with a spatial resolution of 1×1 km (Attorre et al. 2007): mean annual temperature (MeanT), mean minimum temperature of the coldest month (MinT), mean maximum temperature of the hottest month (MaxT), sum of mean monthly precipitation over summer (Ps) and winter months (Pw), and total annual precipitation (Ptot). We also used slope (SLO), derived from the GTOPO30 digital elevation model, geographical coordinates and a simplified geological map, derived from the geological map of Italy at 1:1.250.000 scale provided by the Italian Institute for Environmental Protection and Research, incorporating five main substrata: volcanic, arenaceous, carbonatic, clayey, sandy and conglomeratic.

Data analysis

We used a FMM to cluster vegetation plots, based on the assumption that data originate from one of K potential groups, also referred to as components. Each group is identified by a component, and each component is completely characterized by a distribution with known parametric form and component-specific parameters. When a (multivariate) Gaussian density is used to describe the component-specific distribution of observed plant species

cover, the component is identified by a specific center, defined by the mean vector (as the observed values are on abundance scale, we may hypothesize that similar plots will be characterized by similar values of abundance of the same species), and a specific shape, summarized by the covariance matrix, which allows for varying dependence between cover values corresponding to different plant species for plots in that component. The groups (components) are defined as homogeneous in the sense that they include plots that show similar vegetation as described by the plant species cover. Therefore, the observed plots can be allocated to one of the groups by using a criterion associated with the proximity between plots and group centers. This criterion is based on the posterior probability that a plot comes from that group (component of the finite mixture). The sum of the posterior probabilities over the components for a given plot is equal to 1, meaning that the plot has a varying degree of membership to all clusters in the population. We usually allocate a plot to a given cluster by finding that for which the posterior probability is maximum. At the end of the grouping step, each group will be characterized by a weight defined as the mean of posterior probabilities and refers to the (relative) frequency of plots allocated to that group. These terms can be interpreted as (prior) probabilities that a generic plot is randomly drawn from a "population of plots" belonging to that group (component of the finite mixture). We propose to model these (prior) probabilities as a function of so-called auxiliary variables (see e.g. McLachlan and Peel 2000). Thus, for each plot, the probability that the plot belongs to a group is a function (through a multinomial logistic model) of environmental parameters, as well as of geographical information, represented by class membership of neighboring plots.

After estimating the parameter vectors for the component-specific densities describing observed abundance, and the prior probability models, we derived the updated posterior probabilities as the (normalized) product of the prior information (based on covariates) and the density for that specific component.

These two steps can be jointly performed within the same estimation algorithm (e.g. using Latent Gold software, see Haughton et al. 2009) using multiple maximization sub-steps; we first estimate the group centers and shapes, and, successively and conditionally on the previous results, we estimate the effect of observed covariates on the probability to belong to a given group. A further alternative is based on the so-called two-three-step procedures, see Vermunt (2010). Rather than defining the prior probability of belonging to a cluster as a function of both environmental and geographical variables, according to the latter approach we first estimated the FMM and then built up a model where cluster membership is a function of geographical and environmental variables, through a multinomial logit model. This may be of help when the approach we propose does present convergence issues, and it defines a viable alternative and an approximate approach to model cluster membership as a function of plot-specific geographical and environmental features. For a formal description of the FMM see Attorre et al. (2014).

In this paper, we adapted the FMM to account for a large data matrix, formed by 5,593 vegetation plots and 1,586 species whose percentage cover is recorded. In this case the direct application of a FMM would be difficult, since it would require the computation and inversion of a 1,586 * 1,586 covariance matrix, with a very sparse structure. Looking at the distribution of the number of species observed in each plot, we see that the corresponding median value is equal to 81; if we look at the distribution of the number of plots each species is present in, the median value is equal to 7. The outcome of this is that of 10,402,980 values in the abundance data matrix, we have 10,241,820 (i.e. 98.45%) null values. Thus, rather than applying a FMM to the observed matrix of percentage covers, we fitted this model to a derived matrix, defined by projecting the original data matrix onto the space spanned by the first 20 principal components of the original data matrix using an approximate method (see Baglama and Reichel 2005) for singular value decomposition (SVD) of the observed, sparse, data matrix, using the R package *irlba* (Baglama and Reichel 2019). The number of principal components has been chosen by looking at stability and robustness of the obtained partition; we have considered 5 to 40 eigenvalues and chosen 20 as the best balance between model fit and simplicity/robustness. After employing the sparse SVD, we have extracted the matrix **A** corresponding to the eigenvectors of the covariance matrix of the observed sparse data **X**. We defined the derived matrix **Y**=**XA** and applied to **Y** the FMM with some backfitting to check whether a too high (low) number of dimensions was considered. The FMM model parameters have been estimated using the *mclust* R package (Fraley et al. 2017).

The optimal number of forest groups (components) was obtained according to penalized likelihood criteria (AIC – Akaike 1973; BIC – Schwarz 1978; CAIC – Hurvich and Tsai 1989; AIC3 – Bodzogan 1994). For all criteria, the lower the value of the index the better (more parsimonious) the fit to the observed data.

FMM classification was compared with that obtained by TWINSPAN (Hill 1979). The modified version of TWINSPAN (Roleček et al. 2009), implemented in JUICE (Tichý 2002), was used. This version, which has already been used in several comparative analyses of classification methods (Gauch and Whittaker 1981; Cao et al. 1997; Moss et al. 1999), allowed us to select the same number of groups obtained with the FMM classification. TWINSPAN pseudospecies cut levels for species abundance were set to 0-5-25 percentage scale units and five levels of divisions were chosen.

The obtained groups were characterized according to environmental parameters and diagnostic species, which were determined using the fidelity coefficient (phi) of Tichý and Chytrý (2006). To avoid phi being dependent on the size of the target site group, group size was standardized to equal the average size of all groups present in the data set (Tichý and Chytrý 2006). The phi values vary

independently of the concentration of species occurrence in the plots of individual groups. Statistical significance was obtained by a simultaneous calculation of Fisher's exact test. Species with phi values higher than 0.5 and Fisher's exact test significance lower than 0.001 were deemed to be diagnostic.

Interpretation of groups was supported by Kruskal's non-metric multidimensional scaling (NMDS) ordination (function isoMDS in the MASS R package, Venables and Ripley 2002). Moreover, we produced a predictive map by calculating discriminant functions based on environmental parameters that best discriminate between the estimated groups. These discriminant functions were used, post-estimation, to allocate (to groups) those plots from study areas where no information on plant species covers was available, while covariates describing environmental parameters were derived from available databases at a given resolution. The discriminant functions were estimated using the function *mda* from the R library. A confusion matrix of omission and commission errors was then calculated to evaluate the capacity of environmental factors to discriminate the groups obtained by FMM.

FMM R code and R libraries used for the statistical analyses are included in Suppl. material 1.

Results

FMM identified 24 groups, which were considered optimal according to all penalized likelihood criteria. However, four of these were discarded because they were characterized by few plots (less than 50), and they were quite heterogeneous. Descriptions of their environmental parameters, spatial distribution and syntaxonomic correspondences is presented in Suppl. material 2, while Suppl. material 3 shows mean and standard deviation of environmental parameters and dominant and diagnostic species of each group. With the support of the NMDS result (Figure 1) four main clusters were identified, corresponding to temperate beech forests (A), temperate chestnut-hornbeam forests (B) sub-Mediterranean deciduous forests (C) and evergreen Mediterranean forests (D). The distribution of classified vegetation plots is reported in Suppl. material 4, while the predictive distribution of groups and clusters is shown respectively in Figures 2 and 3.

Cluster A includes groups 8, 2, and 23. The first three can be found in temperate areas at an average altitude greater than 1000 m and are characterized by the dominance of *Fagus sylvatica* in groups 8 and 2, and by the codominance of this species with *Abies alba* in group 23 (Suppl. material 2 and 3). Group 8 is potentially widespread at the highest altitude along the Apennine chain and on the Etna volcano, while at a lower altitude, group 2 is mainly found in the southern part of the peninsula, and group 23 in the central-north (Figure 2). Cluster B includes only group 18, which is co-dominated by *Fagus sylvatica*, *Castanea sativa* and *Carpinus betulus,* with a

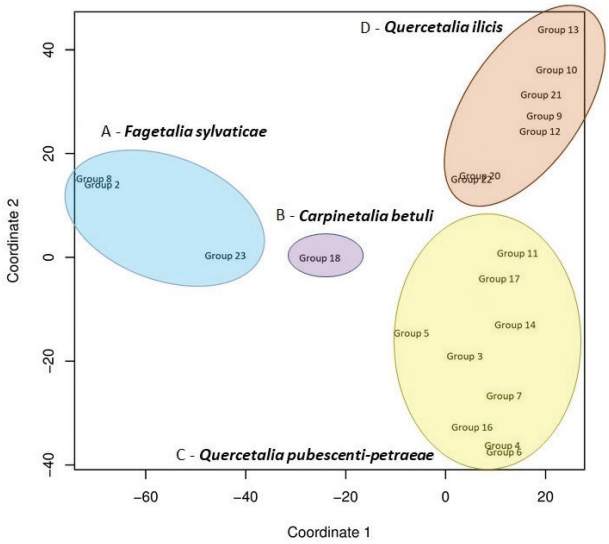

Figure 1. Kruskal's NMDS ordination of the vegetation groups. Due to the high number of plots only the centroids of the groups are shown. Stress values of the two components are 0.32 and 0.18, respectively.

distribution mainly localized in central Italy. Cluster C includes the sub-Mediterranean forests characterized by a high frequency of *Quercus cerris* in all groups, which can be accompanied by other deciduous tree species such as *Ostrya carpinifolia*, *Quercus pubescens* s.l., *Quercus frainetto* and *Fraxinus ornus* (Suppl. material 2 and 3). These groups occupy larger potential areas within an average altitudinal range from the coastal area up to 1000 m a.sl. Some of these can be very localized, such as group 4, characterized by forest stands dominated by *Quercus cerris* in the sub mountain areas of Liguria and northern Tuscany, and group 3, which is characterized by the codominance of *Quercus cerris* and *Ostrya carpinifolia* and is scattered throughout the peninsula (Figure 2). Others are quite widespread such as group 7 characterized by a mixed forest of *Quercus cerris* and *Quercus pubescens*, often with a dominated tree layer of *Carpinus orientalis* and *Erica arborea* and a potential distribution of about 28,000 km^2 mainly in central and southern Italy (Figure 2). Cluster D includes groups 20 and 22 characterized by the dominance of *Quercus suber*. Group 20 is localized in southern Italy and Sicily, while group 22 is potentially distributed in Sardinia and along the Tyrrhenian coast of the peninsula. Other groups within the cluster comprise formations dominated by *Quercus ilex* (Groups 9, 10, 12, 13 and 21). They can be subdivided into two main types: the first one mainly co-dominated by evergreen species at a lower altitude along the coast (Groups 13 and 21) and the second with deciduous tree species such as *Fraxinus ornus*, *Quercus frainetto*, *Quercus pubescens* and *Ostrya carpinifolia,* mainly localized in the inner part of the study area (Groups 9, 10 and 12).

TWINSPAN classification identified three main clusters, dominated by temperate broadleaved deciduous

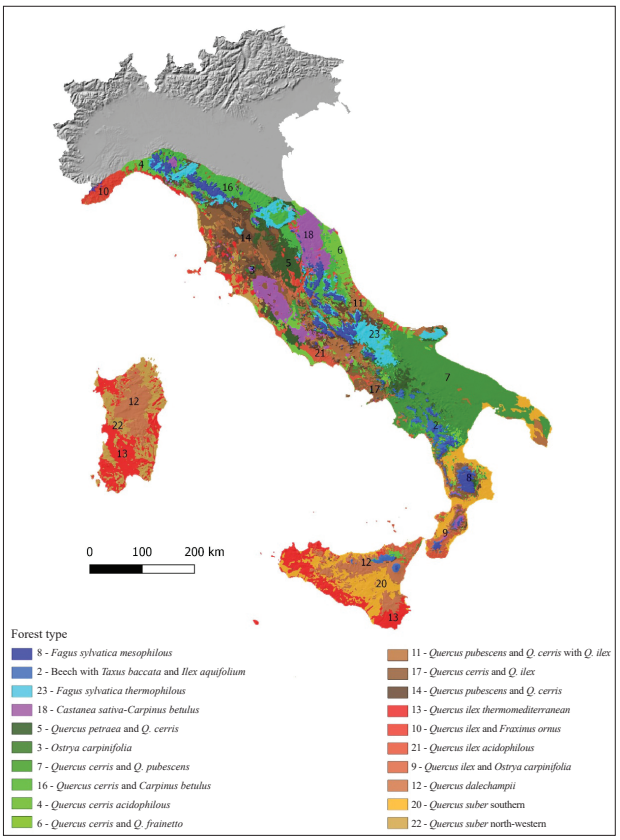

Figure 2. Map of the predictive distribution of the 20 groups based on the discriminant functions applied to environmental factors. The grey color indicates the part of the Italian peninsula not included in the analysis (Alps and the Po Plain).

Figure 3. Map of the potential distribution of the 4 clusters corresponding to main syntaxonomic forest orders recognized for Italy: A – *Fagetalia sylvaticae*, B – *Carpinetalia betuli*, C – *Quercetalia pubescenti-petraeae*, D – *Quercetalia ilicis*.

forests generally dominated by *Fagus sylvatica* (Groups 1–13), evergreen Mediterranean forests dominated by *Quercus suber* and *Quercus ilex* (Groups 14–18) and sub-Mediterranean deciduous forests dominated by *Quercus cerris* (Groups 19–24). The first TWINSPAN cluster corresponds to the four groups of the FMM classification (FMM groups 2, 8, 18 and 23, Table 1). The second cluster includes FMM Mediterranean evergreen groups, clearly differentiating *Quercus suber* and *Quercus ilex* dominated forests. The third TWINSPAN cluster contains all the sub-Mediterranean deciduous forest groups obtained with the FMM classification, group 24 accounting for more than 1000 of these plots.

The confusion matrix built to compare classified versus predicted plots highlighted that, with only some exceptions, environmental factors alone are insufficient to clearly discriminate among the groups identified by the FMM classification (Suppl. material 5). However, a significant difference emerges among clusters: beech forests (Group 2, 8, 23) appear to be better distinguishable, as indicated by the lower omission and commission errors. They are followed by evergreen Mediterranean forests. The poorest results were obtained for sub-Mediterranean deciduous forest types.

Discussion

The choice of an algorithm for the classification of vegetation plots depends on the objective of the classification and each algorithm has advantages and drawbacks (De Cáceres et al. 2015). The results of a classification algorithm can be evaluated by comparison with those of another and with current scientific knowledge on the vegetation type analyzed. In our study, the comparative analysis of FMM and TWINSPAN results highlighted good correspondence only at a high classification level where temperate, deciduous sub-Mediterranean and evergreen Mediterranean forest vegetation clusters were identified (Table 1). At lower levels, significant differences emerged with FMM classification producing groups with an even distribution of plots. Conversely, TWINSPAN split the homogeneous beech forests into many groups but identified two (groups 18 and 24) with 1000 plots each, including almost all the evergreen Mediterranean *Quercus ilex* dominated forests and the sub-Mediterranean deciduous forest dominated by *Quercus cerris* (Figure 4).

Consequently, FMM appears an effective alternative to traditional classification methods, such as TWINSPAN, to support the analysis of complex vegetation systems due to the ability to integrate both species composition and environmental factors into the modelled classificatory process.

Table 1. Comparative matrix between the 24 groups obtained by Finite Mixture Model classification (rows) and the 24 groups by the modified version of TWINSPAN (columns). Colors of the margins (groups) indicate membership to the clusters. Within the matrix, the red color indicates no correspondence among the groups. An increasing correspondence is highlighted by a color gradient from yellow to dark green.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Tot
2	1	5	50	15	12	32	9	21	79	44	4	10	80	0	0	0	0	0	0	0	0	0	0	1	363
8	4	10	19	142	34	18	106	21	47	95	0	0	0	0	0	0	0	0	0	1	0	0	0	0	497
23	0	12	47	28	4	12	3	0	24	35	28	51	132	0	0	0	0	0	2	0	0	1	0	5	384
18	0	3	11	0	6	4	0	0	5	0	30	21	79	0	0	0	2	0	10	0	0	3	1	12	187
3	1	0	0	0	0	0	0	0	0	0	79	42	13	0	0	0	1	0	3	0	1	8	0	50	198
4	0	0	0	0	0	0	0	0	0	0	17	0	1	1	0	0	0	3	11	0	1	10	3	50	97
5	0	0	5	0	0	1	0	0	1	0	27	9	25	0	0	0	0	10	35	0	5	1	1	61	181
6	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	18	0	7	6	1	160	197
7	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	1	15	7	13	1	8	4	9	98	163
11	0	0	0	0	0	0	0	0	0	0	7	3	0	0	0	0	18	59	3	0	0	9	0	205	304
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	39	0	0	0	14	3	323	397
16	1	0	0	0	0	0	0	0	1	0	84	23	81	0	0	0	0	0	5	0	3	2	0	38	238
17	0	0	0	0	0	1	0	0	0	0	6	1	2	7	0	3	11	43	43	0	13	7	3	55	195
9	0	0	0	0	0	0	0	0	0	0	3	2	3	0	0	0	21	31	5	0	22	14	1	11	113
10	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	87	165	4	1	0	26	0	46	333
12	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	7	237	38	2	0	1	16	66	13	381
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	55	390	0	1	0	0	0	2	449
21	0	0	0	0	0	0	0	0	0	0	0	0	0	29	0	28	36	246	0	0	0	1	1	16	357
20	0	0	0	0	0	0	0	0	0	0	0	0	0	18	15	76	19	33	0	1	0	0	2	2	166
22	0	0	0	0	0	0	0	0	0	0	0	0	0	96	44	46	2	56	0	0	0	0	0	0	244
1	1	9	0	0	2	0	0	0	0	0	8	0	0	4	0	0	0	4	16	0	7	0	0	5	56
15	0	0	0	0	0	0	0	0	0	0	0	10	9	0	0	0	0	0	2	0	0	1	0	9	31
19	0	0	0	0	0	0	0	0	0	0	1	3	3	0	0	0	4	0	6	0	1	3	2	10	33
24	0	0	1	0	0	0	0	0	0	0	1	0	1	2	0	2	0	0	7	0	2	1	0	12	29
Tot	8	39	133	185	58	68	118	42	157	174	308	179	429	157	59	164	526	1124	185	5	71	127	93	1184	5593

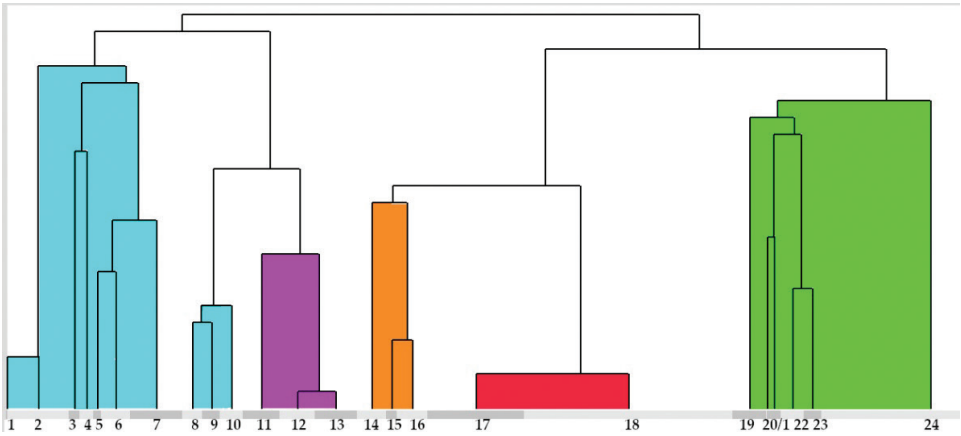

Figure 4. Modified TWINSPAN classification with 24 groups. Light blue color indicates groups belonging to *Fagetalia sylvaticae* (Groups 1–10), purple to *Carpinetalia betuli* (Groups 11–13), orange and red to *Quercetalia ilicis* (Groups 14–18), and green to *Quercetalia pubescenti-petraea* (Groups 19–24).

Moreover, since FMM identifies groups according to their ecological space, a predictive distribution map can also be produced (Figure 2) that better highlights geographic patterns than by viewing the distribution of classified plots alone (Suppl. material 4).

When compared with current syntaxonomic knowledge, the groups obtained by the FMM classification largely corresponded to several alliances and suballiances recognized for Italy according to Mucina et al. (2016) (Table 2). The environmental niche of groups also aligns well with that proposed in the relevant literature, while the floristic composition and the spatial distribution of groups can significantly differ. For instance, in Italy the temperate deciduous forest vegetation characterized by *Fagus sylvatica* and *Quercus* sp. pl. has been traditionally classified on the basis of a distinction between northern and southern syntaxa (see Blasi et al. 2004). This tradition began with Gentile (1970) in the study of beech forests of the Apennines, and was based on the recognition of a number of vicariant closely related species: *Geranium nodosum* (North) / *Geranium versicolor* (South), *Digitalis lutea* (N) / *Digitalis micrantha* (= *D. lutea* subsp. *australis*) (S), *Teucrium scorodonia* (N) / *Teucrium siculum* (S). This phytogeographical distinction was related to a sharp bioclimatic boundary between northern and southern Apennines, the former with no or limited summer drought stress and thus broadly referable to a temperate climate, and the latter with a more pronounced drought stress and

Table 2. Correspondence between the FMM group and the syntaxonomy in Mucina et al. (2016). The alliances are sorted according to an environmental gradient from temperate mesophilous to Mediterranean xeric.

FMM Group	Alliance in Mucina et al. (2016)
2	New alliance?
8	FAG-02B *Fagion sylvaticae* Luquet 1926
23	FAG-02C *Geranio striati-Fagion* Gentile 1970
18	FAG-03 *Carpinetalia betuli* P. Fukarek 1968
3	PUB-01F *Fraxino orni-Ostryion* Tomazic 1940
4	FAG-03C *Erythronio-Carpinion* (Horvat 1958) Marincek in Wallnofer et al. 1993
5	PUB-01L *Crataego laevigatae-Quercion cerridis* Arrigoni 1997
6	PUB-01L *Crataego laevigatae-Quercion cerridis* Arrigoni 1997
7	PUB-01L *Crataego laevigatae-Quercion cerridis* Arrigoni 1997
11	PUB-01G *Carpinion orientalis* Horvat 1958
14	PUB-01G *Carpinion orientalis* Horvat 1958
16	FAG-03C *Erythronio-Carpinion* (Horvat 1958) Marincek in Wallnofer et al. 1993
17	PUB-01L *Crataego laevigatae-Quercion cerridis* Arrigoni 1997
9	PUB-01M *Pino calabricae-Quercion congestae* S. Brullo et al. 1999
10	QUI-01D *Fraxino orni-Quercion ilicis* Biondi, Casavecchia et Gigante in Biondi et al. 2013
12	PUB-01M *Pino calabricae-Quercion congestae* S. Brullo et al. 1999
13	QUI-01A *Quercion ilicis* Br.-Bl. ex Molinier 1934
20	QUI-01E *Erico-Quercion ilicis* S. Brullo et al. 1977
21	QUI-01E *Erico-Quercion ilicis* S. Brullo et al. 1977
22	QUI-01E *Erico-Quercion ilicis* S. Brullo et al. 1977

thus referable to a sub-Mediterranean or supra-Mediterranean climate (Feoli and Lagonegro 1982; Pignatti and Wikus Pignatti 1990). This led to the definition of northern and southern alliances or suballiances, for instance, the northern *Geranio nodosi-Fagion* (= *Cardamino kitaibelii-Fagenion*) and southern *Geranio versicoloris-Fagion* (= *Geranio striati-Fagenion*) (Feoli and Lagonegro 1982; for the nomenclature see Di Pietro et al. 2004).

In our analysis, a more complex pattern emerged: the gradient of different bioclimates, from temperate to sub-Mediterranean, with decreasing water availability and increasing temperature, follows not only the phytogeographical sector but also an altitudinal gradient. For instance, temperate beech forests of the upper altitude are potentially distributed all along the peninsula including the Etna volcano in Sicily (Group 8), while lower altitude beech forests (Groups 2 and 23) are distributed respectively in the south and in the central north (Figure 2). This result substantially agrees with Willner et al. (2017), even though the geographic boundaries between groups 2 and 23 are different because the southern group is more localized than indicated by Willner et al. (2017). Moreover, high altitude beech forests (Group 8) are floristically relatively different from the currently recognized alliances since they include many local endemics from both the north and south Apennines (Suppl. material 3).

Cluster B includes only group 18 and can be referred to the *Carpinetalia betuli* order (Mucina et al. 2016), which is united with *Fagetalia sylvaticae* in the *Carpino-Fagetea* class. NMDS analysis (Fig 1) confirmed its floristic affinity with the beech forests, even though in the Italian peninsula it is spatially and ecologically embedded within the deciduous sub-Mediterranean forests (Suppl. material 3 and Figure 3).

Sub-Mediterranean deciduous oak forests of cluster C are characterized by a complex geographic pattern along the Apennines, which cannot be explained only by the combination of geo-climatic factors, as is highlighted by the very high omission errors of the confusion matrix (Suppl. material 5). These groups show a good correspondence with many alliances and sub-alliances reported in the prodrome of the Italian vegetation (Biondi et al. 2014). Nonetheless, in our study, some syntaxonomic units are split into two or more floristically and ecologically well-defined groups. For instance, the *Cratego laevigati-Quercion cerridis* alliance is split into two groups (6 and 7), with different floristic composition and distinct ecology. Another similarity is represented by the alliance *Carpinion orientalis*, for which three suballiances, *Laburno anagyroidis-Ostryenion, Cytiso sessilifolii-Quercenion pubescentis* and *Lauro nobilis-Quercenion pubescentis* have been identified for Italy (Blasi et al. 2004). In our analysis, they correspond respectively to groups 3, 11 and 14. However, a comprehensive comparison with the *Carpinion orientalis* of the Balkans is still lacking, as well as with the *Quercion pubescenti-petraeae* described by Braun-Blanquet for Provence and Catalonia, which seems very similar to group 14 and to which this has been sometimes referred to (Ubaldi 2003).

The geographic pattern also characterizes the evergreen Mediterranean forests, which are difficult to classify due to the low number of characteristic species, especially in the herbaceous layer. FMM (and also TWINSPAN, see Table 1) clearly differentiated *Quercus suber* and *Quercus ilex* dominated forest vegetation (Figure 1). The former includes groups 20 and 22, one distributed in southern Italy, and the other one in Sardinia and the northern Tyrrhenian coast. A geographic pattern is also evident for evergreen forests dominated by *Quercus ilex*: group 10 is mainly distributed in Liguria and central Italy, group 13 mainly in southern Sardinia and Sicily in the thermo-Mediterranean region, and group 21 includes the coastal forests along both sides of the Italian peninsula. Mixed evergreen and deciduous forests are localized in the supra-Mediterranean region respectively, group 12, co-dominated by *Quercus pubescens* s.l., in Sicily and

Sardinia, and group 9 co-dominated by *Quercus frainetto* very localized in central Italy and Calabria. This classification significantly differs from that currently indicated in the Italian vegetation prodrome, which for the evergreen Mediterranean forests in Italy recognizes only four sub-alliances (Biondi et al. 2003; Bacchetta et al. 2004; Brullo et al. 2008). In our study, we find instead seven groups, which are not exceedingly well characterized from a floristic point of view (even though it must be taken into account the floristic poverty of the *Quercetea ilicis* forests) but are instead perfectly reasonable under an ecological and phytogeographical point of view. For instance, an interesting distinction of both *Quercus suber* and *Quercus ilex* forests in northern-central (22 for *Quercus suber*, and 10 for *Quercus ilex*) and southern groups (20 for *Quercus suber* and 13 for *Quercus ilex*) can be observed. This result has important phytogeographical and syntaxonomic implications that are related to the limits between the meso-Mediterranean and thermo-Mediterranean regions, and it deserves a broader analysis at the continental scale.

The 20 groups can be aggregated in four clusters corresponding to the main syntaxonomic orders recognized for the Italian peninsula: *Carpinetalia betuli, Fagetalia sylvaticae*, *Quercetalia ilicis Quercetalia pubescenti-petraeae* (Figure 3). Their spatial distribution also largely corresponds to the bioclimates recognized by Rivas Martínez for Italy (Rivas Martínez et al. 2004), even though the boundary of the sub-Mediterranean region shifted more south especially in the Apulia region. The bioclimatic limit defined by Rivas Martínez has a better correspondence with the results by Bohn et al. (2003) and Attorre et al. (2014). However, these authors based their biogeographical analyses only on dominant tree species, while in our analysis we included the whole species composition of forest vegetation plots. This also explains why Sardinia is completely classified as *Quercetalia ilicis*, whereas in the previous studies patches of sub-Mediterranean forest vegetation, characterized by stands co-dominated by *Quercus pubescens* s.l. and *Quercus ilex,* were recognized.

Conclusion

Despite a greater computational complexity, Finite Mixture Model seems to be a promising classificatory approach when dealing with the analysis of complex vegetation systems and using a large dataset. This relied on the possibility of modelling in the classification process both the co-occurrence of species and environmental variables so that groups are identified not only based on their species composition, such as in the case of TWINSPAN, but also on their specific environmental niche. These features can effectively highlight geographical patterns as depicted by predictive maps and support the interpretation of classification results.

Data availability

Primary data are stored in the European Vegetation Archive (Chytrý et al. 2016) and the Sapienza University vegetation database (https://www.givd.info/ID/EU-IT-011).

Author contributions

F.A., V.E.C., E.A. and G.F. conceived the study, M.A. and L.M. run the statistical analyses, and N.A., M.D.S., T.S., R.G., C.M., M.M. and F.S. contributed to the interpretation of results.

Acknowledgements

We would like to thank Laura Clarke for revising the text and all those who collected vegetation-plot data in the field and integrated these data in the Sapienza database (https://www.givd.info/ID/EU-IT-011).

References

Agrillo E, Alessi N, Massimi M, Spada F, De Sanctis M, Francesconi F, Cambria VE, Attorre F (2017) Nationwide Vegetation Plot Database - Sapienza University of Rome: State of the art, basic figures and future perspectives. Phytocoenologia 47: 221–229. https://doi.org/10.1127/phyto/2017/0139

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (Eds) International Symposium on Information Theory. Akademiai Kiado, Budapest, HU, 1033–1055.

Attorre F, Alfò M, De Sanctis M, Francesconi F, Bruno F (2007) Comparison of interpolation methods for mapping climatic and bioclimatic variables at regional scale. International Journal of Climatology 27: 1825–1843. https://doi.org/10.1002/joc.1495

Attorre F, Francesconi F, De Sanctis M, Alfò M, Martella F, Valenti R, Vitale M (2014) Classifying and Mapping Potential Distribution of Forest Types Using a Finite Mixture Model. Folia Geobotanica 49: 313–335. https://doi.org/10.1007/s12224-012-9139-8

Bacchetta G, Bagella S, Biondi E, Farris E, Filigheddu R, Mossa L (2004) A contribution to the knowledge of the order Quercetalia ilicis Br.-Bl. ex Molinier 1934 of Sardinia. Fitosociologia 41: 29–51.

Baglama J, Reichel L (2005) Augmented implicitly restarted lanczos bidiagonalization methods. SIAM Journal on Scientific Computing 27: 19–42. https://doi.org/10.1137/04060593X

Baglama J, Reichel L (2019) Irlba: Fast Truncated Singular Value Decomposition and Principal Components Analysis for Large Dense and Sparse Matrices, R package version 2.3.3. https://CRAN.R-project.org/package=irlba.

Biondi E, Casavecchia S, Gigante D (2003) Contribution to the syntaxonomic knowledge of the Quercus ilex L. woods of the Central European Mediterranean Basin. Fitosociologia 40: 129–156.

Biondi E, Blasi C, Allegrezza M, Anzellotti I, Azzella MM, Carli E, Casavecchia S, Copiz R, Del Vico E, … Zivkovic L (2014) Plant communities of Italy: The Vegetation Prodrome. Plant Biosystems 148: 728–814. https://doi.org/10.1080/11263504.2014.948527

Blasi C, Di Pietro R, Filesi L (2004) Syntaxonomical revision of Quercetalia pubescenti-petraeae in the Italian peninsula. Fitosociologia 41: 87–164.

Bohn U, Neuhäuslm R, Gollub G, Hettwer C, Neuhäuslová Z, Raus T, Schlüter H, Weber H (2003) Map of the natural vegetation of Europe. German Federal Agency for Nature Conservation, Bonn, DE.

Bodzogan H (1994) Mixture-model cluster analysis using model selection criteria and a new informational measure of complexity. In: Bodzogan H (Ed.) Proceedings of the first US/Japan conference on the frontiers of statistical modelling: An informational approach. Multivariate statistical modeling. Kluwer Academic Publishers, Dordrecht, NL, 69–113. https://doi.org/10.1007/978-94-011-0800-3_3

Brullo S, Gianguzzi L, La Mantia A, Siracusa G (2008) La classe *Quercetea ilicis* in Sicilia. Bollettino dell'Accademia Gioenia di Scienze Naturali 41: 1–124.

Cao Y, Bark AW, Williams WP (1997) A comparison of clustering methods for river benthic community analysis. Hydrobiologia 347: 25–40. https://doi.org/10.1023/A:1002938721135

Chytrý M, Hennekens SM, Jiménez-Alfaro B, Knollová I, Dengler J, Jansen F, Landucci F, Schaminée JH, Aćić S, … Yamalov S (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. Applied Vegetation Science 19: 173–180. https://doi.org/10.1111/avsc.12191

Conti F, Abbate G, Alessandrini A, Blasi C (2005) An annotated checklist of the Italian vascular flora. Palombi Editori, Roma, IT.

De'ath G (2002) Multivariate regression trees: a new technique for modeling species–environment relationships. Ecology 83: 1105–1117. https://doi.org/10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2

De Cáceres M, Chytrý M, Agrillo E, Attorre F, Botta-Dukát Z, Capelo J, Czúcz B, Dengler J, Ewald E, … Wiser SK (2015) A comparative framework for broad-scale plot-based vegetation classification. Applied Vegetation Science 18: 543–560. https://doi.org/10.1111/avsc.12179

De Cáceres M, Franklin SB, Hunter JT, Landucci F, Dengler J, Roberts DW (2018) Global overview of plot-based vegetation classification approaches. Phytocoenologia 48: 101–112. https://doi.org/10.1127/phyto/2018/0256

Di Pietro R, Izco J, Blasi C (2004) Contribution to the nomenclatural knowledge of *Fagus sylvatica* woodlands of southern Italy. Plant Biosystems 138: 27–36. https://doi.org/10.1080/11263500410001684099

Feoli E, Lagonegro M (1982) Syntaxonomical analysis of beech woods in the Apennines (Italy) using the program package IAHOPA. Vegetatio 50: 129–173. https://doi.org/10.1007/BF00364109

Ferrier S, Guisan A (2006) Spatial modelling of biodiversity at the community level. Journal of Applied Ecology 43: 393–404. https://doi.org/10.1111/j.1365-2664.2006.01149.x

Fraley C, Raftery AE, Scrucca L (2017) mclust: Normal Mixture Modeling for Model-Based Clustering, Classification, and Density Estimation. R package version 5.4. https://CRAN.R-project.org/package=mclust

Gauch HG, Whittaker RH (1981) Hierarchical classification of community data. Journal of Ecology 69: 537–557. https://doi.org/10.2307/2259682

Gentile S (1970) Sui faggeti dell'Italia meridionale (Beech woodlands of Southern Apennines). Atti Dell'istituto Botanico dell'Università Di Pavia 65: 207–306.

Guarino R, Willner W, Pignatti S, Attorre F, Loidi JJ (2018) Spatio-temporal variations in the application of the Braun-Blanquet approach in Europe. Phytocoenologia 48: 239–250. https://doi.org/10.1127/phyto/2017/0181

Haughton D, Legrand P, Woolford S (2009) Review of Three Latent Class Cluster Analysis Packages: Latent GOLD, poLCA, and MCLUST. The American Statistician 63: 81–91. https://doi.org/10.1198/tast.2009.0016

Hennekens SM, Schaminée JHJ (2001) TURBOVEG, a comprehensive data base management system for vegetation data. Journal of Vegetation Science 12: 589–591. https://doi.org/10.2307/3237010

Hill MO (1979) TWINSPAN – A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, NY, US.

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. Biometrika 76: 297–307. https://doi.org/10.1093/biomet/76.2.297

Landucci F, Acosta ATR, Agrillo E, Attorre F, Biondi E, Cambria VE, Chiarucci A, Del Vico E, De Sanctis M, … Venanzoni R (2012) VegItaly: The Italian collaborative project for a national vegetation database. Plant Biosystems 146: 756–763. https://doi.org/10.1080/11263504.2012.740093

Leathwick JR, Elith J, Hastie T (2006) Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecological Modelling 199: 188–196. https://doi.org/10.1016/j.ecolmodel.2006.05.022

McLachlan G, Peel D (2000) Finite mixture models. In: Wiley J (Ed.) Probability and Statistics. Wiley Series, New York, US. https://doi.org/10.1002/0471721182

Médail F, Quézel P (1999) Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. Conservation Biology 13: 1510–1513. https://doi.org/10.1046/j.1523-1739.1999.98467.x

Moss D, Wright JF, Furse MT Clarke RT (1999) A comparison of alternative techniques for prediction of the fauna of running-water sites in Great Britain. Freshwater Biology 41: 167–181. https://doi.org/10.1046/j.1365-2427.1999.00376.x

Mucina L, Bültmann H, Dierßen K, Theurillat JP, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, … Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19: 3–264. https://doi.org/10.1111/avsc.12257

Nieto-Lugilde D, Maguire KC, Blois JL, Williams JW, Fitzpatrick MC (2017) Multiresponse algorithms for community-level modeling: review of theory, applications, and comparison to species distribution models. Methods in Ecology and Evolution 9: 834–848. https://doi.org/10.1111/2041-210X.12936

Pedrotti F (1995) La vegetazione forestale italiana. Atti Convegni Lincei 115: 39–78.

Pesaresi S, Galdenzi D, Biondi E, Casavecchia S (2014) Bioclimate of Italy: application of the worldwide bioclimatic classification system. Journal of Maps 10: 538–553. https://doi.org/10.1080/17445647.2014.891472

Pignatti S, Wikus Pignatti E (1990) Le cenosi a cerro e frainetto della penisola e della Sicilia. Notiziario Fitosociologico 23: 107–124.

Pignatti S (1998) I boschi d'Italia. UTET, Torino, IT.

Rivas Martínez S, Penas A, Díaz TE (2004) Bioclimatic and biogeographic maps of Europe – Bioclimates. Cartographic Service, University of Leon, ES. http://www.globalbioclimatics.org/form/bi_med.htm

Rodwell JS, Evans D, Schaminée JHJ (2018) Phytosociological relationships in European Union policy-related habitat classifications. Rendiconti Lincei 29: 237–249. https://doi.org/10.1007/s12210-018-0690-y

Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. Journal of Vegetation Science 20: 596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x

Scarascia-Mugnozza G, Oswald H, Piussi P, Radoglou K (2000) Forests of the Mediterranean region: gaps in knowledge and research needs. Forest Ecology and Management 132: 97–109. https://doi.org/10.1016/S0378-1127(00)00383-2

Schwarz G (1978) Estimating the Dimension of a Model. The Annals of Statistics 6: 461–464. https://doi.org/10.1214/aos/1176344136

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17: 809–818. https://doi.org/10.1111/j.1654-1103.2006.tb02504.x

Ubaldi D (2003) La vegetazione boschiva d'Italia: Manuale di Fitosociologia forestale. Clueb, Bologna, IT, 1–368.

Vallejo R, Aronson J, Pausas JG, Cortina J (2005) Restoration of Mediterranean woodlands. In: van Andel J, Aronson J (Eds) Restoration ecology: a European perspective. Blackwell Science, Oxford, GB, 193–207. https://doi.org/10.1002/9781118223130.ch11

Venables WN, Ripley BD (2002) Modern Applied Statistics with S, Fourth edition. Springer, New York, US. https://doi.org/10.1007/978-0-387-21706-2

Vermunt JK (2010) Latent Class Modeling with Covariates: Two Improved Three-Step Approaches. Political Analysis 18: 450–469. https://doi.org/10.1093/pan/mpq025

Willner W, Jiménez-Alfaro B, Agrillo E, Biurrun I, Campos JA, Čarni A, Casella L, Csiky J, Ćušterevska R, … Chytrý M (2017) Classification of European beech forests: a Gordian Knot? Applied Vegetation Science 20: 494–512. https://doi.org/10.1111/avsc.12299

Woolley SNC, McCallum AW, Wilson R, O'Hara TD, Dunstan PK (2013) Fathom out: biogeographical subdivision across the Western Australian continental margin – a multispecies modelling approach. Diversity and Distributions 19: 1506–1517. https://doi.org/10.1111/ddi.12119

Yee TW (2004) A new technique for maximum-likelihood canonical gaussian ordination. Ecological Monographs 74: 685–701. https://doi.org/10.1890/03-0078

Yee TW (2006) Constrained additive ordination. Ecology 87: 203–213. https://doi.org/10.1890/05-0283

E-mail and ORCID

Fabio Attorre (fabio.attorre@uniroma1.it), ORCID: http://orcid.org/0000-0002-7744-2195
Vito E. Cambria (Corresponding author, vitoemanuele.cambria@phd.unipd.it), ORCID: http://orcid.org/0000-0003-0481-6368
Emiliano Agrillo (emiliano.agrillo@isprambiente.it), ORCID: http://orcid.org/0000-0003-2346-8346
Nicola Alessi (nicola.alessi@natec.unibz.it)
Marco Alfò (marco.alfo@uniroma1.it), ORCID: http://orcid.org/0000-0001-7651-6052
Michele De Sanctis (michele.desanctis@uniroma1.it), ORCID: http://orcid.org/0000-0002-7280-6199
Luca Malatesta (luca.malatesta@uniroma1.it), ORCID: http://orcid.org/0000-0003-1887-4163
Tommaso Sitzia (tommaso.sitzia@unipd.it), ORCID: http://orcid.org/0000-0001-6221-4256
Riccardo Guarino (riccardo.guarino@unipa.it), ORCID: http://orcid.org/0000-0003-0106-9416
Corrado Marcenò (marceno.corrado@ehu.eus), ORCID: http://orcid.org/0000-0003-4361-5200
Marco Massimi (marco.massimi@hotmail.com)
Francesco Spada (francesco.spada@uniroma1.it)
Giuliano Fanelli (giuliano.fanelli@gmail.com), ORCID: http://orcid.org/0000-0002-3143-1212

Supplementary material

Supplementary material 1
MM R code and R libraries used for the statistical analyses (.R)
Link: https://doi.org/10.3897/VCS/2020/48518.suppl1

Supplementary material 2
Ecological, physiognomic and distributional features, floristic composition and syntaxonomy of groups (.DOCX)
Link: https://doi.org/10.3897/VCS/2020/48518.suppl2

Supplementary material 3
Ecological parameters, dominant and diagnostic species of the groups (.XLSX)
Link: https://doi.org/10.3897/VCS/2020/48518.suppl3

Supplementary material 4
Maps of the distribution of the classified plots of each group (.JPG)
Link: https://doi.org/10.3897/VCS/2020/48518.suppl4

Supplementary material 5
Confusion matrix generated for the accuracy assessment of the potential distribution map of groups (.DOCX)
Link: https://doi.org/10.3897/VCS/2020/48518.suppl5

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 87–102
doi: 10.3897/VCS/2020/38013

RESEARCH PAPER

The lowland seasonally dry subtropical forests in central Argentina: vegetation types and a call for conservation

Sebastián R. Zeballos[1], Melisa A. Giorgis[1,2], Marcelo R. Cabido[1], Alicia T. R. Acosta[3], María del Rosario Iglesias[1], Juan J. Cantero[1,4]

1 *Instituto Multidisciplinario de Biología Vegetal (UNC-CONICET), Córdoba, Argentina*
2 *Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina*
3 *Dipartimento di Scienze, Università degli Studi di Roma Tre, Roma, Italy*
4 *Departamento de Biología Agrícola, Facultad de Agronomía y Veterinaria, UNRC, Córdoba, Argentina*

Corresponding author: Melisa A. Giorgis (mgiorgis@imbiv.unc.edu.ar)

Academic editor: Idoia Biurrun ♦ **Received** 5 July 2019 ♦ **Accepted** 10 February 2020 ♦ **Published** 4 May 2020

Abstract

Aims: The native woody vegetation from the Espinal phytogeographic province in central Argentina, found in subtropical-warm temperate climates, represents part of the southernmost seasonally dry forest in South America. Although this vegetation has been studied for over a century, a complete phytosociological survey is still needed. This lack of knowledge makes its spatial delimitation and the establishment of efficient conservation strategies particularly difficult. The main goals of this study were to classify these forests and assess their current forest cover and to better define the extent of the Espinal phytogeographic province in Córdoba region, central Argentina. **Study area:** Espinal Phytogeographic Province in Córdoba region, central Argentina (ca. 101,500 km^2). **Methods:** We sampled 122 stands following the principles of the Zürich-Montpellier School of phytosociology; relevés were classified through the ISOPAM hierarchical analysis. The extent of the Espinal phytogeographic province was established by overlaying previous vegetation maps, and a map showing the current distribution of forest patches was constructed based on a supervised classification of Landsat images. **Results:** Four woody vegetation types of seasonally dry subtropical forest were identified based on the fidelity and the abundance of diagnostic species: (1) *Aspidosperma quebracho-blanco* forest; (2) *Zanthoxylum coco* forest; (3) *Geoffroea decorticans* forest; and (4) *Prosopis caldenia* forest. These vegetation types were segregated along gradients of temperature and precipitation seasonality and soil-texture and sodium content. The remaining forest patches represent 3.43% of the extent of the Espinal province in Córdoba region of which only 1.05% is represented in protected areas. **Conclusions:** We present a classification of the Espinal forest based on a complete floristic survey. Despite the dramatic forest loss reported, our results show that some forest patches representative of the Espinal are still likely to be found in the area. However, urgent measures should be taken to establish new protected natural areas in order to preserve the last remaining forest patches.

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

central Argentina, chorotype, diagnostic species, dry subtropical forest, Espinal phytogeographic province, exotic species, floristic survey, gradient analysis, vegetation classification, vegetation map, vegetation plot, woody vegetation

PENSOFT.

Copyright *Sebastián R. Zeballos et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Dry tropical and subtropical forests are a potentially extensive set of types in South America (DRYFLOR et al. 2016; Kuemmerle et al. 2017) and are among the most threatened ecosystems in the world, with ca. 10% of their original extent remaining (Bastin et al. 2017). While dry tropical forests have received more attention (Pennington et al. 2000; Linares-Palomino et al. 2015; Dexter et al. 2018), the knowledge of subtropical-warm temperate dry forests distribution and composition is locally fragmented or focused only on woody species instead of on complete floristic inventories (Lewis et al. 2009; Kuemmerle et al. 2017; Silva de Miranda et al. 2018).

Among the seasonally dry subtropical forests in South America the southernmost ones are included in the Espinal phytogeographic province (Cabrera 1976; Morrone 2001) and their phytosociological knowledge is perhaps one of the poorest in the region. The Espinal was distinguished from the Chaco and Pampa phytogeographic provinces for the first time by Cabrera (1953, 1976), who recognized it as a phytogeographic province within the Chaquenian Dominium in Argentina. In addition, Cabrera (1976) defined the Espinal as an "impoverished Chaco" due to the lack of several dominant trees, mainly *Schinopsis lorentzii* and *S. balansae* (i.e, red quebrachos) and a lower tree canopy (Bucher 1982; Cabido et al. 2018). These differences in floristic composition and physiognomy may be due to changes in temperature (mainly a decrease in annual mean temperature and an increase in frost frequency) in the Espinal as a consequence of the increase in latitude (Bucher 1982; Morello et al. 2018).

Currently, the prevailing vegetation of the Espinal is a mosaic of xerophytic deciduous to semi-deciduous forests and shrublands intermingled with grasslands and savanna-like parklands distributed mostly in central and eastern Argentina and, to a lesser extent, in Uruguay and Brazil (Lewis and Collantes 1973; Cabrera 1976; Morello et al. 2018; Oyarzábal et al. 2018). However, given the great extension of the Espinal area (ca. 288,000 km^2; Mateucci 2018), especially in the North-South direction, it shows climatic gradients, including a warmer subtropical and humid climate in its northern extreme, while to the south and west the prevailing climate is warm temperate and dry with marked water deficits (Cabido et al. 2018; Matteucci 2018). This gradient is coupled also with changes in soils with increasing sand content and soil drainage towards the southern extreme (Gorgas and Tassile 2006). This environmental variability results in changes in floristic composition and physiognomy recognized by different authors (Lewis and Collantes 1973; Cabrera 1976; Cabido et al. 2018). Lewis and Collantes (1973) provided the most exhaustive description of the Espinal native vegetation, and identified different units (i.e. districts) based on the physiognomy of the vegetation and the relative abundance of some ubiquitous species of *Prosopis* as well as *Celtis ehrenbergiana* and *Geoffroea decorticants*. Lewis et al. (2009) described the structure of selected tree and shrub populations in several Espinal forest relicts located in a relatively small area, while Noy-Meir et al. (2012) provided complete floristic relevés (comprising both woody and herbaceous species), but restricted to a single remnant patch. Recently, Cabido et al. (2018) reported a classification of woody vegetation in central Argentina and included all Espinal forests in a single vegetation type. Apart from these contributions, there is still lacking a detailed characterization based on a comprehensive phytosociological analysis that includes all vascular plants of the Espinal forest remnants and their relations with environmental determinants.

Historically, the Espinal phytogeographic province was largely forested. Since the beginning of 20th century, these forests have been under heavy pressure (Schofield and Bucher 1986; Boletta et al. 2006; Guida-Johnson and Zuleta 2013; Agost 2015), mainly because the area comprises some of the most suitable soils for agriculture and cattle grazing in the world (Blum and Swaran 2004; Blum 2013). Decades of exploitation driven mainly by timber and firewood extraction (Schofield and Bucher 1986), jointly with the expansion of agribusiness (Arturi 2005; Guida-Johnson and Zuleta 2013; Fehlenberg et al. 2017), have led to the devastation of most of the Espinal forests. Now, only isolated relicts remain (Lewis et al. 2006; Agost 2015; Garachana et al. 2018). These remnants of native woody patches are also threatened by the establishment of several exotic shrub and tree species (Lewis et al. 2004; Giorgis and Tecco 2014; Cabido et al. 2018). These disturbances have resulted in changes in the provision of ecosystem goods and services such as water cycle regulation (Jobbagy et al. 2008), carbon stock (Conti and Díaz 2013) and pollination (Dicks et al. 2016). In addition to the dramatic reduction in Espinal forests, the full extent of protected areas created through official agreements represents only a small fraction of the Espinal in Argentina (ca. 0.03% according to Brown et al. 2006 and Matteucci 2018). Worse, there has been a lack of agreement concerning the real extent of the Espinal phytogeographic province (Lewis and Collantes 1973; Cabrera 1976; Cabido et al. 2018; Morello et al. 2018; Oyarzábal et al. 2018), resulting in maps portraying different sizes, shapes and boundaries; recently Arana et al. (2017) even included the Espinal in the Pampean phytogeographic province. All these issues call for an urgent and detailed description of the main vegetation types combined with an assessment of the current distribution of the Espinal forest remnants.

A great area of the Espinal phytogeographic province occurs in Córdoba province (hereafter, Córdoba region), central Argentina (Matteucci 2018), comprising an outstanding representation of the whole phytogeographic province (Lewis and Collantes 1973; Cabrera 1976). Most of the vegetation types described previously by different authors (Lewis and Collantes 1973; Cabrera 1976) can still be found in Córdoba. The recent paper by Cabido et al. (2018) reported the woody vegetation types for the whole Córdoba region, identifying a single type within the Espinal (i.e. Type 1.3 *Prosopis nigra – Celtis ehrenbergiana – Prosopis caldenia* in Cabido et al. 2018), but recognizing its internal heteroge-

neity. Therefore, the main goal of our study is to expand the classification reported by Cabido et al. (2018) describing the remaining native vegetation types and to assess the spatial extent of the Espinal in Córdoba region, central Argentina. Specifically, our aims were to: (1) classify and characterize the woody native patches of the Espinal based on complete vascular plant surveys; (2) analyze the relationships between the obtained vegetation types and the main regional bioclimatic and edaphic variables; and (3) construct a map of the extent of Espinal phytogeographic province in Córdoba region and assess the current woody vegetation distribution. Additionally, we estimate the area of woody patches of the Espinal in Córdoba region currently included under formal protection (i.e. protected natural areas).

Study area

Currently, the whole distribution area of the Espinal forests is reduced to small and isolated remnants of native woody patches (Cabido et al. 2018; Garachana et al. 2018; Matteucci 2018) in an agricultural matrix, mainly soybean, maize, wheat, sunflower and peanut, with scattered pastures for livestock grazing (mainly cattle). In Argentina, the Espinal phytogeographic province forms a sub-circular belt extended in the central and eastern part of the country; our study area was restricted to the Espinal comprising the lowlands in the central, eastern and southern part of Córdoba region, central Argentina (Figure 1A). The latitude ranges from 30.47° to 34.98°S, while longitude varies from 62.22° to 65.08°W. This area belongs to the Espinal phytogeographic province that borders the dry Chaco forests to the north and the low mountain Chaco vegetation (i.e. sierra Chaco) to the west, and forms a complex and progressive transition towards the Pampa grasslands to the south and east of the province (Figure 1B; Lewis and Collantes 1973; Cabrera 1976). This area occupies the southwestern sector of the Chaco-Pampean geomorphological province (Carignano et al. 2014), comprising two main units: the fluvio-eolian plain, located to the north and east of the study area, and the sandy plain to the southwest of the province. Opposite to tropical ecosystems, in subtropical forests in Argentina, winter and summer seasons are differentiated and freezing is likely to occur, showing a markedly thermal seasonality (Morello et al. 2018). In the study area climate varies from subtropical in the northern extreme to warm temperate in the most southern part (Capitanelli 1979; Matteucci 2018; see climate diagrams in Figure 1B). Rainfall is largely concentrated in the warm season, from October to March, with total annual rainfall ranging from 600 mm (southwestern extreme) to 900 mm (northeastern sector), while the annual mean temperature increases from 16.0 to 17.6 °C in the same direction (De Fina 1992).

Methods

Vegetation data

The vegetation survey was carried out throughout the study area, covering the geographic, topographic and

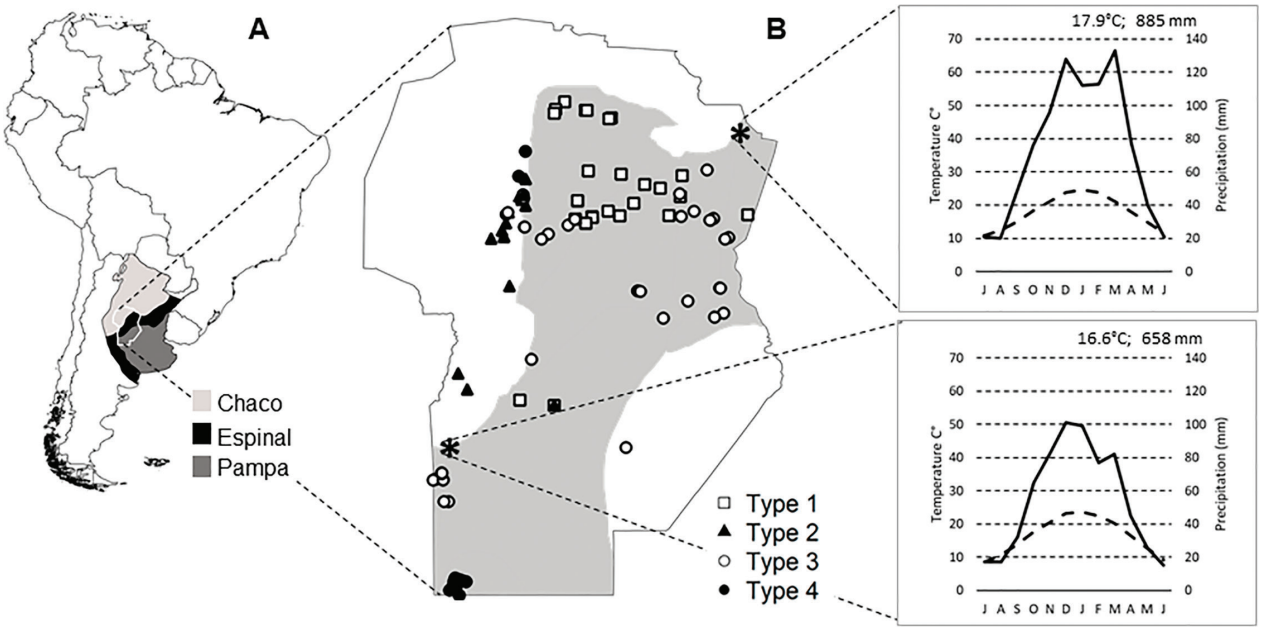

Figure 1. A Location of Córdoba region and Argentina in South-America, showing the location of Espinal, Chaco and Pampa phytogeographic provinces in Argentina based on Cabrera (1976); **B** distribution of sample plots (relevés) in Córdoba region discriminating the four vegetation types: 1) *Aspidosperma quebracho-blanco* forest; 2) *Zanthoxylum coco* forest; 3) *Geoffroea decorticans* forest; and 4) *Prosopis caldenia* forest. In grey, Espinal extent in Córdoba region according to Lewis and Collantes (1973). Two climatic diagrams (see asterisks) representing the northern and southern extremes of the study area are included in the figure (climatic data were obtained from WorldClim database).

ecological variability of the Espinal forests. Sampling followed the Zürich-Montepellier School of phytosociology (Braun-Blanquet 1932). In order to take into account the physiognomic heterogeneity of the vegetation, both conserved and disturbed forests were sampled. Riparian vegetation and grasslands, as well as patches dominated by exotic tree species (with an exotic tree cover of more than 20%) were not considered. Since different authors propose different boundaries for the Espinal phytogeographic province, the vegetation survey was carried out not only in the Espinal area indicated in Figure 1B (Lewis and Collantes 1973), but also in areas included in the Espinal by other authors (Cabrera 1976; Cabido et al. 2018; Morello et al. 2018; Oyarzábal et al. 2018). Our sampling comprised 122 georeferenced 20 m × 20 m plots; 64 samples had already been used for a previous analysis by Cabido et al. (2018), and the additional 58 corresponded to original unpublished data. In each plot, vascular plants were recorded and species cover was estimated using the cover-abundance scale of Braun-Blanquet (1932). The height and cover of the tree, shrub and herb layers were visually estimated. Data were collected during the growing season (summer of Southern Hemisphere) from 2010 to 2019. Endemic taxa at the national level followed Zuloaga et al. (1994, 2008), Cabido et al. (1998), Zuloaga and Morrone (1999a, 1999b) and Chiapella and Demaio (2015), while species nomenclature and their distributional range followed the catalogue of vascular plants of the Southern Cone (Zuloaga et al. 2008) and its online update (http://www.darwin.edu.ar/). All 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 (see also Suppl. material 1: Table S1.1).

To assess the main trends of species distribution patterns and the way in which these trends are represented in the different vegetation types, species chorotypes (groups of species with a similar distribution) were assigned following the criteria of Cabido et al. (1998): Southern-brazilian (1), Chaquenian (2), Low montane (3), Patagonian (4) and Exotic (5). The Southern-brazilian chorotype includes species widely distributed through the lowlands of central and north-eastern Argentina, and in the adjacent territories of Paraguay, Brazil and Uruguay. They may also reach the mountains but sharply decline in number above 1,000 m a.s.l. The Chaquenian chorotype comprises species distributed mainly through the dry Chaco lowland territories of central and north-western Argentina and the whole Chaco-Pampean plain. The Low montane chorotype includes species distributed at low altitudes (lower than 1,500 m) in extra-Andean Mountains of central and north-western Argentina and Bolivia. The Patagonian chorotype species are characterized by ranges extending over the whole Patagonian phytogeographic province, both in Andean and extra-Andean habitats. The Exotic chorotype includes species introduced to Argentina from other areas of the world. For each vegetation type, mean percentage of each chorotype per plot as well as the mean species richness and number of exotics per plot were calculated. Further, species were sorted into life forms as: cactus (c), climber (cl), epiphyte (e), fern (f), grass (g), graminoid (gr), herb (h), succulent herb (hs), parasite (p), palm (pl), shrub (s), subshrub (ss), succulent shrub (rs) and tree (t). The classification of life forms followed previous surveys in central Argentina, slightly modified from Giorgis et al. (2005) and Zuloaga et al. (2008).

Environmental variables

Bioclimatic variables and altitude (Alt) were taken as interpolated values from the WorldClim database (http://www.worldclim.org; Hijmans et al. 2005), at a spatial resolution of 2.5 arc-minutes for continental South America. The bioclimatic variables selected were annual mean temperature (AMT), temperature seasonality (TS), temperature annual range (TAR), precipitation seasonality (PS), precipitation of the warmest quarter (PWaQ), annual precipitation (AP), and precipitation of the driest month (PDM) (see O'Donnell and Ignizio 2012 for details concerning all the bioclimatic variables). These bioclimatic variables were selected because the main climatic constraints for the vegetation in the study area have been shown by Matteucci (2018) to be temperature and precipitation seasonality. In order to obtain data on edaphic variables (i.e. soil type, organic matter, pH, soil depth, clay, lime, fine sand, coarse sand and sodium percentage) for each plot, all the 122 relevés were plotted on digitalized maps of the soils of Córdoba region constructed at the scale of 1:500,000 and 1:50,000 (Gorgas and Tassile 2006; http://visor.geointa.inta.gob.ar/?p=857). The map at the scale 1:50,000 was preferentially used, but since this map still has some gaps (areas not covered at this scale) we completed the data with the map at the scale of 1:500,000. These maps depict soil cartographic units and describe the internal heterogeneity of each unit through representative soil profiles providing results of analysis of their chemical and physical properties.

Spatial analysis: Espinal extent, current woody vegetation distribution and representation on protected areas

In order to establish the extent of the Espinal phytogeographic province within Córdoba region, all available maps by different authors and dates, were overlapped in QGIS (QGIS Development Team 2019) under the same projection system (WGS84). The maps by Lewis and Collantes (1973), Cabido et al. (2018) and Morello et al. (2018), were manually digitalized while the other maps by Cabrera (1976) and Oyarzábal et al. (2018) were available online. The area covered by the overlapping of the different maps was defined as the extent of the phytogeographic province. Since the areas depicted for the Espinal by the different authors differed substantially, their representativeness with respect to the Espinal in the overlapped map was estimated. By means of this procedure, we aimed to

highlight the difficulties of establishing the boundaries of the Espinal when using only the map of any single author.

The area covered by current woody vegetation forest patches was estimated within the overlapped map showing the Espinal extent. Cloud free Landsat 8 OLI data processed to level L1T were acquired from the United States Geological Survey (USGS; http://earthexplorer.usgs.gov/) to assess and map the current distribution of the Espinal woody patches. The spectral bands used in this study included blue (0.45–0.51 μm), green (0.53–0.59 μm), red (0.64–0.67 μm), and near infrared (0.85–0.88 μm). Digital numbers of the Landsat imagery were converted to top-of-atmosphere reflectance according to the instructions provided by the USGS. Ten scenes of this satellite were used to cover the entire area of the Espinal forest in Córdoba region (path 228–229 and row 081, 082, 083, and 084). For each scene, images from April and September 2016 were used. Numerous sites selected during field reconnaissance and high-resolution images in Google Earth were used as the training sites for the supervised classification of the image. The supervised classification of images was performed through Support vector machines (all digital processing was performed using the ENVI (EX 2009) and QGIS software). To reach adequate results, different successive classifications were necessary, masking areas or adding, combining and removing training sites. Post processing was performed by correcting classification inaccuracies and by reducing salt-and-pepper noise, partially due to the high degree of fragmentation of natural vegetation in the study area.

Finally, to assess the actual woody cover of the Espinal area included in the current protected areas system, the boundaries of the natural protected areas were overlapped on the current vegetation map using the shapes of the protected areas obtained from the Argentinean Secretary of Environment and Sustainable Development (https://www.argentina.gob.ar/ambiente/tierra/protegida/mapa), and the Environmental Provincial Secretary.

Data analyses

The ISOmetric feature mapping and Partition Around Medoids (ISOPAM) ordination and classification method was employed to analyze the 122 plots × 616 species matrix. This analysis was used to detect the major vegetation types and their corresponding diagnostic species groups (Schmidtlein et al. 2010; Černý et al. 2015). The ISOPAM is based on the classification of ordination scores from isometric feature mapping (Tenembaum et al. 2000) in which the ordination and partitioning are repeated searching for partitions for maximum discrimination of vegetation units with high overall fidelity of species to groups until a pre-defined stopping criterion is met (e.g., G statistic and number of clusters; Schmidtlein et al. 2010). Hierarchical ISOPAM was run on the Bray-Curtis dissimilarity matrix. This matrix was constructed with the floristic table after transformation of Braun-Blanquet scores to central class values. The maximum number of clusters on each hierarchical level was arbitrarily set to 10 and standardized G statistics to 5. 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 ($p < 0.01$) association 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 species with: 1) phi > 0.2 and a statistically significant ($p < 0.01$) association with a given vegetation type; and 2) constancy > 50%. 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. All bioclimatic data extractions were conducted using the *extract* function on R *version* 3.5.1 (R Core Team 2018). Environmental and edaphic variables with the highest squared correlation coefficient were related to the ISOMAP ordination through the *envift* function from the vegan R-package (http://CRAN.R-project.org/package=vegan). In order to evaluate the differences in mean percentage of each chorotype per plot as well as the differences in the mean species richness and of exotics per plot among the four vegetation types, ANOVAs were performed in R software. Before conducting the analysis, the normality of the data and the homoscedasticity of variances were evaluated and when these requirements were not accomplished the data were natural log transformed.

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). 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. 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.

Results

Floristic composition of vegetation types

The overall number of species recorded was 616 (38 trees, 65 shrubs and 513 belonging to other life forms), comprising 86 families and 353 genera. *Poaceae* (102 species), *Asteraceae* (100), *Fabaceae* and *Solanaceae* (32 species each), *Malvacea*e (31) and *Euphorbiacea*e (24) comprised 52.11% of all encountered species. The most taxonomically diverse genera were: *Solanum* with 14 species, *Baccharis* with 12 species, *Setaria* with 11 species, *Prosopis* and *Nassella* with nine species each, *Euphorbia*, *Lycium* and *Tillandsia* with eight species each, and *Cyperus* and *Opuntia* with six species each. In the 122 stands sampled we

recorded 116 endemic taxa at the national level and 67 exotic species (Table 1; see also Suppl. material 2: Table S2.1 for the extended Table 1).

Table 1. Shortened synoptic table obtained through the ISOPAM classification showing the identified vegetation types along with the percentage constancy and mean Braun-Blanquet cover values based on 122 relevés collected in the Espinal phytogeographic province in Córdoba, central Argentina. Species are sorted by decreasing fidelity within each vegetation type. Dark, medium and light grey indicate phi > 0.2, phi > 0.15 and phi > 0.1, respectively. Only those species with phi ≥ 0.1 in at least one forest type were included in the table. Vegetation types are: 1, *Aspidosperma quebracho-blanco* forest; 2, *Zanthoxylum coco* forest; 3, *Geoffroea decorticans* forest; and 4, *Prosopis caldenia* forest. LF, Life forms: c, cactus; cl, climber; e, epiphyte; f, fern; g, grass; gr, graminoid; h, herb; hs, succulent herb; p, parasite; pl, palm; s, shrub; ss, subshrub; rs, succulent shrub; t, tree. CT, chorotype: 1, Southern-brazilian; 2, Chaquenian; 3, Low montane; 4, Patagonian; 5, Exotic. Symbols: †, endemic species at the national level.

Vegetation type			1	2	3	4
Number of relevés			29	22	50	21
Species	**LF**	**CT**				
Aspidosperma quebracho-blanco	t	2	76^{3}	55^{2}	2^{1}	
Porlieria microphylla	s	2	100^{2}	59^{1}	2^{1}	5^{+}
Senegalia praecox	t	2	38^{2}	45^{2}		
Celtis ehrenbergiana	t	1	100^{3}	95^{2}	76^{2}	86^{1}
Zanthoxylum coco	t	3		73^{2}	4^{2}	
Oplismenus hirtellus	g	1		41^{2}	2^{1}	
Leonurus japonicus	h	5	7^{1}	45^{2}	12^{+}	24^{1}
Chromolaena hookeriana	s	3	17^{+}	55^{2}		
Ipomoea purpurea	cl	1	14^{+}	64^{2}		
Lithraea molleoides	t	3		50^{2}		
Condalia buxifolia	t	3		27^{2}		
Melinis repens	g	5		14^{2}		
Croton lachnostachyus	s	3	14^{1}	82^{1}		
Schinopsis lorentzii	t	1		9^{2}		
Mandevilla pentlandiana	cl	1	7^{+}	73^{1}		
Lorentzianthus viscidus	s	3		59^{1}	2^{+}	
Colletia spinosissima	s	3		9^{2}		
Ligustrum lucidum	t	5	7^{+}	55^{1}	2^{1}	
Gouinia latifolia	g	2	14^{1}	45^{1}		
Paspalum malacophyllum	g	1		18^{2}		
Flourensia thurifera†	s	3		14^{2}		
Passiflora morifolia	cl	1	3^{+}	50^{1}		
Euphorbia berteroana	h	2	3^{+}	45^{1}		
Condalia montana†	t	3	3^{+}	27^{1}		
Ruprechtia apetala	t	3		27^{1}		
Geoffroea decorticans	t	2	79^{1}	50^{2}	90^{3}	81^{2}
Cynodon dactylon	g	5	14^{1}	9^{2}	38^{2}	24^{1}
Sida rhombifolia	ss	1	41^{1}	77^{1}	72^{2}	10^{+}
Sporobolus spartinus	g	2			16^{2}	
Prosopis caldenia†	t	2			10^{2}	90^{3}
Jarava pseudoichu	g	3	17^{2}	50^{1}	20^{1}	81^{4}
Exhalimolobos weddellii	h	1	10^{1}	14^{+}	4^{+}	38^{2}
Carex sororia†	gr	1				52^{2}
Heterotheca subaxillaris	h	5			2^{+}	48^{1}
Nassella tenuissima†	g	3		9^{1}	6^{1}	48^{1}
Carduus acanthoides	h	5			6^{1}	57^{1}
Amelichloa brachychaeta	g	2	7^{1}		4^{1}	48^{1}
Larrea divaricata	s	2	10^{+}		2^{2}	38^{2}
Gamochaeta filaginea	h	1				10^{2}

Four main clusters were obtained from the ISOPAM classification, each representing one vegetation type. Although the sample-size-based rarefaction curves showed that the asymptote was not reached for none of the four vegetation types (Figure 2A), the observed species richness reached a high percentage of the species estimated using the non-parametric estimators (see Suppl. material 3: Table S3.1). Further, the coverage-based rarefaction curves suggested that all vegetation types identified were well represented since the sample coverage percentage showed values higher than 0.85 in all types (Figure 2B, C; Suppl. material 3: Table S3.1).

A description of each vegetation type is provided, with reference to its physiognomy (Figure 3), floristic composition (Table 1) and distribution within the study area (Figure 1B):

Type 1. *Aspidosperma quebracho-blanco* forest. Open forest with shrubs, always dominated by a tree layer with a mean cover of 54% ranging from 10 to 90% (see Suppl. material 4: Table S4.1) and a height that may vary from 5 to 15 m. The shrub layer showed mean cover values of 61% with a height ranging from 1.5 to 5 m; the herb layer showed mean cover values of 56%. The diagnostic species were the native trees *Aspidosperma quebracho-blanco* and *Celtis ehrenbergiana*, accompanied by the native shrubs *Porlieria microphylla* and *Senegalia praecox*. In some forest patches, *Prosopis nigra* may reach high cover values.

This type is restricted to the northernmost sector of the area on loessic plains and gentle eastern slopes of the Sierras del Norte on well to excessively drained soils (Enthic Hapludols and Haplustols). A total of 276 taxa were recorded of which 48 species (17.4%) were endemic, while 10 species were found only in this vegetation unit. Twenty three exotic species were recorded, but they had low constancy and cover in all stands.

Type 2. *Zanthoxylum coco* forest. Open low forests with shrubs alternating with patches dominated by closed shrublands. The tree and shrub layers showed mean cover values of 39 and 51% ranging from 5 to 80% and 20 to 90%, respectively. The height of the tree layer ranged from 4 to 15 m. The herb layer showed mean cover values of 56% (see Suppl. material 4: Table S4.1). The diagnostic species included several life forms as trees (e.g., *Zanthoxylum coco*, *Lithraea molleoides* and *Condalia buxifolia*), shrubs (e.g. *Chromolaena hookeriana* and *Croton lachnostachyus*), grasses (e.g. *Oplismenus hirtellus*) and several climbing species (e.g. *Ipomoea purpurea*, *Mandevilla pentlandiana*, *Passiflora morifolia*, among others). In some valley bottoms *Prosopis alba* may reach high cover values.

This vegetation type is distributed on the eastern lower slopes of Córdoba Mountains, in the transitional zone between the Espinal in the lowlands and the proximate area of the Mountain Chaco Forest. Slopes are gentle to steep, with sandy to rocky and excessively drained soils. The total spe-

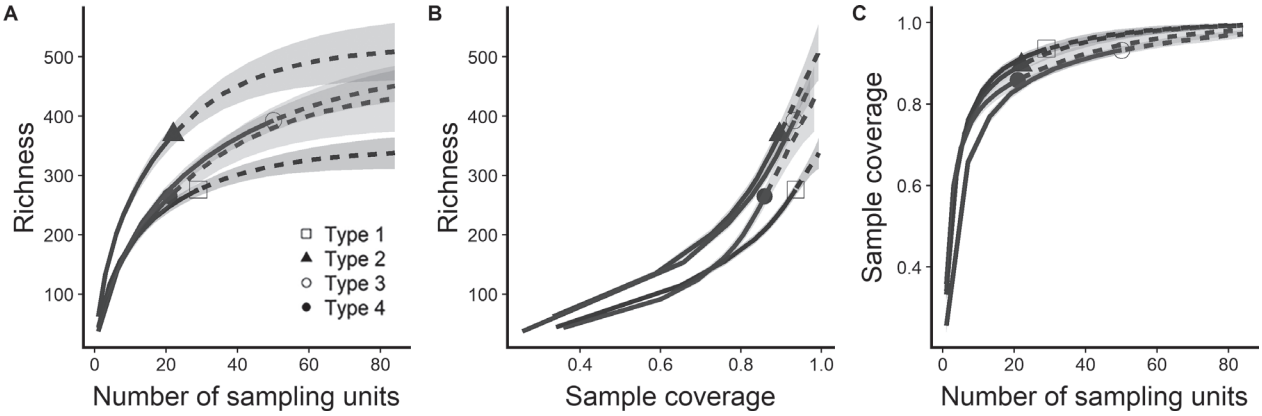

Figure 2. A Sample-size-based and **B** coverage-based rarefaction and extrapolation sampling curves for species richness, and **C** sample completeness curves for each vegetation type. Solid line segments indicate rarefaction and dotted line segments indicate extrapolation (up to a maximum sample size of 80), while shaded areas indicate 95% confidence intervals (based on a bootstrap method with 100 replications).

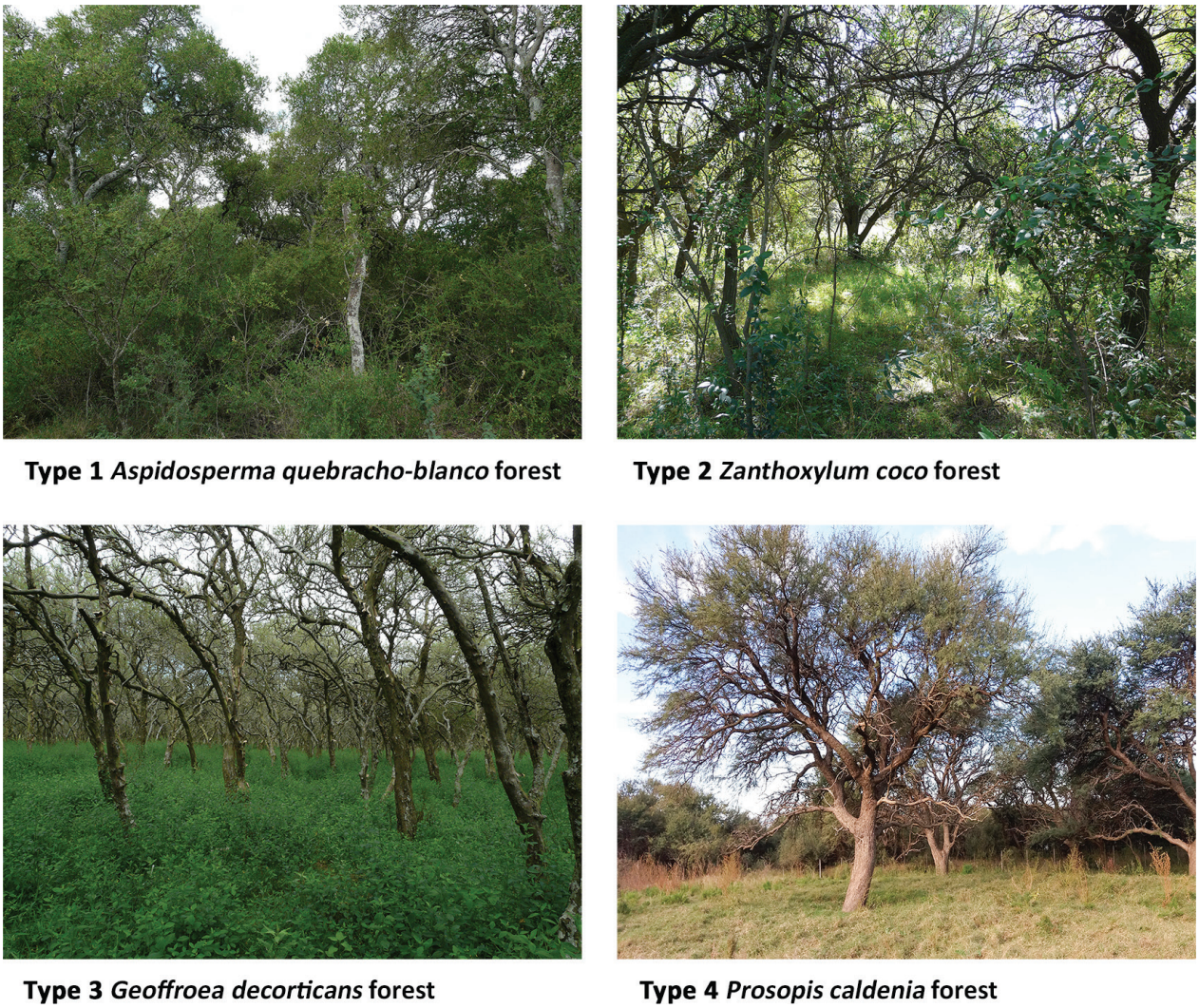

Figure 3. Dominant physiognomy of the four vegetation types described in the Espinal phytogeographic province in Córdoba, central Argentina.

cies richness registered was 369, while the number of endemic species registered was 62 species (16.8%); 11 species were recorded exclusively in this vegetation type. The number of exotic species is relatively low (34 species), but the exotic tree *Ligustrum lucidum* and the exotic herb *Leonurus japonicus* showed high constancy and fidelity to this type.

Type 3. *Geoffroea decorticans* forest. Low open forest with grasses, with well conserved stands intermingled with disturbed patches with lower and more open tree canopy. The tree layer showed a mean cover value of 52% and a height that varied from 4 to 13 m. The shrub and herb layers showed values of 38 and 81%, respectively (see Suppl. material 4: Table S4.1). The diagnostic species were the tree *Geoffroea decorticans*, the grasses *Cynodon dactylon* and *Sporobolus spartinus* and the herb *Sida rhombifolia*. The endemic (Argentina and Uruguay) palm species *Trithrinax campestris* showed its highest relative cover in this vegetation type.

This vegetation type is distributed in the central and eastern part of the study area, on well to moderately well (Haplustols) to imperfectly (Argialbols) drained soils. Differences in soil drainage are associated to internal physiognomic heterogeneity in this type, but also stands in different successional stage may strengthen the internal variability within the *Geoffroea decorticans* forest. A total of 393 species were registered of which 65 (16.5%) were endemics and 11 were recorded only in this vegetation type. Thirty nine species were exotic, with the grass *Cynodon dactylon* showing the highest constancy and relative cover.

Type 4. *Prosopis caldenia* forest. Low open forest with grasses and a tree layer showing a mean cover value of 36% and a height that spans from 5 to 8 m. The shrub layer showed a mean cover of 41%, while the herb layer showed the highest cover value of all vegetation types (93%; see Suppl. material 4: Table S4.1). The diagnostic species were the tree *Prosopis caldenia*, an endemic species from central Argentina, usually associated with *Geoffroea decorticans*, but the latter with low cover values and forming a lower tree layer. In lower and more open canopy sites, patches of grasslands dominated by several diagnostic tussock grasses like *Jarava pseudoichu* and *Nassella tenuissima* can be found.

This vegetation type is restricted to the southern extreme of the study area, on gently undulating sandy plains with lightly to excessively drained soils (Haplustols in gentle slopes; Ustorhtens in sandy summits). This vegetation type showed the lowest species richness (265) of which 47 species were endemic (17.7%) and 18 were registered only in this type. Thirty seven exotic species were recorded; among them, the weeds *Carduus acanthoides* and *Heterotheca subaxilaris* showed high constancy and fidelity to this vegetation type.

Diversity patterns, level of invasion and chorotype distribution across the four forest types

The vegetation types differed in their mean species richness and mean number of exotic species per plot (Figure 4A–B). With 62.1 ± 5.1 species Type 2 (*Zanthoxylon coco* forest) accounted for the highest mean species richness per plot and differed significantly from the other three vegetation types ($F_{(3,118)}$ 12.62; $p < 0.001$). Type 3 (*Geoffroea decorticans* forest) showed the lowest mean species richness per plot (37.4 ±2.2), while Type 1 (*Aspidosperma quebracho-blanco* forest) and Type 4 (*Prosopis caldenia* forest) showed 44.3 ±1.6 and 43.3 ± 2.9 species richness per plot, respectively. The mean number of exotic species per plot varied significantly among vegetation types ($F_{(3,118)}$ 13.96; $p < 0.001$), ranging from 1.7 in Type 1 (*Aspidosperma quebracho-blanco* forest) to 5.7 in Type 4 (*Prosopis caldenia* forest) (Table 1). In all the four vegetation types described significant differences in the representation of the different chorotypes were observed (Figure 4C–F). Among all chorotypes, the Southern-brazilian and Chaquenian were the best represented (Figure 4E–F). Type 2 (*Zanthoxylum coco forest*) showed the highest percentage for the Low montane chorotype differing significantly from the other vegetation types ($F_{(3,118)}$ 10.25; $p < 0.001$). The Patagonian chorotype was represented only by a single species, *Descurainia antarctica*, recorded in Type 4 (*Prosopis caldenia* forest), that differed significantly from the other vegetation types ($F_{(3,118)}$ 3.43; $p < 0.019$). The representation of the Exotic chorotype differed significantly among vegetation types ($F_{(3,118)}$ 14.23; $p < 0.001$) showing the highest values in Type 4 (*Prosopis caldenia* forest), while Type 1 (*Aspidosperma quebracho-blanco* forest) showed the lowest values (Figure 4D). The Southern-brazilian and Chaquenian chorotypes differed significantly among the four vegetation types ($F_{(3,118)}$ 8.86; $p < 0.001$; $F_{(3,118)}$ 20.31; $p < 0.001$, respectively). The Southern-brazilian chorotype showed the highest mean percentage value per plot in Type 3 (*Geoffroea decorticans* forest; Figure 4E); while the Chaquenian chorotype exhibited the highest mean percentage per plot in Type 1 (*Aspidosperma quebracho-blanco* forest; Figure 4F).

Vegetation types and their relationship with environmental variables

The ISOMAP ordination (Figure 5) displays the four vegetation woody types observed in Table 1. The variation in species composition among the four types is related to climatic, edaphic and topographic variables (Table 2). Type 4 (*Prosopis caldenia* forest) stands are plotted on the upper right portion of the ordination diagram, associated with higher temperature annual range and seasonality, lower annual precipitation and precipitation of the warmer quarter, and soils with higher fine sand content and lower lime and clay content. The stands of Type 3 (*Geoffroea decorticans* forest) are plotted on the lower right and central portion of the ordination and their floristic differences can be attributed primarily to soil chemistry (Na content) and depth and to a higher precipitation of the driest month; additional floristic differences within this type are re-

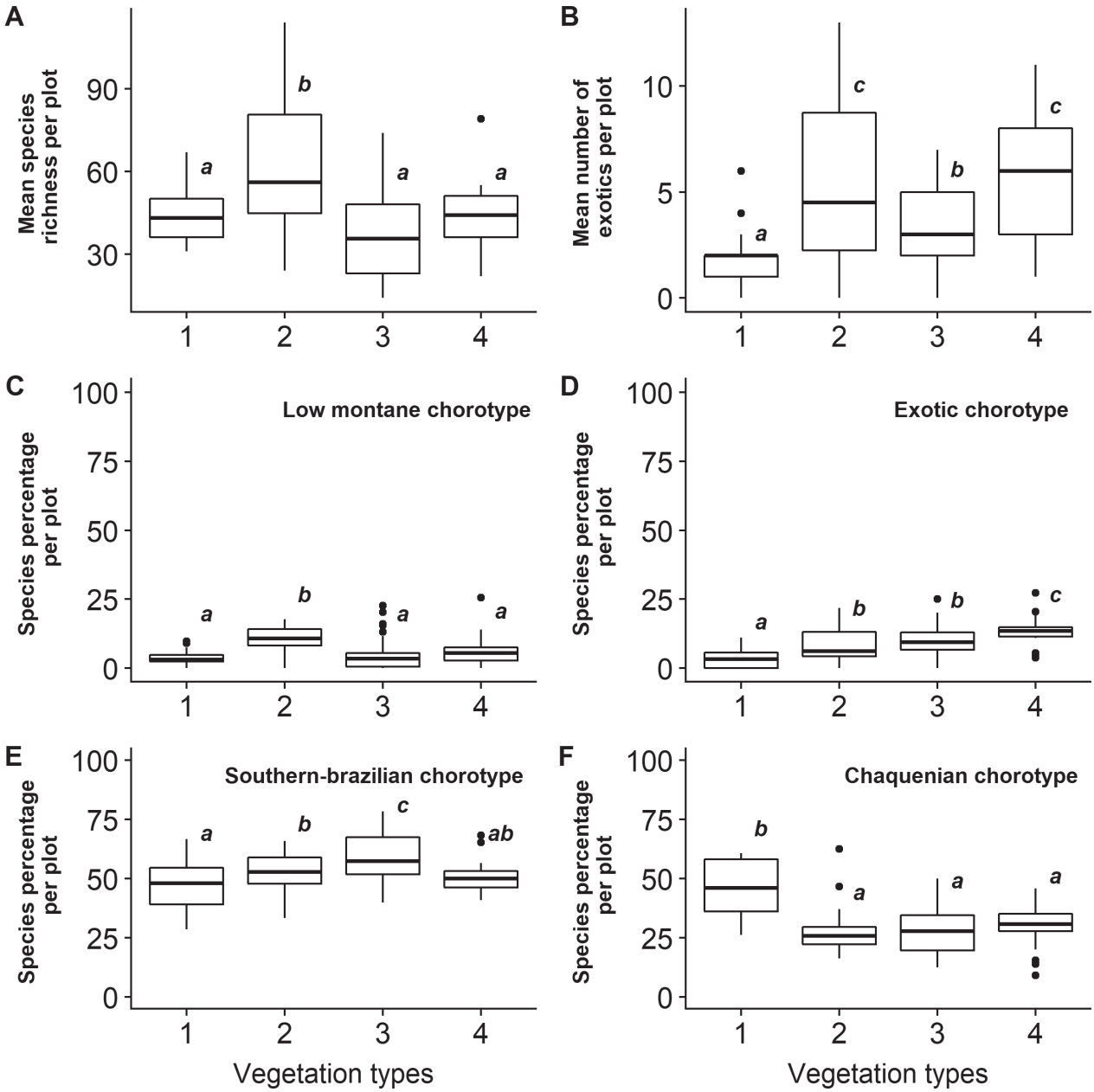

Figure 4. A Mean species richness per plot; **B** mean number of exotic species per plot; **C-F** mean species percentage per plot of different chorotypes for the four vegetation types described in the Espinal phytogeographic province in Córdoba, central Argentina. Vegetation types codes as in Table 1. Different letters indicate significant differences between vegetation types (LSD Fisher, $P < 0.05$).

flected by the dispersion of the stands in the ordination diagram. Stands of Type 2 (*Zanthoxylon coco* forest) are plotted on the left portion of the ordination diagram and its floristic differences are explained by the increase in altitude in the transitional area between true lowland forests and mountain vegetation. Finally, stands of Type 1 (*Aspidosperma quebracho-blanco* forest) are associated with well drained soils with the highest coarse sand content, located in the fluvio-eolian plain in the northern part of the study area. In synthesis, these vegetation types were segregated along gradients of temperature, precipitation, altitude, and of soil-texture and sodium content (Table 2).

Spatial analyses: Espinal extent, current woody vegetation distribution and protected areas

The extent of the Espinal phytogeographic province in the study area, obtained by the overlapping of the previous authors' maps, was 101,550.4 km^2 (Figure 6; Table 3). Further, the comparison of the extent of the Espinal in the overlapped map with previous maps (Figure 6) highlighted the strong differences among authors (Table 3), but the maps by Lewis and Collantes (1973) and Cabido et al. (2018) are most similar (85% similarity) to the Espinal extent used for this study; whereas the maps by the other authors encompass less than 60% (Figure

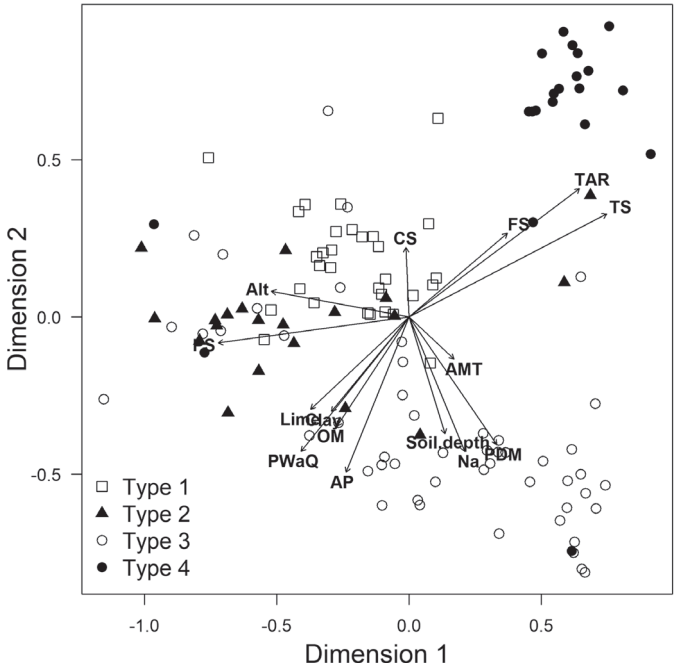

Figure 5. Isometric feature mapping plot (ISOMAP), based on Bray-Curtis dissimilarity of 122 plots × 616 plant species matrix for the Espinal phytogeographic province in Córdoba, central Argentina. Vegetation types codes as in Table 1. Bioclimatic variables with the highest squared correlation coefficient with the sample scores in the ordination space are also reported. Environmental variables: AMT, annual mean temperature; TAR, temperature annual range; TS, temperature seasonality; AP, annual precipitation; PS, precipitation seasonality; PWaQ, precipitation of the warmest quarter; PDM, precipitation of the driest month; Alt, altitude. Edaphic variables: Clay; OM, Organic matter; Soil depth; Na, sodium content; Lime; FS, Fine sand and CS, Coarse sand.

Table 2. Fitted environmental variables onto ISOMAP ordination, reporting their squared correlation coefficient (r^2) and *P*-values based on random permutations of the data. *** and * indicate differences at $p < 0.001$ and $p < 0.05$, respectively.

Environmental variables	r^2
Temperature seasonality (TS)	0.76***
Temperature annual range (TAR)	0.66***
Precipitation seasonality (PS)	0.60***
Precipitation of the warmest quarter (PWaQ)	0.40***
Annual precipitation (AP)	0.34***
Precipitation of the driest month (PDM)	0.31***
Altitude	0.32***
Annual mean temperature (AMT)	0.05*
Lime	0.26***
Fine sand	0.24***
Clay	0.20***
Sodium (Na)	0.26***
Organic matter (OM)	0.22***
Soil depth (SD)	0.18***
Coarse sand	0.07*
pH	0.02

Table 3. Area covered (in km^2) by the extent of the Espinal phytogeographic province (i.e. Overlapped map) and maps by previous authors for Córdoba region, central Argentina. Also shown is the percentage of the extent of the Espinal in the maps by different authors with respect to the overlapped map.

Authors	Espinal extent (km^2)	Percentage extent
Overlapped map	101,550.41	
Lewis and Collantes (1973)	86,455.08	85.13
Cabrera (1976)	55,013.52	54.17
Cabido et al. (2018)	93,653.23	92.22
Morello et al. (2018)	60,356.74	59.43
Oyarzábal et al. (2018)	57,515.67	56.64

6; Table 3). The map showing the current distribution of the woody patches in the study area showed an overall accuracy of about 97% and a Kappa statistic > 0.92. The vegetation map only shows the general spatial pattern of the woody Espinal relicts, because the different vegetation types lacked distinctive reflectance patterns. The total cover of the current woody patches was 3,483.8 km^2 (3.43% of the extent of our version of the Espinal phytogeographic province), of which only 1,071.8 km^2 (31%) are included in the current protected natural areas system.

Discussion

Building on the insights from the previous study by Cabido et al. (2018), the present survey sheds new light on the knowledge of the Espinal forest, recognizing four vegetation types. Moreover, we provide both a map depicting the extent of the Espinal phytogeographic prov-

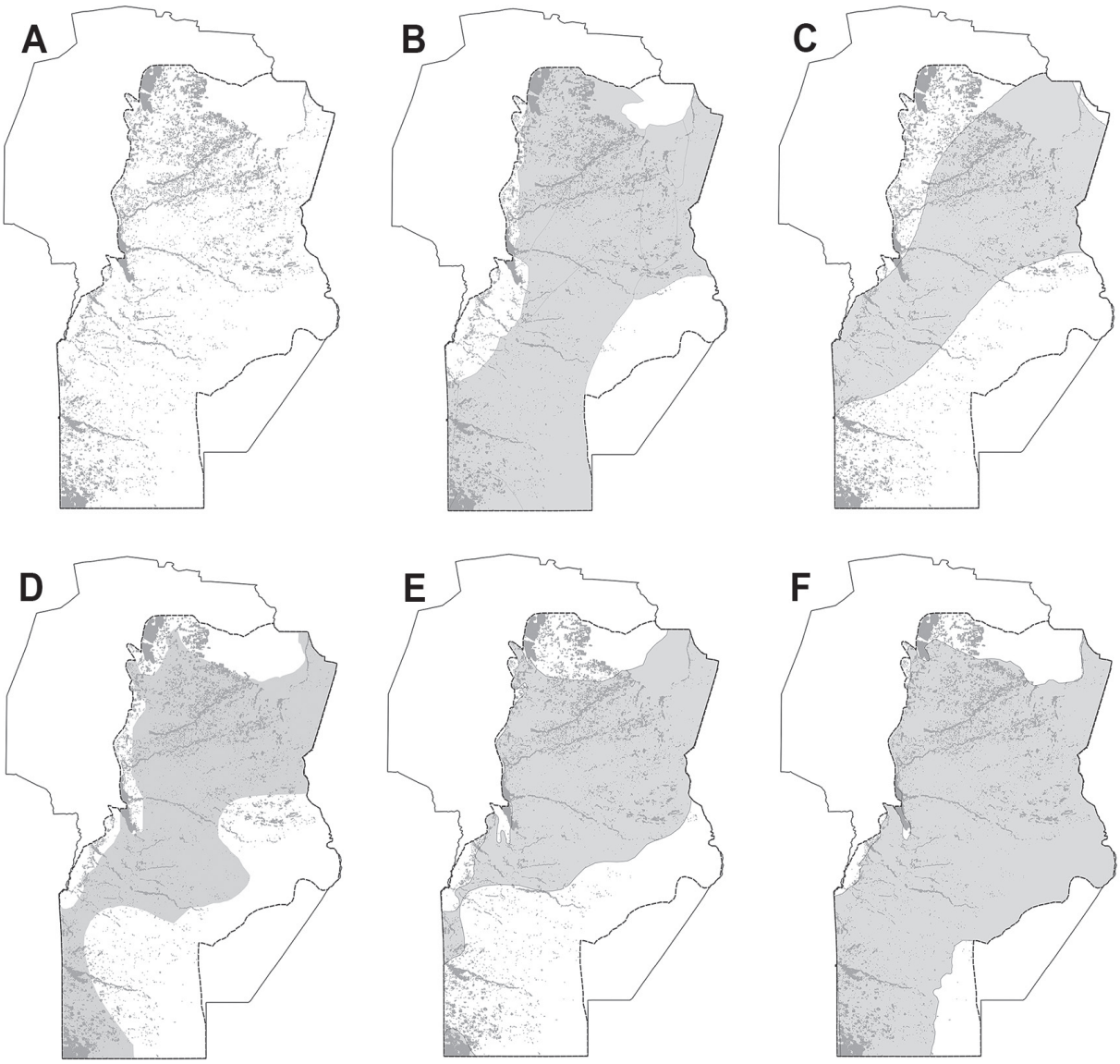

Figure 6. A Overlapped map showing the extent of the Espinal phytogeographic province in Córdoba, central Argentina and the distribution of the current woody vegetation patches; **B-F** Maps of the extent of Espinal in Córdoba by different authors (dark grey): **B** Lewis and Collantes (1973); **C** Cabrera (1976); **D** Morello et al. (2018); **E** Oyarzábal et al. (2018); and **F** Cabido et al. (2018). All maps show the boundaries for the Espinal in the study area resulting from the overlapping of the maps by different authors, together with the current distribution of woody patches.

ince within the study area and an up-to-date map of the current distribution of Espinal forest patches. We should emphasize that the cover of these woody patches represents less than 4% of the extent of the Espinal in Córdoba depicted in both ancient (Cabrera 1953; Lewis and Collantes 1973) and more recent (Cabido et al. 2018; Morello et al. 2018; Oyarzábal et al. 2018) phytogeographic maps. Notwithstanding this dramatic forest loss (Guida-Johnson and Zuleta 2013; Garachana et al. 2018), the representation of the Espinal vegetation types in the current formal system of protected areas is alarmingly low (i.e. 1.05% of the extent of the Espinal in the study area).

Floristic patterns and their relationship with environmental determinants

The changes detected in floristic composition among the four vegetation types are associated mainly to environmental and edaphic variables related to precipitation and temperature seasonality jointly with a soil water availability gradient probably determined by soil texture (i.e. sand, lime and clay content) and sodium content. These conditions vary in the study area in a northeast to southwest direction, in agreement with Matteucci (2018). At the southern extreme of the study area, where the highest temperature oscillation, the lowest precipitation records

and fine sandy soils were registered, the *Prosopis caldenia* forest was identified. Our floristic lists agree with former descriptions and with data reported for La Pampa region, located to the south of our study area (Koutche and Carmelich 1936; Lewis and Collantes 1973). Previous studies have described this vegetation type as "the Pampense" district (Lewis and Collantes 1973) and "the Calden" district (Cabrera 1976; Olson et al. 2001; Oyarzábal et al 2018; Morello et al. 2018). The other three vegetation types share more species among them than with the *Prosopis caldenia* forest and are located under warmer and less dry conditions and on soils with higher clay and lime content. The *Aspidosperma quebracho-blanco* forest, the *Zanthoxylum coco* forest and the *Geoffroea decorticans* forest, were included by Cabrera (1976), Olson et al. (2001), Morello et al. (2018) and Oyarzábal et al. (2018) under the same division ("*Prosopis* district"), while Lewis and Collantes (1973), divided this single unit into six different districts. In the northern part of the study area, *Aspidosperma quebracho-blanco* forest patches are distributed; its identity is determined mainly by species widely distributed in the southern extreme of the Chaco phytogeographic province (e.g. *Aspidosperma quebracho-blanco*, *Prosopis kuntzei*, *Sarcomphalus mistol*, etc.; Sayago 1969). These species confirm the transitional character of the *Aspidosperma quebracho-blanco* forest between the Espinal and Chaco phytogeographic provinces (Cabido et al. 2018). This type shares many species with the *Zanthoxylum coco* forest. The latter is distributed in the western part of the study area, representing a transitional community between the forests on fluvio-eolic sedimentary plains and the low Mountain Chaco Forest (Giorgis et al. 2017; Cabido et al. 2018). Consequently, the diagnostic species group includes several taxa characteristic of the Mountain Chaco Forest district (e.g. *Zanthoxylum coco*, *Lithraea molleoides* and *Croton lachnostachyus*; Cabido et al. 1991; Giorgis et al. 2017), as well as lowland Chaco/Espinal species (e.g. *Condalia buxifolia*; Cabido et al. 2018). Finally, the patches located to the central and eastern sectors of the study area, on soils with the highest sodium content, were classified as the *Geoffroea decorticans* forest. As seen in the ordination diagram in Figure 5, this vegetation type shows additional internal floristic differences partly because of changes in soil drainage and perhaps also due to the influence of differential land use. The dominance of *Geoffroea decorticans* on this vegetation type seems to be promoted by its sprouting roots (Ulibarri et al. 2002) and tolerance to higher sodium soil levels (Karlin et al. 2013). These attributes probably allow *Geoffroea decorticans* to behave as a colonizing species on soils not suitable for agriculture but also over abandoned sites that were previously occupied by forests dominated by *Prosopis alba* and/or *P. nigra* and codominated by *Celtis ehrenbergiana* (Cabido et al. 2018). The advance of *Geoffroea decorticans* over abandoned crop fields was recognized almost 50 years ago by Lewis and Collantes (1973) and more recently by Lewis et al. (2006, 2009). In agreement with these authors and based on our own observations, we predict that perhaps this type will become the dominant vegetation in abandoned fields of the study area if urgent policy measures are not taken into account.

Lewis and Collantes (1973) highlighted the difficulty of differentiating vegetation units within the Espinal based only on the fidelity of species, and they recognized vegetation districts on the basis of physiognomy and the relative abundance of certain dominant plant species. Our results also show that the number of species restricted to a particular vegetation type and, consequently, to be considered as characteristic species (*sensu* Braun-Blanquet 1932) is limited. The small number of exclusive species found could be related to the lack of severe environmental/biogeographic barriers (Bucher 1982), reinforcing the hypothesis stated by Cabrera (1976) concerning the transitional character of the Espinal as an "impoverished Chaco" between the Great Chaco to the north and the Pampas to the south (Bucher 1982). Perhaps as a consequence of the aforementioned lack of barriers to dispersal, a group of ubiquitous species showed high constancy and cover in all four vegetation types (e.g., *Vachellia caven*, *Schinus fasciculatus*, *Setaria lachnea*, and others; see Table 1 and also Suppl. material 2: Table S2.1 for the extended Table 1) and may also explain why the chorotypes Southern-brazilian and Chaquenian are dominant in all the four vegetation types. However, we should not ignore that centuries of human activities (i.e. agriculture and logging; Schofield and Bucher 1986) may have caused the loss and reduction of the range of some characteristic species and, simultaneously, the advance of exotic species that are becoming diagnostic of what we may consider to be "novel ecosystems" (*sensu* Hobbs et al. 2006) with a strong potential to change ecosystem functioning. Another consequence of the intense human activities in the study area is the internal physiognomic heterogeneity observed in all the vegetation types, especially in the *Geoffroea decorticans* forest.

The significant presence of exotic species in the study area has already been reported by different authors (Lewis et al. 2009; Noy-Meir et al. 2012; Cabido et al. 2018). Even though we did not include stands dominated by exotic tree species, a total of 67 exotic taxa, rather evenly distributed (in terms of species richness) among the four vegetation types, were recorded in this study. From a comprehensive list of 40 woody exotic species reported by Giorgis and Tecco (2014) for central Argentina, seven were recorded in this survey. Some of them, such as the trees *Melia azedarach*, *Morus alba* and *Ligustrum lucidum*, showed a high fidelity to the *Zanthoxylum coco* forest. In the same way, the invasive grass *Cynodon dactylon* was identified as a diagnostic species of the *Geoffroea decorticans* forest. Currently, there is general agreement that the advance of exotic species over the Espinal forest is one of the major threats for the conservation of native biodiversity (Lewis et al. 2009; Noy-Meir et al. 2012; Matteucci 2018). The *Prosopis caldenia* forest exhibited the highest mean species richness and proportion of exotics per plot, perhaps because of the

agricultural matrix surrounding these stands since the beginning of the 20th century.

Our floristic survey reported a total of 116 endemic species at the national level, but the number of species restricted only to the study area is almost negligible. Among the highly restricted taxa, *Prosopis caldenia* deserves a special consideration since it is a unique woody species with a very limited range. The conservation status of this species appears as "unspecified" in the Red Lists of the IUCN (http://www.iucn.org); however, its habitat appears to be in "continuing decline in area, extent and/or quality." Delucchi (2006) identifies this species as "vulnerable" due mainly to anthropic activities. Another emblematic taxa recorded in some of the stands sampled in the north and northeast of the study area is the endemic palm *Trithrinax campestris*. Kurtz (1904) and Sayago (1969) reported the high frequency of *Trithrinax campestris* intermingled in forests or in grassland savannas, and Lewis and Collantes (1973) identified a floristic district based in part on the occurrence of this species, but in this study the floristic composition of the patches including *T. campestris* was not clearly differentiated.

Espinal extent, current woody patches distribution and protected areas

Old scientific reports (Lorentz 1876; Kurtz 1904; Frenguelli 1941; Stieben 1946; Cabrera 1953), as well as information compiled from historical documents, oral tradition and more recent contributions (Sayago 1969; Lewis and Collantes1973; Luti et al. 1979), all of them agree in that the Espinal forests dominated the landscape at least until the last decades of the 19th century. From the extent of Espinal province estimated through the overlapped map (ca. 101,500 km^2), a proxy of the potential extent of Espinal forests, only less than 3,500 km^2 (3.43%) of woody patches currently remains. Divergences in the extent of the Espinal phytogeographic province reported by previous authors highlight the difficulties for defining its borders and the need for a comprehensive classification not only for the Espinal vegetation but also neighboring phytogeographic units, such as the Pampa and the Chaco. Regardless of the various phytogeographic maps used to show the comprehensive Espinal extent, it is remarkable that the Espinal woody vegetation has significantly been reduced and fragmented, confirming the dramatic trends for the seasonally dry subtropical forests in South America, already reported by Agost (2015), Cabido et al. (2018) and Garachana et al. (2018).

Finally, our results show that in the study area, the representation of the Espinal forests in formally established natural reserves is almost negligible. The full extent of protected areas comprising well-conserved forest relicts is less than 1,100 km^2 and the figures are even more critical when the whole extent of the Espinal in Argentina is considered (i.e. less than 0.03%; Brown et al. 2006). We should note that these low values are in line with the fact that natural areas developed on flat productive lands have traditionally been excluded from conservation strategies, both at the global (Pressey et al. 2002) and at the regional level (Baldi et al. 2018).

Conclusion

In this study we provide baseline information concerning the floristic heterogeneity and diversity of native forest types of the Espinal forest region in central Argentina. We report four native woody vegetation types segregated along gradients of temperature, precipitation, altitude and soil. Despite the dramatic changes that have taken place since the 19th century, we consider the four vegetation types identified here as representative of the seasonally dry subtropical-warm temperate forests that covered the study area a few centuries ago. Nonetheless, our findings highlight the dramatic reduction in extent and quality of these ecosystems and the need to adopt urgent conservation measures that may stop the conversion of these forests and shrublands to agriculture and grazing lands, as well as the need to take appropriate management actions against invasive exotic species. Recently, the local authorities have established an Agroforestry Plan (Provincial Law 10,467) that compels land owners to plant tree species in at least 2% of their properties in a term of ten years. However, the list of species suggested by the authorities includes exotic trees; whereas, the plan should be restricted to native trees in order to avoid further promoting invasive exotic tree species. The conservation status of the Espinal forests is uncertain and, at this time, its survival depends almost entirely on the good will of private owners. The establishment of new protected areas including the last relicts of these forests should be an essential further step for their conservation.

Author contributions

S.R.Z., M.A.G. and M.R.C. designed the study, S.R.Z., M.A.G., M.R.C. and J.J.C. collected the data; S.R.Z. and M.R.I. performed analyses; S.R.Z., M.A.G. and M.R.C. led the writing; J.J.C. and A.T.A. contributed substantially to revisions.

Acknowledgments

This research was partially supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET); Ministerio de Ciencia y Tecnología de la Provincia de Córdoba (MINCyT – Córdoba, N° 000079/2016 and N° 000007/2019); Secretaría de Ciencia y Tecnología (SECyT – UNC) and Universidad Nacional de Río Cuarto. We express our thanks to three anonymous reviewers and in particular to the Editor, Idoia Biurrun, who made important suggestions that greatly improved the quality of the manuscript.

References

Agost L (2015) Cambio de la cobertura arbórea de la provincia de Córdoba: análisis a nivel departamental y de localidad (periodo 2000–2012). Revista de la Facultad de Ciencias Exactas, Físicas y Naturales 2: 111–123. https://revistas.unc.edu.ar/index.php/FCEFyN/article/view/11502 [accessed 10 Jan 2020]

Arana MD, Martinez GA, Oggero AJ, Natale ES, Morrone JJ (2017) Map and shapefile of the biogeographic provinces of Argentina. Zootaxa 4341: 420–422. https://doi.org/10.11646/zootaxa.4341.3.6

Arturi M (2005) Situación ambiental en la ecorregión Espinal. In: Brown A, Martinez Ortiz U, Acerbi M, Corcuera JF (Eds) La situación ambiental argentina. Fundación Vida Silvestre Argentina, Buenos Aires, AR, 241–246.

Baldi G, Schauman SA, Texeira M, Marinaro S, Martin OA, Gandini P, Jobbágy EG (2018) Nature representativeness in South American protected areas: Country contrasts and conservation priorities. PeerJ 7: e7155. https://doi.org/10.7717/peerj.7155

Bastin JF, Berrahmouni N, Grainger A, Maniatis D, Mollicone D, Moore R, Patriarca C, Picard N, Sparrow, … Castro R (2017) The extent of forest in dryland biomes. Science 356: 635–638. https://doi.org/10.1126/science.aam6527

Blum WE (2013) Soil and land resources for agricultural production: general trends and future scenarios-a worldwide perspective. International Soil and Water Conservation Research 1: 1–14. https://doi.org/10.1016/S2095-6339(15)30026-5

Blum WE, Swaran H (2004) Soils for sustaining global food production. Journal of Food Science 69: crh37–crh42. https://doi.org/10.1111/j.1365-2621.2004.tb15490.x

Boletta PE, Ravelo AC, Planchuelo AM, Grilli M (2006) Assessing deforestation in the Argentine Chaco. Forest Ecology and Management 228: 108–114. https://doi.org/10.1016/j.foreco.2006.02.045

Braun-Blanquet J (1932) Plant sociology. The study of plant communities. McGraw-Hill, New York, US.

Brown A, Martinez-Ortiz U, Acerbi M, Corcuera JF (2006) La situación ambiental argentina 2005. First Edition. Fundación Vida Silvestre Argentina, Buenos Aires, AR.

Bucher EH (1982) Chaco and Caatinga – South American arid savannas, woodlands and thickets. In: Huntley BJ, Walker BH (Eds) Ecology of tropical savannas. Springer, Berlin, Heidelberg, DE, 48–79. https://doi.org/10.1007/978-3-642-68786-0_4

Budka A, Łacka A, Szoszkiewicz K (2018) Estimation of river ecosystem biodiversity based on the Chao estimator. Biodiversity and Conservation 27: 205–216. https://doi.org/10.1007/s10531-017-1429-2

Cabido M, Carranza M, Acosta A, Páez S (1991) Contribución al conocimiento fitosociológico del bosque chaqueño-serrano en la prov. de Córdoba, Argentina. Phytocoenologia 19: 547–566. https://doi.org/10.1127/phyto/19/1991/547

Cabido M, Funes G, Pucheta E, Vendramini F, Díaz S (1998) A chorological analysis of the mountains from Central Argentina. Is all what we call Sierra Chaco really Chaco? Contribution to the study of the flora and vegetation of the Chaco. Candollea 53: 321–331.

Cabido M, Zeballos SR, Zak M, Carranza ML, Giorgis MA, Cantero JJ, Acosta AT (2018) Native woody vegetation in central Argentina: Classification of Chaco and Espinal forests. Applied Vegetation Science 21: 298–311. https://doi.org/10.1111/avsc.12369

Cabrera AL (1953) Esquema fitogeográfico de la República Argentina. Revista del Museo Eva Perón, Botánica 8: 87–168.

Cabrera AL (1976) Regiones fitogeográficas argentinas. In: Kugler WF (Ed.) Enciclopedia argentina de agricultura y jardinería. Acme, Buenos Aires, AR, 1–85.

Capitanelli R (1979) Vegetación. In: Vázquez J, Miatello R, Roque M (Eds) Geografía Física de la provincia de Córdoba. Boldt, Buenos Aires, AR, 45–138.

Carignano C, Kröhling D, Degiovanni S, Cioccale M (2014) Geomorfología Relatorio. XIX Congreso Geológico Argentino, Córdoba, Argentina. https://www.researchgate.net/publication/278242641 [accessed 10 Jan 2020]

Černý T, Kopecký M, Petřik P, Song J, Šrůtek M, Valachovič M, Altman J, Doležal J (2015) Classification of Korean forests: Patterns along geographic and environmental gradients. Applied Vegetation Science 18: 5–22. https://doi.org/10.1111/avsc.12124

Chao A, Chiu CH (2016) Nonparametric estimation and comparison of species richness. In: eLS. John Wiley & Sons Ltd., Chichester, GB. https://doi.org/10.1002/9780470015902.a0026329

Chiapella JO, Demaio PH (2015) Plant endemism in the Sierras of Córdoba and San Luis (Argentina): understanding links between phylogeny and regional biogeographical patterns. PhytoKeys 47: 59–96. https://doi.org/10.3897/phytokeys.47.8347

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13: 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Conti G, Díaz S (2013) Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems. Journal of Ecology 101: 18–28. https://doi.org/10.1111/1365-2745.12012

De Fina AL (1992) Aptitud agroclimática de la República Argentina. Academia Nacional de Agronomía y Veterinaria, Buenos Aires, AR.

Delucchi G (2006) Las especies vegetales amenazadas de la Provincia de Buenos Aires: una actualización. APRONA Boletines Científicos 39: 19–31.

Dengler J, Jansen F, Glöckler F, Peet RK, De Cáceres M, Chytrý M, Ewald J, Oldeland J, Finckh M, ... Spencer N (2011) The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. Journal of Vegetation Science 22: 582–597. https://doi.org/10.1111/j.1654-1103.2011.01265.x

Dexter KG, Pennington RT, Oliveira-Filho AT, Bueno ML, Silva de Miranda PL, Neves DM (2018) Inserting tropical dry forests into the discussion on biome transitions in the tropics. Frontiers in Ecology and Evolution 6: 1–104. https://doi.org/10.3389/fevo.2018.00104

Dicks LV, Viana B, Bommarco R, Brosi B, del Coro Arizmendi M, Cunningham SA, Galleto L, Hill R, Lopes AV, ... Potts SG (2016) Ten policies for pollinators. Science 354: 975–976. https://doi.org/10.1126/science.aai9226

Dryflor BK, Delgado-Salinas A, Dexter KG, Linares-Palomino R, Oliveira-Filho A, Prado D, Pullan M, Quintana C, ... Pennington TR (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353: 1383–1387. https://doi.org/10.1126/science.aaf5080

EX E (2009) ENVI EX User's Guide. Research System, Inc. http://www.harrisgeospatial.com/portals/0/pdfs/enviex/envi_ex_user_guide.pdf [accessed 10 Jan 2020]

Fehlenberg V, Baumann M, Gasparri NI, Piquer-Rodriguez M, Gavier-Pizarro G, Kuemmerle T (2017) The role of soybean production as an underlying driver of deforestation in the South American Chaco.

Global Environmental Change 45: 24–34. https://doi.org/10.1016/j.gloenvcha.2017.05.001

Frenguelli J (1941) Rasgos principales de Fitogeografía Argentina. Revista del Museo de La Plata (Nueva Serie), Botánica 3: 65–181. https://publicaciones.fcnym.unlp.edu.ar/rmlp/article/view/1611

Garachana DM, Aragón R, Baldi G (2018) Estructura espacial de remanentes de bosque nativo en el Chaco Seco y el Espinal. Ecología Austral 28: 553–564. https://doi.org/10.25260/EA.18.28.3.0.767

Giorgis MA, Tecco PA (2014) Árboles y arbustos invasores de la Provincia de Córdoba (Argentina): una contribución a la sistematización de bases de datos globales. Boletín de la Sociedad Argentina de Botanica 49: 581–603. https://doi.org/10.31055/1851.2372.v49.n4.9991

Giorgis MA, Cingolani AM, Gurvich DE, Reynero N, Rufini S (2005) Diferencias en la estructura de la vegetación del sotobosque entre una plantación de *Pinus taeda* L. (Pinaceae) y un matorral serrano (Cuesta Blanca, Córdoba). Kurtziana 31: 39–49.

Giorgis MA, Cingolani AM, Gurvich DE, Tecco PA, Chiapella J, Chiarini F, Cabido M (2017) Changes in floristic composition and physiognomy are decoupled along elevation gradients in central Argentina. Applied Vegetation Science 20: 558–571. https://doi.org/10.1111/avsc.12324

Gorgas JA, Tassile JL (2006) Recursos Naturales de la Provincia de Córdoba LOS SUELOS Nivel de reconocimiento 1: 500.000. INTA – Secretaría de Ambiente de Córdoba, Córdoba, AR.

Guida-Johnson B, Zuleta GA (2013) Land-use land-cover change and ecosystem loss in the Espinal ecoregion, Argentina. Agriculture, Ecosystems & Environment 181: 31–40. https://doi.org/10.1016/j.agee.2013.09.002

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology: A Journal of the Royal Meteorological Society 25: 1965–1978. https://doi.org/10.1002/joc.1276

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, ... Zobel M (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15: 1–7. https://doi.org/10.1111/j.1466-822X.2006.00212.x

Jobbagy EG, Nosetto MD, Santoni CS, Baldi G (2008) El desafío ecohidrológico de las transiciones entre sistemas leñosos y herbáceos en la llanura Chaco-Pampeana. Ecología Austral 18: 305–322.

Karlin MS, Moreno MA, Rollán AA, Bachmeier OA (2013) Causas y efectos de la dinámica hídrica del suelo sobre las comunidades vegetales en Salinas Grandes, Catamarca (Argentina). Multequina 22: 23–36.

Koutche V, Carmelich JNF (1936) Contribución al conocimiento de los bosques de la República Argentina: Estudio Forestal del caldén. Boletín del Ministerio de Agricultura de la Nación 37: 1–4.

Kuemmerle T, Altrichter M, Baldi G, Cabido M, Camino M, Cuellar E, Decarre S, Gasparri I, Gavier-Pizarro G, ... Zak M (2017) Forest conservation: Remember Gran Chaco. Science 355: 465–465. https://doi.org/10.1126/science.aal3020

Kurtz F (1904) Flora de Córdoba. In: Río ME, Achával L (Eds) Geografía de la Provincia de Córdoba, Vol. 1. Compañía Sudamericana de Billetes de Banco, Buenos Aires, 270–343.

Lewis JP, Collantes MB (1973) El espinal periestépico. Ciencia e investigación 29: 360–377.

Lewis JP, Prado D, Noetinger S (2004) Los remanentes de bosques del Espinal en el este de la provincia de Córdoba. Agromensajes 13.

Lewis JP, Pire EF, Barberis I, Prado D (2006) Los bosques del Espinal Periestépico en las proximidades de la localidad de Coronda, provincia de Santa Fe (Argentina). Revista de Investigaciones de la Facultad de Ciencias Agrarias – UNR 10: 13–26.

Lewis JP, Noetinger S, Prado DE, Barberis IM (2009) Woody vegetation structure and composition of the last relicts of Espinal vegetation in subtropical Argentina. Biodiversity and Conservation 18: 3615–3628. https://doi.org/10.1007/s10531-009-9665-8

Linares-Palomino R, Aybar D, Morales Ruiz EJ (2015) Floristics of neotropical seasonally dry forests: a perspective from complete vascular plant inventories. Phytocoenologia 45: 251–267. https://doi.org/10.1127/phyto/2015/0010

Lorentz PG (1876) Cuadro de la vegetación de la República Argentina. Sociedad Anónima de Tipografía, Litografía y Fundición de Tipos, Buenos Aires, AR.

Luti R, Bertrán de Solís MA, Galera MF, Müller de Ferreira N, Berzal M, Nores M, Herrera MA, Barrera JC (1979) Vegetación. In: Vázquez J, Miatello R, Roquem M (Eds) Geografía Física de la provincia de Córdoba. Boldt, Buenos Aires, AR, 297–368.

Matteucci SD (2018) Ecorregión Espinal. In: Morello J, Matteucci SD, Rodríguez AF, Silva M (Eds) Ecoregiones y complejos ecosistémicos argentinos. Second edition. Orientación Gráfica Editora, Buenos Aires, AR, 395–439.

Morello J, Matteucci SD, Rodríguez AF, Silva M (2018) Ecoregiones y complejos ecosistémicos argentinos. Second edition. Orientación Gráfica Editora, Buenos Aires, AR.

Morrone JJ (2001) Biogeografía de América latina y el Caribe. M&T – Manuales & Tesis SEA, vol. 3, Zaragoza, ES.

Noy-Meir I, Mascó M, Giorgis MA, Gurvich DE, Perazzolo D, Ruiz G (2012) Estructura y diversidad de dos fragmentos del bosque de Espinal en Córdoba, un ecosistema amenazado. Boletín de la Sociedad Argentina de Botanica 47: 119–133.

O'Donnell MS, Ignizio DA (2012) Bioclimatic predictors for supporting ecological applications in the conterminous United States. US Geological Survey Data Series 691. https://doi.org/10.3133/ds691 [accessed 10 Jan 2020]

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV, Underwood EC, D´Amigo JA, Itoua I, Strand HE, ... Kassen KR (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. BioScience 51: 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Oyarzábal M, Clavijo J, Oakley L, Biganzoli F, Tognetti P, Barberis I, Maturo HM, Aragon R, Campanello PI, León RJC (2018) Unidades de vegetación de la Argentina. Ecología Austral 28: 40–63. https://doi.org/10.25260/EA.18.28.1.0.399

Pennington TR, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and Quaternary vegetation changes, Journal of Biogeography 27: 261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x

Pressey RL, Whish GL, Barrett TW, Watts ME (2002) Effectiveness of protected areas in north-eastern New South Wales: recent trends in six measures. Biological Conservation 106: 57–69. https://doi.org/10.1016/S0006-3207(01)00229-4

QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org [accessed 10 Jan 2020]

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, AT. https://www.R-project.org/

Sayago M (1969) Estudio fitogeográfico del norte de Córdoba. Boletín Academia Nacional de Ciencias Córdoba 46: 123–427.

Schmidtlein S, Tichý L, Feilhauer H, Faude U (2010) A brute-force approach to vegetation classification. Journal of Vegetation Science 21: 1171–2010. https://doi.org/10.1111/j.1654-1103.2010.01221.x

Schofield CJ, Bucher EH (1986) Industrial contributions to desertification in South America. Trends in Ecology & Evolution 1: 78–80. https://doi.org/10.1016/0169-5347(86)90023-6

Silva de Miranda PL, Oliveira-Filho AT, Pennington RT, Neves DM, Baker TR, Dexter KG (2018) Using tree species inventories to map biomes and assess their climatic overlaps in lowland tropical South America. Global Ecology and Biogeography 27: 899–912. https://doi.org/10.1111/geb.12749

Stieben E (1946) La Pampa: su historia, su geografía, su realidad y porvenir. Peuser, Buenos Aires, AR.

Tenembaum JB, de Silva V, Langford JC (2000) A global geometric framework for nonlinear dimensionality reduction. Science 290: 2319–2323. https://doi.org/10.1126/science.290.5500.2319

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Ulibarri E, Gómez Sosa E, Cialdella A, Fortunato R, Bazzano D (2002) Leguminosas nativas y exóticas. Biota Rioplatense VII. Editorial L.O.L.A., Buenos Aires, AR.

Zuloaga FO, Morrone O (1999a) Catálogo de las plantas vasculares de la República Argentina I. Monographs in Systematic Botany from the Missouri Botanical Garden 60: 1–323.

Zuloaga FO, Morrone O (1999b) Catálogo de las plantas vasculares de la República Argentina II. Monographs in Systematic Botany from the Missouri Botanical Garden 74: 1–1269.

Zuloaga FO, Nicora EG, Rúgolo de Agrasar Z, Morrone O, Pensiero J, Cialdella AM (1994) Catálogo de la familia Poaceae en la República Argentina. Monographs in Systematic Botany from the Missouri Botanical Garden 47: 1–178.

Zuloaga FO, Morrone O, Belgrano MJ (2008) Catálogo de las plantas vasculares del Cono Sur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay). Monographs in Systematic Botany from the Missouri Botanical Garden 107: 1905–1908.

E-mail and ORCID

Sebastián R. Zeballos (sebazeba@hotmail.com)
Melisa A. Giorgis (Corresponding author, mgiorgis@imbiv.unc.edu.ar), ORCID: http://orcid.org/0000-0001-6126-6660
Marcelo R. Cabido (mcabido@imbiv.unc.edu.ar)
Alicia T.R. Acosta (aliciateresarosario.acosta@uniroma3.it), ORCID: https://orcid.org/0000-0001-6572-3187
María del Rosario Iglesias (riglesias@imbiv.unc.edu.ar)
Juan J. Cantero (juanjocantero@gmail.com)

Supplementary material

Supplementary material 1
Analytical table with individual relevés (Table S1.1).
Link: https://doi.org/10.3897/VCS/2020/38013.suppl1

Supplementary material 2
Extended synoptic table (Table S2.1).
Link: https://doi.org/10.3897/VCS/2020/38013.suppl2

Supplementary material 3
Species observed and non-parametric estimators species richness for the four vegetation types (Table S3.1).
Link: https://doi.org/10.3897/VCS/2020/38013.suppl3

Supplementary material 4
Mean cover and height with their respectively standard error and maximum and minimum cover values recorded for tree, shrub and herb layers for the four vegetation types (Table S4.1).
Link: https://doi.org/10.3897/VCS/2020/38013.suppl4

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 103–109
doi: 10.3897/VCS/2020/47180

LONG DATABASE REPORT

ECOINFORMATICS

A new Vegetation-Plot Database for the Coastal Forests of Kenya

Maria Fungomeli[1,2], Anthony Githitho[2], Fabrizio Frascaroli[1,3], Saidi Chidzinga[2], Marcus Cianciaruso[4], Alessandro Chiarucci[1]

1 *Department of Biological, Geological & Environmental Sciences, Alma Mater Studiorum- University of Bologna, Bologna, Italy*
2 *Coastal Forests Conservation Unit, Centre for Biodiversity, National Museums of Kenya, Kilifi, Mombasa, Kenya*
3 *Lòm Research, Rocca d'Arce, Frosinone, Italy*
4 *Department of Ecology, Universidade Federal de Goiás, Brazil*

Corresponding author: Maria Fungomeli (maria.fungomeli2@unibo.it)

Academic editor: Idoia Biurrun ♦ **Received** 9 October 2019 ♦ **Accepted** 5 April 2020 ♦ **Published** 16 June 2020

Abstract

Biodiversity data based on standardised sampling designs are key to ecosystem conservation. Data of this sort have been lacking for the Kenyan coastal forests despite being biodiversity hotspots. Here, we introduce the Kenyan Coastal Forests Vegetation-Plot Database (GIVD ID: AF-KE-001), consisting of data from 158 plots, subdivided into 3,160 subplots, across 25 forests. All plots include data on tree identity, diameter and height. Abundance of shrubs is presented for 316 subplots. We recorded 600 taxa belonging to 80 families, 549 of which identified to species and 51 to genus level. Species richness per forest site varied between 43 and 195 species; mean diameter between 13.0 ± 9.8 and 30.7 ± 20.7 cm; and mean tree height between 5.49 ± 3.99 and 12.29 ± 10.61 m. This is the first plot-level database of plant communities across Kenyan coastal forests. It will be highly valuable for analysing biodiversity patterns and assessing future changes in this ecosystem.

Taxonomic reference: African Plant Database (African Plant Database version 3.4.0).

Abbreviations: DBH = diameter at breast height; GIVD = Global Index of Vegetation-Plot Databases; KECF-VPD = Kenyan Coastal Forests Vegetation Plot Database.

Keywords

Coastal forests, conservation, Global Index of Vegetation-Plot Databases, biodiversity hotspots, Kaya, Kenya, plant species diversity, sacred forests, vegetation plot

PENSOFT.

Copyright *Maria Fungomeli et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

GIVD Fact Sheet: Kenya Coastal Forests Vegetation-Plot Database (KECF-VPD)

GIVD Database ID: AF-KE-001			**Last update:** 2020-03-20
Kenya Coastal Forests Vegetation Plot Database		**Web address:** http://www.givd.info/ID/AF-KE-001	
Database manager(s): Maria Fungomeli (maria.fungomeli2@unibo.it); Alessandro Chiarucci (alessandro.chiarucci@unibo.it)			
Owner: Maria Fungomeli, PhD Student-University of Bologna, Dept of Biology, Geology & Envtal Sci. Senior Curator & Research Scientist, Coastal Forests Conservation Unit, Center for Biodiversity National Museums of Kenya e-mail: mfungomeli@museums.or.ke; maria.fungomeli2@unibo.it; fungomaria@yahoo.com			
Scope: A plant species diversity survey of the Coastal Forests of Kenya. The survey covered 25 forests with details of trees and shrubs species, DBH & Height, georeference of sites & transects. Plants were identified to species level where possible otherwise genus level used.			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): Excel		**Export format(s):** Excel, Open Document, PDF, CSV file	
Plot type(s): nested plots		**Plot-size range:** 50 to 1000	
Non-overlapping plots: 158	**Estimate of existing plots:** 158	**Completeness:** 100%	**Status:** finished
Total no. of plot observations: 158	**Number of sources (biblioreferences, data collectors):** 0		**Valid taxa:** 600
Countries (%): KE: 100%			
Formations: Forest: 100% = Terrestrial: 100%			
Guilds: [NA]			
Environmental data (%): altitude: 100%			
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 2020-03-20 further details and future updates available from http://www.givd.info/ID/AF-KE-001			

Introduction

Eastern African coastal forests are tropical forests known for their rich biodiversity and high levels of endemism, including a concentration of rare and threatened taxa and high diversity of endemic plant and animal species (Wass 1995; Burgess et al. 1998; Lovett 1998; Burgess and Clarke 2000; Myers et al. 2000; Luke 2005; Azeria et al. 2007). According to Burgess and Clarke (2000), this vegetation type hosts more than 4,500 plant species and 1,050 plant genera, the majority of which are woody. This rich biodiversity has been largely attributed to favourable climatic conditions and a wide range of ecological niches (Moomaw 1960; Lovett 1998; Burgess and Clarke 2000; Montagnini and Jordan 2010). Overall, these forests extend along the coastal edge of Eastern Africa along the Indian Ocean stretching from Somalia in the north, through coastal Kenya and Tanzania, and all the way to Mozambique in the south. They have been defined as the "Swahilian centre of endemism", which constitutes a hotspot of endemism in Africa (Burgess et al. 1998; Luke 2005).

For millennia, Eastern African coastal forests have supported livelihoods both locally and regionally and played a major role as high conservation value ecosystems (Wass 1995). However, they are increasingly facing a number of threats which include a growing population and increased anthropogenic activities such as illegal logging, poaching, charcoal burning and agriculture expansion, all activities leading to increased deforestation (Burgess et al. 1998; Burgess and Clarke 2000; Habel et al. 2017). According to Wass (1995) and Burgess et al. (1998), these threats have had severe impacts and resulted in the heavy fragmentation of once connected forests. Some 10% of the original forest cover is estimated to remain, of which only 17% are under some kind of protection (Wass 1995; Burgess and Clarke 2000). Conserving and sustainably managing the remaining forests of the region requires a developed and enhanced biodiversity monitoring system, which is currently lacking. Developing such a system requires baseline biodiversity data, which are currently scant, limited and outdated.

The Kenyan coastal forests fall within the Eastern African coastal forests. Despite their global significance as biodiversity hotspots (Burgess et al. 1998; Myers et al. 2000; Hobohm et al. 2019), systematic biodiversity data survey based on a standard design are still lacking. The first-ever vegetation survey of the coastal forests of Kenya was carried out in 1987 without using a vegetation plot design (Robertson and Luke 1993), with the aim to create a list of species found in these forests (Robertson and Luke 1993; Luke 2005). A standardised dataset based on vegetation plots and suitable for analysing spatial and temporal patterns across the whole area does still not exist. Filling this knowledge gap is even more urgent given the continuing deforestation and the uncertainty of future climate change projections. There is need to undertake ecological studies that can provide baseline data required for sound ecological monitoring and evaluation.

This paper provides a basic description of a new vegetation-plot database, developed as part of a collaboration between the University of Bologna and the National Museums

of Kenya. The database contains data of 25 different forest patches and was developed with the goal to produce a solid sample-based (Chiarucci 2007) overview of the plant communities in the Kenyan coastal forests. The resulting vegetation-plot database represents the first standardised plant data set for these forests and a fundamental tool for future assessments and monitoring of a key biodiversity hotspot.

Study Area: the coastal forests of Kenya in the context of Eastern African forests

The coastal forests of Kenya are part of the Eastern African coastal forests ecoregion and are isolated patches of evergreen to semi-evergreen closed canopy forests. They present unique remnants of indigenous ecosystems and are part of the North Zanzibar-Inhambane Regional Mosaic, which extends from southern Somalia through coastal Kenya to southern Tanzania, including the islands of Zanzibar and Pemba (Burgess et al. 1998, Burgess and Clarke 2000; Githitho 2004; Peltorinne 2004; Luke 2005), and part of the biodiversity hotspot known as the Eastern Arc and Coastal Forests of Kenya and Tanzania (Myers et. al. 2000). They stretch from the north to south along the Kenyan coast, and are mostly found on ancient coral reef bed rocks formed as a result of sea level drops. Therefore, they span over a variety of altitudinal gradients and climatic zones.

The climatic range of the Kenyan coastal forests is tropical with coastal high humidity (Burgess and Clarke 2000). The annual rainfall follows distinctive rainy seasons and generally increases towards the southern coast and at higher altitudes. The rainfall pattern differs from the north to the south. In the northern region, there are two rainy seasons made of long rains (April to June) and short rains (November to December), while in the south, there is only one long rain season between April and June. However, both south and north regions have an annual rainfall variability where the seasons may vary from year to year. Overall, the mean annual rainfall ranges from 900 mm to 1200 mm (Glover et al. 1954; Moomaw 1960; Burgess et al. 1998; Burgess and Clarke 2000). The mean temperature ranges between 30°C during the dry season (December-March) to 25°C during the long rain season (April-September), with relatively cooler temperatures in the southern coast.

It is estimated that approximately 3,170 km^2 of Eastern African coastal forests remains in Somalia, Kenya, Tanzania, Mozambique, Zimbabwe and Malawi. Approximately 20% of these forests are found in Kenya (Burgess et al. 1998; Burgess and Clarke 2000; Azeria et al. 2007). The number of Kenyan coastal forests patches was estimated to be 107 patches in early 1990s (Robertson and Luke 1993; Wass 1995; Burgess et al. 1998; Burgess and Clarke 2000; Githitho 2004; Luke 2005; Azeria et al. 2007).

The size and protection status of the Kenyan coastal forests is highly variable. The two largest remaining forests are Arabuko Sokoke (42,000 ha) and Shimba Hills (25,300 ha), which are government protected forest reserves (Table 1). Other government protected forest reserves include Marenje (1,480 ha), Gogoni (832 ha), Buda (670 ha), Dzombo (650 ha) and Mrima (377 ha). The other forest remnants spread over small patches (10 to 75 ha)

Table 1. Overview of the forest sites included in the Kenyan coastal forest vegetation-plot database, with an indication of their protection status, geographical coordinates, area, number of plots and recorded total species richness per forest site.

Forest ID	Forest name	Protection status	Latitude decimal degree	Longitude decimal degree	Area (ha)	Number of plots	Species richness
Arabuko	Arabuko Sokoke forest	Forest reserve	-3.32138	39.92917	42,000	26	178
Bomu	Kaya Bomu	Sacred forest	-3.93354	39.59635	409	8	154
Buda	Buda forest	Forest reserve	-4.45812	39.39683	670	6	121
Chivara	Kaya Chivara	Sacred forest	-3.69452	39.69132	150	8	140
Chonyi	Kaya Chonyi	Sacred forest	-4.06953	39.53038	200	4	62
Diani	Kaya Diani	Sacred forest	-4.27523	39.58520	20	3	66
Dzombo	Dzombo forest	Forest reserve	-4.42945	39.21545	650	6	90
Fungo	Kaya Fungo	Sacred forest	-3.80068	39.51047	204	4	60
Gandini	Gandini forest	Sacred forest	-4.03443	39.50988	150	5	80
Gogoni	Gogoni forest	Forest reserve	-4.41013	39.47628	832	6	123
Jibana	Kaya Jibana	Sacred forest	-3.84048	39.67382	140	8	195
Kambe	Kaya Kambe	Sacred forest	-3.86766	39.65363	75	6	109
Kauma	Kaya Kauma	Sacred forest	-3.62968	39.73778	75	7	77
Kinondo	Kaya Kinondo	Sacred forest	-4.39427	39.54703	30	3	56
Marenje	Marenje forest	Forest reserve	-4.48458	39.25906	1,480	6	76
Mrima	Mrima forest	Forest reserve	-4.48573	39.26883	377	6	101
Mtswakara	Kaya Mtswakara	Sacred forest	-4.00017	39.51997	248	4	64
Muhaka	Kaya Muhaka	Sacred forest	-4.32568	39.52328	150	5	90
Muvya	Kaya Mudzimuvya	Sacred forest	-3.94175	39.58190	171	4	85
Mwiru	Kaya Mudzimwiru	Sacred forest	-3.95913	39.57372	147	4	70
Ribe	Kaya Ribe	Sacred forest	-3.89922	39.63363	36	5	95
Shimba	Shimba Hills forest	Forest reserve	-4.26940	39.37208	25,300	12	190
Teleza	Kaya Teleza	Sacred forest	-4.14147	39.50342	67	6	91
Tiwi	Kaya Tiwi	Sacred forest	-4.25704	39.59817	10	3	53
Waa	Kaya waa	Sacred forest	-4.19970	39.61565	30	3	43

many of which are considered sacred forests and are managed traditionally and culturally by the local communities (Table 1). These forest patches are locally referred to as *'Kaya'* (Robertson and Luke 1993; Wass 1995; Burgess and Clarke 2000; Githitho 2004; Luke 2005; Metcalfe et al. 2010; Githitho 2016; Luke and Githitho 2016).

Data collection

Sampling was based on a nested plot design consisting of 158 rectangular plots located in 25 forests sites of the Kenyan coastal forests spanning along the coastline, from north to south (Figure 1). The sampling was carried out from November 2018 to June 2019. The forests are a mixture of evergreen to semi-deciduous forests. During field work, we experienced a mix of wet and semi-dry season while in the field with a lot of light rains. Hence performing part of the fieldwork during the dry season did not affect plants identification, as most plants remained leafy and some flowering while the few deciduous were commonly locally known by botanist and could be easily identified.

To standardise sampling intensity, the number of plots per forest site was approximately proportional to the forest site area, although with some variation due to site accessibility and fragmentation. The location of the plots within each forest site was randomised with minor adaptations due to accessibility. A minimum distance of 200 m between plots per site was maintained to maximise spatial variation. The plots were laid with a north-south orientation, had a standard size of 10 m × 100 m and were further sub-divided into twenty 10 m × 5 m subplots for a total of 3,160 subplots across the entire study system. We sampled and identified at the species level all woody plant individuals with diameter at breast height (DBH) ≥ 5 cm (mostly trees) rooted within each subplot. For each tree, besides DBH, we also measured the height with a hand held clinometer (Suunto PM-5), or a calibrated measuring pole (50 m) in areas with dense forests where clinometer was difficult to use. Woody plant individuals with DBH < 5 cm, mostly shrubs, were sampled and identified in two of the twenty subplots within a plot, where one was randomly selected in the northern half (subplots 1–10) and the second in the southern half (subplots 11–20) of the plot. The abundance of shrub species was assessed by counting the number of individual shoots rooted within the subplot.

Plants were identified on-site to the species or at least genus level by local botanists and with the use of botanical manuals using standard references for the area (Noad and Birnie 1990; Beentje 1994; Luke 2005). When on-site identification was not possible, voucher specimens were collected for subsequent identification on the lab with the help of herbarium specimens. Finally, Global Positioning Systems (GPS) devices were used for recording the geographical coordinates and altitude of forest sites and plots (start and end points), and shrub subplots.

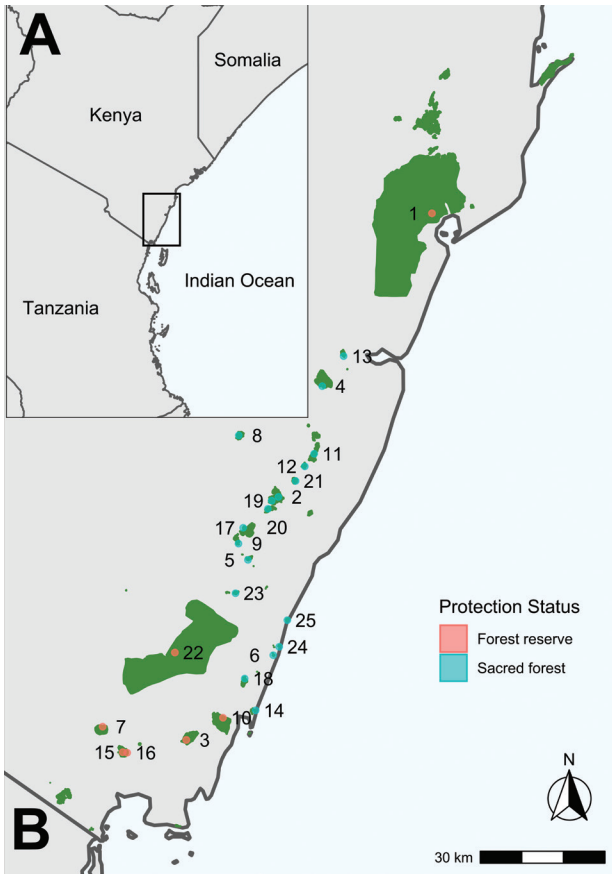

Figure 1. A Map of Eastern Africa area highlighting the coastal area of Kenya. **B** Coastal forests of Kenya spanning from North to South (all forests identified by green colour with and without numbers), the numbered are the sampled sites with their protection status. 1 = Arabuko, 2 = Bomu, 3 = Buda, 4 = Chivara, 5 = Chonyi, 6 = Diani, 7 = Dzombo, 8 = Fungo, 9 = Gandini, 10 = Gogoni, 11 = Jibana, 12 = Kambe, 13 = Kauma, 14 = Kinondo, 15 = Marenje, 16 = Mrima, 17 = Mtswaka, 18 = Muhaka, 19 = Muvya, 20 = Mwiru, 21 = Ribe, 22 = Shimba, 23 = Teleza, 24 = Tiwi, 25 = Waa.

Database content

The Kenyan coastal forests vegetation-plot database (KE-CF-VPD) is registered at the Global Index of Vegetation Database (http://www.givd.info/ID/AF-KE-001). It consists of vegetation data collected in 158 nested plots across 25 forests sites (Table 1). The total subplots were 3,160. The sampled forest sites are characterised by different area sizes and protection status, with seven government state forest reserves (377 to 42,000 ha) and 18 sacred sites (10 to 409 ha). Overall, the database includes 40,913 occurrence records relative to a total of 600 distinct taxa belonging to 80 families. 549 species were identified at the specific level and 51 at the genus level belonging to 43 genera. For taxonomy consistency and to avoid misspelt names, plant species names were standardised using the TAXONSTAND package in R statistical software (Cayuela et al. 2017).

In total, 19 families had more than 10 species (Table 2) with *Rubiaceae* presenting the highest number of spe-

Table 2. List of the most diverse families in the Kenyan coastal forests vegetation-plot database, defined as those having at least 10 different recorded species.

Family	Number of species
Rubiaceae	63
Leguminosae	61
Malvaceae	34
Euphorbiaceae	30
Annonaceae	24
Moraceae	23
Sapindaceae	22
Apocynaceae	20
Sapotaceae	18
Rutaceae	17
Celastraceae	16
Combretaceae	16
Lamiaceae	16
Capparaceae	15
Ebenaceae	14
Acanthaceae	12
Phyllanthaceae	12
Salicaceae	11
Anacardiaceae	10

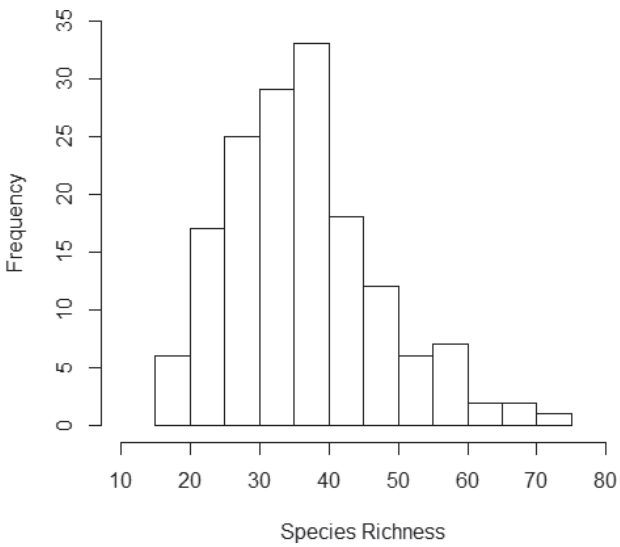

Figure 2. Distribution of species richness per plot in the Kenyan coastal forests vegetation-plot database (n = 158 plots).

cies (63), followed by *Leguminosae* (61), *Malvaceae* (34) and *Euphorbiaceae* (30). Species richness per site varied between 43 species at Waa sacred forest to 195 species at Jibana sacred forest (Table 1). The Shimba Hills and Arabuko forest reserves, the largest forest sites, were the richest after Jibana. The number of species increased relative to the area, as expected given the species-area relationship perspective. Some small forest areas, like Jibana, also exhibited high species richness, likely because other factors different from area may have a strong impact in driving local species richness.

The frequency distribution of species richness per plot showed a slightly right-skewed distribution (Figure 2), with the highest number of plots harbouring between 35–40 species. The most frequent trees in plots across all sites were *Uvaria acuminata* and *Haplocoelum inoploeum* (Table 3). *Hymenaea verrucosa* exhibited the highest mean DBH and height. The shrubs *Monanthotaxis fornicata* and *Synaptolepis kirkii* were among the 20 most frequent woody species in plots (Table 3).

Basic forest structure varied across sites (Table 4). The highest mean DBH was recorded at Mtswaka sacred forest while the lowest at Chivara sacred forest. Kambe sacred forest exhibited the highest mean height, while Diani sacred forest the lowest. There was a high variation in tree heights from the small to tallest within sites, creating mean heights that would depict a bush rather than a forest, but this is not the case given the large mean DBH recorded. The largest number of tree individuals was sampled at Arabuko and Shimba forest reserves, the largest ones, and where more plots were sampled, while the lowest at Muvya sacred forest.

Conclusion

The KECF-VPD database represents the first vegetation dataset collected according to a standardised plot-based design across Kenyan coastal forests. This database represents a snapshot of the vegetation in a relevant fraction of the existing forest patches in the region. As such, the database provides the best available picture of the current patterns of woody plant biodiversity of these forests. Since the sampling design was based on different scale levels (forest sites, plots and subplots), the database also offers a unique opportunity for exploring the patterns and determinants of plant diversity in the Kenyan Coastal forests across spatial scales. These data will provide a tool and baseline for assessing future changes in the study system.

Future perspectives

The current KECF-VPD database covers 25 Kenyan coastal forests. There is potential to extend the survey to the remaining coastal forests not covered by this research. The database is presently being explored for analysing species diversity data, in terms of species-area relationships, beta diversity and species composition. A successive phase will also be to develop a biodiversity monitoring platform for these forests. Such a platform could be shared with the institutions, organisations and communities working and living around these forests to promote their conservation and sustainable management. Furthermore, integrating socio-economic aspects into the research would be essential to capture local level forest use by adjacent communities and their attitude towards forest management and conservation.

Data availability

The database is presently stored at the University of Bologna. Its availability is currently restricted to the PhD pro-

Table 3. List of the 20 most frequent species per plot (n = 158 plots), including family, habit, number of plots in which they have been recorded, and DBH and height (mean ± standard deviation) for species with DBH ≥ 5cm.

Species	Family	Habit	Number of plots	DBH (mean ± sd) (cm)	Height (mean ± sd) (m)
Uvaria acuminata	*Annonaceae*	tree	95	7.4 ± 2.13	7.54 ± 7.08
Haplocoelum inoploeum	*Sapindaceae*	tree	94	11.9 ± 7.46	5.51 ± 2.71
Polysphaeria parvifolia	*Rubiaceae*	tree	69	5.6 ± 0.57	2.75 ± 0.67
Salacia elegans	*Celastraceae*	liana	69	7.3 ± 1.87	7.14 ± 2.78
Combretum schumannii	*Combretaceae*	tree	66	18.5 ± 16.97	9.24 ± 5.74
Hymenaea verrucosa	*Leguminosae*	tree	66	33.9 ± 21.36	15.73 ± 8.50
Landolphia kirkii	*Apocynaceae*	liana	66	9.5 ± 3.79	8.21 ± 3.33
Monanthotaxis fornicata	*Annonaceae*	shrub	66	–	–
Synaptolepis kirkii	*Thymelaeaceae*	shrub	64	–	–
Cassipourea euryoides	*Rhizophoraceae*	tree	63	14.7 ± 8.64	8.21 ± 4.02
Asteranthe asterias	*Annonaceae*	tree	57	6.2 ± 1.60	3.09 ± 1.03
Manilkara sansibarensis	*Sapotaceae*	tree	57	18.2 ± 11.43	9.41 ± 5.06
Cola minor	*Malvaceae*	tree	56	12.8 ± 7.79	5.75 ± 3.18
Grewia plagiophylla	*Malvaceae*	tree	56	12.2 ± 5.71	5.15 ± 2.30
Pyrostria bibracteata	*Rubiaceae*	tree	56	8.6 ± 5.38	4.25 ± 2.46
Combretum illairii	*Combretaceae*	liana	54	11.1 ± 13.82	6.00 ± 5.51
Lecaniodiscus fraxinifolius	*Sapindaceae*	tree	54	20.4 ± 15.06	8.29 ± 5.15
Deinbollia borbonica	*Sapindaceae*	tree	52	6.7 ± 1.75	2.90 ± 0.66
Allophylus pervillei	*Sapindaceae*	tree	51	7.0 ± 1.92	3.36 ± 0.83
Suregada zanzibariensis	*Euphorbiaceae*	tree	51	7.0 ± 2.23	3.83 ± 1.42

Table 4. Basic structural data of the Kenyan coastal forest sites expressed as mean **(±** standard deviation) of the DBH and height, and number of measured trees (n).

Site	DBH (mean ± sd) (cm)	Height (mean ± sd) (m)	n
Arabuko	15.3 ± 12.55	7.73 ± 4.74	2163
Bomu	25.2 ± 22.28	9.99 ± 8.07	275
Buda	16.6 ± 15.14	7.94 ± 6.28	658
Chivara	13.0 ± 9.80	7.26 ± 4.78	539
Chonyi	17.3 ± 15.91	6.79 ± 5.10	216
Diani	16.0 ± 23.26	5.49 ± 3.99	412
Dzombo	18.9 ± 20.84	7.71 ± 5.77	470
Fungo	17.0 ± 14.80	8.74 ± 5.74	208
Gandini	17.3 ± 12.02	7.39 ± 4.45	270
Gogoni	17.5 ± 16.80	7.50 ± 6.10	709
Jibana	18.6 ± 19.45	9.71 ± 7.95	972
Kambe	24.5 ± 25.37	12.29 ± 10.61	274
Kauma	13.4 ± 28.18	7.29 ± 4.67	253
Kinondo	19.5 ± 17.83	9.56 ± 6.92	468
Marenje	16.3 ± 14.18	7.81 ± 5.91	579
Mrima	15.7 ± 15.56	7.12 ± 5.72	485
Mtswaka	30.7 ± 20.71	11.76 ± 7.42	176
Muhaka	24.1 ± 20.97	10.52 ± 8.39	414
Muvya	24.8 ± 20.57	10.69 ± 8.90	110
Mwiru	24.6 ± 20.19	10.64 ± 6.79	153
Ribe	15.5 ± 17.67	7.62 ± 5.74	299
Shimba	15.6 ± 17.16	7.51 ± 6.04	1345
Teleza	17.9 ± 11.03	8.83 ± 5.03	556
Tiwi	14.3 ± 17.73	5.59 ± 3.93	464
Waa	15.8 ± 11.84	6.47 ± 4.10	410

ject within which it was developed. Possible uses by other interested researchers are presently limited on the bases of specific agreement to be discussed with the database administrators. After an embargo period, the data will be contributed to sPlot – the global vegetation plot database (Bruelheide et al. 2019).

Author contributions

A.C conceptualised the idea and provided overall supervision. M.F, F.F and A.C developed the field work sampling design. A.G guided on overall study area briefing, forest sites selection and accessibility. M.F carried out the field work, collected, compiled, standardised data and prepared the manuscript. S.C contributed to field sampling and plant specimen identification. M.C reviewed the species data and verified taxonomy for African and tropical vegetation species. All authors contributed to the final manuscript.

Acknowledgements

Authors are indebted to University of Bologna, Department of Biological, Geological and Environmental Sciences, International Association of Butterfly Exhibitors and Suppliers, National Museums of Kenya, Nature Kenya and WWF-Kenya for funding and logistical support received. Special thanks to Geoffrey Mashauri and Abbas Shariff for assistance in plant identification We are grateful to Lawrence Chiro and Abdulrahman Matano (Coastal forests conservation unit-NMK); Dr Tito E. Mbuvi and Joseph Muthini (Kenya Forest Research Institute); George Wara and Blessingtone Magangha (Kenya Forest Service) for field sampling assistance. We would like to acknowledge Prof. Idoia Biurrun and two other anonymous reviewers for comments and suggestions on previous version of the manuscript, and Megan J. McNellie for linguistic editing.

References

African Plant Database (2019) Conservatoire et Jardin botaniques de la Ville de Genève, Geneva, CH and South African National Biodiversity Institute, Pretoria, ZA (version 3.4.0). https://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php/ [accessed 9 Dec 2019]

Azeria ET, Sanmartin I, Stephan AS, Carlson A, Burgess ND (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. Biodiversity and Conservation 16: 883–912. https://doi.org/10.1007/s10531-006-9022-0

Beentje HJ (1994) Kenya Trees, Shrubs and Lianas. National Museums of Kenya, Nairobi, 722 pp.

Bruelheide H, Dengler J, Jiménez-Alfaro B, Purschke O, Hennekens SM, Chytrý M, Pillar VD, Jansen F, Kattge J, ... Winter M (2019) sPlot: A new tool for global vegetation analyses. Journal of Vegetation Science 30: 161–186.

Burgess ND, Clarke GP, Rodgers WA (1998) Coastal forests of Eastern Africa: status, endemism patterns and their potential causes. Biological Journal of the Linnean Society 64: 337–367. https://doi.org/10.1111/j.1095-8312.1998.tb00337.x

Burgess ND, Clarke GP [Eds] (2000) The Coastal Forests of Eastern Africa. IUCN, Gland, CH and Cambridge, UK, 443 pp.

Cayuela L, Stein A, Oksanen J (2017) Taxonstand: Taxonomic standardization of plant species names. R package version 2.1. https://CRAN.R-project.org/package=Taxonstand [accessed 15 July 2019]

Chiarucci A (2007) To sample or not to sample? That is the question for the vegetation scientist. Folia Geobotanica 42: 209–216. https://doi.org/10.1007/BF02893887

Githitho AN (2004) The coastal terrestrial forests of Kenya: A report on resources threats and investments. A report to WWF Eastern coastal forest programme. http://coastalforests.tfcg.org/pubs/CFResource-Ken.pdf [accessed 3 Oct 2019]

Githitho AN (2016) Listing the sacred Mijikenda *kaya* Forests as UNESCO World Heritage Sites: The Long Journey, Journal des africanistes [En ligne], 86-1, mis en ligne le 10 avril 2018. http://journals.openedition.org/africanistes/4971 [accessed 3 Oct 2019]

Glover J, Robinson P, Henderson JP (1954) Provisional maps of the reliability of annual rainfall in East Africa. Quarterly Journal of the Meteorological Society 80: 1–607. https://doi.org/10.1002/qj.49708034609

Habel J, Constanza I, Zamora C, Teucher M, Hornetz B, Shauri H, Mulwa R, Lens L (2017) East African coastal forest under pressure. Biodiversity and Conservation 26: 2751–2758. https://doi.org/10.1007/s10531-017-1375-z

Hobohm C, Janišová M, Steinbauer MJ, Landi S, Field R, Vanderplank S, Beierkuhnlein C, Grytnes J-A, Vetaas OR, … Chiarucci A (2019) Global endemics-area relationships of vascular plants. Perspectives in Ecology and Conservation 17: 41–49. https://doi.org/10.1016/j.pecon.2019.04.002

Lovett JC (1998) Eastern Tropical African Centre of Endemism: A Candidate for World Heritage Status. Journal of East African Natural History 87: 359–366. https://doi.org/10.2982/0012-8317(1998)87[359:ETACOE]2.0.CO;2

Luke WRQ (2005) Annotated check-list of the plants of the Shimba Hills, Kwale District, Kenya. Journal of East African Natural History 94: 5–121. https://doi.org/10.2982/0012-8317(2005)94[5:ACOTPO]2.0.CO;2

Luke WRQ, Githitho AN (2016) Biodiversity and the Kaya forests. In: Hoorweg J, Muthiga N (Eds) Recent Advances in Coastal Ecology: Studies from Kenya. African Studies Centre, Leiden, 293–301. https://www.oceandocs.org/bitstream/handle/1834/9014/ktf70ex1253933-067-20

Metcalfe K, French-Constant R, Gordon I (2010) Sacred sites as hotspots for biodiversity: The Three Sisters Cave complex in coastal Kenya. Oryx 44: 118–123. https://doi.org/10.1017/S0030605309990731

Moomaw JC (1960) A Study of the Plant Ecology of the Coast Region of Kenya, East Africa. Government Printer, Nairobi, 62 pp. https://edepot.wur.nl/493400

Montagnini F, Jordan CF (2010) Tropical Forest Ecology. Springer, Berlin, 295 pp. https://doi.org/10.1007/b138811

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1038/35002501

Noad T, Birnie A (1990) A Fully Illustrated Field Guide: Trees of Kenya. General Printers Ltd, Nairobi, 350 pp.

Peltorinne P (2004) The forest types of Kenya. In: Pellikka P, Ylhäisi J, Clark B (Eds) Taita Hills and Kenya, 2004 – seminar, reports and journal of a field excursion to Kenya [Expedition reports of the Department of Geography 40]. University of Helsinki, Helsinki, 8–13.

Robertson SA, Luke WRQ (1993) The vegetation and conservation status of Kaya coastal forests in Kenya. WWF, Nairobi, 425 pp. https://www.africabib.org/rec.php?RID=K00001940

Wass P [Ed.] (1995) Kenya's indigenous forests: status, management and conservation. IUCN, Gland, CH and Cambridge, UK, 220 pp. https://portals.iucn.org/library/sites/library/files/documents/FR-014.pdf

E-mail and ORCID

Maria Fungomeli (Corresponding author, maria.fungomeli2@unibo.it), ORCID: https://orcid.org/0000-0002-8963-6405
Anthony Githitho (anthony.githitho@yahoo.com)
Fabrizio Frascaroli (fabrizio@lomonlus.org)
Saidi Chidzinga (chidzinga@gmail.com)
Marcus Cianciaruso (cianciaruso@gmail.com), ORCID: https://orcid.org/0000-0001-5866-5345
Alessandro Chiarucci (alessandro.chiarucci@unibo.it), ORCID: https://orcid.org/0000-0003-1160-235X

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 111–122
doi: 10.3897/VCS/2020/48228

RESEARCH PAPER

Grasslands on Coastal Headlands in New South Wales, south eastern Australia

John T. Hunter[1]

1 *School of Environmental and Rural Science, University of New England, Armidale, New South Wales, Australia*

Corresponding author: John T. Hunter (jhunter8@bigpond.com)

Academic editor: Zdeňka Lososová ♦ **Received** 6 November 2019 ♦ **Accepted** 14 May 2020 ♦ **Published** 16 June 2020

Abstract

Aims: To use unsupervised techniques to produce a hierarchical classification of grasslands on coastal headlands of New South Wales in eastern Australia. **Methods:** A dataset of 520 vegetation plots scored on cover and placed across grasslands on coastal headlands (ca. 2000 km of coastline). Vegetation assemblages were identified with the aid of a clustering method based on group averaging and tested using similarity profile analysis (SIMPROF) using Bray-Curtis similarity. A hierarchical schema was developed based on EcoVeg hierarchy and was circumscribed using positive and negative diagnostic taxa via similarity percentage analysis (SIMPER) and importance based on summed cover scores and frequency. Mapping the occurrences grasslands was initially constructed using remote sensing which was verified and modified with on ground observations. **Results:** One group *Themeda – Pultenaea – Zoysia – Cynodon* grasslands and heathy grasslands was defined to include all coastal headland grassland vegetation of the New South Wales, and within this, three alliances and ten associations. Only one of the circumscribed associations is represented within the current state classification schema. In total 107 ha were mapped of which 68 ha occurred within secure conservation tenure. **Conclusions:** A number of unique and rare grassland assemblages on coastal headlands have to date gone undescribed. The most common alliance constitutes approximately 87% of extant grassland occurrences but is currently the only type listed as endangered and afforded protection. Although *Poa* spp. are listed as a threat to *Themeda* dominated assemblages on headlands data from this study suggest that this is unlikely to be the case.

Taxonomic reference: PlantNET (http://plantnet/10rbgsyd.nsw.gov.au/; accessed June 2019).

Abbreviations: BC Act = Biodiversity Conservation Act; NMDS = non-metric multidimensional scaling; NSW = New South Wales; PCT = Plant Community Type; SIMPER = similarity percentage analysis; SIMPROF = Similarity profile analysis.

Keywords

Australia, EcoVeg, Grassland, Headlands, New South Wales

Introduction

Natural temperate grasslands cover 7% of continental landmasses with approximately 4% within protected areas (Henwood 2010). In the Australian context and in particular in NSW temperate grasslands are a highly threatened and restricted vegetation type of which less than 3% remains in good condition with patches often under 10 ha in size (Baines and Dunford 2008; Hunter and Hunter 2016). Grasslands are some of the best studied vegetation types within Australia (Williams et al. 2015). Even so little is known about the dynamics of most species and well-known species are likely to have more nuanced responses to disturbance and competition that currently is portrayed (Moore et al. 2019; Price et al. 2019).

PENSOFT.

Copyright *John T. Hunter*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Potentially the most restricted grassland type within Australia are those found on coastal headlands and sea cliffs. These closed tussock and sod tussock grasslands have been recognised as unique by a number of authors (Beadle 1981; Kirkpatrick 1981; Opie et al. 1984; Myerscough and Carolin 1986; Adam et al. 1990; Griffith et al. 2003; Keith 2004; Tozer et al. 2010; Hunter and Hunter 2017a). Generally, such grasslands occur on more nutrient rich soils with a higher proportion of clay content than comparable areas containing heaths in similar landscape positions (Kirkpatrick 1977; Beadle 1981; Adam et al. 1990).

Grasslands on headlands are thought by some authors to be a dis-climax community created by Aboriginal burning which were subsequently then kept open by European management (Morris et al. 1990). Others, however, have argued that the grasslands are natural and a product of nutrient rich soils, exposure and salt spray (Beadle 1981; Adam et al. 1990). Furthermore, the often-protected nature of headlands, steepness of slopes, prevailing onshore winds during summer months and salt spray are likely to retard fire spread suggesting areas of grassland would have occurred and persisted even without fire (Adam et al. 1990). The presence of long-lived obligate seeding prostrate shrubs endemic to these grasslands suggest that the community is not a dis-climax created by regular burning (Hunter and Hunter 2017b; Hunter 2018).

The most comprehensive survey and analysis of the vegetation of coastal headlands in south eastern Australia was conducted by Adam et al. (1990) who surveyed 613 plots (1×1, 2×2 or 4×4 m plots along transects). This survey was restricted to the southern half of the New South Wales (NSW) coastline and sampled all vegetation assemblages including rushlands and heaths. The subsequent analyses derived one purely grassland and two broadly 'grassland' like assemblages, one circumscribed by *Themeda triandra* (syn. *T. australis*), one by *Lomandra longifolia* and the other by *Ficinia nodosa* (syn. *Isolepis nodosa*) and the introduced grass *Stenotaphrum secundum*. The description of the *Themeda triandra* community by Adam et al. (1990) was used as a basis for the listing of the endangered ecological community *Themeda* grassland on sea cliffs and coastal headlands in the NSW North Coast, Sydney Basin and South East Corner Bioregions on the NSW *Biodiversity Conservation* Act 2016 (https://www.environment.nsw.gov.au/). The vegetation types of Adam et al. (1990) were considered to be provisional and were not given an official designation but are likely fall within the level of alliance or above. A subsequent floristic analysis was performed on 117 (2×2 m) plots placed only within grasslands on headlands in the northern half of the NSW coastline by Hunter and Hunter (2017b). This additional analysis described three *Themeda triandra* dominated assemblages and an additional four others. As Adam et al. (1990) and Hunter and Hunter (2017b) were describing northern and southern parts of the NSW coast some overlap between types occurs but geographical and thematic differences make direct comparison less clear. A further analysis of 352 (2×2 m) plots sampling only grassland on headlands was performed by Hunter (2018). These later analyses highlighted a number of factors that influenced composition and dominance such as distance from seaward edge, altitude, wind shear, grazing, fire and direct and indirect facilitation by adjacent taller shrubs (Hunter and Hunter 2017a, b, 2019; Hunter 2018).

A number of threats have been listed as potentially affecting the survival of these unique vegetation types which include; weed invasion, too frequent or infrequent fires, invasion from native shrubs, mowing, trampling, lack of tenure security, overgrazing by abundant macropods, competition from native *Poa* (particularly *Poa poiformis*), coastal development and pasture improvement. Many of these threats are still current in urban and semi-urban localities (e.g. weed invasion, trampling, coastal development, pasture improvement), however, others have been shown to be non-critical threats and even important to the diversity and persistence of these systems. For example, tall shrub occurrence and grazing by abundant macropods have been positively implicated for the maintenance and persistence of biodiversity (Hunter and Hunter 2017a, b, 2019) and low frequency fire may also not be a critical threat (Hunter and Hunter 2017b, Hunter 2018).

Thus far no fully comprehensive investigation across the entire range of these unique, and in part legally protected endangered grasslands, has occurred within NSW (Adam et al. 1990; Hunter and Hunter 2017a). Management decisions are currently being made without full comprehension of their full floristic components, distribution and natural variation across their range. It is essential, especially for communities considered threatened, that a fundamental understanding of their distribution, rarity and floristic interrelationships with co-occurring types be gained (Franklin et al. 2016; Jensen et al. 2016). Even within areas considered relatively well surveyed, many highly restricted systems are likely to be poorly sampled and incompletely treated within current classifications, leading to misunderstandings of their placement, function, importance and rarity (Hunter and Lechner 2017; Hunter and Hunter 2017a). Even though these grasslands occur in the most highly populated jurisdictions in Australia they have up until recently been very poorly sampled. Currently the NSW Plant Community Type (PCT) classification schema describes four coastal headland grasslands all collectively described as *Themeda australis* Sod Tussock Grasslands within the hierarchy of Maritime Grasslands (Class) and Temperate Grasslands (Formation) (https://www.environment.nsw.gov.au/). The designations of Class and Formation have been developed in isolation from that of association and no divisions occur between Class and Association thus the links between these hierarchical levels is not fully resolved (Gellie et al. 2017).

Within this investigation an attempt is made to provide a more comprehensive plot-based assessment of the

floristic relationships between grass dominated communities on coastal headlands along the entire NSW coastline. Hierarchical classification systems facilitate integrated understanding of relationships between vegetation assemblages and also allow conceptualisations at different ranks to match scales at which management and investigations may be applied, from local to global (Gellie et al. 2017; De Cáceres et al. 2018; Faber-Langendoen et al. 2018). Here I provide a hierarchical classification based on unsupervised analysis of plot data producing a consistent classification section (CCS) for a unified vegetation type (De Cáceres et al. 2015). Mapping of natural remnants is also undertaken using on ground and remote sensing techniques in order to better understand the distribution, area of occupancy and reservation status of these grasslands.

Methods

Study region

The study region encompasses the NSW coastal headlands and sea cliffs (ca. 2,000 km of coastline; Figure 1) in eastern Australia. Headlands occur as isolated island like rocky protrusions separated by long distances of beaches and dunal landscapes (Figure 2). Field investigations were carried out from northern and eastern Tasmania to south eastern Queensland. Although headlands also occur within south eastern Queensland, eastern Victoria and north and eastern Tasmania no sampling was undertaken in these areas due to the comparative paucity of grassland assemblages. Though largely rainfall is aseasonal the region has slightly higher rainfall in summer in the northern locations becoming more winter dominant in the southern parts of the study area. Rainfall varies from 816 to 1711 mm per year with average annual temperatures from 14 to 21°C. Winds tend to be offshore during winter months and onshore during summer (Adam et al. 1990).

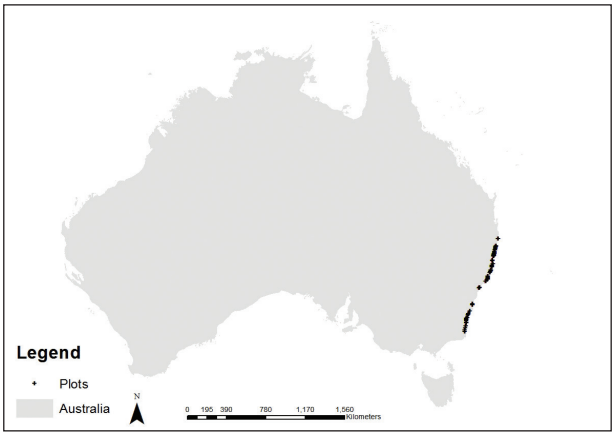

Figure 1. Location of 520 plots placed on coastal headlands in New South Wales, Australia.

Field sampling

Survey plots of a 2 × 2 m dimension were placed randomly within vegetation in which Poaceae taxa was visually assessed to cover a minimum of 50% of the patch to be surveyed. Where possible a minimum of three plots were placed in a random stratified way (to ensure coverage of aspect and distance from seaward edge) on each headland with a minimum distance of 10 m between plots. Larger headlands with larger grass dominated patches received more plots. All plots were surveyed by the author. The survey was conducted over a period of four years from 2015–2019 during Spring to Summer (November and February) of each year. Most accessible headlands were visited at least once. Species nomenclature follows that of PlantNET (http://plantnet.rbgsyd.nsw.gov.au/; accessed January 2019). Vascular plant taxa were scored using overlapping percent cover and frequency. Frequency was determined by dividing the plot into 16 subplots (50 cm × 50 cm) where the rooted presence and absence of each species was scored in each subplot. The majority of plot data has been submitted for hosting in 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).

Mapping

Imagery including ADS40 (Coffs Harbour 2009 – 50 cm resolution) and World Imagery (WGS84 1 m resolution supplied by ESRI) was used within ArcGIS 10.6 (ESRI Inc) to map potential grasslands on headlands on the mainland and nearby off shore islands. The majority of accessible headlands were visited between 2015 and 2019 and mapping re-adjusted based on on-ground observations of extent. In some cases, exact boundaries of grasslands were mapped with a hand held GPS. Mapping was conducted over all land tenures but restricted to within the NSW jurisdiction. Mapping was conducted for the purpose of understanding how much grassland in total occurs within protected lands. Based on the resolution of the imagery available it is not possible to map to individual community type.

Statistical analysis

Primer E (ver. 7.0.11; Quest Research Limited; Ivybridge, Devon, UK) was used for data exploration, whereby an initial triangular resemblance matrix using Bray-Curtis similarity co-efficient was created after dispersion weighting and square root transformation. Clustering was achieved through group averaging and the similarity profile tested using similarity profile analysis (SIMPROF) permutation tests (9999 iterations). SIMPROF tests the statistical significance of every node within a dendrogram starting from the top and (all points within a single group) and high-

Figure 2. Bare Bluff, an example of the island like headlands and grassland sampling plot locations from the North Coast Bioregion of NSW.

lighting only those groups which show within group multivariate structure. The EcoVeg (Faber-Langendoen et al. 2014) approach was used to define hierarchical levels and guide nomenclature. The type and density of data available allowed for the circumscription of vegetation types from medial Group down to alliance and associations.

Similarity percentage analysis (SIMPER) identifies the species driving differences between selected types. SIMPER uses the Bray-Curtis similarity measure (Primer E ver. 7.0.11; Quest Research Limited; Ivybridge, Devon, UK) to identify positively and negatively diagnostic taxa across vegetation types. Taxa with combined high fidelity and cover were also identified and listed for diagnostic purposes and type delineation. Attempts to place current eastern Australian state based noncultural units was derived by comparing diagnostic and non-diagnostic taxa from SIMPER results. The results of the analyses were used to define mid to lower level classification levels (Macrogroup, Group and Alliance) based on EcoVeg terminology. It should be noted that although EcoVeg uses the alliance and association as does the Braun-Blanquet approach, the nomenclatural and procedural roles are distinct.

Results

A total of 520 plots were placed with approximately across 90 headlands. 326 vascular plant taxa from within 75 families were found within plots. An average of 15 and a maximum of 27 taxa were recorded per plot. The current survey is the first to encompass the entirety of the NSW coastline and also the first unified hierarchical classification for this vegetation type. Association was defined at a Bray-Curtis similarity of 23% (Figure 3). Splicing the dendrogram at 23% similarity allowed all associations to be delineated at a level which shows statistical evidence of multivariate structure and enabled the circumscription of ten associations within three alliances (Figures 4–6) and a single group (Table 1). The Alliances separate assemblages found in areas with a higher water table, with Alliances 2 and 3 largely separating northern and southern floristic elements with the dominant grasses in general possessing different photosynthetic pathways (Table 1). All described vegetation units would be included within the defined Class – Maritime Grasslands. Three associations appear to have no equivalent in any published resources (Tables 2, 3). The other seven associations have broadly or more directly synonymous types described from disparate literature sources (Table 2). Association 3.5 constitutes the most widely distributed vegetation type found along much of the NSW coastline and is the type most commonly described within previous analyses and literature (Tables 1–3).

A total of 604 'grassland' mapping polygons were created constituting 107 ha of which 72 ha were within the National Reserve system or other forms of registered con-

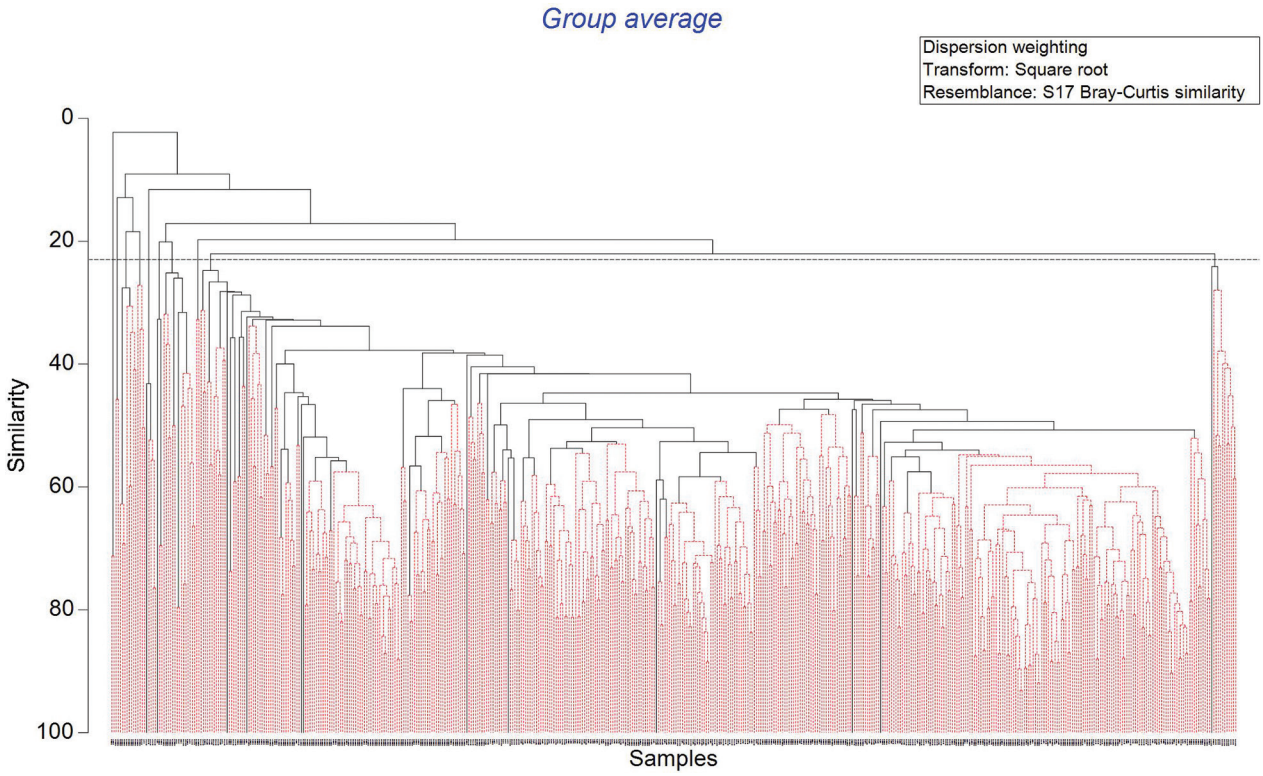

Figure 3. SIMPROF cluster analysis of the full dataset from grasslands of coastal headlands NSW in south eastern Australia showing association level recognition.

Figure 4. Alliance 1 *Hemarthria uncinata – Pteridium esculentum* NSW North Coast Bioregion Sod Tussock Grasslands (Broughton Island National Park).

Table 1. Circumscription of grasslands on coastal headlands of New South Wales within south eastern Australia. Descriptions 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. Common taxa are listed in decreasing order of cumulative frequency and cover within each identified group.

Hierarchy	Positive diagnostic (SIMPER)	Negative diagnostic (SIMPER)	Common taxa	Notes and distribution
Group: Scientific Name: *Themeda – Pultenaea – Zoysia - Cynodon* grasslands & heathy grasslands Colloquial: Grasslands of South East Australian Coastal Headlands	NA	NA	*Themeda triandra, Pultenaea maritima, Hibbertia vestita, Zoysia macrantha, Polymeria calycina, Cynodon dactylon, Viola banksii, Pimelea linifolia, Gonocarpus humilis, Goodenia rotundifolia, Entolasia stricta, Imperata cylindrica, Ficinia nodosa, Hydrocotyle hirta, Lobelia anceps.*	Restricted to the south east Australian coastal headlands commonly south from Noosa in Qld to near Bega of the south coast of NSW, though minor occurrences may occur as far south as Tasmania and north of Noosa.
Alliance 1: Scientific Name: *Hemarthria uncinata – Pteridium esculentum* NSW North Coast Bioregion Sod Tussock Grasslands **Association 1–1:** Scientific Name: *Hemarthria uncinata – Pteridium esculentum* Sod Tussock Grasslands	*Hemarthria uncinata, Pteridium esculentum, Imperata cylindrica, Ficinia nodosa, Parsonsia lanceolata.*	*Themeda triandra, Hibbertia vestita, Zoysia macrantha, Pultenaea maritima, Polymeria calycina, Viola banksii, Cynodon dactylon, Pimelea linifolia, Zieria prostrata, Lobelia anceps, Goodenia rotundifolia. Gonocarpus humilus.*	*Hemarthria uncinata, Pteridium esculentum, Imperata cylindrica, Ficinia nodosa, Parsonsia lanceolata, Stephania japonica, Hydrocotyle hirta.*	Sample plots restricted to Broughton Island within the NSW North Coast Bioregion. Likely also to occur on sands with a high-water table on the mainland within the same bioregion.
Alliance 2: Scientific Name: *Cynodon dactylon – Microlaena stipoides* North Coast and South East Coast Bioregion Grassy Shrublands & Grasslands	*Microlaena stipoides, Cynodon dactylon, Poa poiformis, Eragrostis leptostachya, Ficinia nodosa, Schoenus nitens, Glycine clandestina, Hydrocotyle sibthorpioides, Sporobolus creber, Crassula sieberiana.*	*Themeda triandra, Hibbertia vestita, Pultenaea maritima, Polymeria calycina, Zieria prostrata, Goodenia rotundifolia, Gonocarpus humilis.*	*Cynodon dactylon, Microlaena stipoides, Poa poiformis, Eragrostis leptostachya, Viola banksii, Zoysia macrantha, Ficinia nodosa, Micromyrtus ciliata, Lobelia anceps, Glycine clandestina, Schoenus nitens.*	Often dominated by the C_3 *Microlaena stipoides.* Found most commonly as grasslands in the open south of Narooma within the South East Corner Bioregion. Found as far north as Coffs Harbour within sheltered sites adjacent shrublands.
Association 2–1: Scientific Name: *Cynodon dactylon – Viola banksii* Grassland	*Cynodon dactylon, Viola banksii, Schoenus nitens, Bothriochloa decipiens, Schoenus apogon, Lobelia anceps, Centipeda minima*	*Themeda triandra, Hibbertia vestita, Pultenaea maritima, Zieria prostrata, Goodenia rotundifolia, Gonocarpus humilus, Imperata cylindrica, Poa poiformis.*	*Cynodon dactylon, Viola banksii, Schoenus nitens, Bothriochloa decipiens, Zoysia macrantha, Schoenus apogon, Lobelia anceps, Pimelea linifolia, Themeda triandra, Hydrocotyle hirta.*	Constituting the disjunct northern occurrence of this Group. Generally found in more frequently disturbed sheltered sites where *Themeda triandra* has been excluded and/or on sites where sand deposition has occurred.
Association 2–2: Scientific Name: *Zoysia macrantha – Ficinia nodosa* Grassy Shrublands and Grassland	*Zoysia macrantha, Ficinia nodosa, Zieria cytisoides, Westringia fruticosa, Crassula sieberiana, Sporobolus creber.*	*Themeda triandra, Hibbertia vestita, Pultenaea maritima, Polymeria calycina, Viola banksii, Cynodon dactylon, Pimelea linifolia, Zieria prostrata, Goodenia rotundifolia, Schoenus apogon.*	*Zoysia macrantha, Ficinia nodosa, Lobelia anceps, Zieria cytisoides, Westringia fruticosa, Sporobolus creber, Crassula sieberiana, Themeda triandra.*	Generally restricted to South East Corner Bioregion in the Eden area but may occur further north in favourable areas. *Zoysia macrantha* is a common species along the entire coast that is a highly salt tolerant species. Generally occurring closer to the seaward edge. The combination with *Ficinia nodosa* indicates a generally higher moisture availability of sites.
Association 2–3: Scientific Name: – *Poa poiformis - Microlaena stipoides* Grassland	*Poa poiformis, Microlaena stipoides, Eragrostis leptostachya, Cynodon dactylon, Ficinia nodosa, Glycine clandestina, Hydrocotyle sibthorpioides, Dichondra repens, Oxalis perennans, Lobelia anceps, Rytidosperma racemosum, Cheilanthes sieberi.*	*Themeda triandra, Hibbertia vestita, Zoysia macrantha, Pultenaea maritima, Polymeria calycina, Viola banksii, Pimelea linifolia, Zieria prostrata, Goodenia rotundifolia, Gonocarpus humilis.*	*Microlaena stipoides, Poa poiformis, Eragrostis leptostachya, Cynodon dactylon, Ficinia nodosa, Glycine cladestina, Lobelia anceps, Hydrocotyle sibthorpioides, Oxalis perennans, Entolasia stricta, Dichondra repens.*	Generally restricted to the South East Corner Bioregion. Dominated by C_3 grasses and in particular *Poa poiformis* which is largely confined to the most southern parts of the continent. Generally found where rainfall is higher and more aseasonal or winter dominant.

Hierarchy	Positive diagnostic (SIMPER)	Negative diagnostic (SIMPER)	Common taxa	Notes and distribution
Alliance 3: Scientific Name: *Themeda – Hibbertia – Pultenaea* South East Qld to South East Coast Bioregions Shrubby Grassland, Prostrate Heathy Grasslands & Sod Tussock Grasslands	*Themeda triandra, Hibbertia vestita, Pultenaea maritima, Polymeria calycina, Pimelea linifolia, Zieria prostrata, Goodenia rotundifolia, Hydrocotyle hirta, Gonocarpus humilis, Poranthera microphylla, Podolobium scandens, Pultenaea myrtoides, Senecio spathulatus.*	*Microlaena stipoides, Poa poiformis, Hemarthria uncinata, Eragrostis leptostachya, Pteridium esculentum, Schoenus nitens, Hydrocoytle sibthorpioides, Bothriochloa decipiens, Sporobolus creber.*	*Themeda triandra, Hibbertia vestita, Pultenaea marítima, Zoysia macrantha, Polymeria calycina, Viola banksii, Cynodon dactylon, Pimelea linifolia, Zieria prostrata, Gonocarpus humilis, Goodenia rotundifolia, Lobelia anceps.*	Found across the entire study area from the South East Queensland Bioregion to the South East Corner Bioregion.
Association 3–1: Scientific Name: *Cynodon dactylon – Viola banksii – Micromyrtus ciliata* Shrubby Grassland & Grassland	*Cynodon dactylon, Viola banksii, Hydrocotyle hirta, Micromyrtus ciliata, Parsonsia straminea, Hydrocotyle laxiflora, Dichondra repens, Lobelia purpurascens, Crassula sieberiana.*	*Themeda triandra, Hibbertia vestita, Zoysia macrantha, Pultenaea maritima, Pimelea linifolia, Zieria prostrata, Lobelia anceps, Goodenia rotundifolia, Gonocarpus humilis, Schoenus apogon, Ficinia nodosa, Imperata cylindrica, Poa poiformis, Lomandra longifolia, Microlaena stipoides, Carex breviculmis, Entolasia stricta.*	*Cynodon dactylon, Viola banksii, Hydrocotyle hirta, Micromyrtus ciliata, Polymeria calycina, Parsonsia straminea, Hydrocotyle laxiflora, Lobelia purpurascens, Dichondra repens, Hibbertia vestita, Themeda triandra.*	Found from the North Coast Bioregion (Coffs Harbour) to the Sydney Basin (Ulladulla). Often occurring in disturbed sites or heavily disturbed in the past.
Association 3–2: Scientific Name: *Zoysia macrantha – Aotus ericoides* Grassland	*Zoysia macrantha, Aotus ericoides, Imperata cylindrica, Centella asiatica, Commelina cyanea, Actinotus helianthi, Dianella congesta, Einadia hastata, Baumea juncea, Wahlenbergia littoricola.*	*Themeda triandra, Hibbertia vestita, Pultenaea maritima, Polymeria calycina, Viola banksii, Cynodon dactylon, Zieria prostrata, Lobelia anceps, Goodenia rotundifolia, Gonocarpus humilis, Ficinia nodosa.*	*Zoysia macrantha, Aotus ericoides, Imperata cylindrica, Themeda triandra, Centella asiatica, Dianella congesta, Actinotus helianthi, Commelina cyanea, Pimelea linifolia, Baumea juncea, Einadia hastata.*	Restricted to the NSW North Coast Bioregion occurring north of Coffs Harbour. Occurring in higher salt deposition areas. *Aotus ericoides* and *Actinotus helianthi* become prominent associated species in these northern locales but are largely absent further south.
Association 3–3: Scientific Name: *Zoysia macrantha – Themeda triandra* Shrubby Grassland & Sod Tussock Grassland	*Zoysia macrantha, Wollastonia uniflora, Viola banksii, Zieria prostrata, Poa poiformis, Lomandra longifolia, Podolobium scandens, Plectranthus cremnus, Senecio spathulatus, Atriplex cinereas.*	*Pultenaea marítima, Cynodon dactylon, Hydrocoytle hirtus, Pultenaea myrtoides, Aotus ericoides. Westringia fruticosa.*	*Zoysia macrantha, Themeda triandra, Wollastonia uniflora, Hibbertia vestita, Viola banksii, Plectranthus cremnus, Poa poiformis, Zieria prostrata, Podolobium scandens, Lomandra longifolia, Senecio spathulatus, Pimelea linifolia.*	More common assemblage than Assemblage 3.2 found within the NSW North Coast Bioregion (Coffs Harbour) to the South East Coast Bioregion (Bega). In higher salt deposition areas closer to seaward edge. Prostrate shrubs generally less prominent in this assemblage. *Atriplex cinereas* found only in the southern locales.
Association 3–4: Scientific Name: *Themeda triandra – Microlaena stipoides* Shrubby Grassland & Sod Tussock Grassland	*Microlaena stipoides, Cynodon dactylon, Commelina cyanea, Melaleuca armillaris, Bulbine bulbosa, Goodenia bellidifolia, Westringia fruticosa, Crassula sieberiana.*	*Hibbertia vestita, Zoysia macrantha, Pultenaea maritima, Polymeria calycina, Pimelea linifolia, Zieria prostrata, Lobelia anceps, Goodenia rotundifolia, Gonocarpus humilis, Ficinia nodosa, Imperata cylindrica.*	*Themeda triandra, Microlaena stipoides, Cynodon dactylon, Commelina cyanea, Schoenus apogon, Melaleuca armillaris, Goodenia bellidifolia, Bulbine bulbosa.*	Found within the South East Corner Bioregion. Small occurrences within the Moruya area. This assemblage occurs at the cross over of *Themeda* dominated assemblages to the north and *Microlaena* dominated assemblages to the south.
Association 3–5: Scientific Name: *Themeda triandra – Pultenaea maritima* Prostrate Heathy Grassland & Sod Tussock Grassland	*Themeda triandra, Polymeria calycina, Pultenaea maritima, Goodenia rotundifolia, Lobelia anceps, Pultenaea myrtoides.*	*Zoysia macrantha, Microlaena stipoides, Zieria prostrata, Poa poiformis, Hemarthria uncinata, Eragrostis leptostachya, Aotus ericoides, Micromyrtus ciliatus.*	*Themeda triandra, Pulteanea marítima, Hibbertia vestita, Polymeria calycina, Zoysia macrantha, Viola banksii, Cynodon dactylon, Pimelea linifolia, Zieria prostrata, Goodenia rotundifolia, Gonocarpus humilis, Lobelia anceps.*	The most common assemblage found from South East Qld to the South East Corner Bioregion. Largely dominated by *Themeda triandra* throughout its range this community type has a wide ecological amplitude but primarily found on higher nutrient soils e.g. basalt derived.
Association 3–6: Scientific Name: *Themeda triandra – Zieria prostrata* Prostrate Heathy Grassland, Shrubby Grassland & Sod Tussock Grassland	*Zieria prostrata, Hibbertia vestita, Viola banksii, Acacia sophorae, Schoenus apogon, Kunzea capitata, Gonocarpus humilis, Entolasia stricta, Leptospermum* sp., *Lomandra multiflora, Baumea juncea, Cynodon dactylon.*	*Lobelia anceps, Imperata cylindrica, Lomandra longifolia, Ficinia nodosa, Pultenaea myrtoides.*	*Themeda triandra, Zieria prostrata, Hibbertia vestita, Acacia sophorae, Viola banksii, Polymeria calycina, Zoysia macrantha, Pultenaea maritima, Pimelea linifolia, Schoenus apogon, Cynodon dactylon, Gonocarpus humilis.*	Restricted to the NSW North Coast Bioregion occurring north of Diamond Head. Generally distinguished by the presence of *Zieria prostrata* this assemblage often occurs closer to and is protected by dense taller shrub patches.

Figure 5. Alliance 2 *Cynodon dactylon – Microlaena stipoides* North Coast and South East Coast Bioregion Grassy Shrublands & Grasslands (Eurobodalla National Park).

Table 2. Comparison with existing classifications within eastern Australia. Plant Community Types (PCT), class and formation are part of the current New South Wales vegetation classification schema; Regional Ecosystems comprise the Queensland equivalent of associations.

Hierarchy	Previous published classification units
Group: Scientific Name: *Themeda – Pultenaea – Zoysia - Cynodon* grasslands & heathy grasslands Colloquial: Grasslands of South East Australian Coastal Headlands	Contained within Class - Maritime Grasslands (Keith 2004).
Association 1–1: *Hemarthria uncinata – Pteridium esculentum* Sod Tussock Grasslands	Not previously circumscribed.
Association 2–1: Scientific Name: *Cynodon dactylon – Viola banksii* Grassland	Not previously circumscribed.
Association 2–2: Scientific Name: *Zoysia macrantha – Ficinia nodosa* Grassy Shrublands and Grassland	Contained within 3: *Isolepis nodosa – Stenotaphrum subsecundum* Community (Adam et al. 1990).
Association 2–3: Scientific Name: – *Poa poiformis - Microlaena stipoides* Grassland	Contained within *Poa poiformis* Alliance (Beadle 1981); 3: *Isolepis nodosa – Stenotaphrum subsecundum* Community (Adam et al. 1990).
Association 3–1: Scientific Name: *Cynodon dactylon – Viola banksii – Micromyrtus ciliata* Shrubby Grassland & Grassland	In part Assemblage 5: *Cynodon dactylon – Viola banksii – Zoysia macrantha* and 6: *Viola banksii – Schoenus apogon – Zoysia macrantha* (Hunter and Hunter 2017a).
Association 3–2: Scientific Name: *Zoysia macrantha – Aotus ericoides* Grassland	Not previously circumscribed.
Association 3–3: Scientific Name: *Zoysia macrantha – Themeda triandra* Shrubby Grassland & Sod Tussock Grassland	Equivalent to Assemblage 4: *Zoysia macrantha – Melanthera biflora – Viola banksii* (Hunter and Hunter 2017a).
Association 3–4: Scientific Name: *Themeda triandra – Microlaena stipoides* Shrubby Grassland & Sod Tussock Grassland	Equivalent to 5.1.5 *Themeda australis* on Headlands Alliance (Beadle 1981); Possibly contained within 5: *Monotoca elliptica – Banksia integrifolia* Community (Adam et al. 1990).
Association 3–5: Scientific Name: *Themeda triandra – Pultenaea maritima* Prostrate Heathy Grassland & Sod Tussock Grassland	Equivalent to 5.1.5 *Themeda australis* on Headlands Alliance (Beadle 1981); Headland Thicket (Myerscough and Carolin 1986); 2: *Themeda australis* Community and in part 7: *Westringia fruticosa* Community (Adam et al. 1990); Community No. 14: *Themeda australis* Sod Grassland (Griffith et al. 2003); PCT 897 & 898: Kangaroo Grass Sod Tussock Grassland of Coastal areas of the Sydney Basin, PCT 1272: *Themeda australis* Sod Tussock Grassland of the NSW North Coast Bioregion, PCT 1513: Kangaroo Grass Sod Tussock Grassland of Coastal Areas of the North Coast (Benson 2006); GL: Headland Grassland of South East NSW (Tozer et al. 2010); Assemblage 1–3: 1 *Themeda triandra – Polymeria calycina – Pultenaea maritima*, 2 *Themeda triandra – Viola banksii – Cynodon dactylon*, 3 *Themeda triandra – Viola banksii – Cynodon dactylon* (Hunter and Hunter 2017).
Association 3–6: Scientific Name: *Themeda triandra – Zieria prostrata* Prostrate Heathy Grassland, Shrubby Grassland & Sod Tussock Grassland	Equivalent to 5.1.5 *Themeda australis* on Headlands Alliance (Beadle 1981); Assemblage 1–3: 1 *Themeda triandra – Polymeria calycina – Pultenaea maritima* (Hunter and Hunter 2017).

Figure 6. Alliance 3 *Themeda – Hibbertia – Pultenaea* South East Qld to South East Coast Bioregions Shrubby Grassland, Prostrate Heathy Grasslands & Sod Tussock Grasslands (Moonee Beach Nature Reserve).

Table 3. Comparison of species density and general environmental data and average percent cover synoptic table of Grasslands of South East Australian Coastal Headlands. 1–1 *Hemarthria uncinata – Pteridium esculentum*, 2–1 *Cynodon dactylon – Viola banksii*, 2–2 *Zoysia macrantha – Ficinia nodosa*, 2–3 *Poa poiformis – Microlaena stipoides*, 3–1 *Cynodon dactylon – Viola banksii – Micromyrtus ciliata*, 3–2 *Zoysia macrantha – Aotus ericoides*, 3–3 *Zoysia macrantha – Themeda triandra*, 3–4 *Themeda triandra – Microlaena stipoides*, 3–5 *Themeda triandra – Pultenaea maritima*, 3–6 *Themeda triandra – Zieria prostrata*. Climatic data was derived from ANUCLIM 6.1.1 (Xu and Hutchinson 2011) modelled using the variables easting, northing and altitude.

Association	1–1	2–1	2–2	2–3	3–1	3–2	3–3	3–4	3–5	3–6
Number of plots	2	2	2	8	7	7	3	15	463	12
Species density (4 m^2)	5–6 (6)	5–17 (12)	11–11 (11)	13–21 (16)	4–20 (13)	9–12 (11)	4–19 (13)	13–19 (16)	2–27 (11)	13–25 (18)
Average sward height	55	11	34	24	30	30	17	40	23	15
Mean Annual Temperature (°C)	18.1	20.8–21.2	14.4	17.5–19.3	19.1–20.6	21.1–21.4	17.9–21.4	18.4–18.9	17.8–22.1	20.4–21.7
Annual Precipitation (mm)	1488–1490	1583–1711	862–863	817–1074	1179–1671	1390–1646	988–1711	891–978	941–1875	1559–1730
Association 1–1										
Hemarthria uncinata	100	0	0	0	0	0	0.5	0	0	0
Pteridium esculentum	29	0	0	0	0	0	0.2	0	0.1	0
Imperata cylindrica	16	0	0	0.1	0	14.3	0.5	0	0.9	0
Association 2–1										
Cynodon dactylon	0	85	0	15.4	29.1	0	0	15	2.3	4
Viola banksii	0	30	0	0.8	7.9	0	6	1.5	3.4	8.2
Schoenus nitens	0	12.5	0	0	0	0	0	0	0.3	0
Bothriochloa decipiens	0	7.5	0	0	0	0	0	0	0	0
Association 2–2										
Westringia fruticosa	0	0	35	0	0	0	0	1	0.5	0
Zieria cytisoides	0	0	15	0	0	0	0	0	0	0
Paspalum dilatatum	0	0	8.5	0.1	0	0	0.1	1	0.2	0.8
Association 2–3										
Microlaena stipoides	0	0	0	40.9	0	0	0.5	25	0.1	1.8
Poa poiformis	0	0	0	31	0	0	4.9	0	0.4	0
Eragrostis leptostachya	0	0	0	20.6	0	0	0.1	0.5	0	0

Association	1–1	2–1	2–2	2–3	3–1	3–2	3–3	3–4	3–5	3–6
Association 3–1										
Stenotaphrum secundatum	0	0	5	0.8	71.7	0	0.1	0	0.4	0
Hydrocotyle hirta	0.5	1.5	0	0	7.9	0	0.1	0	1	0.2
Micromyrtus ciliata	0	0	0	0	7.1	0	0	0	0	0
Association 3–2										
Zoysia macrantha	0	4	25	0	0	86.7	56.3	0	4.6	7.3
Aotus ericoides	0	0	0	0	0	50	0	0	0.3	0
Centella asiatica	0	0	0	0	0	4.7	0	0	0.1	0
Dianella congesta	0	0	0	0.1	0	4	0	0.5	0.3	0
Actinotus helianthi	0	0	0	0	0	4	0	0	0.3	0
Association 3–3										
Wollastonia uniflora	0	0	0	0	0	0	15	0	0.1	0
Plectranthus cremnus	0	0	0	0	0	0	8	0	0	0
Podolobium scandens	0	0	0	0	0	0	4.5	0	0.6	1.6
Lomandra longifolia	0	0.5	0	0.5	0	0	4.3	0	0.9	0
Senecio spathulatus	0	0	0	0	0	0	3.6	0	0.4	0
Association 3–4										
Commelina cyanea	0	0	0	0.3	0.4	3.3	0	25	0.3	0
Sporobolus fertilis	0	0	0	0	0	0	0	25	0	0
Plantago lanceolata	0	0	0.5	0.1	0	0	0	2	0	0.1
Bulbine bulbosa	0	0	0	0	0	0	0	2	0	0
Goodenia bellidifolia	0	0	0	0	0	0	0	2	0	0
Melaleuca armillaris	0	0	0	0	0	0	0	2	0	0
Association 3–5										
Themeda triandra	0	1.5	0.5	0	0.6	8.3	22.8	29	88.5	29.1
Pultenaea maritima	0	0	0	0	0	0	0.7	0	7.9	4.8
Hibbertia vestita	0	0.5	0	0	1	0	7.9	0	7.8	16.6
Lobelia anceps	0	3	2	2.5	0	0	0.5	0	1.3	0.4
Association 3–6										
Zieria prostrata	0	0	0	0	0	0	4.8	0	1.4	26
Acacia sophorae	0	0	0	0.3	0	0	0	0	0.2	8.8
Banksia integrifolia	0	0	0	0.1	0	0	0.1	0	0.1	8.3
Polymeria calycina	0	1	0	0	3.7	1.3	2.1	0	6	7.8
Hypochaeris radicata	0	2.5	2.5	1.5	0.1	0	1.6	0	0.5	5.2
Pimelea linifolia	0	2	0	0	0.1	2.7	3.5	0	2.5	4.8
Schoenus apogon	0	3	0	0.1	0	0	1.3	2	1	4.4
Gonocarpus humilis	0	0	0	0	0	0	0.5	0	1.3	3.8
Entolasia stricta	0	0	0	1.5	0	0	1.1	0	0.9	3.5
Dichondra repens	0	0	0	1.5	1.6	0	1.1	1.5	0.8	2.8
Leptospermum liversidgei	0	0	0	0	0	0	0	0	0	2.5
Goodenia rotundifolia	0	0	0	0	0	0	0.1	0	1.3	2.4
Lomandra multiflora	0	0	0	0	0	0	0.3	0	0.1	2.4
Baumea juncea	0	0	0	0	0	2	0	0	0.1	2.1
Viola betonicifolia	0	0	0	0.3	0	0	0	0	0.1	2.1

servation tenure. Ninety-three (87%) mapped hectares (68 ha within reserves) was found to conform to the listed endangered ecological community based on plot data and on-ground assessment. Inclusion within the endangered community was easily assessed as the main criterion is a dominance of *Themeda triandra*. Only 24 mapped stands were over one hectare in size with the largest being 5.3 ha.

Discussion

Previously, no comprehensive vegetation survey and classification has been attempted on coastal grassland vegetation on coastal headlands along their whole range of occurrence in NSW. This study has derived ten distinct associations. At least three of the assemblages have no synonymous descriptions one of these is considered to be at the group level within this analysis (Table 2). A further three assemblages were only recently circumscribed during an earlier analysis of a subset of this same dataset (Hunter and Hunter 2017b). Although four Plant Community Types (PCT) are currently recognised on coastal headlands within the NSW classification system, all of these types would fall within a single association in the analysis presented here (Association 3.5; Table 2). Thus, currently only one of the associations described here is included within the state-based classification schema. Association 3.5 *Themeda triandra – Pultenaea maritima* Prostrate Heathy Grassland and Sod Tussock Grassland is the most widespread, has been described by numerous authors (Table 2) and constitutes what is circumscribed by the endangered community listing. The other nine associations herewith are more restricted and rarer but have no protection under current legislation (Table 1).

The ten associations were found to fall within three distinct alliances. Alliance 1 was only found as isolated examples where the water table was found close to the surface and was found to have no shrubby elements distinguishing it from the other two alliances. Alliance 2 and 3 though they overlap in distribution likely due to exposure and local site conditions largely represent northern and southern floristic elements. Within Alliance 2 the dominant grasses were largely of the C_3 photosynthetic pathway (Table 1). The diversity of shrubs was lower within Alliance 2 with *Micromyrtus ciliata* being the most common associated low shrub (Table 1). Alliance 3 in contrast is largely dominated by C_4 grasses and a high diversity of associated prostrate or low growing shrubs.

Collectively these grasslands on headlands are highly restricted with the extant distribution being approximately 107 ha along more than 2,000 km of coastline. Though they are restricted they appear to be well reserved with at least 64% (73% of the listed endangered *Themeda* type) of the known area of occurrence falling with public reserves. Although these grasslands are highly disjunct and small in area, they are better reserved than almost any other vegetation type within NSW. Despite previous suggestions, lack of tenure security is likely not a threat for the *Themeda* dominated grasslands.

Currently invasion and competition by native *Poa* spp., in particular *Poa poiformis*, is listed as threat to the more common *Themeda triandra* dominated assemblages. Management actions have been enacted to counteract the threat of *Poa* invasion. *Poa* spp. were rare on coastal headlands and *Poa poiformis* was only sampled in 26 plots (0.05%) and only dominated four and is described here within its own association *Poa poiformis – Microlaena stipoides* Grassland which is highly restricted in southern NSW. Observations made during this survey would suggest that *Poa* spp. are not a threat to *Themeda triandra* assemblages. In context *Poa poiformis* assemblages are significantly rarer and more threatened in NSW and have a general distribution along the cooler and more temperate southern coasts of Australia. *Themeda triandra* is more common and dominant in northern locales. *Themeda triandra* has a C_4 and *Poa poiformis* a C_3 photosynthetic pathway and it is suggested that *Themeda triandra* is naturally less dominant in southern locations with *Poa poiformis* becoming more naturally abundant further south. Southern NSW is the expected location for floristic turnover between *Poa poiformis* and *Themeda triandra* dominated assemblages which has been misinterpreted as invasion. It is suggested here that *Poa poiformis* is therefore not a threat to the endangered listed *Themeda triandra*-dominated assemblages and is more likely a rare occurrence that warrants protection within NSW rather than eradication from headlands within the state.

Conclusion

This comprehensive analysis of the full distribution of grassland occurrences on headlands within NSW has highlighted significant gaps in our knowledge. Three associations have not previously been described but more importantly nine associations have no corresponding type within the NSW state-wide classification. All of these nine previously uncharacterised types are much more restricted and threatened than the more common *Themeda triandra*-dominated association and remain unprotected. This fuller survey has also allowed a better interpretation of floristic distribution and dominance and cast doubt on *Poa* spp. invasion as a listed threatening process. Even areas considered to be generally well surveyed may have undervalued and under protected vegetation types.

Data availability

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).

Acknowledgements

I wish to thank Vanessa Hunter for assisting in the collection of all plot data. The author has no support funding to report.

References

Adam P, Stricker P, Wiecek BM, Anderson DJ (1990) The vegetation of seacliffs and headlands in New South Wales, Australia. Australian Journal of Ecology 15: 515–547. https://doi.org/10.1111/j.1442-9993.1989.tb01459.x

Baines G, Dunford M (2008) Grassland modelling in the Southern Tablelands. Report to National Recovery Team for Natural Temperate Grassland Environment ACT.

Beadle NCW (1981) The Vegetation of Australia. Gustav Fischer, Stuttgart. https://doi.org/10.1007/978-94-009-8629-9_23

Bruelheide H, Dengler J, Jiménez-Alfaro B, Purschke O, Hennekens SM, Chytrý M, Pillar VD, Jansen F, Kattge J, … Zverev A (2019) sPlot – a new tool for global vegetation analysis. Journal of Vegetation Science 30: 161–186. https://doi.org/10.1111/jvs.12710

De Cáceres M, Chytry M, Agrillo E, Attorre F, Botta-Dukát Z, Capelo J, Czúz B, Dengler J, Ewald J, Faber-Langendoen D, … Wiser SK (2015) A comparative framework for broad-scale plot-based vegetation classification. Applied Vegetation Science 18: 543–560. https://doi.org/10.1111/avsc.12179

De Cáceres M, Franklin S, Hunter JT, Landucci F, Dengler J, Roberts D (2018) Global overview of plot-based vegetation classification approaches. Phytocoenologia 48: 101–112. https://doi.org/10.1127/phyto/2018/0256

Faber-Langendoen D, Keeler-Wolf T, Meidinger D, Tart D, Hoagland B, Josse C, Navarro G, Ponomarenko S, Saucier J-P, … Comer P (2014) EcoVeg: a new approach to vegetation description and classification. Ecological Monographs 84: 533–561. https://doi.org/10.1890/13-2334.1

Faber-Langendoen D, Baldwin K, Peet RK, Meidinger D, Muldavin E, Keeler-Wolf T, Josse C (2018) The EcoVeg approach in the Americas: U.S., Canadian and international Vegetation Classifications. Phytocoenologia 48: 215–237. https://doi.org/10.1127/phyto/2017/0165

Franklin SB, Hunter JT, De Cáceres M, Dengler J, Landucci F, Krestov P (2016) Introducing the IAVS Vegetation Classification Working Group. Phytocoenologia 46: 5–8. https://doi.org/10.1127/phyto/2016/0116

Gellie NJH, Hunter JT, Benson JS, Kirkpatrick JB, Cheal DC, McCreery K, Brocklehurst P (2017) Overview of plot-based vegetation classification approaches within Australia. Phytoceonologia 48: 251–272. https://doi.org/10.1127/phyto/2017/0173

Griffith SJ, Bale C, Adam P, Wilson R (2003) Wallum and related vegetation on the NSW North Coast: description and phytosociological analysis. Cunninghamia 8: 202–252. https://www.rbgsyd.nsw.gov.au/getmedia/6f182458-bb5f-41f6-be3a-b9c1569e24b7/Volume-8(2)-2003-Cun8Gri202-252.pdf.aspx

Henwood WD (2010) Toward a strategy for the conservation and protection of the World's temperate grasslands. Greater Plains Research 20: 121–134. https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=2073&context=greatplainsresearch

Hunter JT (2018) Complexities of shrub encroachment: are shrubs important for the maintenance of diversity in *Themeda*-dominated assemblages on coastal headlands in Australia. Journal of Coastal Conservation 22: 667–677. https://doi.org/10.1007/s11852-018-0599-8

Hunter JT, Hunter VH (2016) Tussock and sod tussock grasslands of the New England Tablelands Bioregion of eastern Australia. Pacific Conservation Biology 22: 12–19. https://doi.org/10.1071/PC15037

Hunter JT, Hunter VH (2017a) Floristics, dominance and diversity within the threatened *Themeda* grassy headlands of the North Coast Bioregion of New South Wales. Pacific Conservation Biology 23: 71–80. https://doi.org/10.1071/PC16013

Hunter JT, Hunter VH (2017b) The complex nature of headland shrub encroachment: the case of *Zieria prostrata*. Ecological Management and Restoration 18: 115–119. https://doi.org/10.1111/emr.12255

Hunter JT, Hunter VH (2019) High macropod populations at Look At Me Now Headland, North Coast NSW: implications for endangered *Themeda triandra*-grasslands on headlands. Cunninghamia 19: 97–106. https://doi.org/10.7751/cunninghamia.2019.008

Hunter JT, Lechner AM (2017) A multi-scale, hierarchical, ecoregional and floristic classification of arid and semi-arid ephemeral wetlands in New South Wales, Australia. Freshwater and Marine Science 69: 418–431. https://doi.org/10.1071/MF17006

Jensen F, Bergmeier E, Dengler J, Janišová M, Krestov, P, Willner W (2016) Vegetation classification: a task for our time. Phytocoenologia 46: 1–4. https://doi.org/10.1127/phyto/2016/0134

Keith DA (2004) Ocean Shores to Desert Dunes: The Native Vegetation of New South Wales and the ACT. Department of Environment and Conservation (NSW), Hurstville, Sydney.

Kirkpatrick JB (1977) The disappearing Heath. Tasmanian Conservation Trust, Hobart.

Kirkpatrick JB (1981) Coastal, heath and wetland vegetation. In: Jackson WD (Ed.) The Vegetation of Tasmania. Australian Academy of Science, Canberra, 36–54.

Moore NA, Camac JS, Morgan JW (2019) Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses. New Phytologist 221: 1424–1433. https://doi.org/10.1111/nph.15480

Morris EC, Skelton NJ, Durham SJ (1990) Vegetation of three headlands of the central coast of New South Wales – Norah, Wamberal and Wybung Heads. Wetlands Australia 9: 49–67. https://doi.org/10.31646/wa.201

Myerscough PJ, Carolin RC (1986) The vegetation of the Eurunderee Sand Mass, headlands and previous islands of the Myall Lakes Area, New South Wales. Cunninghamia 1: 399–466. https://www.rbgsyd.nsw.gov.au/getmedia/00e0c638-27be-4448-9c3a-c63ec790fde5/Volume-1(4)-1986-Myerscough399-466.pdf.aspx

Opie AM, Gullan PK, van Berke SC, van Rees H (1984) Vegetation of the Western Port catchment. Muelleria 5: 289–346.

Price JN, Good MK, Schultz NL, Guja LK, Morgan JW (2019) Multivariate drivers of diversity in temperate Australian native grasslands. Australian Journal of Botany 67: 367–380. https://doi.org/10.1071/BT18190

Tozer MG, Turner K, Keith D, Tindall D, Pennay C, Simpson C, MacKenzie B, Beukers P, Cox S (2010) Native vegetation of southeast NSW: a revised classification and map for the coast and eastern tablelands. Cunninghamia 11: 359–406. https://www.rbgsyd.nsw.gov.au/getmedia/b4f021cf-86e9-4eca-8f2e-058a7e574a3a/Volume-11(3)-2010-Cun113Toz359-406.pdf.aspx

Williams NSG, Marshall A, Morgan JW (2015) Land of Sweeping Plains: Managing and Restoring the Native Grasslands of South-eastern Australia. CSIRO Publishing: Melbourne, Victoria. https://doi.org/10.1071/9781486300822

Xu T, Hutchinson M (2013) ANUCLIM Version 6.1. Fenner School of Environment and Society, Australian National University, Canberra. http://fennerschool.anu.edu.au/files/anuclim61.pdf

E-mail and ORCID

John T. Hunter (jhunter8@bigpond.com)**, ORCID:** https://orcid.org/0000-0001-5112-0465

Supplementary material

Supplementary material 1

Mapped hectares of and tenure of mapped occurrences.
Link: https://doi.org/10.3897/VCS/2020/48228.suppl1

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 123–137
doi: 10.3897/VCS/2020/38629

RESEARCH PAPER

Vegetation Classification Exercise for the Pawnee National Grasslands, USA

Scott B. Franklin[1], Michael Scheibout[2], Jozef Šibik[3]

1 *School of Biological Sciences, University of Northern Colorado, Greeley, Colorado, USA*
2 *Union University, Jackson, Tennessee, USA*
3 *Institute of Botany, Slovak Academy of Sciences, Bratislava, Slovakia*

Corresponding author: Scott B. Franklin (scott.franklin@unco.edu)

Academic editor: David W. Roberts ♦ **Received** 29 July 2019 ♦ **Accepted** 30 September 2020 ♦ **Published** 16 November 2020

Abstract

Aims: Vegetation classifications are useful for a variety of management purposes as well as scientific exploration. Local classifications are common throughout the United States but only recently have been integrated into a national classification system, which is now expected for local classifications. **Study Area:** The Pawnee National Grasslands (PNG) in northeastern Colorado, USA, has not been classified using plot data, and is thus a gap on the baseline knowledge of the PNG plant communities that hinders impact assessment of various anthropogenic activities. **Methods:** Here, we use 128 plots to classify the vegetation of the PNG using a two-step process: first, classifying the PNG plots alone to characterize local uniqueness, and then employing a semi-supervised classification with an additional 64 plots from areas to the north and east of the PNG, using standard classification procedures. **Results:** We document on the PNG the occurrence of two Classes, three Subclasses, four Formations, five Divisions, six Macrogroups, seven Groups and eight Alliances and Associations already described in the USNVC. **Conclusions:** The PNG is dominated by the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association, which we further subdivide and describe as three local subassociations. The mixed-grass concepts in the USNVC do not exist in the PNG.

Taxonomic reference: Hazlett (1998).

Syntaxonomic reference: USNVC (2016).

Abbreviations: BLM = Bureau of Land Management; CPER = Central Plains Experimental Range; ESA = Ecological Society of America; EST = Ecological Site Type; GPS UTM = Global Positioning System Universal Transverse Mercator; NEON = National Ecological Observatory Network; PNG = Pawnee National Grasslands; USNVC = United States Vegetation Classification.

Keywords

Colorado, Pawnee, semi-supervised classification, shortgrass, steppe, USNVC, vegetation

Introduction

Classification of vegetation provides a common language to compare communities among regions, an inventory to assess change, and a baseline for land stewardship decisions (ESA Panel 2015). Vegetation classifications are useful for: (1) documenting complex vegetation patterns, (2) developing hypotheses about processes shaping such patterns, (3) mapping vegetation and related ecosystem properties, (4) surveying, monitoring and reporting plant and animal communities, and (5) developing management and conservation strategies

PENSOFT.

Copyright *Scott B. Franklin et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

(De Cáceres et al. 2015). While several initial efforts toward mapping and vegetation data collection are available for the Pawnee National Grasslands, there is no plot-based classification, despite the area including the Central Range Experiment Station of the United States Agricultural Research Service and a National Ecological Observatory Network (NEON) site. Here we present a plot-based classification that follows recent standards of the United States (Jennings et al. 2009; Faber-Langendoen et al. 2014) as well as international standards (De Cáceres and Wiser 2012; De Cáceres et al. 2015).

Baker (1984) provided a preliminary list of the natural vegetation communities for the entire state of Colorado, but gave no descriptions of the communities themselves. Johnson (1987) described 13 potential natural associations (in this case, cover types) based on previous literature. Hazlett (1998) described habitats based on vegetation occurrences integrated with site abiotic characteristics, but did not use plot data and thus performed no analyses. With the multiple uses of the PNG, from grazing to missile silos to the recent oil and natural gas boom, a consistent and standards-conforming classification of vegetation communities is needed for land stewardship decisions. The Colorado Vegetation Classification Project, an effort of the Bureau of Land Management (BLM) and the Colorado Department of Wildlife (http://www.arcgis.com/home/item.html?id=893739745fcd4e05af8168b7448cda0c), produced a classification using 1993–1997 Landsat Thematic Mapper imagery that was processed using an unsupervised classification procedure. Field-gathered GPS data were used to label and group the final classes. Based on that classification on broad-based life forms, the PNG lies in the Herbaceous Riparian (only one subclass, Sedge) or Grass/Forb Rangeland, including several subclasses pertinent to the PNG: Grass Dominated Herbaceous Rangeland, Forb Dominated Herbaceous Rangeland, Grass/Forb Mix Herbaceous Rangeland, Tall-grass Prairie, Mid-grass Prairie, Short-grass Prairie, Disturbed Rangeland and Sparse Grass/Blowouts. These are general names for large-scale vegetation communities and, thus, are likely not specific enough for local land stewards.

The Vegetation Subcommittee of the Federal Geographic Data Committee has developed a standard for vegetation classification in the United States (FGDC 2008), as well as descriptions of the approach (Jennings et al. 2009; Faber-Langendoen et al. 2009; Franklin et al. 2012; Faber-Langendoen et al. 2014), and the resulting United States National Vegetation Classification (USNVC) was released in February of 2016 (http://usnvc.org/website-launch/). The USNVC has already been successfully used to develop state-and-transition models of landscape change (Kudray and Cooper 2005) by standardizing the definition of states, develop habitat suitability maps and high-quality vegetation maps essential for biodiversity stewardship and research (Evens and Keeler-Wolf 2014), and improve the sharing of vegetation information among agencies for intra- and interagency management, such as mapping of vegetation and fuels in the LandFire program (https://my.usgs.gov/eerma/data/index/4f4e486ee4b07f02db50bea7).

Classification systems around the world are being developed and used for such purposes (Bruelheide and Chytrý 2000; Rodwell 2006), but small-scale, unconnected classifications within and among countries, and in the United States, within and among governmental units, have been the bane of developing regional classifications and the identification of community concepts over the range of their occurrence. Such is the problem in many areas of the United States and a standardized effort is needed to both corroborate USNVC concept descriptions and fill in the holes of the USNVC. Peet and Roberts (2013) define nine primary components of vegetation classification: 1) project planning, 2) data acquisition, 3) data preparation, 4) community entitation, 5) cluster assessment, 6) community characterization, 7) community determination, 8) classification integration, and 9) classification documentation. The advent of the USNVC has changed how researchers in the US approach these components; specifically, regarding classification integration recognizing that integration may also affect the iterative process of entitation and assessment. Because the USNVC concept descriptions are meant to cover the range of characteristics of a community concept, while collected data are potentially from a restricted area such as a park (as is the case in this study), documenting variations on that concept that are specific to the location may be beneficial to local stewards. However, that does not suggest the community concept itself be changed, as currently accepted concepts should only be modified after careful reflection (Jennings et al 2009; Peet and Roberts 2013).

An important element of any classification is the heterogeneity of the landscape, such that many different vegetation types may be found in a small geographic area. Further, one of the main uses of such classifications is mapping that provides information to stakeholders to make stewardship decisions (ESA Panel 2015), and this mapping level tends to be at the Macrogroup scale of the USNVC (combinations of moderate sets of diagnostic plant species and diagnostic growth forms that reflect biogeographic differences; FGDC 2008). While we fully expect the Great Plains Shortgrass Prairie to dominate the PNG landscape, we also expect to find more arid (e.g., Arid West Interior Freshwater Marsh) and more mesic types (e.g., Great Plains Flooded Forest).

The objective of this research was to develop a plot-based vegetation classification of the natural and semi-natural vegetation communities in the Pawnee National Grasslands in accordance with the USNVC. We followed standard procedures for data acquisition, used a variety of multivariate analyses for community entitation and determination, and integrated our community concepts with those of the USNVC, following the standards of Peet and Roberts (2013) and De Cáceres et al. (2015). We predicted that vegetation would be strongly affected by topography, especially slope positions that affect moisture levels, and that repeating patterns of vegetation communities would be found throughout the PNG landscape (i.e., community concepts would be recognizable).

Study area

The Pawnee National Grasslands (PNG), administered by the USDA Forest Service, covers 79,876 ha in Weld County, Colorado, between 40°36' and 41°00' N latitude and between 103°34' and 104°48' W longitude (Figure 1). The grasslands are a mosaic pattern of private and public lands; both are used for grazing, oil and gas extraction, and house below-ground nuclear missiles. Included within the PNG are the Central Plains Experimental Range (CPER; 6057 ha), a research area administered by the Agricultural Research Service (now also part of the National Ecological Observation Network, NEON) and the Shortgrass Steppe Long-term Ecological Research site (now maintained by Colorado State University).

Climate is continental, but large air masses from maritime areas may move across the area. Crabb (1981) reported an average air temperature of -2°C during the winter with an average daily minimum temperature of -10°C; during summer months, average air temperature is 21°C with an average daily maximum temperature of 31°C.

The Pawnee National Grasslands also lie in the rainshadow of the Rocky Mountains to the west. Mean annual precipitation for the study area is 305–380 mm; average annual snowfall is 102 mm (Crabb 1981). Wind-driven snow often accumulates on leeward sides of hills (typically southeastern sides), around shrubs, and near roads; meltdown, especially in rocky or sandy soil, results in water penetration to greater depths at these locations (Hazlett 1998). The PNG lies within Kuchler's (1964) Shortgrass Steppe, dominated by C_4 grasses, and two of his four potential natural vegetation types may occur on the PNG: the overwhelmingly dominant *Bouteloua-Buchloe* Type and the *Artemisia-Schizachyrium* Type on deep sandy soils. The Shortgrass Steppe is typically dominated by graminoids (> 60%) with less than 20% cover of succulents, dwarf shrubs, and herbaceous dicots (Laurenroth 2008). Classifications of portions of the PNG, e.g. the Central Plains Experimental Range, suggest only a handful of vegetation community types (Moir and Trlica 1976). The PNG falls in the Loamy Plains (*Atriplex canescens/ Bouteloua gracilis-Pascopyrum smithii*) Ecological Site Type (EST), part of the Central High Plains (https://esis.sc.egov.usda.gov/Welcome/pgESDWelcome.aspx). The EST classification includes discrete biological and physical factors that denote specific vegetation/soil/physical characteristics that respond similarly to management and disturbance. In addition, Hazlett (1998) differentiated six habitat types on the Pawnee: (1) open steppe (> 80% of study area), (2) sandy soils (~5%), (3) breaks and barrens

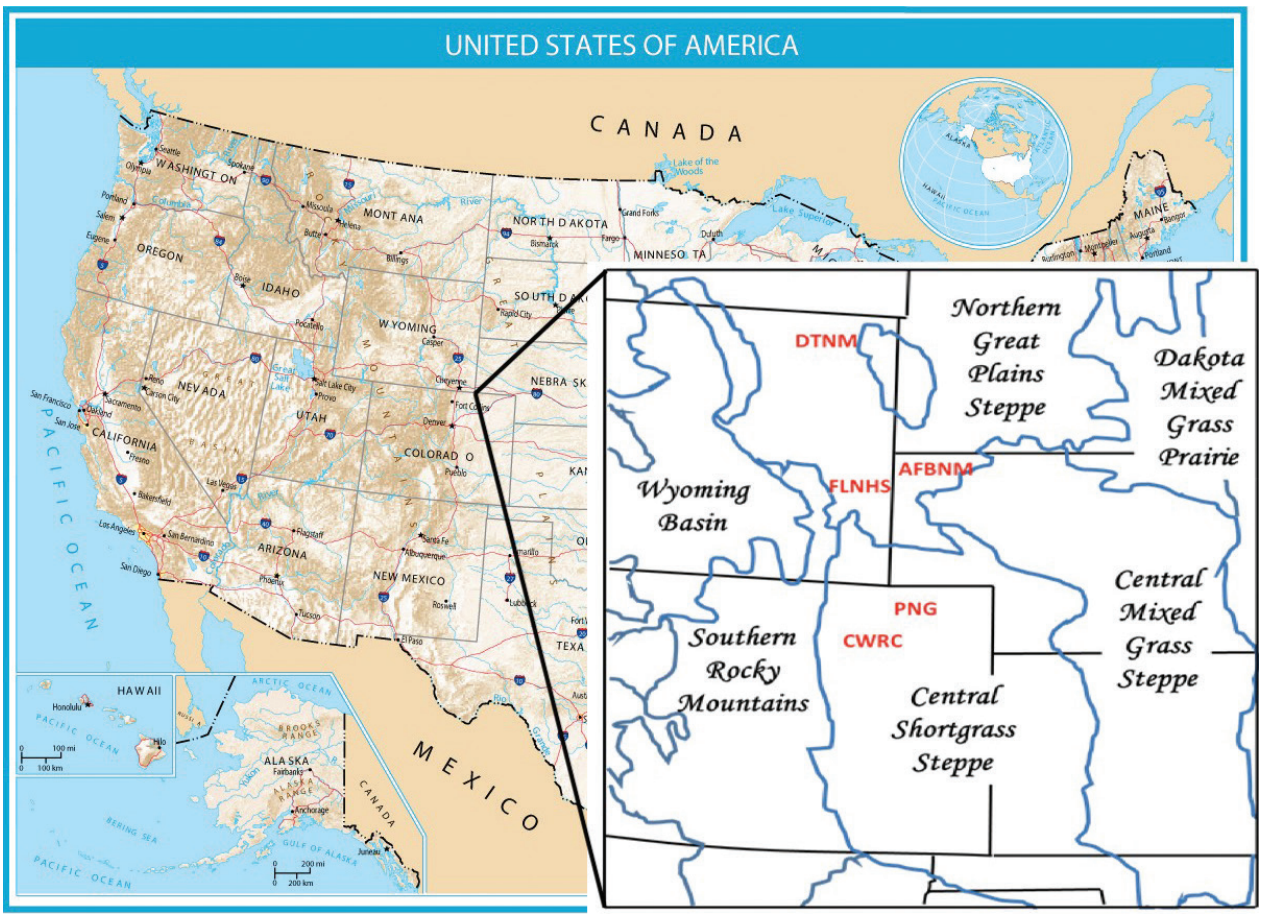

Figure 1. Location of Pawnee National Grasslands (PNG). Inset includes NatureServe Ecoregions of study area and additional plot data locations and studies: Classification of Natural Riparian/Wetland Plant Associations for Colorado (CWRC, throughout CO), Fort Laramie National Historic Site (FLNHS), Agate Fossil Beds National Monument (AFBNM), and Devil's Tower national Monument (DTNM).

(<2%), (4) cliffs and ravines (<2%), (5) riparian (~5%), and (6) roadsides and disturbed soils (< 5 %).

In general, the elevation of the Colorado Piedmont, an uplifted Cretaceous shale physiography that includes the PNG, declines from the mountain foothills toward the east at a rate of about 2 m km^{-1}; the highest elevation is 1,935 m in the northwestern portion near the "Chalk Bluffs" and the lowest elevation is 1,310 m in the southeastern portion around South Pawnee Creek. Most of the soils on the Pawnee National Grassland are shallow to deep loams that are well drained (Crabb 1981). Over most of the area is a loamy, wind-mixed veneer layer of soil of varying depths. These soils are underlain by a variable pattern of shale and sandstone bedrock materials. Barren rock or gravel areas of shale and sandstone can be exposed when erosive wind removes upper layers of soil. In addition, past tectonics and water erosion have exposed ravine "break" areas with rock exposed on the sides of the ravine. Sandy soils occur along stream terraces and on leeward sides of some hills (Hazlett 1998).

Swale areas often have finer textured soils than ridgetops, as mobile soil particles, such as silt and clay, have eroded from higher topographic positions and have been deposited in lower areas. This difference in soil texture is sometimes reflected by a greater abundance of *Buchloe dactyloides* in swales. In addition, some drainages, playas, and riparian areas have an accumulation of salts on or near the surface and thus host alkaline-tolerant plant species. Maps and detailed descriptions of the soil series types that occur in this study area can be found in Crabb (1981).

GIS techniques have been shown to be useful in determining distribution of plant and animal communities (Rotenberry et al 2006; Sangermano and Eastman 2006). The initial phase of this project used GIS map layers to develop an ecological land type classification that was subsequently used to stratify field plots (Kupfer and Franklin 2000). Map layers included elevation, bedrock geology, and soil classification obtained from the State of Colorado (http://coloradogeologicalsurvey.org/geologic-mapping/gis-data/). Plots (see below) were positioned within all 100 m elevation zones (1300–1800 m, which also was essentially an east to west gradient) and on all major parent materials (dune sand, gravel, sandstone, shale). We examined geology, soils, and topographic factors in an attempt to place plots in all environments (i.e., land types) of the Pawnee National Grasslands. Some noticeable trends are important (Figure 2). The western portion of the Pawnee is dominated by Cretaceous shales and the eastern portion by Tertiary sandstone; the eastern portion also contains some quaternary gravel and sand. There is also a general gradient in elevation, decreasing from west to east.

Methods

Field Data Collection

We obtained plots from all respective land types, but we purposefully did not set plots near roads, and the number of plots was fewer from habitats of lesser extent (e.g., riparian areas). Finally, discussion with Vernon Kohler (USFS, pers. comm.) and Don Hazlett (Denver Botanic Garden, pers. comm.) suggested vegetatively unique areas for plot locations. A posi-plot (positioned plot; Weaver and Robertson 1981) method was used to locate plots, first based on ecological land types and habitat types, and subsequently on visual vegetation communities. The GPS points for each of the community types were imported into ArcGIS and physical characteristics for each of these points were identified. In ArcGIS, plot locations were used to determine topographic characteristics (slope, aspect, elevation), soil type and rock type. Aspect was transformed following Beers et al. (1966).

101 plots were located based on visual homogeneity of vegetation (both dominant taxa and structure) and site characteristics, then randomly located within that area. Plot sampling followed the Carolina Vegetation Survey method (Peet et al. 1998). Plots were 0.1 ha; 20 m × 50 m made up of ten 10 m × 10 m modules unless vegetation heterogeneity constricted the size. If the area was small, modules were essentially 'fit' to the area to maintain homogenous vegetation within the plot. Within four intensive modules, subplots of 5 m × 5 m, 2 m × 2 m, 1 m × 1 m, and 0.3 m × 0.3 m were established in two corners (these corners were marked with GPS UTM coordinates; Peet et al. 1998). Presence of all taxa was described for each plot scale; cover of taxa was recorded for the 1 m × 1 m plots using the following cover scale (0–1%, 1–2%, 2–5%, 5–10%, 10–15%, 15–25%, 25–50%, 50–75%, 75–90%, >90%). Cover data were transformed to median values and averaged for all intensive modules for each plot prior to analyses. Both cover (estimated by module and averaged for the plot) and diameter at breast height (dbh) were recorded by species for all individual woody stems > 2.5 cm dbh. Cover values were used in all analyses.

In addition to the above data set, plots taken for a mountain plover study (Derner et al. 2009) with areas under heavy grazing were included in the analysis to determine the extent of differences among those communities and other steppe communities. These data were acquired with the permission of Paul Stapp, who had produced that canopy cover data in 27 fields; cover values for each field were derived from 30 1 m^2 quadrats spaced every 10 m along three 100 m transects. Data were transformed to median cover class values (Scale used for data collection: 0–5%, 6–15%, 16–25%, 26–40%, 41–60%, >60%) and averaged by pasture. These 27 plots along with the 101 plots make up the Pawnee-only data set (n=128).

Classification Protocol

Pawnee-Only Community Classification Analyses

We classified the data into 'plot-groups' using a hierarchical cluster analysis using the Sorenson dissimilarity measure and the Flexible Beta group linkage method

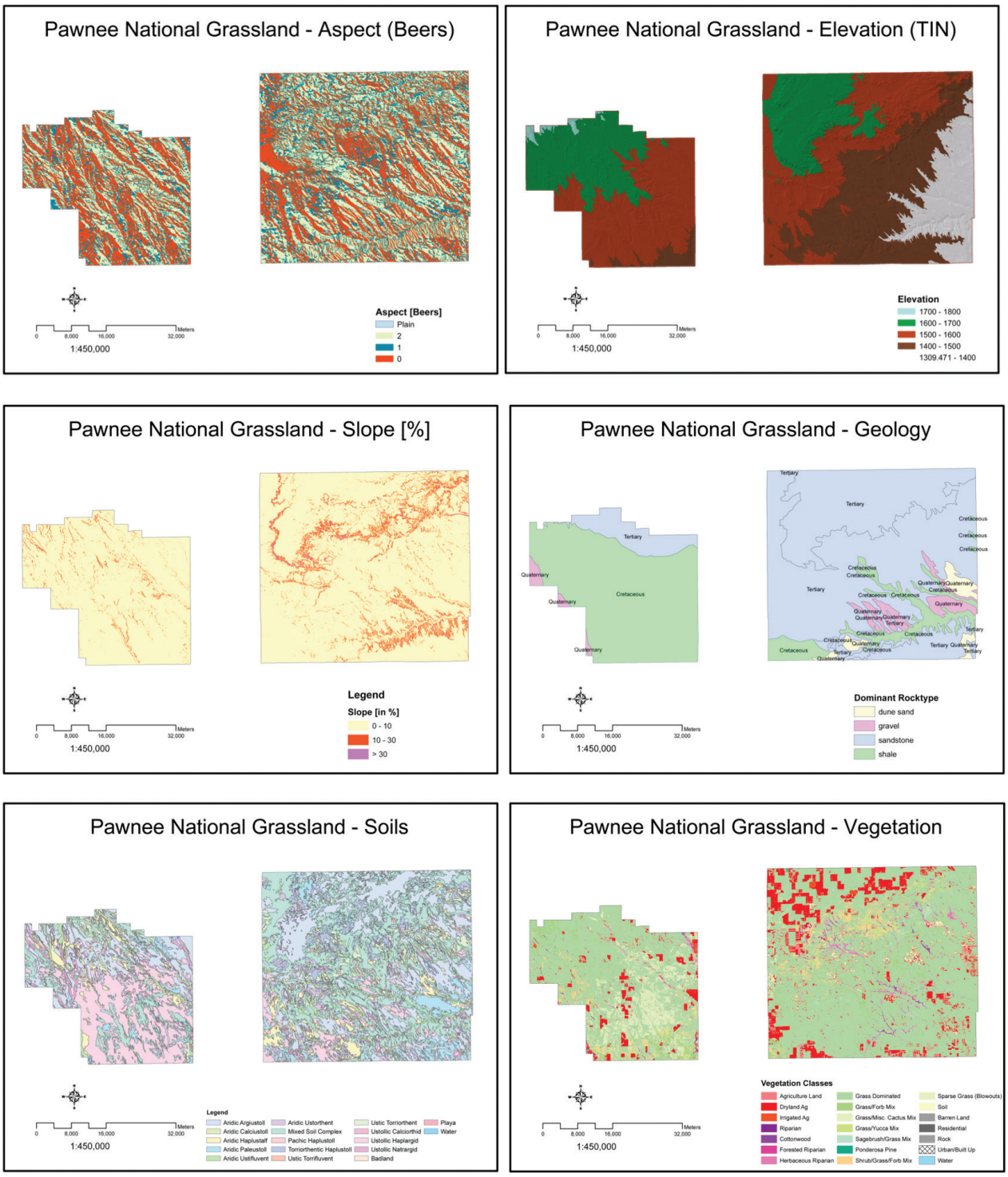

Figure 2. GIS maps of aspect, elevation, slope, soil type and vegetation type of the Pawnee National Grasslands (PNG). The two polygons represent the east and west sections of the PNG. Beers et al. (1966) transformation was used for aspect, ranging from 0 (SW) to 2 (NE); elevation ranges from 1309–1800 in 100 m intervals; slope ranges from low (0–10%) to medium (10–30%) to steep (>30%); vegetation and soild are based on previous classifications (see text).

(Beta = -0.25): data were square-root transformed prior to analysis using PCORD (McCune and Mefford 1999). We determined the number of plot-groups using Optim-Class Type 1 (Tichý et al. 2009) using the Juice 7.0.102 Program (http://www.sci.muni.cz/botany/juice/); the method compares clustering results obtained with different methods and numbers of clusters to determine which solution is optimal in terms of the number of diagnostic species. Given an optimal number of clusters we determined diagnostic species by analysis of frequency and fidelity (phi coefficient) using the Juice program. The phi coefficient is a measure of fidelity independent of sample size. Values range from -1 to 1 and positive values indicate species occur within groups more often than expected by

chance; higher values mean a greater degree of joint fidelity (Chytrý et al. 2002). Diagnostic species were those one to six species with the highest frequency and phi coefficient, chosen subjectively as meaningful.

We expected a gradient-driven distribution of vegetation related to a complex of environmental factors, including geological characteristics (soil type, rock type, % bare ground) and topographic characteristics (latitude, longitude, slope position, aspect). We promoted an ordinal scale to an interval scale for soil type, rock type, slope position, and site type, essentially from poor to less poor environmental conditions based on our knowledge of the area. We did not have data to assess scale so chose a simple linear scale and interpret the results conservatively. Soil Type included badland (1), Aridisol (2), Mollisol (3), mixed soil (4), Alfisol (5), and Entisol (6). Rock type included dune sand (1), sandstone (2), gravel (3) and shale (4). Slope position was coded 1 for convex ridgetop, 2 for flat slope, and 3 for concave ravine. Site Types were numbered from driest to most mesic: (1) blowout, (2) steppe hilltop, (3) steppe, (4) steppe buffalo wallow, (5) rock outcrop, (6) ridgetop, (7) draw slope, (8) ravine, (9) playa, and (10) riparian. Environmental data were related to vegetation groups through Canonical Correspondence Analysis and Nonmetric Multidimensional Scaling (using the Sorenson Index), species-environment correlations using 999 Monte-Carlo simulations, and descriptive statistics; all in PCORD. As a check on how strongly classified groups were tied to particular environments, we used a forward stepwise discriminant analysis (using SAS) to test if classified plot-groups could be predicted with site data, using the same promoted interval scale.

Semi-supervised Classification Analysis

Initial classification analyses showed eight plot-groups with four very small ones (including less than four plots), albeit these groupings were very different from other classified groups. After initial interpretation, we concluded these plots were all from rare mesic areas of the Pawnee National Grasslands. Accordingly, we compared PNG plots that made up the four small plot-groups with plots that had been previously classified elsewhere, a sort of semi-supervised classification (Tichý et al. 2014). For this, we retrieved an additional 64 plots from four other research projects within VegBank (Peet et al. 2013) with a query for plots containing the dominant and potentially diagnostic species of our small groups *Pascopyrum smithii*, *Carex nebrascensis*, *Eleocharis* species, and restricted to plots in the Great Plains (not foothills or mountains). These included the Agate Fossil Beds National Monument (AGFO; n=3) National Park Service Mapping Project in Nebraska (Project Contributer Jim Drake) and Devils Tower National Monument (DETO; n=6) National Park Service Mapping Project in Wyoming (Project Contributer Jim Drake), Fort Laramie National Historic Site (FOLA; n=34) National Park Service Mapping Project in Wyoming (Project Contributer Jim Drake), and the Classification of Natural Riparian/Wetland Plant Associations for Colorado (CWRC; n=21; Project Contributer Anonymous; Kittel et al. 1999).

Because all data were in VegBank there were relatively few taxonomy issues and these were vetted accordingly (e.g., *Arabis* = *Boechera, Agropyron smithii* = *Pascopyrum smithii*). However, several taxa were merged or deleted either due to questionable identification (unknown species) or too few individuals from the different study locations. For *Carex* or *Juncus* only, if species were unknown, those individual species observations were deleted, leaving only identified species data. We chose to merge taxa which were ecologically similar in their environment and when several plots did not identify them to species level (Suppl. material 1); most of these species also had very few individuals of one or more of the merged taxa. Such groupings of species make the results more conservative by increasing similarity among locations.

As with the Pawnee-only data set, we classified the full data set (all 128 Pawnee plots and 64 additional plots; n=192) using a hierarchical cluster analysis using the Sorenson distance measure and Flexible Beta (Beta = -0.25) group linkage method: data were square-root transformed prior to analysis. We determined the number of groups using OptimClass Type 1 (Tichý et al. 2009). Although we lacked sufficient data for a true semi-supervised analysis, we used the previously classified plot data (already published and in VegBank) to compare to our data within the cluster analysis.

Classification Integration with the USNVC Classification System

Classification integration was mostly a comparison of our plot-groups with those described in the USNVC version 2.01 and known to occur in Colorado. The regional analysis provided several previously-classified plots and those concepts were compared to the plots from the PNG and integrated when possible. For those plots not clearly linked with previously classified plots, i.e., most of the steppe plots, our classified plot-group characteristic species were compared with described concepts and integrated; that is, we used characteristic species to compare our plot-groups to the USNVC classification and placed our plot-groups into the USNVC entities to which they matched most closely. Thus, the integration was non-quantitative.

Results

Pawnee National Grasslands Analysis

Analysis identified either 4 (Figure 3A) or 10 (Figure 3B) plot-groups (based on top two results that were not very different in their species fidelities) for the Pawnee-only plots. The main division was between the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association (Groups 2, 3 and 4; Figure 3A) and mesic vegetation communi-

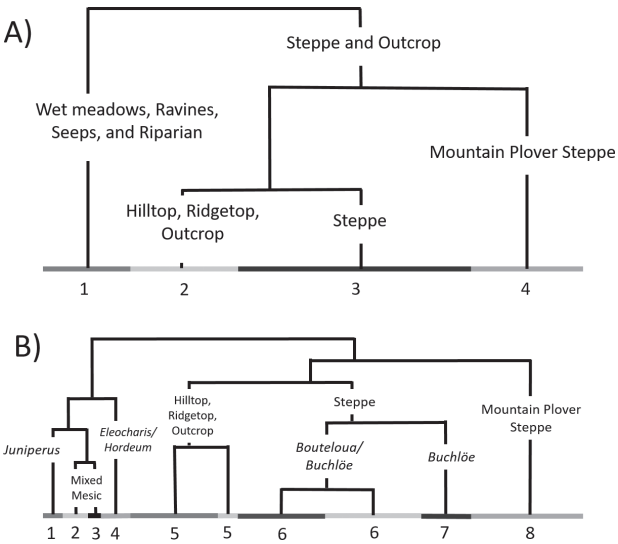

Figure 3. Dendrogram of Pawnee National Grassland plots showing the two peaks suggested by OptimClass. A) four groups suggested by OptimClass; B) 10 groups suggested by OptimClass with coalition of two sets based on the lack of indicator species.

ties (Group 1; Figure 3A). The initial interpretation of the 10-group dendrogram yielded two plot-groups that completely lacked indicator flora. Thus, we merged two sets of plot-groups (5 and 6) as shown in Figure 3B. Interpretation is thus based on these eight plot-groups with clear indicator species. The eight-group dendrogram essentially splits those two major groups into four plot-groups each (Figure 3B), but there is some difficulty in that there were so few plots of the mesic plot-groups; total plots = 20, each plot-group ranged from 3 to 7 plots. Thus, we discuss the mesic plot-groups only briefly here and more substantially in the regional analysis section. The eight plot-groups were also distinguished in an NMDS analysis (two dimensions, stress=20.517, p = 0.001; Figure 4A). Mesic sites were scattered throughout the bottom and left of the ordination plot and steppe sites were at the top and to the right, generally.

Albeit small in numbers of plots, and indeed limited in geographic distribution in the Pawnee National Grasslands (PNG), the diversity of vegetation in more mesic areas is high. Group 1, which contains mesic sites in scarp areas, had the second highest number of species despite having only three plots (Table 1). The highest diversity occurred in the other group that included scarp and outcrop plots, suggesting these sites have high heterogeneity and high diversity. The lowest diversity was found in the plots from the mountain plover studies (Table 1), typically prairie dog colonies, although one of our plots taken in a prairie dog colony was associated with Group 6, and we ended up combining plot-groups 6 and 8 based on their similarity of dominant and diagnostic species (especially *Bouteloua gracilis* and *Opuntia polyacantha*, Tables 1, 2). We attribute the lower diversity in the plover plots to smaller plot sizes from that study (30 m^2 compared to 100 m^2 for our plots).

Because the USNVC nomenclature is based on both dominant and diagnostic species, we examined dominance based on cover and fidelity of species in relation to the eight plot-groups (Table 2). However, the first four mesic plot-groups are heterogeneous in their dominant species; for example, Plot-Group 1 has *Juniperus scopulorum* and *Carex nebrascensis* dominating, but *J. scopulorum* was only found in one of the three plots. Thus, we do not suggest the average values or indicator species are correct for these plot-groups and instead discuss them further in the regional analysis section below.

Species- and Community-Environment Relationships

Canonical Correspondence Analysis showed a significant species-environment correlation (0.839; p=0.001) for axis 1 only (the first axis had the only significant relationship with environment as well, 0.533, p=0.001; axis 2 = 0.352; Figure 4B). The first axis was correlated with site types,

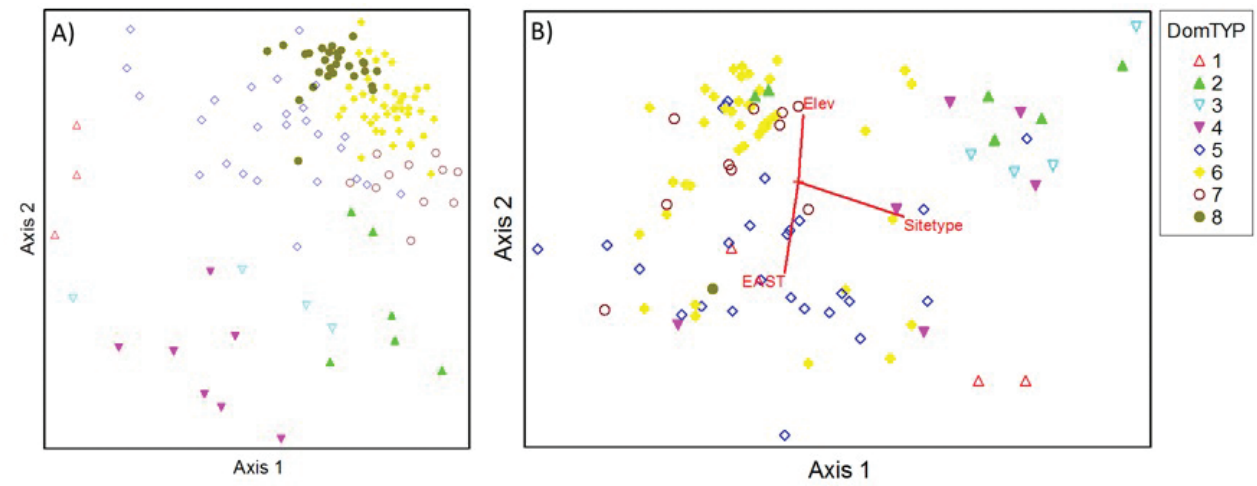

Figure 4. Non-metric multidimensional scaling (A) and canonical correspondence (B) analyses of 128 plots from Pawnee National Grasslands, CO. DomTyp refers to the plot-groups delineated from the analyses.

Table 1. Dominant species (average cover values > 1%) of the eight plot-groups found in the Pawnee National Grasslands, CO. Bold indicates highest average cover values.

	1	2	3	4	5	6	7	8
Taxa	**n = 3**	**n = 6**	**n = 4**	**n = 7**	**n = 26**	**n = 43**	**n = 11**	**n = 28**
Carex nebrascensis	**20.7**							
Junipurus scopulorum	**12.7**				0.8			
Rhus trilobata	8.0				2.3			
Toxicodendron rydbergii	7.4				0.1			
Nassella viridula	6.2				1.0			
Agropyron cristatum	6.0		0.1		1.5	0.7	0.1	
Symphoricarpus occidentalis	2.7							
Rosa woodsii	1.5	0.7						
Prunus virginiana	1.4				0.1			
Solidago canadensis	1.3							
Sporobolus airoides		**19.8**	1.0		0.2			
Poa sp.	0.3	7.7	2.3	0.1	0.2			
Glycyrrhiza lepidota	0.8	6.4						
Populus deltoides		6.3						
Distichlis spicata		5.0	0.4		0.3			
Rosa woodsii		4.0						
Elymus canadensis	0.2	3.7						
Juncus balticus		3.3						
Thermopsis rhombifolia		1.3						
Eleocharis acicularis			**4.5**					
Erigeron sp.			4.0					
Schoenoplectus pungens			2.3					
Phalaris canariensis			2.0					
Lemna minor			2.0					
Eleocharis palustris			**5.1**	**8.6**			0.9	
Polygonum sp.			0.2	**5.7**				
Thlaspi arvense				**5.4**				
Hordeum jubatum				**5.2**		1.0	0.2	
Rorippa curvipes			0.3	4.0			0.6	
Rumex crispis				4.0				
Ambrosia psilostachya	0.2	0.1		3.3	0.1			
Bassia scoparium				2.8	0.1			
Potentilla sp.				1.2				
Heliantus annuus				1.2				
Ribes aurea	0.7				3.0			
Schizachyrium scoparium	0.2				1.8			
Cercocarpus montanus					1.5			
Hesperostipa comata			0.3		1.3	0.9	0.2	2.0
Bouteloua gracilis	0.1	1.9	0.3	0.1	**6.8**	**23.4**	2.3	**17.5**
Buchloe dacyloides		0.7			4.3	**21.6**	**28.7**	1.6
Opuntia polyacantha					0.7	8.3	4.8	0.8
Atriplex canescens						3.5		
Yucca glauca	0.9				2.9	3.3		
Aristida purpurea					0.6	2.7	0.4	0.4
Atriplex canescens					0.1	2.2		
Pascopyrum smithii	0.1	6.1	3.1	0.2	4.4	2.7	**10.4**	0.9
Sporobolus cryptandrus					0.3	0.9	1.9	0.2
Carex duriuscula		0.7		0.8	0.1	0.4	1.9	
Artemisia frigida	0.1				0.7	0.2	1.8	0.5
Community Diversity								
Richness	32	25	19	13	**40**	24	16	11
Pielou Evenness	0.47	0.49	0.71	0.60	**0.72**	0.53	0.55	0.45
Shannon Diversity	1.56	1.56	2.07	1.45	**2.58**	1.64	1.44	1.06
Simpson Diversity	0.64	0.66	0.77	0.65	**0.82**	0.69	0.63	0.47

suggesting vegetation was structured by a moisture gradient. Averages by plot-group also show a clear pattern in site type for the mesic communities compared to the steppe communities (Table 3). Axis 2 was correlated (albeit insignificantly) positively with elevation and negatively with easterly longitude since the Pawnee decreases in elevation from west to east; however, the gradient was not so evident by plot-group since many of these plot-groups are found throughout the PNG. There are apparently subtle changes in the flora from west to east. Since there is also a general increase in moisture from west to east, we examined floral changes along this longitudinal gradient. Of 213 species, 42 showed a significant positive correlation with easting and two showed a negative correlation. Correspondingly,

Table 2. Diagnostic species frequencies and fidelity values (phi coefficient × 100 superscripted) for the eight plot-groups found in the Pawnee National Grasslands, CO.

Plot-group	1	2	3	4	5	6	7	8
Number of plots	**n = 3**	**n = 6**	**n = 4**	**n = 7**	**n = 26**	**n = 43**	**n = 11**	**n = 28**
Carex nebrascensis	67 ^{49}	17		14				
Toxicodendron rydbergii	100 ^{38}				19 ^{3}			
Solidago canadensis	33 ^{25}			14				
Prunus virginiana	100 ^{23}				15	5		
Rosa woodsii	100 ^{22}	17			8			
Rhus trilobata	100 ^{23}	17			54 ^{21}	5		
Nassella viridula	67 ^{20}				38 ^{14}	2	9	
Parthenocissus quinquefolia	67 ^{19}				4			
Celtis laevigata	67 ^{18}							
Sporobolus airoides	33	83 ^{47}	25		8	9		
Distichlis spicata		83 ^{30}	75 ^{5}		4	5		
Juncus balticus		33 ^{30}						
Elymus canadensis	67 $^{0.0}$	33 ^{28}			4			
Glycyrrhiza lepidota	67 ^{11}	33 ^{24}			4			
Thermopsis rhombifolia		17 ^{21}						
Equisetum laevigata		50 ^{17}	25	14	4			
Eleocharis acicularis			25 ^{32}					
Lemna minor			50 ^{28}					
Schoenoplectus pungens			75 ^{27}			10		
Ranunculus cymbalaria			75 ^{27}					
Phalaris canariensis			25 ^{24}					
Circium floodmanii			100 ^{20}					
Polygonum sp.			50 ^{4}	100 ^{30}	8			
Eleocharis palustris		17	75 ^{18}	57 ^{29}			27	4
Rorippa curvipes		17	50	71 ^{28}	4		27	
Bassia scoparia				86 ^{25}	8	5	4	
Ambrosia psilostachya	67 ^{3}	50		86 ^{25}	23			
Hordeum jubatum				86 ^{20}	8	5		
Schizachyrium scoparium	33	17			54 ^{25}	5		
Buchloe dactyloides		50			65	100 ^{34}	100 ^{19}	57
Opuntia polyacantha	33	17			73	100 ^{25}	55	100
Bouteloua gracilis	67	83	50	29	96	100 ^{24}	91	100
Lichen					19	58	45	89 ^{14}

Table 3. Average (and standard deviations) environmental values by plot-group: bold values are the highest and lowest values among plot-groups. Plot-group 8 is not shown as only one plot had environmental data. We developed ordinal scales for soil type, rock type, slope position, and site type, essentially from poor to less poor environmental conditions. Soil Type included badland (1), Aridisol (2), Mollisol (3), mixed soil (4), Alfisol (5), and Entisol (6). Rock type included dune sand (1), sandstone (2), gravel (3) and shale (4). Slope position included 1 for convex ridgetop, 2 for flat slope, and 3 for concave ravine. Site Types were numbered from driest to most mesic: (1) blowout, (2) steppe hilltop, (3) steppe, (4) steppe buffalo wallow, (5) rock outcrop, (6) ridgetop, (7) draw slope, (8) ravine, (9) playa, and (10) riparian.

Plot-group	1	2	3	4	5	6	7
Number of plots	**n = 3**	**n = 6**	**n = 4**	**n = 7**	**n = 26**	**n = 43**	**n = 11**
Easting	**604978**	**527119**	535261	566184	585591	556341	559331
	(20316)	**(6260)**	(14063)	(25462)	(28906)	(28821)	(28001)
Northing	**4521855**	4516970	4520876	4519157	**4512413**	4515685	4516816
	(14049)	(6867)	(2379)	(12819)	**(11184)**	(9643)	(9601)
Elevation (m)	**1483**	**1633**	1600	1533	1514	1573	1565
	(58)	**(41)**	(58)	(41)	(112)	(87)	(116)
Soil	4.0	3.5	**4.3**	4.2	3.8	3.4	**2.9**
	(0)	(1.4)	**(2.1)**	(1.5)	(0.9)	(1.1)	**(0.3)**
Rock	**2.0**	**1.0**	1.5	1.8	1.9	1.5	1.6
	(0)	**(0)**	(0.6)	(0.8)	(0.6)	(0.6)	(0.5)
Aspect	**1.3**	**0.5**	1.0	0.7	0.9	**1.3**	**0.4**
	(1.2)	**(0.8)**	(1.2)	(1.0)	(0.9)	**(0.9)**	**(0.7)**
Slope	**2.0**	1.0	1.0	1.0	1.3	1.1	1.0
	(1.0)	(0)	(0)	(0)	(0.5)	(0.3)	(0)
% Bare Ground	18	9.2	24.3	**47.5**	35.2	19.2	**43.0**
	(31.8)	(11.0)	(35.0)	**(37.1)**	(24.1)	(9.8)	**(33.0)**
Site Type	8.7	7.3	**9.5**	7.8	5.4	3.6	**3.1**
	(3.2)	(3.4)	**(1.0)**	(2.6)	(2.5)	(1.8)	**(0.9)**

38 showed a negative correlation with elevation and one showed a positive correlation. A total of 19 species showed a negative correlation with northing and only two a positive relationship. Taken together, there is a strong suggestion of a longitudinal gradient (most likely moisture-driven) to which species are responding, but the gradient does not render distinct vegetation types.

We examined the ability to classify plot-groups with environmental data through stepwise discriminant analysis (Table 4); sitetype, longitude, percent bare ground and slope together significantly discriminated vegetation types. While some plot-groups seem to have distinct abiotic requirements (e.g., Groups 1, 3, 6 and 7), others were much less distinct.

Table 4. Number of observations and percent of plots (in parentheses) classified correctly based on environmental data. Model results from discriminant analysis given at the bottom of table. Group 8 was excluded due to low numbers and variability within group.

Plot-group	1	2	3	4	5	6	7
1	**2**				1		
	(66.7)				(33.3)		
2		1	**3**			2	
		(16.7)	**(50.0)**			(33.3)	
3		1	**3**				
		(25.0)	**(75.0)**				
4		1	**2**	**2**			1
		(16.7)	**(33.3)**	**(33.3)**			(16.7)
5	7		1	2	**9**	3	4
	(26.9)		(3.9)	(7.7)	**(34.6)**	(11.5)	(15.4)
6	3	1		1	3	**29**	4
	(7.3)	(2.4)		(2.4)	(7.3)	**(70.7)**	(9.8)
7						**6**	4
						(60.0)	(40.0)

Discriminant Analysis Results

Variable	Partial R^2	F	p>F
Sitetype	0.44	10.13	<0.0001
Easting	0.36	6.93	<0.0001
% Bare Ground	0.25	4.17	0.0005
Slope	0.18	2.73	0.0132

Semi-supervised Regional Analysis

The regional analysis clearly separated more mesic communities from mixed grass and short grass steppe (Figure 5). The rather striking difference of flora affirms the classification on the Pawnee sites as shortgrass steppe and generally negates the occurrence of mixed grass communities in the Pawnee National Grasslands; only two plots from outside of the Pawnee were classified with Pawnee plots (Groups 3 and 4; Figure 5) and only one Pawnee plot was classified with the mixed grass macrogroup (Groups 1 and 2; Figure 5). The bottom line is that while elements of the mixed grass are present in PNG (e.g., *Hesperostipa comata and Pascopyrum smithii*), they never reach sufficient cover to be called mixed grass. The one plot from the Pawnee situated with Plot-Group 1 of the regional analysis (Figure 5) and Plot-Group 5 of the Pawnee analysis (Figure 3) was closely related to the *Hesperostipa comata-Bouteloua gracilis-Carex filifolia* Grassland Association, but it is evident how different this association is from those typical of the Pawnee. In addition, the *Bouteloua gracilis-Buchloe dactyloides* Great Plains Shortgrass Prairie Macrogroup was separated from the *Hesperostipa comata-Pascopyrum smithii-Festuca hallii* Grassland Macrogroup to the north and east.

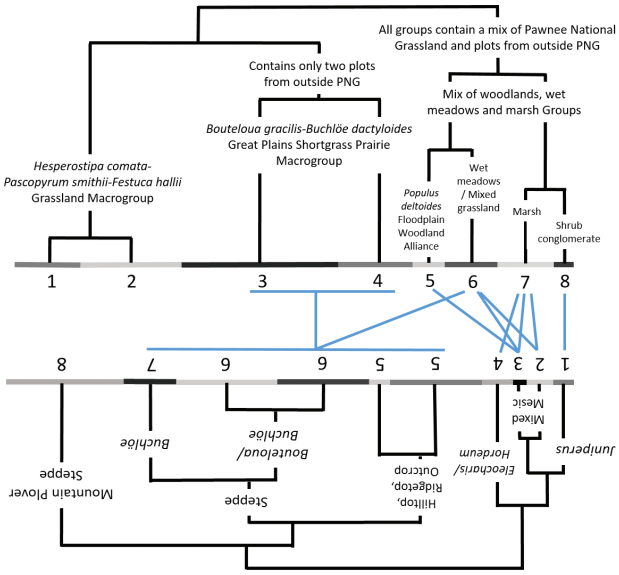

Figure 5. Regional analysis (right-side up) including all Pawnee National Grassland plots and plots from other local studies. The figure also depicts the relationship of plots in the Regional analysis to the Pawnee-only dendrogram (upside down).

This semi-supervised classification allowed us to characterize our few plots of mesic sites with known classified plots of similar flora from outside the PNG because mesic sites tend to be less zonal than drier sites. For example, the one plot from the Pawnee situated with Plot-Group 5 of the regional analysis linked that plot to the *Populus deltoides/Panicum virgatum-Schizachyrium scoparium* Floodplain Woodland Association.

Seven PNG plots were located in Group 6 of the regional analysis, which included a mix of *Pascopyrum smithii* and *Hesperastipa comata* USNVC associations, but also included the *Carex nebrascensis* Wet Meadow Association and the *Juncus balticus* Wet Meadow Association. We interpret this as an 'in-between' concept, with more mesic than usual mixed grass associations and drier than usual wet meadow associations. Supporting this conjecture, four of the seven plots, including three relic buffalo wallows, were classified with other shortgrass steppe plots (Group 6) in the Pawnee-only classification. In addition, one plot was situated in Plot-Group 5 with other scarp plots, and only two plots in Plot-Group 2 with other riparian sites (see below).

All three plots from PNG in Plot-Group 8 of the regional analysis resulted in their own Plot-Group 1 of the Pawnee-only analysis. The three plots previously classified included the *Populus deltoides/Panicum virgatum-Schizachyrium scoparium* Woodland Association, the *Juniperus scopulorum/Cornus sericea* Woodland Associ-

ation, and the *Rhus trilobata/Pascopyrum smithii* Shrub Association. However, perhaps the closest USNVC concept is the *Juniperus scopulorum/Cornus sericea* Woodland Association that is supposed to occur here, except that none of our plots had >40% *Juniperus* cover. The plot-group actually shows the heterogeneity of scarp locations (although the plots were not located together), with one plot a seep dominated by *Carex nebrascensis* (and seems to fit the *Carex nebrascensis* Wet Meadow concept), another a riparian zone dominated by *Juniperus scopulorum* and *Rhus trilobata*, and the third near the scarp itself dominated by *Rhus trilobata* and *Rosa woodsii*. We suggest these belong to a new *Rhus trilobata* Alliance, but more data are needed for description of the concept. The difference between this concept and Plot-Group 5 of the Pawnee-only analysis is the presence of *Bouteloua gracilis* and *Buchloe dactyloides* in Plot-Group 5, while they are essentially absent from Plot-Group 1 of the regional analysis.

Plot-Group 7 of the regional analysis was also a mix of mesic communities based on previous designations. Indeed, PNG plots from this regional plot-group were split into Plot-Groups 2, 3, and 4 in the Pawnee-only analysis. Plot-Group 4 of the Pawnee-only analysis was most closely associated with the *Eleocharis palustris* Marsh Association and the *Hordeum jubatum* Marsh Association, with a couple of plots fitting each of those descriptions.

Plot-Groups 2 and 3 of the Pawnee-only analysis were not closely associated with any previously-classified plots. Plot-Group 2 occurs in riparian, ravine, and mesic steppe areas that, based on the dominance and fidelity of *Sporobolus airoides* and *Distichilis spicata*, have finer-textured, saline soils. This plot-group is most similar to the *Sporobolus airoides-Distichilis spicata* Wet Meadow Association, but the current USNVC description is mainly from New Mexico and should be updated to include the larger geographic area to which the type is found. Plot-Group 3 may indeed be from the mixed grass area, as it seems to fit best the *Pascopyrum smithii-Eleocharis* species Wet Meadow Association, typical of playa and periodically flooded grasslands mainly north of PNG. However, since this association does not generally have *Schoenoplectus pungens*, we suggest that at least one of the plots within this plot-group belongs to the *Schoenoplectus pungens* Marsh Association; plots more typical of permanent rather than periodic wetlands such as margins of ponds.

USNVC Concepts in the Pawnee National Grasslands

While we do not have enough plot data to characterize all of these concepts, we provide a list of those USNVC concepts that we have evidence for in the Pawnee National Grasslands (Table 5). We document plots from two Classes, three Subclasses, four Formations, five Divisions, six Macrogroups, seven Groups and eight Alliances and

Table 5. USNVC concepts evidenced by plots within the Pawnee National Grasslands, CO.

Class	**Mesomorphic Shrub and Herb Vegetation**							**Mesomorphic Tree Vegetation**
Subclass	Shrub & Herb Wetland					Temperate & Boreal Grassland & Shrubland		Temperate & Boreal Forest & Woodland
Formation	Temperate to Polar Freshwater Marsh, Wet Meadows & Shrubland			Salt Marsh		Temperate Grassland & Shrubland		Temperate Flooded & Swamp Forest
Division	Western North American Temperate and Freshwater Marsh, Wet Meadows & Shrubland			Great Plains Saline Marsh		Central North American Grassland & Shrubland	Western North American Grassland & Shrubland	Eastern North American – Great Plains Flooded & Swamp Forest
Macrogroup	Arid West Interior Freshwater Marsh	Western North American Montane-Subalpine-Boreal Marsh, Wet Meadow and Shrubland		Great Plains Saline Wet Meadow & Marsh		Great Plains Shortgrass Prairie	Southern Rocky Mountain Montane Shrubland	Great Plains Flooded Forest
Group	Arid West Interior Freshwater Marsh	Vacouverian-Rocky Mountain Montane Wet Meadow & Marsh		Great Plains Saline Wet Meadow & Marsh	Western Great Plains Saline Meadow	*Bouteloua gracilis-Buchloe dactyloides-Pleuraphis jamsii* Great Plains Prairie	Southern Rocky Mountain Mountain-mahogony – *Mixed* Foothill Shrubland	Great Plains Cottonwood – Green Ash Floodplain Forest
Alliance	*Schoenoplectus americanus-Schoenoplectus acutus-Schoenoplectus californicus* Marsh	*Carex nebrascensis-Carex vesicaria-Carex pellita* Wet Meadow	*Juncus balticus-Juncus mexicanus* Wet Meadow	*Pascopyrum smithii – Distichlis spicata – Hordeum jubatum* Wet Meadow	*Sporobolus airoides* Great Plains Marsh	*Bouteloua gracilis-Buchloe dactyloides* Shortgrass Prairie	*Fallugia paradoxa-Rhus trilobata* Shrubland	*Populus deltoides* Floodplain Woodland
Association	*Schoenoplectus pungens* Marsh n=1	*Carex nebrascensis* Wet Meadow n=1	*Juncus balticus* Wet Meadow n=1	*Pascopyrum smithii – Eleocharis spp.* Wet Meadow N=3	*Sporobolus airoides* Northern Plains Marsh n=6	*Bouteloua gracilis-Buchloe dactyloides* Grassland N=54	*Rhus trilobata-Ribes cerneum* Shrubland n=26	*Populus deltoides/Panicum virgatum-Schizachyrium scoparium* Floodplain Woodland n=1
Pawnee Plot-Group	*2/3/4*	*5/6/7*	*5/6/7*	*3*	*2*	*5/6/7*	*1*	*2*
Regional Plot-Group	*7*	*6*	*6*	*6*	*6*	*3/4*	*8*	*5*

Table 6. Local subassociations of the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association of the Pawnee National Grasslands, CO.

***Bouteloua gracilis-Buchloe dactyloides* Grassland Association**								
Local Subassociation Name								
Pawnee-Only Plot-Group 5			*Pawnee-Only Plot-Groups 6,8*			*Pawnee-Only Plot-Group 7*		
Rhus trilobata/Schizachirium scoparium-Bouteloua spp. Outcrop			*Bouteloua gracilis-Buchloe dactyloides* Steppe			*Buchloe dactyloides-Pascopyrum smithii* Steppe		
Local Subassociation Diagnostic Species								
Diagnostic	**Constant**	**Dominant**	**Diagnostic**	**Constant**	**Dominant**	**Diagnostic**	**Constant**	**Dominant**
Schizachirium Scoparium;		*Pascopyrum smithii*;	*Bouteloua gracilis*;		*Buchloe dactyloides*;		*Buchloe dactyloides*	*Buchloe dactyloides*;
Rhus trilobata		*Yucca glauca*;	*Opuntia polyacantha*;		*Bouteloua gracilis*;			*Pascopyrum smithii*
		Schizachyrium scoparium;	*Buchloe dactyloides*;		*Opuntia polyacantha*;			
		Cercocarpus montanus;			*Hordeum jubatum*			
		Bouteloua gracilis;						
		Buchloe dactyloides;						
		Agropyron cristatum						
Local Subassociation Environmental Description								
Rock outcrops on ridgetops, scarps and draws resulting in heterogeneously-mesic conditions			Typical steppe concept			Swales and lower areas with finer-textured soils		

Associations. Abridged descriptions of these USNVC associations are in Suppl. material 2.

We have substantial data to characterize the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association dominating the PNG. Because these data are from a limited area within the entire range of the Association, we simply document here the characteristics typical for the PNG. In addition, we present characteristics of three local subassociations that may be helpful for local management (Table 6; Suppl. material 3). One subassociation occurs on rocky outcrops that harbor more moisture at least heterogeneously. Thus, species such as *Rhus trilobata* and *Schizachirium scoparium* are common, while *Pascopyrum smithii* maintains more cover in this type than other types we describe here. These areas are quite diverse and probably deserve some attention for conservation. Another local subassociation appears to be dominated by *Buchloe dactyloides* while *Pascopyrum smithii* is again higher in cover, at least compared to other types. These communities appear to be related to shallow swales and likely finer-textured soils within the steppe complex. While we did not find a diagnostic species for the plots from the mountain plover study, except perhaps lichen, the dominance of *Bouteloua gracilis* and the lack of diversity, along with overall low total vegetation cover (averaged 27.8% cover; 72.2% bare ground) suggests these sites differ due to grazing. However, we consider these disturbed communities simply a subset of the *Bouteloua gracilis-Buchloe dactyloides* Steppe local subassociation (Suppl. material 3).

Discussion

We used plot data to document the occurrence of two USNVC Classes, three Subclasses, four Formations, five Divisions, six Macrogroups, seven Groups and eight Alliances and Associations on the PNG, ranging from mesomorphic tree vegetation (i.e., *Populus* woodlands along riparian zones) to mesomorphic shrub and herb vegetation dominated by the wide-ranging shortgrass steppe species *Bouteloua gracilis* and *Buchloe dactyloides*. The latter is the matrix of the landscape with fragments of more mesic conditions nested within, ranging from standing water locations (e.g.. farm ponds) dominated by *Schoenoplectus pungens* or *Sporobolus airoides* under greater salinity, to *Carex*, *Juncus*, *Eleocharis*, and *Pascopyrum smithii* dominance in swales with varying levels of periodic moisture during the growing season.

Our plot-groups relate to those outlined by Hazlett (1998). Our *Buchloe dactyloides-Pascopyrum smithii* Steppe and *Bouteloua gracilis-Buchloe dactyloides* Steppe local subassociations together match his Open Steppe and Sandy Soils habitats, and our *Rhus trilobata-Ribes cernuum* Shrubland association matches his Cliffs and Ravines habitat. We suggest that his Breaks and Barrens habitat relates to our *Rhus trilobata/Schizachirium scoparium-Bouteloua* spp. Outcrop local subassociation, and that the remainder of our vegetation concepts relate to his Riparian habitat. For the latter, we clearly defined a number of different vegetation types within his one habitat, which is not surprising due to the azonal nature of more mesic locations (Faber-Langendoen et al. 2014). Baker (1984) appeared to take a strong splitter approach with grasslands and developed several associations from the many possible dominants at small scales (< 10 m^2). For *Bouteloua*-dominated types, he recognizes two, similar to our two local subassociations; *Bouteloua gracilis* Shortgrass Prairie and *Bouteloua gracilis-Buchloe dactyloides* Shortgrass Prairie, but also types like the *Hordeum jubatum* Plains Grassland. The unique barrens and outctrops are noted by associations such as the *Arenaria hookeri* Barrens and *Rhus trilobata-Ribes cereum /Schizachyrium scoparium* Shrub Association, but also at

least two mixed prairie associations; *Stipa comata* Mixed Prairie and *Schizachyrium scoparium* Mixed Prairie. As did we, he also recognized several mesic types, including *Juncus balticus* Wetland, *Carex nebrascensis-Juncus balticus* Wetland, *Carex nebrascensis-Catabrosa aquatica-Juncus balticus* Spring Wetland, *Eleocharis palustris* Wetland, *Sporobolus airoides* Salt Meadow, and *Distichlis spicata* var. *stricta* Salt Meadow, as well as several *Populus deltoides* Forest/Woodland associations that are not clearly related to those on the PNG. There are two considerations with these comparisons. First, the previous studies are expert-based classifications and not plot-based. Further, at least for Baker (1984), that classification was for the entire state of Colorado, although we still believe he split concepts too finely compared to the current USNVC. Regardless, direct comparisons are difficult.

We propose local subassociations that may be helpful for land stewardship, but not as a change to the *Bouteloua gracilis-Buchloe dactyloides* Grassland Association concept. Our limited geographic reference for this concept does not allow any major changes, but that same geographic size suggests local subassociations may exist (Jennings et al. 2009). These groups have clear characteristic species and environments that may be of interest for conservation management.

Our 'semi-supervised' classification was successful in that it let us classify several rarer (in our dataset) plots. The ability to compare previously-classified plots with unknown plots (Tichý et al. 2014) in the same analysis allowed for a much better entitation and cleared up nearly all of our questions from the Pawnee-only analysis, and such analyses are needed to improve all future local classification efforts. One major conclusion from this analysis is that the mixed-grass concepts in the USNVC do not exist in the PNG. While the Colorado vegetation map suggests these communities are part of the PNG landscape, we argue that the vegetation composition and structure as a whole are different and should be considered so as the lines demarking the Shortgrass Steppe Ecoregion suggest (Sayre et al. 2009).

There are of course limitations to our study and this classification exercise. First, while the plot data are solid, the low number of plots (n=101+27) for the area of the PNG is a concern. Especially for the types where we have little data, additional plots are warranted. Further, while we thoroughly traversed the PNG looking for different vegetation associations, we may have missed certain associations that occur in the PNG, notably the four-wing saltbush (*Atriplex canescens*) lowlands as well as purposefully ignoring ruderal communities that are generally restricted to roadsides and highly disturbed sites in the PNG (Kotanen et al. 1998). The occurrence of the four-wing saltbush type seems to be rare, mainly on low-lying areas of private lands in the northeastern corner of the PNG (pers. obs.) and perhaps due to coarser soils (Dodd et al. 2002) or grazing intensity (Cibils et al. 2000; Hart 2001), or simply previous disturbance (Coffin et al. 1996; Augustine et al. 2017).

Finally, a thorough assessment of the abiotic characteristics of these sites is warranted, since soil texture (Dodd and Lauenroth 1997; Dodd et al. 2002) and moisture (Boutton et al. 1980) are known to affect vegetation community composition and structure on the PNG but were not examined on a site-specific basis here. While abiotic factors would not affect our plot-based vegetation classification, environmental data would be useful for interpreting the vegetation patterns.

Finally, we make a plea here that all vegetation scientists with full-species plot data place those data into VegBank or another public database. While we were able to relate some of our more mesic concepts to plots from other studies, little plot data existed for the typical shortgrass steppe communities dominated by *Bouteloua* species. Our data represent a small geographic fraction of the area this concept covers and a regional analysis would be beneficial for the PNG and the USNVC (Palmquist et al. 2016).

Data availability

All data are in VegBank (http://www.vegbank.org).

Author contributions

SBF collected and analyzed data and wrote initial paper; MS collected and analyzed data and edited paper; JS helped with analyses and edited paper.

Acknowledgements

We honor thank Don Hazlett for helping find some of the unique vegetation locations, his insight to Pawnee National Grasslands, and his help with identification of plant specimens – his presence will be greatly missed. We thank Bruce Hoagland and James Van Kley for their friendly reviews of earlier versions of this manuscript. This research was partially funded by NSF-ROA grant and a Provost Grant from the University of Northern Colorado.

References

Augustine DJ, Derner JD (2012) Disturbance regimes and mountain plover habitat in shortgrass steppe: Large herbivore grazing does not substitute for prairie dog grazing or fire. The Journal of Wildlife Management 76: 721–728. https://doi.org/10.1002/jwmg.334

Augustine DJ, Derner JD, Milchunas D, Blumenthal D, Porensky LM (2017) Grazing moderates increases in C3 grass abundance over seven decades across a soil texture gradient in shortgrass steppe. Journal of Vegetation Science 28: 562–572. https://doi.org/10.1111/jvs.12508

Baker WL (1984) A preliminary classification of the natural vegetation of Colorado. Great Basin Naturalist 44: No. 4, Article 11.

Beers TW, Dress PE, Wensel LC (1966) Aspect transformation in site productivity research. Journal of Forestry 64: 691–692. https://doi.org/10.1093/jof/64.10.692

Boutton TW, Harrison AT, Smith BN (1980) Distribution of biomass of species differing in photosynthetic pathway along an altitudinal transect in southeastern Wyoming grassland. Oecologia 45: 287–298. https://doi.org/10.1007/BF00540195

Bruelheide H, Chytrý M (2000) Towards unification of national vegetation classifications: A comparison of two methods for analysis of large data sets. Journal of Vegetation Science 11: 295–306. https://doi.org/10.2307/3236810

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13: 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Cibils AF, Swift DM, Hart RH (2000) Gender-related differences of shrubs in stands of Atriplex canescens with different histories of grazing by cattle. Journal of Arid Environments 46: 383–396. https://doi.org/10.1006/jare.2000.0692

Coffin D, Lauenroth W, Burke I (1996) Recovery of vegetation in a semi-arid grassland 53 years after disturbance. Ecological Applications 6: 538–555. https://doi.org/10.2307/2269390

Crabb JA (1981) Soil survey of Weld County, Colorado northern part. USDA Soil Conservation Service and Forest Service in cooperation with Colorado Agricultural Experiment Station, Washington D.C., US.

De Cáceres M, Wiser SK (2012) Towards consistency in vegetation classification. Journal of Vegetation Science 23: 387–393. https://doi.org/10.1111/j.1654-1103.2011.01354.x

De Cáceres M, Chytrý M, Agrillo E, Attorre F, Botta-Dukát Z, Capelo J, Czúcz B, Dengler J, Ewald J, Faber-Langendoen D, … Wiser S (2015) A comparative framework for broad-scale plot-based vegetation classification. Applied Vegetation Science 18: 543–560. https://doi.org/10.1111/avsc.12179

Derner JD, Lauenroth WK, Stapp P, Augustine DJ (2009) Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. Rangeland & Ecological Management 62: 111–118. https://doi.org/10.2111/08-008.1

Dodd MB, Lauenroth WK (1997) The influence of soil texture on the soil water dynamics and vegetation structure of a shortgrass steppe ecosystem. Plant Ecology 133: 13–28. https://doi.org/10.1023/A:1009759421640

Dodd MB, Lauenroth WK, Burke IC, Chapman PL (2002) Associations between vegetation patterns and soil texture in the shortgrass steppe. Plant Ecology 158: 127–137. https://doi.org/10.1023/A:1015525303754

ESA Panel (2015) How can a national vegetation classification help ecological research and management? Frontiers in Ecology and the Environment 13: 185–186. https://doi.org/10.1890/15.WB.006

Evens J, Keeler-Wolf T (2014) Vegetation mapping is essential in conserving rare desert plant species and plant communities. Fremontia 42: 11–14.

Faber-Langendoen D, Keeler-Wolf T, Meidinger D, Hoagland B, Josse C, Navarro G, Ponomarenko S, Saucier J-P, Weakley A, Comer P (2014) EcoVeg: a new approach to vegetation description and classification. Ecological Monographs 84: 533–61. https://doi.org/10.1890/13-2334.1

Faber-Langendoen, D, Tart, DL, Crawford RH (2009) Contours of the revised US National Vegetation Classification standard. Bulletin of the Ecological Society of America 90: 87–93. https://doi.org/10.1890/0012-9623-90.1.87

FGDC (Federal Geographic Data Committee) (2008) National Vegetation Classification Standard, Version 2 FGDC-STD-005-2008. Vegetation Subcommittee, Federal Geographic Data Committee, FGDC Secretariat, US Geological Survey. Reston, VA, US.

Franklin S, Faber-Langendoen D, Jennings M, Keeler-Wolf T, Loucks O, Peet R, Roberts D, McKerrow A (2012) Building the United States National Vegetation Classification. Annali Di Botanica 2: 1–9.

Hart R (2001) Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. Plant Ecology 55: 111–118. https://doi.org/10.1023/A:1013273400543

Hazlett D (1998) Vascular plant species of the Pawnee National Grassland. General Technical Report RMRS-GTR-17. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Ft. Collins, CO, 26 pp. https://doi.org/10.2737/RMRS-GTR-17

Jennings MD, Faber-Langendoen D, Loucks OL, Peet RK, Roberts D (2009) Standards for associations and alliances of the U.S. National Vegetation Classification. Ecological Monographs 79: 173–199. https://doi.org/10.1890/07-1804.1

Johnson B (1987) Plant associations of Region Two, Edition 4: Potential plant communities of Wyoming, South Dakota, Nebraska, Colorado, and Kansas. USDA Forest Service Rocky Mountain Region R2-ECOL-87-2. Lakewood, CO, US. https://doi.org/10.5962/bhl.title.150478

Kittel G, Van Wie E, Damm M, Rondeau R, Kettler S, McMullen A, Sanderson J (1999) A Classification of Riparian Wetland Plant Associations of Colorado: User Guide to the Classification Project. Colorado Natural Heritage Program, Colorado State University, Fort Collins, CO, US.

Kotanen P, Bergelson J, Hazlett D (1998) Habitats of native and exotic plants in Colorado shortgrass steppe: a comparative approach. Canadian Journal of Botany 76: 664–672. https://doi.org/10.1139/b98-036

Kudray G, Cooper S (2005) *Linking the National Vegetation Classification System to NRCS ecological sites in southeastern Montana.* Report prepared for the Bureau of Land Management by Montana Natural Heritage Program, Natural Resource Information System, Montana State Library. Montana Natural Heritage Program. Helena, MT, US. https://doi.org/10.5962/bhl.title.55626

Küchler AW (1964) Potential Natural Vegetation of the Conterminous United States. American Geographical Society, New York, US. 116 pp.

Kupfer JA, Franklin SB (2000) Implementation and evaluation of an ecological land type classification system, Natchez Trace State Forest, western Tennessee, USA. Landscape and Urban Planning 49: 179–190. https://doi.org/10.1016/S0169-2046(00)00070-0

Laurenroth WK (2008) Vegetation of the Shortgrass Steppe. In: Laurenroth WK, Burke IC (Eds) Ecology of the shortgrass steppe, Oxford University Press, NY, US, 70–83.

McCune B, Mefford MJ (1999) PC-ORD. Multivariate Analysis of Ecological Data, Version 4.0. MjM Software Design, Gleneden Beach, OR, US. 237 pp.

Moir WH, Trlica MJ (1976) Plant communities and vegetation pattern as affected by various treatments in shortgrass prairies of northeastern Colorado. Southwestern Naturalist 21: 359–371. https://doi.org/10.2307/3669721

Palmquist KA, Peet RK, Carr SC (2016) Xeric Longleaf Pine Vegetation of the Atlantic and East Gulf Coast Coastal Plain: an Evaluation and Revision of Associations within the U.S. National Vegetation Classification. Proceedings of the US National Vegetation Classification 1: 1–1.

Peet R, Roberts D (2013) Classification of natural and semi-natural vegetation. In: van der Maarel E, Franklin J (Eds) *Vegetation Ecology. Second Edition*. Oxford University Press, New York, US, 28–70. https://doi.org/10.1002/9781118452592.ch2

Peet RK, Lee MT, Jennings MD, Faber-Langendoen D (Eds) (2013) VegBank – a permanent, open-access archive for vegetation-plot data. Biodiversity & Ecology 4: 233–241. https://doi.org/10.7809/b-e.00080

Peet R, Wentworth T, White P (1998) A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63: 262–274.

Rodwell JS (2006) *National Vegetation Classification: User's Handbook*. Joint Nature Conservation Committee, Peterborough, UK.

Rotenberry JT, Preston KL, Knick ST (2006) GIS-Based niche modeling for mapping species' habitat. Ecology 87: 1458–1464. https://doi.org/10.1890/0012-9658(2006)87[1458:GNMFMS]2.0.CO;2

Sangermano F, Eastman R (2006) Linking GIS and ecology – the use of mahalanobis typicalities to model species distribution. Physical Geography 19: 474–499.

Sayre R, Comer P, Warner H, Cress J (2009) A new map of standardized terrestrial ecosystems of the conterminous United States. U.S. Geological Survey Professional Paper 1768, 17 pp. https://doi.org/10.3133/pp1768

Tichý L, Chytrý M, Botta-Dukát Z (2014) Semi-supervised classification of vegetation: preserving the good old units and searching for new ones. Journal of Vegetation Science 25: 1504–1512. https://doi.org/10.1111/jvs.12193

Tichý L, Chytrý M, Hájek M, Talbot SS, Botta-Dukát Z (2009) OptimClass: Using species-to-cluster fidelity to determine the optimal partition in classification of ecological communities. Journal of Vegetation Science 20: 1–13.

USNVC [United States National Vegetation Classification] (2016) United States National Vegetation Classification Database, V2.0. Federal Geographic Data Committee, Vegetation Subcommittee, Washington DC. http://usnvc.org/ [accessed Jan–Apr 2016]

Weaver GT, Robertson P (1981) Regrowth of *Quercus prinus* and associated tree species following regeneration harvesting in the Ozark Hills of Illinois. Bulletin of the Torrey Botanical Club 108: 166–179. https://doi.org/10.2307/2484896

E-mail and ORCID

Scott Franklin (Corresponding author, scott.franklin@unco.edu), ORCID: https://orcid.org/0000-0003-3922-8857
Michael Schiebout (mschiebout@uu.edu)
Jozef Šibik (jozef.sibik@savba.sk), ORCID: https://orcid.org/0000-0002-5949-862X

Supplementary material

Supplementary material 1
List of taxa used in the classification of the Pawnee National Grasslands, CO
Link: https://doi.org/10.3897/VCS/2020/38629.suppl1

Supplementary material 2
Abridged USNVC concept descriptions
Link: https://doi.org/10.3897/VCS/2020/38629.suppl2

Supplementary material 3
Subassociation descriptions based on plot data from current study in Pawnee National Grasslands
Link: https://doi.org/10.3897/VCS/2020/38629.suppl3

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 139–144
doi: 10.3897/VCS/2020/56372

FORUM PAPER

What is an alliance?

Wolfgang Willner[1]

1 *Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria*

Corresponding author: Wolfgang Willner (wolfgang.willner@univie.ac.at)

Academic editor: Idoia Biurrun ♦ **Received** 10 July 2020 ♦ **Accepted** 5 October 2020 ♦ **Published** 16 November 2020

Abstract

The alliance is the basic unit of the EuroVegChecklist, and it often serves as the lowest rank in broad-scale vegetation surveys. However, there is hardly any literature about the concept and definition of this syntaxonomic rank, leading to uncertainty in its application. Here, I explore the original association concept of Braun-Blanquet, which was based on absolute character species, and I show that this concept is more or less identical with the units that we now call alliances. By also incorporating the concept of central syntaxa, I propose the following definition: "An alliance is a moderately broad vegetation unit that either has one or several absolute character taxa or that can be interpreted as the central alliance of an order." The one-to-one relationship between character taxa and vegetation units gives the latter a clear biogeographical and evolutionary meaning. Restrictions to the validity of character taxa – either to certain geographical areas or to physiognomic types – cause theoretical and practical problems and should be avoided. Possible exceptions are species with similar frequency in two formations or species introduced to other continents.

Taxonomic reference: Euro+Med PlantBase (http://ww2.bgbm.org/EuroPlusMed/) [accessed 1 July 2020].

Keywords

Alliance, Braun-Blanquet approach, character species, EuroVegChecklist, phytosociology, syntaxonomy, vegetation classification

Introduction

The alliance is the basic unit of the EuroVegChecklist (EVC; Mucina et al. 2016), and it is frequently used as the smallest unit in supra-regional phytosociological revisions (e.g., Čarni et al. 2009; Peterka et al. 2017). However, there is very little literature about the concept and definition of this syntaxonomic rank.

The alliance (in German: Verband) was introduced by Braun-Blanquet (1921) as a synonym to "association group" (Assoziationsgruppe), meaning a group of floristically related associations. The effective start of the alliance concept was 1926, when several important monographs were published (and many of those alliance names are still in use) (Braun-Blanquet 1926; Braun-Blanquet and Jenny 1926; Koch 1926; Luquet 1926). None of those monographs, or subsequent works provided an explicit definition for the units above the rank of association, but the general agreement was that an alliance should have supra-regional character species that are shared by some or all of its associations. Textbooks of phytosociology (e.g., Pavillard 1935; Braun-Blanquet 1964; Westhoff and van der Maarel 1978) did not much elaborate on the topic. Unlike the association concept, which has been the subject of heated debates in the phytosociological literature (Dengler 2003; Willner 2006; Guarino et al. 2018), the evolution of the alliances was much smoother, although their number has steadily grown over the last century. In recent years, the alliance has also been adopted in classification systems not using the traditional Braun-Blanquet approach (Jennings et al. 2009; Faber-Langendoen et al. 2014).

In the absence of a commonly agreed definition for the alliance (at least in Europe), recent decades have witnessed an increasing tendency of splitting long-established alli-

PENSOFT.

Copyright *Wolfgang Willner*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

ances and describing new ones lacking supra-regional or absolute character species. The EuroVegChecklist (Mucina et al. 2016) lists 1108 alliances (excluding those of vegetation dominated by non-vascular plants), which is an increase of ca. 20% compared to the overview of Rodwell et al. (2002). To enable the evaluation of all proposed alliances, we need objective criteria. Therefore, I propose to revisit Braun-Blanquet's original association concept and transform it into a definition of the alliance which is both operational and theoretically founded.

Braun-Blanquet's original association concept – more like the modern alliances

After preliminary considerations on the subject (Braun 1913; Braun and Furrer 1913), Braun-Blanquet presented a first, fully developed association concept in his thesis (Braun 1915). Based on the definition given by Flahault and Schröter (1910), he emphasised that the association is primarily a floristic unit. He then identified three components of the floristic composition of a vegetation unit: dominant, constant and characteristic species. The third category (called "character species" hereafter) was defined as those species which were either restricted to a certain association (character species of first order) or had at least their optimum therein (character species of second order). Braun-Blanquet argued that the character species should have the highest weight in the delimitation of the associations, as they represented the ecology and evolution of the vegetation unit better than the dominant and constant species. Thus, he defined the association as "a vegetation unit of definite floristic composition which, by the presence of character species, exhibits an ecological independence" (translated from French and German).

The only higher rank used by Braun (1915) was the "association group" ("groupe d'associations"). Like the association, the association group had its own character species, i.e. species with broader ecological amplitude, common to several or all associations of the group while being rare or absent outside the group. Braun-Blanquet argued that, unlike the formations, which are defined by physiognomic criteria, vegetation units defined by character species contain not only ecological but also biogeographical and evolutionary information.

Despite the fact that the "association group" was synonymised with the alliance in Braun-Blanquet (1921), the groups of Braun (1915) basically correspond to classes in the modern phytosociological system. The associations, on the other hand, are more or less identical to units that we now call alliances (see Suppl. material 1). This was not because most alliances were represented by only one association in his study area (the Cévennes in southern France). Instead the extensive discussion of the variability and distribution of each association proves that Braun (1915) indeed perceived the associations as much broader units than in his later works. For example, under the "Association à *Potentilla caulescens* et *Saxifraga cebennensis*", he wrote (translated from French): "The Pyrenees on one side and the Alps on the other, present not only races but also different altitudinal forms." About the "Association du hêtre", he noted: "Wherever we encountered beech forests, from the Baltic Sea to the Alps and the Pyrenees, nearly the same phanerogamous species formed the understorey. We can hardly recognize them as distinct regional variants. […] The distinction of two main races of the association seems possible today, however. Several beech companions have a clearly southern distribution and do not exceed north of the latitude of Paris and Central Germany. […] The variant of northern Europe contrasts with the southern race by its poverty in special elements."

Braun-Blanquet's second association concept

The original definition of character species did not include any geographical restriction. Indeed, the whole idea of associations as biogeographical-evolutionary units relies on the one-to-one relationship between the species and the vegetation unit. However, while being a brilliant theoretical concept, the associations defined in this way turned out to be too broad for detailed vegetation studies. In the years following Braun-Blanquet's thesis, the original association concept was gradually and almost surreptitiously transformed by using "regional character species" instead of absolute ones. The new concept was made official in a footnote in volume 5 of the "Prodrome of plant communities" (Braun-Blanquet and Moor 1938): "In the progress of phytosociological studies it has become evident that the associations are individualised by regional and even more or less local character species rather than by absolute ones. The character species of the alliances and orders, in contrast, have a much more general validity. They only occur in other alliances and orders in a constitutive manner if they are distributed over two or more big circles of vegetation (eurosiberian circle, mediterranean circle etc.)" (translated from German).

Therefore, for the purpose of the association concept, the validity of character species was restricted to "floristically homogenous regions", often not larger than a particular valley in the Alps. This allowed Braun-Blanquet to maintain his original definition of the association, which requires at least one character species for each association, while in fact they were only defined by differential species. The concept is best illustrated in Braun-Blanquet's monograph of the inner-alpine dry valleys (Braun-Blanquet 1961), where the vicariant associations of an alliance mostly have the same regional character species that are in fact character species of the alliance. Thus, the new associations were basically geographical subdivisions of the alliance, whereas the old associations became the alliances. This concept worked surprisingly well, despite

the fact that nobody could give a clear definition of a "floristically homogenous region" (Willner 2006), and the original association concept was forgotten.

Back to the roots: towards an operational definition of the alliance

According to Braun-Blanquet, the character species of alliances have a much more general validity than those of the association, being geographically constrained only by the "circle of vegetation." The latter, however, remained an elusive concept that has not been used in the phytosociological literature for many decades. In fact, geographical restrictions to the validity of character species are very problematic for both practical and theoretical reasons. On the one hand, any delimitation of areas of validity is arbitrary, circular or based on external criteria not derived from the vegetation itself. On the other hand, the one-to-one relationship between taxa and vegetation units is destroyed, thus weakening the biogeographical and evolutionary significance of the syntaxonomic system. I therefore suggest that we abandon all geographical restrictions and only use absolute character taxa for higher syntaxa. The term "*character taxa*" underlines the fact that subspecies may be used to define higher syntaxa as long as they are really genetically different. In certain cases, the use of supraspecific taxa might also be reasonable, e.g. in vegetation types characterised by closely related species with narrow geographical ranges (Deil 1994).

An "*absolute character taxon*" is a taxon which has its global optimum in the syntaxon in question. Obviously, a taxon can only be an absolute character taxon of exactly one syntaxon. Possible exceptions could be cryptic taxa (i.e., morphologically indistinguishable, but genetically isolated infraspecific entities), and species introduced to other continents and genetically differentiated from their native range (e.g. *Robinia pseudoacacia* in Europe; Bouteiller et al. 2019). Such cases could be seen as "subspecies in statu nascendi" and used as character taxa of higher syntaxa, provided that the latter are sufficiently different in their overall species composition. In contrast, geographically isolated ranges without accompanying genetic differentiation would not be sufficient to use a character taxon for two different syntaxa.

Building upon these ideas, and incorporating the concept of central syntaxa (see below), I propose the following definition:

"An alliance is a moderately broad vegetation unit that either has one or several absolute character taxa or that can be interpreted as the central alliance of an order."

There are several aspects in this definition that need further explanation. The term "*moderately broad vegetation unit*" refers to the relative position of the alliance in the syntaxonomic hierarchy, being intermediate between the more narrowly defined association and the broader units above. Indeed, analogous definitions should be adopted for the order and class level, the latter being broad and very broad vegetation units, respectively, though physiognomic considerations might come into play at these ranks as well (see below). A more precise specification of the range of compositional variability covered by an alliance seems hardly possible and even undesirable given the extreme differences among different types of vegetation.

A "*central syntaxon*" is a syntaxon which has the diagnostic species of the next higher unit but is only negatively differentiated from the next similar units of the same rank. Per definition, there can be only one central syntaxon within each higher unit. The concept was introduced by Dierschke (1981) for associations bearing the character species of the alliance, but lacking character species of their own. Later, Dengler et al. (2005) argued that the same logic can be applied to higher syntaxa. Indeed, many alliances adopted in the literature are central syntaxa, although this fact is often obscured by the enumeration of "regional character species." A prominent example is the *Galio odorati-Fagion* (Central European basiphytic beech forests) which is only negatively differentiated from their counterparts in southern Europe (Willner et al. 2017). It contains most of the character species of the order *Fagetalia sylvaticae* but has no character species of its own. A potential argument against central alliances could be that in this way the delimitation of the alliances becomes dependent on the orders, and therefore the system would have to be developed top-down instead of bottom-up. However, in reality, syntaxonomy is always a combination of top-down and bottom-up perspectives. Regional and national monographs often disagree on the syntaxonomic rank at which a species is characteristic (e.g., the same species is considered as characters species for an alliance in one study and for the whole order in another study). The appropriate rank for each species can only be determined by a broad-scale comparison. Thus, an alliance previously considered to have several character species of its own might turn out to be the central alliance of the order. However, as there can be only one central alliance per order, it could also mean that several alliances must be merged. The same logic applies to the orders within a class.

It is now widely recognised that floristically defined units should be constrained by certain structural types or formations, although the exact number and definition of the latter remains a matter of debate (Theurillat et al. 1995; Dengler et al. 2005; Faber-Langendoen et al. 2014; Willner 2017). Thus, some authors proposed that the same species could be character species within two different formations or structural types (Dengler et al. 2005). However, formation-specific character species are in fact a special case of shared differential species rather than true character species. They should only be used if a species is similarly frequent and vital within two formations and therefore would not be suitable as character species of a single syntaxon. For instance, the dwarf-shrub *Erica carnea* grows with equally high constancy and cover

within dry pine forests and in treeless dwarf-shrub heaths of Central Europe. Thus, if pine forests and dwarf-shrub heaths are classified in different classes, *Erica carnea* could not be used as unique character species of any syntaxon. However, it might be accepted as formation-specific character species for both a pine-forest and a dwarf-shrub syntaxon. On the other hand, species that clearly have their optimum outside of forests and only occasionally occur under a tree canopy, or just as successional relics, should not be used as formation-specific character species of forest syntaxa, as they could not survive in the absence of their true, treeless habitat. Alliances solely based on formation-specific character species should be avoided unless there is no other reasonable solution.

Another issue that needs further attention is the frequency of the character species within the alliance. Since alliances are usually not only defined by character but also by differential species, the absence of character species in some associations is not a problem. However, is a single character species with restricted geographical range and very low constancy sufficient to raise a vegetation unit to alliance rank? Without putting forward precise threshold values, I suggest as a minimum requirement that at least one character species of the alliance should either occur in most associations with low (<20%) to moderate (20–60%) constancy or in some associations with high (>60%) constancy. Transgressive character species of associations are, by definition, character species of the alliance (Westhoff and van der Maarel 1978; Dengler et al. 2005). In any case, the alliance is not necessarily the lowest syntaxon that has a character species.

The biogeographical meaning of higher syntaxa

The proposed alliance concept emphasises the importance of intensive floristic definitions of higher syntaxa (De Cáceres et al. 2015), and the special role of character species for these definitions. As already indicated by Braun (1915), vegetation units based on coherent groups of character species are more than arbitrary boxes of similar plant communities. The one-to-one relationship between character species and vegetation units gives the latter a clear biogeographical and even evolutionary meaning. Associations, in contrast, often lack true character species. They are temporally less stable, especially in regions strongly affected by the climatic fluctuations of the Pleistocene. Therefore, from a global perspective, alliances could be perceived as more fundamental units than the associations, although the latter are formally the basic units of the phytosociological system. However, there are cases that may differ, such as vegetation types characterised by highly competitive, often monodominant species (e.g. marsh vegetation). In such vegetation, associations are mostly defined by the dominance of a single transgressive species, and the alliances by the frequent co-occurrence of these species as well as by differential species from other classes, while specific alliance species are lacking (Landucci et al. 2020). In these cases, the associations might be regarded as more fundamental than the alliances.

Syntaxa are abstract units, but the patterns behind them are real. Well-supported groups of character species (i.e., frequently co-occurring species with similar habitat requirements and similar geographical ranges) could be interpreted, to some degree, as natural entities reflecting a common biogeographical history of the species. However, despite the recent advances in phylogenetics and historical biogeography, the evolution of higher syntaxa has gained little attention in the scientific literature (but see Deil 1999, 2014 for some attempts in this direction). There are four possible mechanisms of "syntaxon evolution", which in most cases will act simultaneously: (i) speciation, (ii) extinction, (iii) adaptation of species to new habitats, and (iv) species migration (see Wiens 2012 for a similar model). For instance, isolation over long time periods might result in a previously wide-spread syntaxon being split into two or more syntaxa, each with its own set of character species. Alternatively, new habitats or areas might become available which are colonised by existing species. This colonisation might be accompanied by evolutional changes, leading to new species or subspecies, which subsequently become character taxa of new syntaxa (Figure 1). The alpine plant radiation, triggered by the uplift of high mountain systems during the late Tertiary (Hughes and Atchison 2015), has probably given rise to the numerous classes and orders of high-mountain vegetation described from Europe and other continents. Alliances might rather reflect the migration, extinction and speciation events caused by the climatic oscillations of the Pleistocene (Comes and

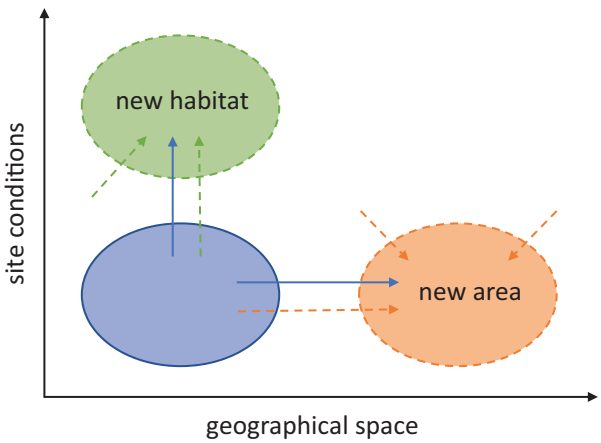

Figure 1. Two simple scenarios for the emergence of new syntaxa. Blue circle: old syntaxon. Green and orange circles: newly emerging syntaxa. Solid blue arrows: species colonising and adapting to a new habitat or area. Dashed arrows: colonisation coupled with evolutionary changes, leading to new species or subspecies, which become character taxa of the new syntaxa.

Kadereit 1998; Willner et al. 2009, 2017). Adaptation to a new habitat might shift the ecological niche of a species in such way that its optimum lies no longer in its original but in a new syntaxon. For instance, *Arrhenatherum elatius*, now the main character species of nutrient-rich mesic grasslands of Europe and almost exclusively found in anthropogenic habitats, is thought to have originated from nutrient-rich scree communities (Ellenberg 2009). Thus, a syntaxon can be much younger than its character species, but obviously it cannot be older. It is safe to assume that the age of alliances, orders and classes varies from a few hundred years in case of some types of anthropogenic vegetation to millions of years in case of old natural habitats.

Conclusions and outlook

Braun-Blanquet's original association concept provides a promising basis for defining the alliance. Otherwise, any grouping of associations could become an alliance, and the "inflation of higher syntaxa" (Pignatti 1995) could go on forever. However, there is more than just a practical need for this concept. The one-to-one relationship between character species and higher syntaxa offers the opportunity for integrating phytosociology and biogeographical-evolutionary studies, a scientific field that has hardly been explored.

The EuroVegChecklist (Mucina et al. 2016) was accompanied by expert-derived diagnostic species lists for the classes. The task of evaluating these species lists using large plot data sets and identifying the diagnostic species for the alliances and orders is still in the early stages. Optimally, this should be done with a simultaneous revision of the syntaxonomic system. The alliance concept outlined in this paper could serve as a helpful tool for these exercises.

Acknowledgements

I'm grateful to Idoia Biurrun, Federico Fernández-González and two anonymous reviewers for their valuable comments on a previous draft of the manuscript, and to Don Faber-Langendoen for checking the English and providing additional comments.

References

Bouteiller XP, Verdu CF, Aikio E, Bloese P, Dainou K, Delcamp A, De Thier O, Guichoux E, Mengal C, ... Mariette S (2019) A few north Appalachian populations are the source of European black locust. Ecology and Evolution 9: 2398–2414. https://doi.org/10.1002/ece3.4776

Braun J (1913) Die Vegetationsverhältnisse der Schneestufe in den Rätisch-Lepontischen Alpen. Ein Bild des Pflanzenlebens an seinen äußersten Grenzen. Neue Denkschriften der Schweizerischen Naturforschenden Gesellschaft 48: 1–347.

Braun J (1915) Les Cévennes méridionales (Massif de l'Aigoual): étude phytogéographique. Thèse présentée à la Faculté des sciences de Montpellier. Société Générale d'Imprimerie, Genève, CH.

Braun J, Furrer E (1913) Remarques sur l'étude des groupements de plantes. Bulletin de la Société Languedocienne de Géographie 36: 20–41.

Braun-Blanquet J (1921) Prinzipien einer Systematik der Pflanzengesellschaften auf floristischer Grundlage. Jahrbuch der St. Gallener Naturwissenschaftlichen Gesellschaft 57: 305–351.

Braun-Blanquet J (1926) Le 'climax complexe' des landes alpines (*Genisto-Vaccinion* du Cantal). Arvernia 2: 29–48.

Braun-Blanquet J (1961) Die inneralpine Trockenvegetation. Gustav Fischer, Stuttgart, DE.

Braun-Blanquet J (1964) Pflanzensoziologie. Grundzüge der Vegetationskunde. 3rd edition. Springer, Wien, AT. https://doi.org/10.1007/978-3-7091-8110-2

Braun-Blanquet J, Jenny H (1926) Vegetationsentwicklung und Bodenbildung in der alpinen Stufe der Zentralalpen. Denkschriften der Schweizerischen Naturforschenden Gesellschaft 63: 183–349.

Braun-Blanquet J, Moor M (1938) Verband des *Bromion erecti*. Prodromus der Pflanzengesellschaften 5, Montpellier, FR.

Čarni A, Košir P, Karadžić B, Matevski V, Redžić S, Škvorc Ž (2009) Thermophilous deciduous forests in Southeastern Europe. Plant Biosystems 143: 1–13. https://doi.org/10.1080/11263500802633881

Comes HP, Kadereit JW (1998) The effect of Quaternary climatic changes on plant distribution and evolution. Trends in Plant Science 3: 432–438. https://doi.org/10.1016/S1360-1385(98)01327-2

De Cáceres M, Chytrý M, Agrillo E, Attorre F, Botta-Dukát Z, Capelo J, Czúcz B, Dengler J, Ewald J, ... Wiser SK (2015) A comparative framework for broad-scale plot-based vegetation classification. Applied Vegetation Science 18: 543–560. https://doi.org/10.1111/avsc.12179

Deil U (1994) Klassifizierung mit supraspezifischen Taxa und symphylogenetische Ansätze in der Vegetationskunde. Phytocoenologia 24: 677–694. https://doi.org/10.1127/phyto/24/1994/677

Deil U (1999) Synvikarianz und Symphylogenie. Zur Evolution von Pflanzengesellschaften. Berichte der Reinhold-Tüxen-Gesellschaft 11: 223–244.

Deil U (2014) Rock communities and succulent vegetation in Northern Yemen (SW Arabia) – ecological, phytochorological and evolutionary aspects. Phytocoenologia 44: 193–234. https://doi.org/10.1127/0340-269X/2014/0044-0590

Dengler J (2003) Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtigung der Vegetationsklassifikation [Archiv naturwissenschaftlicher Dissertationen 14]. Martina Galunder-Verlag, Nümbrecht, DE.

Dengler J, Berg C, Jansen F (2005) New ideas for modern phytosociological monographs. Annali di Botanica, nuova serie, 5: 193–210.

Dierschke H (1981) Zur syntaxonomischen Bewertung schwach gekennzeichneter Pflanzengesellschaften. In: Dierschke H (Ed.) Syntaxonomie (Rinteln 31.3.–3.4.1980). Berichte der Internationalen Symposien der Internationalen Vereinigung für Vegetationskunde. Cramer, Vaduz, LI, 109–122.

Ellenberg H (2009) Vegetation ecology of Central Europe, 4th ed. Cambridge University Press, Cambridge, UK.

Faber-Langendoen D, Keeler-Wolf T, Meidinger D, Tart D, Hoagland B, Josse C, Navarro G, Ponomarenko S, Saucier J-P, … Comer P (2014) EcoVeg: a new approach to vegetation description and classification. Ecological Monographs 84: 533–561. https://doi.org/10.1890/13-2334.1

Flahault C, Schröter C (1910) Rapport sur la nomenclature phytogéographique. In: Wildeman ED (Ed.) Actes du III. Congrès International de Botanique, Bruxelles 1910. De Boeck, Bruxelles, BE, 131–142.

Guarino R, Willner W, Pignatti S, Attorre F, Loidi JJ (2018) Spatio-temporal variations in the application of the Braun-Blanquet approach in Europe. Phytocoenologia 48: 239–250. https://doi.org/10.1127/phyto/2017/0181

Hughes CE, Atchison GW (2015) The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. New Phytologist 207: 275–282. https://doi.org/10.1111/nph.13230

Jennings MD, Faber-Langendoen D, Loucks OL, Peet RK, Roberts D. (2009) Standards for associations and alliances of the U.S. National Vegetation Classification. Ecological Monographs 79: 173–199. https://doi.org/10.1890/07-1804.1

Koch W (1926) Die Vegetationseinheiten der Linthebene unter Berücksichtigung der Verhältnisse in der Nordostschweiz. Systematisch-kritische Studie. Jahresberichte der St. Gallischen Naturwissenschaftlichen Gesellschaft 61 (2): 1–144.

Landucci F, Šumberová K, Tichý L, Hennekens S, Aunina L, Biță-Nicolae C, Borsukevych L, Bobrov A, Čarni A, ... Chytrý M (2020) Classification of the European marsh vegetation (*Phragmito-Magnocaricetea*) to the association level. Applied Vegetation Science 23: 297–316. https://doi.org/10.1111/avsc.12484

Luquet A (1926) Essai sur la géographie botanique de l'Auvergne. Les associations végétales du Masif des Monts-Dores. Presses Universitaires France, Paris, FR.

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, ... Tichý L (2016) Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (Suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Pavillard J (1935) Éléments de sociologie végétale (phytosociologie). Hermann, Paris, FR.

Peterka T, Hájek M, Jiroušek M, Jiménez-Alfaro B, Aunina L, Bergamini A, Dítě D, Felbaba-Klushyna L, Graf U, ... Chytrý M (2017) Formalized classification of European fen vegetation at the alliance level. Applied Vegetation Science 20: 124–142. https://doi.org/10.1111/avsc.12271

Pignatti S (1995) A new spirit in phytosociology. Annali di Botanica 53: 9–21.

Rodwell JS, Schaminée JHJ, Mucina L, Pignatti S, Dring J, Moss D (2002) The diversity of European vegetation – An overview of phytosociological alliances and their relationships to EUNIS habitats. National Reference Centre for Agriculture, Nature and Fisheries [Report no. EC-LNV 2002(054)], Wageningen, NL.

Theurillat J-P, Aeschimann D, Küpfer P, Spichiger R (1995) The higher vegetation units of the Alps. Colloques Phytosociologiques 23: 189–239.

Westhoff V, van der Maarel E (1978) The Braun-Blanquet Approach. In: Whittaker RH (Ed.) Classification of Plant Communities. Dr. W. Junk, The Hague, NL, 287–399. https://doi.org/10.1007/978-94-009-9183-5_9

Wiens JJ (2012) Why biogeography matters: historical biogeography vs. phylogeography and community phylogenetics for inferring ecological and evolutionary processes. Frontiers of Biogeography 4: 128–135. https://doi.org/10.21425/F54313269

Willner W (2006) The association concept revisited. Phytocoenologia 36: 67–76. https://doi.org/10.1127/0340-269X/2006/0036-0067

Willner W (2017) Classification of the Austrian forest and shrub communities: concepts, methods and experiences. Documents Phytosociologiques 6: 44–50.

Willner W, Di Pietro R, Bergmeier E (2009) Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. Ecography 32: 1011–1018. https://doi.org/10.1111/j.1600-0587.2009.05957.x

Willner W, Jiménez-Alfaro B, Agrillo E, Biurrun I, Campos JA, Čarni A, Casella L, Csiky J, Ćušterevska R, ... Chytrý M (2017) Classification of European beech forests: a Gordian Knot? Applied Vegetation Science 20: 494–512. https://doi.org/10.1111/avsc.12299

E-mail and ORCID

Wolfgang Willner (wolfgang.willner@univie.ac.at), ORCID: https://orcid.org/0000-0003-1591-8386

Supplementary material

Supplementary material 1
Associations in Braun (1915) and corresponding syntaxa in the EuroVegChecklist (Mucina et al. 2016).
Link: https://doi.org/10.3897/VCS/2020/56372.suppl1

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 145–147
doi: 10.3897/VCS/2020/60352

REPORT

First Report of the European Vegetation Classification Committee (EVCC)

Idoia Biurrun[1], Wolfgang Willner[2]

1 *Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain*
2 *Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria*

Corresponding author: Idoia Biurrun (idoia.biurrun@ehu.es)

Academic editor: Florian Jansen ♦ **Received** 3 November 2020 ♦ **Accepted** 10 November 2020 ♦ **Published** 17 December 2020

Abstract

The European Vegetation Classification Committee (EVCC) was established in 2017 by the European Vegetation Survey to maintain and update a standard phytosociological classification of European vegetation. Vegetation scientists can send proposals for modification of specific parts of the EuroVegChecklist, which is used as a baseline. The proposals are accepted or rejected based on recommendations issued by a specialist group and after voting by EVCC members. Here we report the results of the first voting, which took place from 4 June to 4 July 2020. EVCC members voted on the recommendations issued for three proposals of change concerning spring and dune vegetation, and mediterranean grasslands. As a result, EVCC accepted to modify the classes *Ammophiletea* and *Helichryso-Crucianelletea*, but rejected to include the alliance *Philonotidion seriatae* and the class *Charybdido pancratii-Asphodeletea ramosi*. These rejections are not final, and similar proposals can be submitted again with new data supporting the proposed changes.

Abbreviations: EVCC = European Vegetation Classification Committee; SG = Specialist Group.

Keywords

Alliance, class, European Vegetation Survey, EuroVegChecklist, EVCC, order, phytosociology, syntaxonomy

Introduction

European phytosociology has traditionally been characterised by a pluralism of national and regional traditions (Guarino et al. 2018). The idea to develop a coherent overview of vegetation units for the whole of Europe was revived by the formation of the IAVS working group 'European Vegetation Survey' in 1992, and a first preliminary compilation was published by Rodwell et al. (2002). In the following years, these attempts were intensified, culminating in the publication of the 'EuroVegChecklist' (Mucina et al. 2016).

In 2017, the European Vegetation Classification Committee (hereafter EVCC) was established by the European Vegetation Survey to maintain and update a standard phytosociological classification of European vegetation, taking the EuroVegChecklist as a baseline. The EVCC involves experts whose expertise collectively covers most European vegetation types and most European regions. Its tasks are: (a) receiving proposals for changes of specific parts of the EuroVegChecklist; (b) organising the reviewing of these proposals by international expert groups; and (c) deciding about acceptance or rejection of the proposals.

Currently, the EVCC has the following 69 members: Emiliano Agrillo, Iva Apostolova, Fabio Attorre, Christian Berg, Erwin Bergmeier, Edoardo Biondi, Idoia Biurrun, Carlo Blasi, Richard Boeuf, Salvatore Brullo, Helga Bültmann, Juan Antonio Campos, Jorge Capelo, Andraž Čarni, Milan Chytrý, János Csiky, Fred Daniëls, Jürgen Dengler, Yakiv Didukh, Panayotis Dimopoulos, Romeo Di Pietro, Nikolai Ermakov, Giuliano Fanelli, Federico Fernández-González, Dan Gafta, Rosario Gavilán, Dan-

PENSOFT.

Copyright *Idoia Biurrun, Wolfgang Willner*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

iela Gigante, Gian Pietro Giusso del Galdo, Valentin Golub, Riccardo Guarino, Michal Hájek, Rense Haveman, Dmytro Iakushenko, Adrian Indreica, Ute Jandt, Monika Janišová, Jan Jansen, John Janssen, Borja Jiménez-Alfaro, Zygmunt Kącki, Anna Kuzemko, Flavia Landucci, Javier Loidi, Zdeňka Lososová, Corrado Marcenò, Vlado Matevski, José Antonio Molina, Ladislav Mucina, Vladimir Onipchenko, Sandro Pignatti, Valerijus Rašomavičius, John Rodwell, Jan Roleček, Solvita Rūsina, Daniel Sánchez Mata, Arnoldo Santos Guerra, Joop Schaminée, Jozef Šibík, Urban Šilc, Željko Škvorc, Vladimir Stupar, Kateřina Šumberová, Massimo Terzi, Gilles Thébaud, Jean-Paul Theurillat, Ioannis Tsiripidis, Rossen Tzonev, Milan Valachovič, and Wolfgang Willner.

Any vegetation scientist can send a proposal for modification of a specific part of the EuroVegChecklist, typically based on published scientific papers. The EVCC establishes a Specialist Group (SG) for each proposal received. Each SG consists of at least three members of the EVCC whose expertise is close to the topic of the proposal, led by a Coordinating Editor assigned by the Secretary (or Deputy Secretary) of the EVCC. Based on the discussion within the SG, the Coordinating Editor prepares a recommendation about the proposal, which can be 'Accept' or 'Reject'. Once a year, the EVCC members are asked to vote about the recommendations. More details about the whole procedure are available in the document approved at the EVS Business Meeting in Bilbao on 14 September 2017 (available at http://euroveg.org/download/EuroVegChecklist-update-procedures-2017-09-14-APPROVED.pdf).

Here we report the results of the first voting, which took place from 4 June to 4 July 2020. In this voting, EVCC members were asked to vote on the recommendations issued for three proposals of change.

Report on proposals, recommendations and voting

Proposal 001 – Inclusion of the alliance *Philonotidion seriatae* in the EuroVegChecklist

Author of proposal: Dirk Hinterlang
Date of proposal: 5 October 2017

Summary of proposal: The author suggests to include the alliance *Philonotidion seriatae* Hinterlang 1992 in the EuroVegChecklist, where it is currently indicated as syntaxonomic synonym of the alliance *Swertio perennis-Anisothecion squarrosi* Hadač 1983.
Supporting publication: Hinterlang (2017).

Specialist Group: Michal Hájek (Coordinating Editor), Ladislav Mucina, Jürgen Dengler, José Molina, Christian Berg, Milan Valachovič, Jozef Šibík.

Recommendation (23 February 2018): The SG suggested to reject the proposal, but to reconsider the decision if additional material is provided which clearly demonstrates the floristic independence of *Swertio-Anisothecion squarrosi* and *Philonotidion seriatae* (i.e., own diagnostic species) at a wider geographical scale.

Voting: The recommendation of the Specialist Group was confirmed by the EVCC.

Proposal 002 – Inclusion of the class *Charybdido pancratii-Asphodeletea ramosi* in the EuroVegChecklist

Authors of proposal: Edoardo Biondi, Simona Casavecchia, Simone Pesaresi, Roberta Gasparri and Nello Biscotti
Date of proposal: 27 February 2018

Summary of proposal: The authors suggest to include the new class *Charybdido pancratii-Asphodeletea ramosi* Biondi et al. 2016 with its two new orders *Asphodeletalia ramosi* Biondi in Biondi et al. 2016 and *Bellido sylvestris-Arisaretalia vulgaris* Biondi in Biondi et al. 2017 in the EuroVegChecklist.

Supporting publications: Biondi et al. (2016), Biondi et al. (2017).

Specialist Group: Andraž Čarni (Coordinating Editor), Jorge Capelo, Romeo Di Pietro, Giuliano Fanelli, Ladislav Mucina, Jozef Šibík.

Recommendation (11 November 2019): The SG noted that this proposal goes beyond merely accepting a new class into the EuroVegChecklist. It also contains syntaxonomic changes of concern for the classes *Lygeo-Stipetea* Rivas-Mart. 1978 and *Trifolio-Geranietea* T. Müller 1962. A proposal of a new class should be clearly ecologically and floristically argued. The floristic delimitation would be unequivocally addressed if a synoptic table was presented that would document the status of the new class in relation to other, floristically similar classes. The SG identified at least two classes towards which the *Charybdido-Asphodeletea* should be delimited, namely towards the *Lygeo-Stipetea* and the *Trifolio-Geranietea*. Therefore, the SG recommended rejection, but encouraged the authors to provide additional evidence for their proposal by means of synoptic tables.

Voting: The Recommendation of the Specialist Group was confirmed by the EVCC.

Proposal 003 – Modification of the classes *Ammophiletea* and *Helichryso-Crucianelletea* in the EuroVegChecklist

Authors of proposal: Corrado Marcenò and Milan Chytrý
Date of proposal: 18 October 2019

Summary of proposal: The authors suggest to rearrange the syntaxonomic framework of European dune vegetation. They propose to modify the classes *Ammophiletea* Br.-Bl. et Tx. ex Westhoff et al. 1946 and *Helichryso-Crucianelletalia maritimae* Géhu et al. in Sissingh 1974. The main change would be the inclusion of the *Honckenyo-Elymetea arenarii* Tx. 1966 and *Elymetalia*

gigantei Vicherek 1971 as separate class and order, respectively.

Supporting publications: Boşcaiu (1975), Sburlino et al. (2013), Marcenò et al. (2018).

Specialist Group: Juan Antonio Campos (Coordinating Editor), Erwin Bergmeier, Jürgen Dengler, Rense Haveman.

Recommendation (7 February 2020): The SG concluded that Marcenò et al. (2018) convincingly demonstrated that the variation in species composition of European and Mediterranean coastal dune vegetation is strongly affected by the geographic component (differentiation between Atlantic, Mediterranean and Black Sea regions). TWINSPAN classification and DCA clearly supported the main separation between the Atlantic–Baltic and Mediterranean–Black Sea dune vegetation. This vegetation pattern is also supported by phylogeographic studies (Kadereit et al. 2005; Kadereit and Westberg 2007) carried out on some widely distributed dune species such as *Cakile maritima*, *Eryngium maritimum*, *Euphorbia paralias*, which point to the importance of the Strait of Gibraltar as a barrier in the gene flow of many coastal species. Therefore, the SG recommend acceptance of the proposal with minor wording adjustments that were accepted by the authors of the proposal.

Voting: The recommendation of the Specialist Group was confirmed by the EVCC. The proposal is therefore accepted.

Summary and outlook

The modifications as indicated in Proposal 003 will be implemented in the next EuroVegChecklist update. However, we would like to emphasise that the rejection of Proposals 001 and 002 is not final. In both cases, the main reason why the expert committees recommended rejection was the lack of a pan-European revision with synoptic tables. Thus, it is possible that the same or similar proposals are submitted again when new data supporting the proposed changes have been presented.

Two more proposals are now in the evaluation process. We would like to remind vegetation scientists who are willing to submit a proposal to follow the abovementioned procedures, especially regarding the documentation supporting the proposal, e.g., scientific papers including synoptic tables showing the floristic delimitation between the target syntaxon/syntaxa and other related ones.

Proposals have to be sent to the acting EVCC Secretary or Deputy Secretary (see http://euroveg.org/evc-committee).

Author contributions

W.W. planned the report, I.B. wrote it with important inputs from W.W.

References

Biondi E, Pesaresi S, Galdenzi D, Gasparri R, Biscotti N, del Viscio G, Casavechia S (2016) Post-abandonment dynamic on Mediterranean and sub-Mediterranean perennial grasslands: the edge vegetation of the new class *Charybdido pancratii-Asphodeletea ramosi.* Plant Sociology 53: 3–18.

Biondi E, Pesaresi S, Gasperri R, Biscotti N, del Viscio G, Bonsanto D, Casavecchia S (2017) New contributions to the class *Charybdido pancratii-Asphodeletea ramosi* Biondi 2016. Plant Sociology 54: 137–144.

Boşcaiu N (1975) Aspecte de vegetaţie din reservaţia dunelor maritime de la Agigea [Vegetation aspects from the Agigea sea dune reserve]. Studii şi Comunicări, Muzeul Bruckenthal, Ştiinţele Naturii, Sibiu, 19: 81–93.

Guarino R, Willner W, Pignatti S, Attorre F, Loidi J (2018) Spatio-temporal variations in the application of the Braun-Blanquet approach in Europe. Phytocoenologia 48: 239–250. https://doi.org/10.1127/phyto/2017/0181

Hinterlang D (2017) *Montio-Cardaminetea* (C 6). Quell- und Waldsumpf-Gesellschaften [Synopsis der Pflanzengesellschaften Deutschlands. Heft 12]. Göttingen, DE, 110 pp.

Kadereit JW, Westberg E (2007) Determinants of phylogeographic structure: a comparative study of seven coastal flowering plant species across their European range. Watsonia 26: 229–238.

Kadereit JW, Arafeh R, Somogyi G, Westberg E (2005) Terrestrial growth and marine dispersal? Comparative phylogeography of five coastal plant species at a European scale. Taxon 54: 861–876. https://doi.org/10.2307/25065567

Marcenò C, Guarino R, Loidi J, Herrera M, Isermann M, Knollová I, Tichý L, Tzonev RT, Acosta ATR, Chtyrý M (2018) Classification of European and Mediterranean coastal dune vegetation. Applied Vegetation Science 21: 533–559. https://doi.org/10.1111/avsc.12379

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, ... Tichý L (2016) Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (Suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Rodwell JS, Schaminée JHJ, Mucina L, Pignatti S, Dring J, Moss D (2002) The diversity of European vegetation – An overview of phytosociological alliances and their relationships to EUNIS habitats. National Reference Centre for Agriculture, Nature and Fisheries [Report no. EC-LNV 2002(054)], Wageningen, NL, 167 pp.

Sburlino G, Buffa G, Filesi L, Gamper U, Ghirelli L (2013) Phytocoenotic diversity of the N-Adriatic coastal sand dunes – The herbaceous communities of the fixed dunes and the vegetation of the interdunal wetlands. Plant Sociology 50: 57–77.

E-mail and ORCID:

Idoia Biurrun (Corresponding author, idoia.biurrun@ehu.es), ORCID: https://orcid.org/0000-0002-1454-0433.
Wolfgang Willner (wolfgang.willner@univie.ac.at), ORCID: https://orcid.org/0000-0003-1591-8386.

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 149–150
doi: 10.3897/VCS/2020/60520

SHORT DATABASE REPORT ECOINFORMATICS

Eastern European Steppe Database

Denys Vynokurov[1], Yakiv Didukh[1], Olga Krasova[2], Hennadiy Lysenko[3], Igor Goncharenko[4], Iryna Dmytrash-Vatseba[5], Olga Chusova[1], Dariia Shyriaieva[1], Vitalii Kolomiychuk[6], Ivan Moysiyenko[7]

1 *M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine*
2 *Kryvyi Rih Botanical Garden of National Academy of Sciences of Ukraine, Kryvyi Rih, Ukraine*
3 *Department of Biology, Gogol State University of Nizhyn, Nizhyn, Ukraine*
4 *Institute for Evolutionary Ecology, National Academy of Sciences of Ukraine, Kyiv, Ukraine*
5 *Halych National Nature Park, Krylos, Ukraine*
6 *O.V. Fomin Botanical Garden, the National Taras Shevchenko University, Kyiv, Ukraine*
7 *Department of Botany, Kherson State University, Kherson, Ukraine*

Corresponding author: Denys Vynokurov (denys.vynokurov@gmail.com)

Academic editor: Florian Jansen ♦ **Received** 8 November 2020 ♦ **Accepted** 12 November 2020 ♦ **Published** 21 December 2020

Abstract

The Eastern European Steppe Database (GIVD ID EU-00-030) includes 6961 vegetation plots of dry grassland vegetation from Eastern Europe (Steppe and Forest-Steppe zones, mountain regions), mainly from Ukraine (4579 relevés), Russia (2403 relevés) and Moldova (203 relevés). 3912 vegetation plots are from different literature sources (66 sources), 219 are from the phytosociological card-index of the M.G. Kholodny Institute of Botany, NAS of Ukraine, 2830 relevés are authors' relevés. They were established in 1935-2019 years. The database comprises mainly the vegetation of the class *Festuco-Brometea* (around 95% of the dataset), and a small proportion of *Koelerio-Corynephoretea canescentis*, *Artemisietea vulgaris*, *Crataego-Prunetea*. The taxonomy of vascular species is given according to Cherepanov (1995) for vascular plants, Ignatov and Afonina (1992) for bryophytes and identification guides of the USSR (1971–1978) and Russia (1996, 1998) for lichens. The database is part of the European Vegetation Archive.

Keywords

Dry grassland, Eastern Europe, forest-steppe zone, steppe, steppe zone

PENSOFT.

Copyright *Denys Vynokurov et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

GIVD Fact Sheet

GIVD Database ID: EU-00-030			**Last update:** 2020-11-09
Eastern European Steppe Database		**Web address:**	
Database manager(s): Denys Vynokurov (denys.vynokurov@gmail.com)			
Owner: Denys Vynokurov			
Scope: The database includes the relevés of different types of grasslands from Ukraine. Criteria for inclusion: plot size from 1 to 100 m2 and clear geographic location			
Abstract: The Eastern European Steppe Database (GIVD ID EU-00-030) includes 6961 vegetation plots of dry grassland vegetation from Eastern Europe (Steppe and Forest-Steppe zones, mountain regions), mainly from Ukraine (4579 relevés), Russia (2403 relevés) and Moldova (203 relevés). 3912 vegetation plots are from different literature sources (66 sources), 219 are from the phytosociological card-index of the M.G. Kholodny Institute of Botany, NAS of Ukraine, 2830 relevés are authors' relevés. They were established in 1935-2019 years. The database comprises mainly the vegetation of the class Festuco-Brometea (around 95% of the dataset), and a small proportion of Koelerio-Corynephoretea canescentis, Artemisietea vulgaris, Crataego-Prunetea. The taxonomy of vascular species is given according to Cherepanov vascular plants checklist (1995), bryophytes – M. Ignatov & O. Afonina checklist (1992) and lichens – identification guides of the USSR (1971–1978) and Russia (1996, 1998).			
Availability: free upon request		**Online upload:** no	**Online search:** no
Database format(s): TURBOVEG		**Export format(s):** TURBOVEG, Excel	
Plot type(s): normal plots		**Plot-size range:** 4 to 625	
Non-overlapping plots: 6961	**Estimate of existing plots:** 6961	**Completeness:** 100%	**Status:** completed and continuing
Total no. of plot observations: 6961	**Number of sources (biblioreferences, data collectors):** 66		**Valid taxa:** 0
Countries (%): UA: 62.5; RU: 34.1; MD: 2.9			
Formations: Non Forest: 100% = Terrestrial: 100% (Non arctic-alpin: 100% [Natural: 43%; Semi-natural: 57%])			
Guilds: all vascular plants: 95%; bryophytes (terricolous or aquatic): 1%; lichens (terricolous or aquatic): 1%			
Environmental data (%): altitude: 23; slope aspect: 49; slope inclination: 46; microrelief: 0; surface cover other than plants (open soil, litter, bare rock etc.): 0; other soil attributes: 0; soil pH: 0; land use categories: 0; soil depth: 0			
Performance measure(s): presence/absence only: 0%; cover: 100%; number of individuals: 0%; measurements like diameter or height of trees: 0%; biomass: 0%; other: 0%			
Geographic localisation: GPS coordinates (precision 25 m or less): 20%; point coordinates less precise than GPS, up to 1 km: 75%; small grid (not coarser than 10 km): 0%; political units or only on a coarser scale (above 10 km): 5%			
Sampling periods: before 1920: 0%; 1920-1929: 0%; 1930-1939: 0.07%; 1940-1949: 0.01%; 1950-1959: 0.04%; 1960-1969: 0.3%; 1970-1979: 4.48%; 1980-1989: 6.51%; 1990-1999: 2.33%; 2000-2009: 22.07%; 2010-2019: 28.65%; unknown: 35.54%			
Information as of 2020-12-14 further details and future updates available from http://www.givd.info/ID/EU-00-030			

E-mail and ORCID

Denys Vynokurov (Corresponding author: denys.vynokurov@gmail.com), ORCID: https://orcid.org/0000-0001-7003-6680
Yakiv Didukh (ya.didukh@gmail.com)
Olga Krasova (kras.kbs.17@gmail.com)
Hennadiy Lysenko (lysenko_gena@yahoo.com)
Igor Goncharenko (goncharenko.ihor@gmail.com), ORCID: https://orcid.org/0000-0001-5239-3270
Iryna Dmytrash-Vatseba (iradmytrash@ukr.net)
Olga Chusova (olgachusova28@gmail.com)
Dariia Shyriaieva (darshyr@gmail.com), ORCID: https://orcid.org/0000-0001-7140-7201
Vitalii Kolomiychuk (vkolomiychuk@ukr.net)
Ivan Moysiyenko (ivan.moysiyenko@gmail.com), ORCID: https://orcid.org/0000-0002-0689-6392

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 151–153
doi: 10.3897/VCS/2020/61348

SHORT DATABASE REPORT

ECOINFORMATICS

Balkan Vegetation Database (BVD) – updated information and current status

Kiril Vassilev[1], Hristo Pedashenko[1], Alexandra Alexandrova[2], Alexander Tashev[2], Anna Ganeva[1], Anna Gavrilova[16], Armin Macanović[14], Assen Assenov[4], Antonina Vitkova[1], Beloslava Genova[7], Borislav Grigorov[4], Chavdar Gussev[1], Ermin Mašić[14], Eva Filipova[10], Gana Gecheva[7], Ina Aneva[1], Ilona Knollová[5], Ivaylo Nikolov[6], Georgi Georgiev[7], Georgi Gogushev[8], Georgi Tinchev[20], Ivan Minkov[7], Kalina Pachedzieva[3], Katerina Mincheva[7], Koycho Koev[9], Mariyana Lyubenova[3], Marius Dimitrov[2], Media Gumus[15], Momchil Nazarov[1], Nadezhda Apostolova-Stoyanova[18], Nikolay Nikolov[4], Nikolay Velev[1], Petar Zhelev[2], Plamen Glogov[10], Rayna Natcheva[1], Rossen Tzonev[3], Senka Barudanović[14], Sofia Kostadinova[4], Steffen Boch[11], Stephan Hennekens[12], Stoyan Georgiev[13], Stoyan Stoyanov[1], Todor Karakiev[21], Tijana Ilić[19], Veronika Kalníková[17], Veselin Shivarov[1], Vladimir Vulchev[1]

1 *Department of Plant and Fungal Diversity and Resources, Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria*
2 *Department of Dendrology, Faculty of Forestry, University of Forestry, Sofia, Bulgaria*
3 *Department of Ecology and Environmental Protection, Faculty of Biology, Sofia University "St. Kliment Ohridski", Sofia, Bulgaria*
4 *Department of Landscape Ecology and Environmental Protection, Faculty of Geology and Geography, Sofia University "St.Kliment Ohridski", Sofia, Bulgaria*
5 *Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic*
6 *Directorate Central Balkan National Park, Gabrovo, Bulgaria*
7 *Department of Ecology, Faculty of Biology, Plovdiv University "Paisii Hilendarski", Plovdiv, Bulgaria*
8 *Regional Forest Directorate Blagoevgrad, Blagoevgrad, Bulgaria*
9 *Departmant of Botany and Teaching Methods in Biology, Faculty of Biology, Plovdiv University "Paisii Hilendarski", Plovdiv, Bulgaria*
10 *Forest Research Institute, Bulgarian Academy of Science, Sofia, Bulgaria*
11 *Biodiversity and Conservation Biology, WSL Swiss Federal Research Institute, Birmensdorf, Switzerland*
12 *Alterra, Wageningen UR, Wageningen, The Netherlands*
13 *Field Crop Institute, Chirpan, Bulgaria*
14 *Depatment of Biology, Faculty of Science, University of Sarajevo, Sarajevo, Bosnia and Herzegovina*
15 *Institute of Oceanology, Bulgarian Academy of Science, Varna, Bulgaria*
16 *Faculty of Pharmacy, Medicinal University, Pleven, Bulgaria*
17 *Beskydy Protected Landscape Area Administration, Rožnov pod Radhoštěm, Czech Republic*
18 *Directorate of Vitosha Nature Park, Sofia, Bulgaria*
19 *Institute of Botany and Botanical Garden "Jevremovac", University of Belgrade, Belgrade, Serbia*
20 *11A Yordan Stubel str., Sofia, Bulgaria*
21 *4 Viktor Yugo str., Sofia, Bulgaria*

Corresponding author: Kiril Vassilev (kiril5914@abv.bg)

Academic editor: Jürgen Dengler ♦ **Received** 24 November 2020 ♦ **Accepted** 26 November 2020 ♦ **Published** 21 December 2020

Abstract

The Balkan Vegetation Database (BVD; GIVD ID: EU-00-019) is a regional database, which was established in 2014. It comprises phytosociological relevés covering various vegetation types from nine countries of the Balkan Peninsula (Albania – 153 relevés, Bosnia and Herzegovina – 1715, Bulgaria – 12,282, Greece – 465, Croatia – 69, Kosovo – 493,

PENSOFT.

Copyright *Kiril Vassilev et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Montenegro – 440, North Macedonia – 13 and Serbia – 2677). Currently, it contains 18,306 relevés (compared to 9.580 in 2016), and most of them (82.8%) are geo-referenced. The database includes both digitized relevés from the literature (65.6%) and unpublished data (34.5%). Plot size is available for 84.7% of all relevés. During the last four years some "header data information" was improved e.g. elevation (now available for 83.4% of all relevés), aspect (67.7%), slope (66%), total cover of vegetation (54.3%), cover of tree, shrub, herb, bryophyte and lichen layers (27.1%, 20.1%, 40.2%, 11.5% and 2.1%), respectively. Data access is either semi-restricted (65.6%) or restricted (34.4%). Most relevés (84.6%) are classified to syntaxa of different levels. The database has been used for numerous studies with various objectives from floristic, vegetation and habitat-related topics, to macroecological studies at the local, regional, national, continental and global levels. During the last four years, BVD data were requested from 111 different projects via the EVA and sPlot databases.

Keywords

Balkan Peninsula, Balkan vegetation, conservation, TURBOVEG, vegetation plot, vegetation classification

GIVD Fact Sheet

GIVD Database ID: EU-00-019			**Last update:** 2020-11-24
Balkan Vegetation Database		**Web address:**	
Database manager(s): Kiril Vassilev (kiril5914@abv.bg); Hristo Pedashenko (hristo_pedashenko@yahoo.com)			
Owner: Kiril Vassilev, Hristo Pedashenko, Alexandra Alexandrova, Alexander Tashev, Anna Ganeva, Anna Gavrilova, Armin Macanović, Assen Assenov, Antonina Vitkova, Beloslava Genova, Borislav Grigorov, Chavdar Gussev, Ermin Mašić, Eva Filipova, Ganna Gecheva, Ina Aneva, Ilona Knollová, Ivaylo Nikolov, Georgi Georgiev, Georgi Gogushev, Georgi Tinchev, Ivan Minkov, Kalina Pachedzieva, Katerina Mincheva, Koycho Koev, Mariyana Lubenova, Marius Dimitrov, Media Gumus, Momchil Nazarov, Nadezhda Apostolova-Stoyanova, Nikolay Nikolov, Nikolay Velev, Petar Zhelev, Plamen Glogov, Rayna Natcheva, Rossen Tzonev, Senka Barudanović, Sofia Kostadinova, Steffen Boch, Stephan Hennekens, Stoyan Georgiev, Stoyan Stoyanov, Todor Karakiev, Tijana Ilić, Veronika Kalníková, Veselin Shivarov, Vladimir Vulchev			
Scope: Balkan Vegetation Database includes 18,306 relevés i.e. all vegetation types are considered, except the dry grasslands (which are in the Balkan Dry Grassland Database) from 9 Balkan countries (Albania – 153 relevés, Bosnia and Herzegovina - 1715, Bulgaria – 12,282, Greece – 465, Croatia – 69, Kosovo - 493, Montenegro – 440, North Macedonia – 13 and Serbia - 2677).			
Abstract:			
Availability: according to a specific agreement		**Online upload:** yes	**Online search:** yes
Database format(s): TURBOVEG		**Export format(s):** TURBOVEG	
Plot type(s): normal plots		**Plot-size range:** 0.2 to 8000	
Non-overlapping plots: 18307	**Estimate of existing plots:** 18307	**Completeness:** 100%	**Status:** completed and continuing
Total no. of plot observations: 18307	**Number of sources (biblioreferences, data collectors):** 340		**Valid taxa:** 09573
Countries (%): BG: 67.09; RS: 14.62; KO: 2.69; ME: 2.40; AL: 0.84; BA: 9.37; GR: 2.54; HR: 0.38; MK: 0.07			
Formations: Forest: 29% // Non Forest: 71% = Aquatic: 4%; Terrestrial: 66%			
Guilds: all vascular plants: 100%; bryophytes (terricolous or aquatic): 16%; lichens (terricolous or aquatic): 7%			
Environmental data (%): altitude: 83.4; slope aspect: 67.7; slope inclination: 66; other soil attributes: 0.6; soil pH: 0.02; land use categories: 11.21; soil depth: 17			
Performance measure(s): presence/absence only: 0%; cover: 100%; number of individuals: 0%; measurements like diameter or height of trees: 10.19%; biomass: 0%; other: 0%			
Geographic localisation: GPS coordinates (precision 25 m or less): 22.71%; point coordinates less precise than GPS, up to 1 km: 4.03%; small grid (not coarser than 10 km): 41.31%; political units or only on a coarser scale (above 10 km): 14.75%			
Sampling periods: before 1920: 0.01%; 1920-1929: 0.58%; 1930-1939: 0.32%; 1940-1949: 2.16%; 1950-1959: 14.91%; 1960-1969: 8.20%; 1970-1979: 7.22%; 1980-1989: 6.43%; 1990-1999: 14.29%; 2000-2009: 14.87%; 2010-2019: 27.15%; unknown: 3.86%			
Information as of 2020-11-24 further details and future updates available from http://www.givd.info/ID/EU-00-019			

Acknowledgements

Development of the Balkan Vegetation Database was supported by IAVS, EVS and EDGG in 2016-2018, the National Scientific Program "Young scientists and Post-doctoral students" (contracts No. 22-0078/22.04.2019 and DCM 577/17.08.2018), the National Science Fund (contract DCOST 01/7/19.10.2018) and the bilateral project "Study of ruderal flora and vegetation on the territory of Bulgaria and Romania".

E-mail and ORCID

Kiril Vassilev (Corresponding author, kiril5914@abv.bg), ORCID: https://orcid.org/0000-0003-4376-5575
Hristo Pedashenko (hristo_pedashenko@yahoo.com)
Alexandra Alexandrova (alex4eto_f@abv.bg)
Alexander Tashev (altashev@abv.bg), ORCID: https://orcid.org/0000-0001-8193-4371
Anna Ganeva (annaganeva8@gmail.com)
Anna Gavrilova (any_gavrilova@abv.bg)
Armin Macanović (arminmacanovic@yahoo.com), ORCID: https://orcid.org/0000-0002-8915-7818
Assen Assenov (asseni.assenov@gmail.com), ORCID: https://orcid.org/0000-0002-7899-3562
Antonina Vitkova (vitkova17@abv.bg)
Beloslava Genova (beloslava111@abv.bg)
Borislav Grigorov (borislav.g.grigorov@gmail.com), ORCID: https://orcid.org/0000-0002-5936-3573
Chavdar Gussev (chgussev@gmail.com)
Ermin Mašić (erminmasic@hotmail.com), ORCID: https://orcid.org/0000-0001-5383-2431
Eva Filipova (eveto_filipova@abv.bg), ORCID: https://orcid.org/0000-0002-2591-2642
Ganna Gecheva (ggecheva@mail.bg)
Ina Aneva (ina.aneva@abv.bg), ORCID: https://orcid.org/0000-0002-6476-5438
Ilona Knollová (ikuzel@sci.muni.cz), ORCID: https://orcid.org/0000-0003-4074-789X
Ivaylo Nikolov (ivodimnik@abv.bg)
Georgi Georgiev (g_man92@abv.bg)
Georgi Gogushev (gogushev_g@abv.bg)
Georgi Tinchev (tinchev70@abv.bg)
Ivan Minkov (platoplam2014@abv.bg)
Kalina Pachedzhieva (kalina.pachedjieva@gmail.com)
Katerina Mincheva (k.mincheva42@gmail.com)
Koycho Koev (koev_k@mail.bg)
Mariyana Lyubenova (ryana_l@yahoo.com)
Marius Dimitrov (mariusdimitrov@abv.bg)
Media Gumus (med_i@abv.bg)
Momchil Nazarov (mnazarov357@gmail.com)
Nadezhda Apostolova-Stoyanova (apostolova_nadejda@abv.bg)
Nikolay Nikolov (nikolay.niikolov@gmail.com)
Nikolay Velev (nikolay.velev@abv.bg), ORCID: https://orcid.org/0000-0001-6812-3670
Petar Zhelev (petar.zhelev@ltu.bg), ORCID: https://orcid.org/0000-0002-4273-3400
Plamen Glogov (pglogov@abv.bg)
Rayna Natcheva (raynanatcheva@yahoo.com)
Rossen Tzonev (rossentzonev@abv.bg), ORCID: https://orcid.org/0000-0001-8112-1354
Senka Barudanović (sebarudanovic@gmail.com)
Sofia Kostadinova (sofiq_borisova@abv.bg)
Steffen Boch (steffen.boch@wsl.ch), ORCID: https://orcid.org/0000-0003-2814-5343
Stephan M. Hennekens (stephan.hennekens@wur.nl)
Stoyan Georgiev (stogeorgiev@abv.bg)
Stoyan Stoyanov (tjankata@abv.bg), ORCID: https://orcid.org/0000-0001-9245-0727
Todor Karakiev (karakiev@abv.bg)
Tijana Ilić (tijana.d.ilic@gmail.com), ORCID: https://orcid.org/0000-0002-8259-2024
Veronika Kalníková (v.kalnikova@seznam.cz), ORCID: https://orcid.org/0000-0003-2361-0816
Veselin Shivarov (v.shivarov@abv.bg), ORCID: https://orcid.org/0000-0001-8469-4254
Vladimir Vulchev (vlado@bio.bas.bg)

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 155–161
doi: 10.3897/VCS/2020/59869

LONG DATABASE REPORT ECOINFORMATICS

DUMIRA – a management related vegetation plot database of Dutch military ranges

Iris de Ronde[1], Rense Haveman[1], Anja van der Berg[1], Tom van Heusden[1]

1 *Section Nature, Expert Centre Technique, Central Government Real Estate Agency, Ministry of the Interior and Kingdom Relations, Wageningen, the Netherlands*

Corresponding author: Iris de Ronde (iris.deronde@wur.nl)

Academic editor: Florian Jansen ♦ **Received** 20 October 2020 ♦ **Accepted** 19 November 2020 ♦ **Published** 21 December 2020

Abstract

In this paper we describe the historical background and contents of the DUMIRA vegetation plot database (GIVD-code EU-NL-003). It contains 13,046 relevés, collected between 1995 and 2018 at military ranges in the Netherlands, and it is updated regularly with new data. Historical circumstances led to the placement of military ranges at the most nutrient poor, dry, sandy soils, and as a result, the database is built up mainly by plots of *Calluno-Ulicetea* and *Nardetea* heathlands, *Koelerio-Corynephoretea* grasslands, and *Quercetea robori-petraeae* woodlands. These classes account for more than 50% of the database. Coastal communities (*e.g.* from the *Juncetea maritimae* and the *Therosalicornietea*) and scrubs (*e.g.* the *Lonicero-Rubetea plicati* and *Salicetea arenariae*) are other important sources. Notably, throughout the database, *Rubus* species are identified to species level. Although the DUMIRA database was initially used for management related vegetation mapping projects, the data gave rise to several more scientific studies and papers.

Taxonomic reference: Van der Meijden (2005) for vascular plants; Van de Beek et al. (2014) for *Rubus*; Kleukers et al. (2004) for *Orthoptera*.

Syntaxonomic reference: Mucina et al. (2016).

Abbreviations: DUMIRA = Vegetation plot database of Dutch Military Ranges; GIVD = Global Index of Vegetation-plot Databases; MoD = Ministry of Defence.

Keywords

Coastal vegetation, database, DUMIRA, grassland, heathland, management, military ranges, Netherlands, relevé, *Rubus*, scrub, TURBOVEG

Introduction

Vegetation research has a long tradition in the Netherlands, as was described in the long database report of The Dutch National Vegetation Database (Schaminée et al. 2012). As is clear from the overview in the Global Index of Vegetation-plot Databases (GIVD: www.givd.info/info_organisation.xhtml), with 600,000 plot records in this database, the Netherlands is the most extensively sampled country in Europe. From the beginning of the vegetation survey in this country, most attention was paid to natural and semi-natural systems, but until the 1990's, military training areas and air-fields were hardly sampled, mostly due to access restrictions. Sporadically, the vegetation was mapped for operational purposes (e.g. the estimation of the carrying capacity of the soil for military vehicles) or the evaluation of land use changes. These *ad hoc* mapping projects were replaced by a systematic and regular vegetation mapping project in 1996 after a two-year pilot period. This project has a long history though.

Most Dutch military areas were acquired between 1850 and 1920, when, mainly as a result of ongoing mechanisa-

PENSOFT.

Copyright *Iris de Ronde et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

tion and the development of larger and heavier equipment, the need for larger areas for field exercises for the Dutch army increased. For obvious reasons, the most suitable areas were extensive and uncultivated common lands, consisting mainly of heath- and woodlands, and open dune areas, which coincidentally became available at that time (Gilissen 2013). As a consequence of the Inclosure Act ("Markenwet") of 1886, common lands were divided and sold, and the former Ministry of War claimed the cheapest areas, which evidently included the very poor, sandy soils, practically unsuitable for agriculture. In the twentieth century, with ongoing urbanization and the introduction of mineral fertilizer, the claim on land became more and more problematic, but over time the Dutch government was able to acquire tens of thousands of hectares of land as military training areas and air fields. After World War II, training exercises intensified, and increasingly heavier equipment was used. The introduction of so-called "free-for-all areas" – zones without any restriction for driving – had a very destructive influence on the vegetation.

In the nineteen-seventies, growing environmental awareness led to the sentiment that the army, with its intensified exercises, was partly responsible for the decline of species and ecosystems. This awareness eventually led to a more leading role of the national government in environmental and nature conservational policy. In 1994, a collaboration between the former Ministry of Agriculture, Nature and Food Quality and the Ministry of Defence (MoD) resulted in a project aiming at the survey of nature in military areas (Haveman 2012), focussing on breeding birds, butterflies and vegetation. From the start of the project, data collection served practical goals, *i.e.* management advice, decision making in spatial developments of the MoD areas, and the conservation of natural values, but not for answering of scientific questions as such. In a relatively short period of about 10 years, all larger military training areas, airbases and firing ranges were mapped, and from 2004 the first areas were revisited for the monitoring of the most important values. Nowadays a team of 8 ecologists is working on the monitoring of natural values on military areas, employed by the Central Government Real Estate Agency, part of the Ministry of the Interior and Kingdom Relations.

The basis for the vegetation monitoring is formed by the sequential mapping of the vegetation, in scale ranging mostly from 1:2,500 to 1:10,000. The mapped vegetation types are based on a set of local vegetation plot data (relevés). Practically from the beginning of the project, the relevé data is stored in a TURBOVEG-database (Hennekens and Schaminée 2001). Although the data from this database is used mainly in local typologies and for detailed descriptions of plant communities in military areas, the data is also used in several other large projects, of which the revision of the national classification (Schaminée et al. 2017) might be the most important one. The data and maps are also used for nature conservation policy, e.g. as a basis for the mapping of habitats in the framework of Natura 2000. More than 25 Dutch military ranges are designated as Natura-2000 sites, comprising more than half of the total area of the 25,000 ha of training areas, airfields and firing ranges.

GIVD Fact Sheet

GIVD Database ID: EU-NL-003			**Last update:** 2020-11-09
Dutch Military Ranges Vegetation Database (DUMIRA)		**Web address:**	
Database manager(s): Iris de Ronde (Iris.deRonde@wur.nl); Rense Haveman (Rense.Haveman@wur.nl)			
Owner: Central Government Real Estate Agency, Ministry of the Interior and Kingdom relations			
Scope: Vegetation plot database of military ranges in the Netherlands, mainly grasslands, heathlands and acidophilous forests. Also scrubs and salt marshes are well represented.			
Abstract:			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): TURBOVEG		**Export format(s):** TURBOVEG	
Plot type(s): normal plots, time series		**Plot-size range:** 0.01 to 54909	
Non-overlapping plots: 13046	**Estimate of existing plots:** 13046	**Completeness:** 100%	**Status:** completed and continuing
Total no. of plot observations: 13587	**Number of sources (biblioreferences, data collectors):** 1		**Valid taxa:** 1995
Countries (%): NL: 100			
Formations: Forest: 12% = Semi-aquatic: 1%; Terrestrial: 11% // Non Forest: 92% = Aquatic: 1% (Haline water: 0%; Fresh water: 1%); Semi-aquatic: 8% (Haline water: 2%; Fresh water: 7%); Terrestrial: 83% (Non arctic-alpin: 83% [Natural: 20%; Semi-natural: 61%; Anthropogenic: 2%])			
Guilds: all vascular plants: 100%; bryophytes (terricolous or aquatic): 75%; lichens (terricolous or aquatic): 25%			
Environmental data (%): altitude: 0; slope aspect: 43; slope inclination: 23; microrelief: 0; surface cover other than plants (open soil, litter, bare rock etc.): 15; other soil attributes: 0; soil pH: 0; land use categories: 0; soil depth: 0			
Performance measure(s): presence/absence only: 0%; cover: 100%; number of individuals: 0%; measurements like diameter or height of trees: 0%; biomass: 0%; other: 0%			
Geographic localisation: GPS coordinates (precision 25 m or less): 90%; point coordinates less precise than GPS, up to 1 km: 7%; small grid (not coarser than 10 km): 1%; political units or only on a coarser scale (above 10 km): 3%			
Sampling periods: before 1920: 0%; 1920-1929: 0%; 1930-1939: 0%; 1940-1949: 0%; 1950-1959: 0%; 1960-1969: 0%; 1970-1979: 0%; 1980-1989: 0%; 1990-1999: 9%; 2000-2009: 60%; 2010-2019: 31%; unknown: 0%			
Information as of 2020-12-14 further details and future updates available from http://www.givd.info/ID/EU-NL-003			

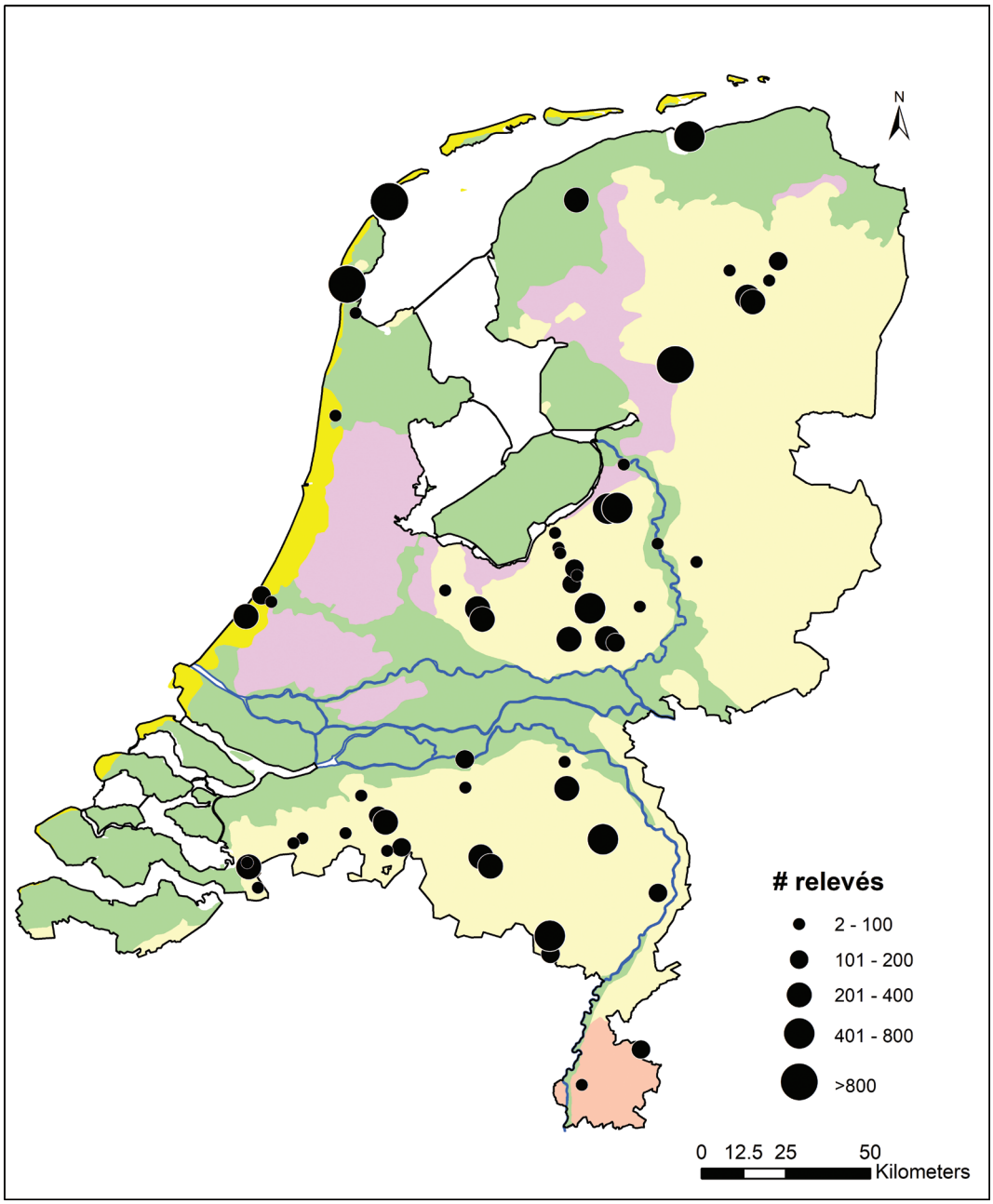

Figure 1. Distribution of relevés in the DUMIRA database made between 1995 and 2018. Dark yellow = coastal dunes; yellow = Pleistocene sands; green = marine and river clays; purple = fen peat; light orange = loess and limestone.

DUMIRA Database

As of November 2020, the vegetation plot database of Dutch Military Ranges (DUMIRA, registered in the GIVD as EU-NL-003) consists of 13,046 relevés, all from military areas in the Netherlands (Figure 1). Data collection started in 1995 and new data is added regularly, preferably annually. Over the years, data collection changed from pure analogue (on paper) to completely digital (tablets). Between 1995 and 2000, the relevés are lacking coordinates, or the coordinates are estimated at square kilometre level. From 2000 onwards, the coordinates were assessed with a GPS, and thus are much more accurate. From 2008, relevés are collected with electronic notebooks, using TURBOVEG CE, or, recently, TURBOVEG SD (Hennekens 2018). Almost two thirds of the number of relevés in the database date back to the time period 2000–2009, in which the focus was on the first inventory of the ranges. The actual number of relevés per year fluctuates considerably (Figure 2), which is the effect of the method used: relevés are collected in years prior to the actual mapping of the vegetation. Over the years, ten people contributed to the data collection; the authors of this paper contributed almost 75% of the total number of relevés. Less than 5% of the relevés are permanent plots, recorded in the 17-level Barkman, Doing and Segal scale (Barkman et al. 1964), which is basically a more detailed, modified Braun-Blanquet-scale. The large bulk of the relevés, however, is recorded

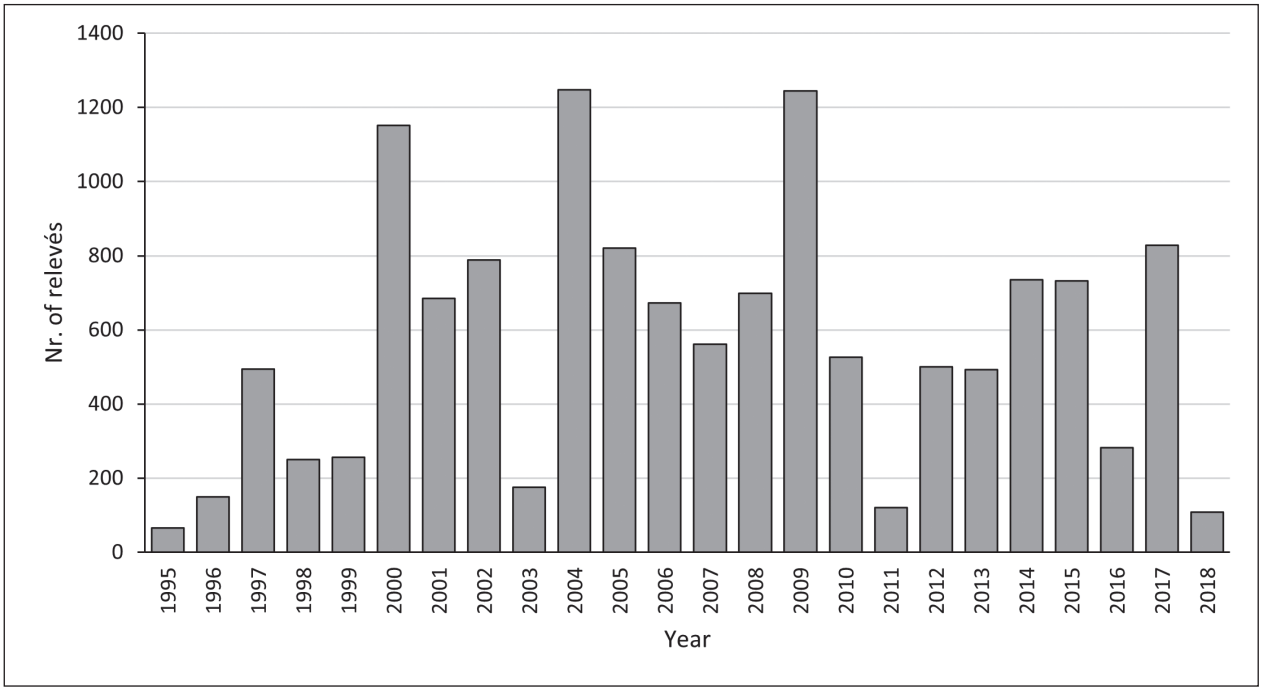

Figure 2. Number of relevés per year in the DUMIRA vegetation plot database.

in a slightly modified 9-scales form of the well-known Braun-Blanquet scale (Westhoff et al. 1995). About 18% of the relevés are indicated in the database as stratified random plots. The location of these relevés is not based on a field decision, but randomly chosen beforehand from the study area. Subsequently such sets of random plots are used to test the change in species composition in relatively homogeneous areas, for example in grasslands on airfields where reduction of the productivity is the main goal (De Ronde and Haveman 2008). Throughout, terrestrial mosses and lichens are included in the relevés. Especially in oligotrophic systems poor in vascular plants (like heathlands and inland dune communities), and in pioneer ecosystems (*e.g.* in pioneer dune slacks), cryptogams have proved to be important for the recognition and delimitation of communities. In the database, relevés of basal communities and transitional stages are well represented, since the relevés were intended to be used for mapping purposes from the beginning. Each relevé in the database is assigned to a phytosociological unit from the check list of Dutch plant communities (Schaminée et al. 2017) using the identification program ASSOCIA (van Tongeren et al. 2008).

As pointed out in the introduction, the military areas are not a reflection of the average Dutch landscape and its corresponding vegetation. Most training areas are found on dry, nutrient poor, sandy soils, which were not suitable for agriculture (see Figure 1 for the distribution of the relevés over the soil types). As a result of this unbalanced representation, relevés from peatlands, brooks, ponds, meadows, calcareous grasslands and mesic deciduous forests are either completely lacking, or seriously underrepresented in the DUMIRA database compared to the national database. In contrast, the DUMIRA database includes mainly data from dry grasslands on sandy soils (*Koelerio-Corynephoretea* Klika 1941) and more in detail silicicolous tussock grasslands of the *Corynephorion* Klika 1931 and meso-xerophytic closed grasslands of the *Sedo-Cerastion arvensis* Sissingh & Tideman 1960, dry inland heathlands (*Calluno-Genistion pilosae* P. Duvigneaud 1945), temperate Atlantic acidophilous oak forests of the *Quercion roboris* Malcuit 1929, pastures and meadows of the *Molinio-Arhenatheretea* Tx. 1937, and matgrass-swards of the *Violion caninae* Schwickerath 1944. Figure 3 shows the five classes with the highest numbers of relevés in the database, with all subordinate alliances represented with relevés in the database. As is clear from this figure, over two-thirds of the relevés of the *Koelerio-Corynephoretea*, *Calluno-Genistion*, *Quercion roboris* and *Violion caninae* can be assigned at alliance-level. Although the *Molinio-Arrhenatheretea* are well represented in the database at class level, over 90% of the relevés assigned to this class can only be classified at the order level or higher, which is a strong indication of the poor and fragmentary development of these grasslands at the Dutch military ranges, which is in correspondence with the initially nutrient poor environment.

Not included in the 5 largest classes in the database are the coastal communities of the *Therosalicornietea* Tx. 1958, *Juncetea maritimi* Br.-Bl. & Tx. 1952, *Honckenyo-Elymetea arenarii* Tx. 1966 (sub nomine *Ammophiletea* Br.-Bl et Tx. ex Westhoff et al. 1946), *Saginetea maritimae* Westhoff et al. 1962 and *Caricion viridulo-trinervis* Julve ex Hájek & Mucina 2015, but summarised these classes are represented with 1459 relevés. The majority of these relevés originate from two large training areas at the Wadden islands of Texel and Vlieland, located in highly dynamic young coastal landscapes. Another key characteristic of the DUMIRA database is the attention paid to shrub

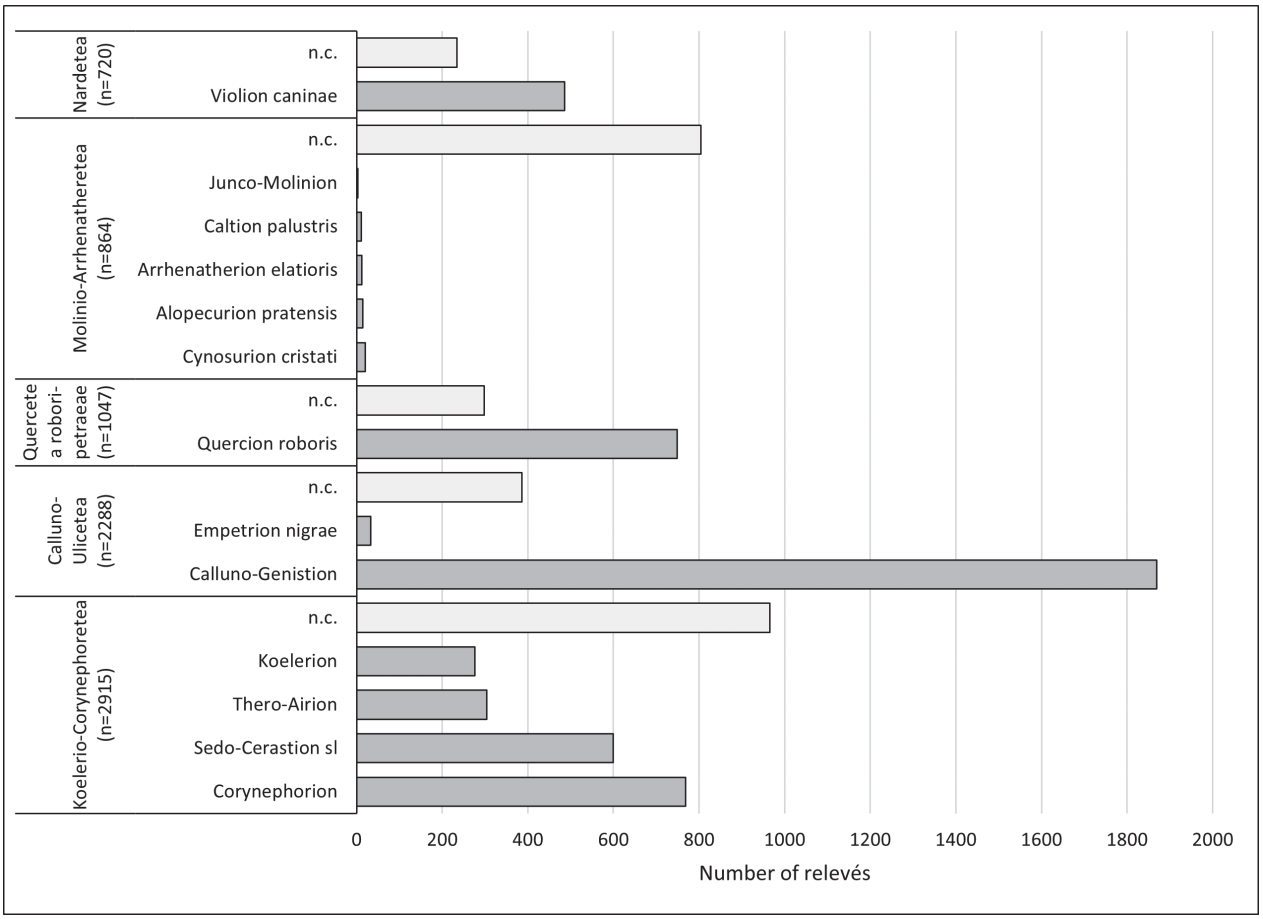

Figure 3. Number of relevés in the DUMIRA vegetation plot database for the five most sampled vegetation classes in the database per alliance. Dark grey bars represent the number of relevés assigned to the given alliance, light grey bars (n.c.= not classified) could not be assigned to one of the alliances.

communities of the *Salicetea arenariae* Weber 1999, *Lonicero-Rubetea plicati* Haveman et al. 1999, *Rhamno-Prunetea* Rivas Goday & Borja Carbonell ex Tüxen1952, and *Franguletea* Doing ex Westhoff 1969 (1294 relevés). Associated with this, but not limited to the scrub communities, *Rubus* apomicts are named at species level in the relevés; we think this is a unique feature of the DUMIRA database in comparison to most other vegetation databases. In the DUMIRA database, 1797 relevés contain 96 brambles species from *Rubus* subgen. *Rubus*; *Rubus plicatus* (n = 911) and *Rubus gratus* (n = 713) are the most frequently recorded species, again affirming the poor nutrient status of most soils in Dutch military areas.

Output

From 1995 onward, vegetation maps are made of more than 60 military areas, ranging from a few to several thousand hectares, and some of these areas have been mapped for the third time already. Most of the maps are published as internal reports, but they are also made available for external organisations (mostly the provincial administration) for the monitoring of the area and quality of Natura 2000 habitats, and the article 17 reporting to the EU. The DUMIRA database has further been the basis for many broad to very specialised studies, mostly published as internal reports, *e.g.* large overviews concerning the contribution of the MoD areas to the nature in the Netherlands, recommendations on the management of airfield grasslands, the habitat requirements of endangered species in Natura 2000 areas, and a landscape ecological analysis of the large military range at the Wadden Island of Texel.

Although the DUMIRA database has a very practical basis, with its main use in the daily mapping practise of military ranges, the data also gave rise to papers on a wide range of subjects, some of which we mention here. One category of published papers is dealing with rare species or species of special (nature conservation) interest, like *Mibora minima* (Haveman and de Ronde 2012). More often, the mapping of military ranges led to syntaxonomical discussions, sometimes urging the need for studies beyond the strict borders of the military areas. Two examples are the *Rubetum taxandriae* Haveman & De Ronde 2012 (class *Lonicero-Rubetea* Haveman et al. 2012), and the *Senecioni ovati-Rubetum iuvenis* Haveman et al. 2014 (alliance *Athyrio filicis-feminae-Rubion idaei* Haveman et al. 2014, class *Crataego-Prunetea* Tx. 1962, Haveman et al. 2014), two bramble scrub associations, which were recognised for the first time on military areas, but both

have a wider distribution in western Europe. Further investigations in the mountainous areas of Europe might reveal more associations belonging to the later mentioned alliance (Haveman et al. 2014). The vegetation mapping practice not only led to new insights in the classification of bramble scrubs though. In a recently published revision of the National Vegetation Classification (Schaminée et al. 2017), the treatment of several classes (*e.g.* the *Nardetea* Rivas Goday & Borja Carbonell 1966, *Calluno-Ulicetea* Br.-Bl. et Tx. ex Klika & Hadač 1944, *Lonicero-Rubetea plicati*, and the *Salicetea arenariae*) was based on the insights gained during the mapping of the vegetation on military ranges, and to a considerable extent on relevés from the DUMIRA database.

Occasionally, the data in the DUMIRA database is used to describe the habitat of rare animal species in the Netherlands. An example is given by the description of the species composition of the plant communities at the Oldebroekse Heide, a large heathland remnant harbouring the westernmost population of *Gampsocleis glabra* (*Orthoptera*) in Europe (Van der Berg et al. 2000).

Final remarks

The DUMIRA database is an active database which is complemented regularly with new relevés from military areas. As before, most relevés will be collected for mapping purposes, but more specific studies will probably be carried out. As is shown in the above, the database was built in a period of 25 years in a project aiming at subsequent vegetation mapping of the military ranges in the Netherlands. The first goal has never been the scientific study of the synsystematics of one or more biomes, formations or classes, but the database merely grew as a by-product of the mapping of the vegetation, in service of practical conservation questions. Comprising over 13,000 relevés, it has shown to be of important value however, even for more (descriptive) scientific questions. Although a rather recent branch on the phytosociological tree, large databases can contribute to our understanding of the vegetation, especially of large scale patterns (e.g. Wagner et al. 2017). But more than 80 years ago, the "Altmeister" of phytosociology, Reinhold Tüxen, in the preface of the dissertation of the Dutch forester and phytosociologist W.H. Diemont, appointed the value of vegetation mapping as an instrument to "sharpen the eye", as a result of which the fine details in the vegetation, below the association and subassociation level, are observed, and understood (Tüxen 1938). This remark still hasn't lost its value: for the understanding of the almost endless variation in the vegetation, and its relation to the landscape, vegetation mapping is difficult to replace. In the light of the still growing pressure on the landscape and its natural inhabitants, the value of vegetation mapping can hardly be overestimated. We hope and believe that in the future the DUMIRA database will serve both these two goals: first of all the understanding of small scale variation in the vegetation and its causes, as an instrument for the conservation of natural values, and, as a good second, also a more synthetic overview of the vegetation over larger, regional to continental, areas.

Author contributions

I.R. and R.H. conceived the idea and outline of the text, I.R. wrote the first concept. R.H. and I.R. edited several text versions and all authors checked and improved the final concept of the manuscript. All authors contributed to the database.

Acknowledgements

We express our gratitude to Nathan Churm (Wyverstone, UK) for the linguistic proof-reading of the manuscript.

References

Barkman JJ, Doing H, Segal S (1964) Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. Acta Botanica Neerlandica 13: 394–419. https://doi.org/10.1111/j.1438-8677.1964.tb00164.x

De Ronde I, Haveman R (2008) Problems in vegetation monitoring in nature management practice: two case studies. Annali di Botanica nuova serie VII: 78–84.

Gilissen N (2013) Missie Natuur. Natuur en landschap op defensieterreinen. [Mission Nature. Nature and landscape at military ranges] KNNV Uitgeverij, Zeist, NL, 224 pp.

Haveman R (2012) Defensie als natuurbeheerder. [The military as nature conservationist] In: Van der Vlis I (Ed.) Militairen op de Veluwe. Boom, Amsterdam, 121–148.

Haveman R, de Ronde I (2012) Nieuwe vindplaatsen van *Mibora minima* (L.) Desv. (Dwerggras) in de Texelse duinen. [New finds of *Mibora minima* (L.) Desv. In the dunes of Texel]. Gorteria 36: 18–21. http://natuurtijdschriften.nl/search?identifier=537534

Haveman R, De Ronde I, Weeda EJ (2012) The *Rubetum taxandriae* ass. nov. (*Lonicero-Rubion silvatici*, *Lonicero-Rubetea plicati*), a new bramble association from the Belgian and Dutch Campine. Tuexenia 32: 55–65. https://www.tuexenia.de/wp-content/uploads/2017/08/Tuexenia-32.zip

Haveman R, de Ronde I, Weeda EJ (2014) Ecologie, verspreiding en syntaxonomie van Nederlandse struwelen. II. Bramenrijke kapvlaktebegroeiingen. [Ecology, distribution and syntaxonomy of Dutch scrubs. II. Rubus-rich clearings]. Stratiotes 46: 5–40.

Hennekens SM (2018) TurbovegSD v1.3., 2 pp. https://www.synbiosys.alterra.nl/turboveg/android/ManualTurbovegSD.pdf

Hennekens SM, Schaminée JHJ (2001) TURBOVEG, a comprehensive data base management system for vegetation data. Journal of Vegetation Science 12: 589–591. https://doi.org/10.2307/3237010

Kleukers R, Van Nieukerken E, Odé B, Willemse L, Van Wingerden W (2004) De sprinkhanen en krekels van Nederland (Orthop-

tera). [Grasshoppers and crickets in the Netherlands (Orthoptera)]. Nederlandse Fauna 1. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey, Leiden, NL, 415 pp.

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, ... Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (Suppl. 1): 3–264. https://10.1111/avsc.12257

Schaminée JHJ, Haveman R, Hommel PWFM, Janssen JAM, de Ronde I, Schipper PC, Weeda EJ, Dort KWv, Bal D (2017) Revisie Vegetatie van Nederland. [Revision Vegetation of the Netherlands]. Stratiotes 50/51: 5–20.

Schaminée JHJ, Hennekens SM, Ozinga WA (2012) The Dutch National Vegetation Database. Biodiversity & Ecology 4: 201–210. https://doi.org/10.7809/b-e.00077

Tüxen R (1938) Vorwort des Herausgebers. Mitteilungen der Floristisch-soziologischen Arbeitsgemeinschaft in Niedersachsen 4: n.p.

Van de Beek A, Bijlsma RJ, Haveman R, Meijer K, de Ronde I, Troelstra A, Weeda EJ (2014) Naamlijst en verspreidingsgegevens van de Nederlandse bramen (*Rubus* L.). [Checklist and distribution data of Dutch brambles (*Rubus* L.)]. Gorteria 36: 108–171. http://natuurtijdschriften.nl/search?identifier=537555

Van der Berg A, Haveman R, Hornman M (2000) De Kleine wrattenbijter *Gampsocleis glabra* herondekt in Nederland (Orthoptera: Tettigoniidae). [Heath Bush cricket *Gampsocleis glabra* rediscovered in the Netherlands (Orthoptera: Tettigoniidae)]. Nederlandse Faunistische Mededelingen 11: 1–12. https://www.repository.naturalis.nl/record/215240

Van der Meijden R (2005) Heukels' Flora van Nederland. [Heukels' Flora of the Netherlands]. Wolters-Noordhoff, Groningen/Houten, NL, 685 pp.

Van Tongeren O, Gremmen N, Hennekens S (2008) Assignment of relevés to pre-defined classes by supervised clustering of plant communities using a new composite index. Journal of Vegetation Science 19: 525–536. https://doi.org/10.3170/2008-8-18402

Wagner V, Chytrý M, Jiménez-Alfaro B, Pergl J, Hennekens S, Biurrun I, Knollová I, Berg C, Vassilev K, Rodwell JS (2017) Alien plant invasions in European woodlands. Diversity and Distributions 23: 969–981. https://doi.org/10.1111/ddi.12592

Westhoff V, Schaminée JHJ, Stortelder AHF (1995) De analytische fase van het vegetatieonderzoek. [The analytic phase of the vegetation study]. In: Schaminée JHJ, Stortelder AHF, Westhoff V (Eds) De vegetatie van Nederland Deel 1: Inleiding tot de plantensociologie – grondslagen, methoden en toepassingen. Opulus Press, Uppsala, SE, 63–80.

E-mail and ORCID

Iris de Ronde (Corresponding author, iris.deronde@wur.nl), ORCID: https://orcid.org/0000-0002-6008-6956
Rense Haveman (rense.haveman@wur.nl), ORCID: https://orcid.org/0000-0001-9127-4549
Anja van der Berg (anja.vanderberg@wur.nl)
Tom van Heusden (tom.vanheusden@wur.nl), ORCID: https://orcid.org/0000-0003-4851-7714

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 163–167
doi: 10.3897/VCS/2020/59977

FORUM PAPER

The concept of vegetation class and order in phytosociological syntaxonomy

Javier Loidi[1]

1 *Department of Plant Biology and Ecology, University of the Basque Country (UPV/EHU), Bilbao, Spain*

Corresponding author: Javier Loidi (javier.loidi@ehu.eus)

Academic editor: Wolfgang Willner ♦ **Received** 23 October 2020 ♦ **Accepted** 27 November 2020 ♦ **Published** 21 December 2020

Abstract

In order to stabilize the defining concepts of the higher rank syntaxonomic units such as class or order, the criteria of floristic content and unity of origin are enunciated. This is done with the aim of preventing the fragmentation of the large classes and the subsequent typological inflation. For orders, the criterion of specific floristic content is discussed, with orders that have been described to encompass seral secondary forests or the separation of forest vegetation from that which is dominated by shrubs rejected, due to their weak floristic characterization. These criteria have been applied to two forest vegetation classes: the European temperate (*Querco-Fagetea*) and the Mediterranean (*Quercetea ilicis*). For the first, it is argued in favor of maintaining a single class for all temperate deciduous forests in Europe instead of dividing them into four. Within this single class five orders are distinguished: *Fagetalia*, *Quercetalia roboris*, *Quercetalia pubescenti-petraeae*, *Alno-Fraxinetalia* and *Populetalia albae*, rejecting the orders that have been proposed for secondary forests because they have few characteristic taxa. For the sclerophyllous and macchia forests of Mediterranean Europe, the *Quercetea ilicis* class can be split into two or three geographical orders, rejecting the *Pistacio-Rhamnetalia alaterni* as a shrubby physiognomic unit.

Taxonomic reference: Castroviejo S (coord. gen.) (1986–2012) Flora iberica 1–8, 10–15, 17–18, 21. Real Jardín Botánico, CSIC, Madrid, ES.

Syntaxonomic reference: Mucina et al. (2016).

Keywords

Floristic content, *Quercetea ilicis*, *Querco-Fagetea*, syntaxonomy, unity of origin, vegetation class, vegetation order

Introduction

The concept of vegetation class needs to be formalized in such a way that instability is prevented. The higher rank syntaxonomic units, such as classes, as far as they represent the fundamental parts of the ecological and floristic variability in a given territory, should have a well-defined ecology and a sufficient biological content (Pignatti et al. 1995). In terms of phytosociological syntaxonomy, each class should have a certain number of characteristic taxa; a minimal "floristic content". As syntaxonomy reflects the floristic and ecologic relationships between the subordinate units, the higher rank units should include a significant content of a specific flora. This is particularly important in the case of classes, but it is also valid for orders. The number of taxa required to fulfill these minimal requirements are variable and must be estimated in the context of the vegetation types involved. Species rich vegetation, such as the *Querco-Fagetea* or *Molinio-Arrhenatheretea*, would need a longer list of characteristic taxa to justify the classes and orders, while species poor vegetation, such as the *Calluno-Ulicetea* or *Cytisetea scopario-striati*, have fewer taxa available for this purpose and it is usually difficult to distinguish more than one or two orders within a class in such cases.

PENSOFT.

Copyright *Javier Loidi*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

The syntaxonomic scheme structuring a class is the expression of the ecological and dynamic diversity occurring within it, but, to a certain extent, it can also express a certain biogeographical-evolutionary background. The floristic set characterizing a class has potentially originated in a particular evolutionary episode that occurred in a particular geographical area under specific environmental conditions. We could hypothesize a type of "unity of origin" in the floristic element characteristic of the class. This eco-evolutionary background should prevent us from making arbitrary decisions which are not based on real patterns in nature.

I will illustrate these ideas with a short discussion on the classes *Querco-Fagetea* and *Quercetea ilicis*.

The class *Querco-Fagetea*

The recent publication of the EuroVeg checklist (Mucina et al. 2016) has revived the question of the syntaxonomic structuring of temperate deciduous forests in Europe. Contrary to the concept of a broad class *Querco-Fagetea sylvaticae*, maintained by several European phytosociologists (Mucina et al. 1993, Stortelder et al. 1999), Mucina et al. (2016) decided to accept the division of this syntaxon into four European forest classes: *Quercetea robori-petraeae*, *Carpino-Fagetea sylvaticae*, *Quercetea pubescentis* and *Alno glutinosae-Populetea albae*. A different approach was presented by Rivas-Martínez et al. (2011), who proposed one class for non-riparian forests and another one for riparian forests. Other approaches have included all the fen alder and riparian ash forests in a specific class, the *Alnetea glutinosae* (Berg et al. 2004). A solution to this controversy requires the application of clear and objective criteria. Here, I advocate the recognition of a single class that includes most of the deciduous forests of Europe. This is supported by three broad arguments that are discussed:

1. Biogeographical-evolutionary criterion: common origin and evolution. The current European deciduous forests descend from the deciduous forests that occupied a wide area in the extratropical latitudes of the Northern Hemisphere in the first half of the Tertiary. They encompassed the territories of ancient North America and those of Eurasia. In that time they were connected by the proximity of the land masses that formed Laurasia (Axelrod 1983). The separation of North America and Eurasia and the subsequent climatic changes that occurred in the late Tertiary, gave rise to the fragmentation of that continuous zone into the three current ones: (i) North America (basically the eastern half of the USA and the southeast of Canada), (ii) Europe (to which are added areas of western Asia bordering the Black and Caspian seas), and (iii) East Asia (Sino-Japanese region comprising northeast China, the Korean peninsula, the south of the Russian Far East and the Japanese archipelago). This general context shows that the European temperate deciduous forests have a common origin followed by a common evolutionary history up to the present. Since the phytosociological class is the highest unit of the system, this unity of origin should be reflected in a single class *Querco-Fagetea sylvaticae*. The diversity existing within it can be represented by lower syntaxonomic ranks, such as the order and the alliance.

2. Floristic criterion: common set of characteristic species. After being isolated from the American and East Asian deciduous forests, the European ones shared the climatic oscillations of the Pleistocene. It is generally assumed, since Gray (1878) and Reid (1935), that the European forest flora was impoverished as a result of the extinctions that occurred during the Pleistocene glaciations, whose effects were intensified by the east-west disposition of the mountain ranges. Later it was postulated that these extinctions must have been more severe in the siliceous flora than in the basiphilous one, because the siliceous territories, located mainly in the north and in the center of Europe, suffered more from the climatic rigors of the glaciations than those in the south of the continent where base-rich rocks are more abundant, allowing the basiphilous flora to find more refuge areas and suffer fewer extinctions (Chytrý et al. 2003). In spite of these differences, there is a set of specific forest plants occurring throughout the European temperate deciduous forests, regardless of the substrates on which they are found, from northwestern Iberia to the Hyrcanian region south of the Caspian sea. No less than 25 forest species, from herbs such as *Athyrium filix-femina*, *Stellaria holostea*, *Poa nemoralis or Brachypodium sylvaticum*, to shrubs such as *Rubus caesius*, *Daphne laureola* or *Frangula alnus* and trees such as *Acer campestre*, *Fraxinus excelsior*, *Quercus robur*, *Taxus baccata* or *Ulmus glabra*, are common to most regions where these forests exist.

3. Application criterion: coherence in the presentation. Syntaxonomy has to be presented to non-phytosociologists in a useful and coherent way. It is very difficult to argue, in a teaching context, that forests dominated by the same species belong to different classes. This is also valid in other fields such as conservation, vegetation mapping or land management and planning. If we recognize four separate classes, there would be forests of *Fagus sylvatica* and *Quercus petraea* or *Q. robur* that would be classified into different classes. This would be unusual compared to other phytosociological syntaxonomy and further explanation would be required for students, land managers and other stakeholders, adding inconsistency and discrediting the system.

Riparian and fen forests

Riparian forests are different in several aspects from most other deciduous forests. There are three main eco-topographical positions within them: the lower bed, usually occupied by willow scrub, the upper bed, normally populated by alder and poplar forests, and the floodplain, usually dominated by ashes and elms. The forests belonging to the second and third level can be included in the class *Querco-Fagetea sylvaticae* because they share a high number of species with the non-hygrophilous deciduous forests. However, due to their floristic and ecological spec-

ificity, they have been grouped in various ways by different authors, e.g. as a class of their own (*Alno glutinosae-Populetea albae*; Mucina et al. 2016) or joined together with the willow scrub formations of the lower river bed (*Salici purpureae-Populetea nigrae*; Rivas-Martínez et al. 2011). Concerning this second option, the nemoral *Querco-Fagetea* species are very rare in the willow scrub of the lower river bed. This lower level is subject to very frequent flooding episodes which cause strong erosion by the river current, preventing the edaphic development of the soil horizons and making the establishment of these herbaceous nemoral species impossible. Therefore, the lower-bed willow scrub vegetation would better be grouped in the independent class *Salicetea purpureae*, leaving the rest to be included in the *Querco-Fagetea*.

The non-willow scrub perifluvial forests separate clearly into two large biogeographic-climatic units which are represented by two orders: the eurosiberian *Alno-Fraxinetalia excelsioris*, and the mediterranean *Populetalia albae* (Biurrun et al. 2016). The proposal to join riparian forests with alder fen forests into one class *Alnetea glutinosae* (Berg et al. 2004) can be supported using floristic arguments, the dilemma is whether to recognize the class *Alnetea glutinosae* including only the *Alnus* fen forests, or to add the riparian humid ash forest to that class. The decision on how to establish the limit between two units, which have a certain number of plants in common, should also take account of the biogeographic context, as far as there are floristic arguments for either keeping them separated or joining them. The *Alno-Fraxinetalia* occur in many areas of southern Europe where the *Alnetalia* are lacking. The areas where both units coexist add weight to the argument to consider both as a single class, separated from the rest of *Querco-Fagetea*. However, in areas where humid forests all belong to the *Alno-Fraxinetalia* or to the *Populetalia albae* and the *Alnetalia* fen forests are absent, the recognition of a single class *Querco-Fagetea* could be a better solution. As the *Alnetalia* forests have peaty soils with stagnant anoxic water, there are a number of plants specifically adapted to that situation. Overall, I suggest maintaining a single class for all European deciduous forests: basiphilous, acidophilous, sub-mediterranean and riparian, but excluding the lower-bed willow scrub that are grouped in the *Salicetea purpureae* and the fen alder forests grouped in the *Alnetea glutinosae*.

Secondary forests

Several proposals to classify secondary forests have been published. Willner et al. (2016) described the order *Lonicero periclymeni-Betuletalia pubescentis*, which partially corresponds to the previously described *Betulo pendulae-Populetalia tremulae* (Rivas-Martínez et al. 2002). Both descriptions encompass secondary forests which have become established after a certain level of disturbance. Both are also very poorly defined floristically, with the *Betulo pendulae-Populetalia tremulae* including a few tree species of the genus *Betula*, *Populus tremula* or *Corylus avellana*. The rest of the flora is unspecific to secondary forests and occurs in many other units of the European deciduous forest, or even in forest mantles or shrublands. The floristic definition of these orders is significantly poorer than that of the other orders such as the *Fagetalia sylvaticae*, *Quercetalia pubescenti-petraeae*, *Quercetalia roboris* or *Alno-Fraxinetalia excelsioris*. These orders have a clear ecological character and they have been long recognized. Secondary forests are short-lived, filling a short time window in the succession and therefore can hardly develop a specific understory flora. Before humans started transforming the landscape at the beginning of the Neolithic age, the forests of temperate Europe were overwhelmingly primary; the secondary forests only occurred after natural disturbance episodes, which were much less frequent and less extensive than after the spread of agriculture and domesticated cattle herds. Thus, they temporarily occupied naturally disturbed patches cleared by wildfire, animal herbivory, windfalls, tree disease, etc. As their floristic differentiation is weak, it would be more consistent to frame these secondary forests in associations and alliances, rather than in one or two orders.

For the reasons stated, I believe that maintaining the unity of deciduous forests in the rank of a class would be a reflection of their unity of origin and their physiognomic and ecological similarity. This argument is also supported by a significant set of species that inhabit all of them. Additionally, secondary forests do not deserve the order status due to their weak floristic characterization. I propose that within the *Querco-Fagetea* class there are five European orders: *Fagetalia sylvaticae*, *Quercetalia roboris*, *Quercetalia pubescenti-petraeae*, *Alno-Fraxinetalia excelsioris* and *Populetalia albae*.

The class *Quercetea ilicis*

This class encompasses the sclerophyllous arboreal and shrubby vegetation in the Mediterranean region of Europe, the Middle East, and north Africa. It is a relatively species-poor unit with few herbaceous elements, due to summer drought stress and persistent shading of the understory. Distinguishing the different orders within this class has always been controversial, particularly in the western Mediterranean portion. Many of the genuine species of this class have a wide distribution across the whole Mediterranean region. In the central and eastern portion of the Mediterranean two orders have been recognized: *Quercetalia calliprini* and *Pinetalia halepensis* and for the central-western area the *Quercetalia ilicis* has been described. Rivas-Martínez (1975) described the order *Pistacio lentisci-Rhamnetalia alaterni* with representation throughout the Mediterranean. This order includes the sclerophylle macchia vegetation which can act as a mantle for the arboreal communities, i.e. their first seral stage, as well as potential vegetation in the areas where climatic or edapho-topographic conditions impede the establishment of a true forest. In Mucina et al. (2016) the *Quercus*-dominated forest communities remained in the order *Quercetalia ilicis* or the *Quercetalia calliprini*. However, it should be

noted that some specialists in Mediterranean vegetation have published opposing views (Bolòs and Vigo 1984). The characteristic species listed by Rivas-Martínez (1975) frequently occur in forests: *Asaparagus horridus*, *Chamaerops humilis*, *Clematis cirrhosa*, *C. flammula*, *Daphne gnidium*, *Euphorbia characias*, *Jasminum fruticans*, *Myrtus communis*, *Osyris alba*, *O. lanceolata*, *Pistacia lentiscus*, *P. terebinthus*, *Rhamnus alaternus*, *R. lycioides*, but the order *Pistacio-Rhamnetalia* was described based on physiognomical criterion more than floristic citerion. In our opinion, it is more sustainable and consistent to separate the *Quercetea ilicis* into geographic orders, with the orders supported by the different endemic species which provide a firm floristic basis and confer stability to the syntaxonomy.

The relationship between the *Pistacio-Rhamnetalia* and *Quercetalia ilicis* seems to parallel that of the order *Prunetalia spinosae* and the rest of the *Querco-Fagetea*. When the order *Pistacio-Rhamnetalia* was described (Rivas-Martínez 1975), the *Prunetalia spinosae* was still accepted as an order of the *Querco-Fagetea* by most European phytosociologists, following the original concept of Tüxen (1952). The argument for establishing the *Pistacio-Rhamnetalia* was a physiognomic one (shrublands versus forests), following the criterion accepted at that time for the *Prunetalia spinosae*. However, more recently the general opinion regarding temperate forests and forest mantles has changed, and most authors have started to accept a separate class for the spiny hedges: *Rhamno-Prunetea*, restricting the *Querco-Fagetea* to forests. At the same time, with increased knowledge of the *Quercetea ilicis*, particularly in northern Africa (Quézel et al. 1988, 1992), a significant number of associations with a tree layer (*Pinus halepensis*, *Juniperus turbinata*, *Tetraclinis articulata*, etc.) have been described and attributed to the *Pistacio-Rhamnetalia*. Thus, the initial separation of forests and shrubland was broken and the separation of *Pistacio-Rhamnetalia* from *Quercetalia ilicis* became inconsistent.

The *Rhamno-Prunetea* is a relatively well defined class because it has few plants in the herb layer, in strong contrast to the *Querco-Fagetea*. Concerning the shrub species, it is true that many of them are shared between both classes, particularly with the order *Quercetalia pubescenti-petraeae*, but in the other orders, such as *Fagetalia*, most of these shrub species grow with diminished vitality. They hardly produce flowers and fruits and their populations are maintained by the constant seed rain provided by birds, as they are mostly endozoochorous. The spiny shrubs occurring inside the forests are therefore maintained by a metapopulational dynamic as sink populations. These shrub species need high light levels to produce a good set of fruit and fertile seeds.

The *Pistacio lentisci-Rhamnetalia alaterni* is quite different from the *Prunetalia spinosae* in this respect as the shrub species exhibit good vitality within most forests. It is impossible to recognize truly characteristic shrub or tree taxa within the *Pistacio lentisci-Rhamnetalia alaterni* and the herb species are limited and generally unspecific.

Acknowledgements

I wish to thank Jim Martin for the linguistic editing and suggestions in the text and the comments of an anonymous reviewer that have helped me to arrive at a better version of the manuscript, but I am especially grateful to Wolfgang Willner for his in-depth review and participation in the production of a more complete and scientifically sound final version.

References

Axelrod DI (1983) Biogeography of oaks in the Arcto-Tertiary Province. Annals of the Missouri Botanical Garden 70: 629–657. https://doi.org/10.2307/2398982

Berg C, Dengler J, Abdank A, Isserman M (2004) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefärdung – Textband. Weissdorn-Verlag. Jena, DE.

Biurrun I, Campos JA, García-Mijangos I, Herrera M, Loidi J (2016) Floodplain forests of the Iberian Peninsula: Vegetation classification and climatic features. Applied Vegetation Science 19: 336–354. https://doi.org/10.1111/avsc.12219

Bolós O, Vigo J (1984) Flora dels Països Catalans. Vol. 1. Ed. Barcino. Barcelona, ES.

Chytrý M, Tichý L, Roleček J (2003) Local and regional patterns of species richness in central European vegetation types along the pH/calcium gradient. Folia Geobotanica 38: 429–442. https://doi.org/10.1007/BF02803250

Gray A (1878) Forest geography and archaeology. American Journal of Sciences and Arts, Ser. 3, 16: 85–95, 183–196. https://doi.org/10.2475/ajs.s3-16.93.183

Mucina L, Bültmann H, Dierßen K, Theurillat J P, Raus T, Čarni A, Šumerová K, Willner W, Dengler J, ... Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Mucina L, Grabherr G, Wallnöfer S (1993) Die Pflanzengesellschaften Österreichs. Teil III. Wälder und Gebüsche. Gustav Fischer, Jena, DE.

Pignatti S, Oberdorfer E, Schaminée JHJ, Westhoff V (1995) On the concept of vegetation class in phytosociology. Journal of Vegetation Science 6: 143–152. https://doi.org/10.2307/3236265

Quézel P, Barbero M, Benabid A, Loisel R, Rivas-Martínez S (1988) Contribution à l'étude des groupements pré-forestiers et des matorrals rifaines. Ecologia Mediterranea 14: 77–122. https://doi.org/10.3406/ecmed.1988.1208

Quézel P, Barbero M, Benabid A, Rivas-Martínez S (1992) Contribution à l'étude des groupements forestiers et pré-forestiers du Maroc oriental. Studia Botanica 10: 57–90.

Reid EM (1935) Discussion on the origin and relationship of the British flora. Proceedings of the Royal Society of London, series B, Biological Sciences 118: 197–214. https://doi.org/10.1098/rspb.1935.0054

Rivas-Martínez S (1975) La vegetación de la clase Quercetea ilicis en España y Portugal. Anales del Instituto Botánico Cavanilles 31(2): 205–259.

Rivas-Martínez S, Díaz TE, Fernández-González F, Izco J, Loidi J, Lousã M, Penas A (Eds) (2002) Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomical checklist of 2001. Itinera Geobotanica 15: 5–922.

Rivas-Martínez S, Asensi A, Garretas B, Mesa J, Valle F, Cano E, Costa M, Díaz T, Fernández Prieto JA, ... Soriano P (2011) Mapa de series, geoseries y geopermaseries de vegetación de España (Memoria del mapa de vegatación potencial de España), Parte II. Itinera Geobotanica 18: 5–424.

Stortelder AHF, Schaminée JHJ, Hermy M (1999) Querco-Fagetea. In: Stortelder AHF, Schaminée JHJ, Hommel PWFM (Eds) De vegetatie van Nederland, deel 5, plantengemeenschappen van ruigten, struwelen en bossen, Opulus, Uppsala, SE, 287–331.

Tüxen R (1952) Hecken und Gebüsche. Mitteilungen der Geographischen Gesellschaft Hamburg 50: 85–117.

Willner W, Solomeshch A, Čarni A, Bergmeier E, Ermakov N, Mucina L (2016) Description and validation of some European forest syntaxa – a supplement to the EuroVegChecklist. Hacquetia 15: 15–25. https://doi.org/10.1515/hacq-2016-0005

E-mail and ORCID

Javier Loidi (Corresponding author, javier.loidi@ehu.eus), ORCID: https://orcid.org/0000-0003-3163-2409

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 169–170
doi: 10.3897/VCS/2020/61419

SHORT DATABASE REPORT

ECOINFORMATICS

Arable Weeds and Management in Europe

Jana Bürger[1], Helen Metcalfe[2], Christoph von Redwitz[3], Alicia Cirujeda[4], Silvia Fogliatto[5], Guillaume Fried[6], Denise Fu Dostatny[7], Bärbel Gerowitt[1], Michael Glemnitz[8], José Luis González-Andújar[9], Eva Hernández Plaza[9], Jordi Izquierdo[10], Michaela Kolářová[11], Jevgenija Ņečajeva[12], Sandrine Petit[13], Gyula Pinke[14], Matthias Schumacher[15], Lena Ulber[3], Francesco Vidotto[5]

1 *Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany*
2 *Sustainable Agricultural Sciences, Rothamsted Research, Harpenden, Hertfordshire, United Kingdom*
3 *Institute for Plant Protection in Field Crops and Grassland, Julius Kühn-Institute (JKI), Federal Research Centre for Cultivated Plants, Braunschweig, Germany*
4 *Plant Protection Unit, Centro de Investigación y Tecnología Agroalimentaria de Aragón (CITA), Zaragoza, Spain*
5 *Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino, Grugliasco, Italy*
6 *Anses – Laboratoire de la Santé des Végétaux, Unité Entomologie et Plantes invasives, Montferrier-sur-Lez, France*
7 *Plant Breeding and Acclimatization Institute, National Research Institute, Błonie, Poland*
8 *Leibniz Centre for Agricultural Landscape Research (ZALF), Research Area II ("Land Use and Governance"), Müncheberg, Germany*
9 *Instituto de Agricultura Sostenible (CSIC), Córdoba, Spain*
10 *School of Agriculture of Barcelona, Polytechnic University of Catalunya, Castelldefels, Spain*
11 *Department of Agroecology and Crop Production, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Prague, Czech Republic*
12 *Institute for Plant Protection Research 'Agrihorts', Latvia University of Life Sciences and Technologies, Jelgava, Latvia*
13 *Agroécologie, AgroSup Dijon, INRAE, Université de Bourgogne Franche-Comté, Dijon, France*
14 *Faculty of Agricultural and Food Sciences, Széchenyi István University, Mosonmagyaróvár, Hungary*
15 *Department of Weed Science, Institute of Phytomedicine, University of Hohenheim, Stuttgart, Germany*

Corresponding author: Jana Bürger (jana.buerger@uni-rostock.de)

Academic editor: Jürgen Dengler ♦ **Received** 27 November 2020 ♦ **Accepted** 2 December 2020 ♦ **Published** 21 December 2020

Abstract

"Arable Weeds and Management in Europe" is a collection of weed vegetation records from arable fields in Europe, initiated within the Working Group Weeds and Biodiversity of the European Weed Research Society (EWRS). Vegetation-plot data from this scientific community was not previously contributed to databases. We aim to prove the usefulness of collection for large scale studies through some first analyses. We hope to assure other weed scientists who have signalled willingness to share data, and plan to construct a full data base, making the data available for easy sharing. Presently, the collection has over 60,000 records, taken between 1996 and 2015. Many more studies for potential inclusion exist. Data originate mostly from studies exploring the effect of agricultural management on weed vegetation. The database is accompanied with extensive meta-data on crop and weed management on the surveyed fields. The criteria for inclusion were a minimum amount of information on the cultivated crop, and a georeference. Most fields were surveyed repeatedly, i.e. transects, multiple random plots, or repeated visits. All surveys aimed to record the complete vegetation on the plots. Sometimes, taxa were identified only to genus level, due to survey dates very early in the vegetation period. Plant taxonomy is standardized to the Euro+Med PlantBase.

Keywords

agriculture, arable weed, Europe, management, segetal plant, vegetation-plot database

PENSOFT.

Copyright *Jana Bürger et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

GIVD Fact Sheet

GIVD Database ID: EU-00-033			**Last update:** 2020-12-02
Arable Weeds and Management in Europe		**Web address:**	
Database manager(s): Jana Bürger (jana.buerger@uni-rostock.de)			
Owner: Members of the EWRS Working Group Weeds and Biodiversity			
Scope: Weed vegetation survey data, complemented with data on agricultural management of the surveyed fields.			
Abstract: Arable Weeds and Management in Europe is a collection of weed vegetation records from arable fields in Europe, collected through an initiative within the Working Group Weeds and Biodiversity of the European Weed Research Society (EWRS). Plot-vegetation data from this particular scientific community has not previously been collected in a data base. The initiators aim to prove the usefulness of collection for large scale studies through some first analyses, to assure other weed scientists who have signaled willingness to share data. Presently, the collection has 59839 records, from approx. 5000 fields, starting from the early 1990s. Many more studies for potential inclusion exist. Data originate mostly from studies exploring the effect of agricultural management on weed vegetation. It is accompanied with extensive meta-data on crop and weed management on the surveyed fields, provided by the farmers. The criteria for inclusion were a minimum requirement of meta data on the cultivated crop, and a georeference to the location. Plot sizes range mainly from 1m² to 2000m², but sometimes a larger area of the field was surveyed (0.5-1ha). Most fields were surveyed repeatedly, for example with 10 plots per fields, transects from edge to interior, or with multiple visits per cropping season. All surveys aimed to record the complete vegetation on the plots. Sometimes, taxa were identified only to genus level, due to survey dates very early in the vegetation period. The taxonomy was harmonized according to the Euro+Med database.			
Availability: not yet available		**Online upload:** no	**Online search:** no
Database format(s): Excel		**Export format(s):** Excel, CSV file	
Plot type(s): normal plots, time series		**Plot-size range:** 0.125 to 20000	
Non-overlapping plots: 41850	**Estimate of existing plots:** 80000	**Completeness:** 52%	**Status:** emerging
Total no. of plot observations: 60475	**Number of sources (biblioreferences, data collectors):** 32		**Valid taxa:** 1260
Countries (%): CZ: 0.5; DE: 13; ES: 1; FR: 32.5; GB: 40; HU: 5; LV: 1.5; PL: 1; IT: 2.5			
Formations: Non Forest: 100% = Terrestrial: 100% (Non arctic-alpin: 100% [Anthropogenic: 100%])			
Guilds: all vascular plants: 100%			
Environmental data (%): altitude: 9; other soil attributes: 80; soil pH: 32; other attributes: soil type, soil texture, clay/silt/sand content, nitrogen content, soil organic matter content			
Performance measure(s): cover: 15%; number of individuals: 85%			
Geographic localisation: point coordinates less precise than GPS, up to 1 km: 90%; political units or only on a coarser scale (above 10 km): 10%			
Sampling periods: 1990-1999: 1.5%; 2000-2009: 88%; 2010-2019: 10%			
Information as of 2020-12-02 further details and future updates available from http://www.givd.info/ID/EU-00-033			

Acknowledgements

J.B. was funded by Deutsche Forschungsgemeinschaft under the grant number BU 3097/1-1.

E-mail and ORCID

Jana Bürger (Corresponding author, jana.buerger@uni-rostock.de), ORCID: https://orcid.org/0000-0003-3898-6664
Helen Metcalfe (helen.metcalfe@rothamsted.ac.uk), ORCID: https://orcid.org/0000-0002-2862-0266
Christoph von Redwitz (christoph.redwitz@julius-kuehn.de), ORCID: https://orcid.org/0000-0002-1591-5081
Alicia Cirujeda (acirujeda@aragon.es), ORCID: https://orcid.org/0000-0001-9646-8422
Silvia Fogliatto (silvia.fogliatto@unito.it), ORCID: https://orcid.org/0000-0002-7309-8550
Guillaume Fried (guillaume.fried@anses.fr), ORCID: https://orcid.org/0000-0002-3653-195X
Denise Fu Dostatny (d.dostatny@ihar.edu.pl), ORCID: https://orcid.org/0000-0002-6544-1531
Michael Glemnitz (mglemnitz@zalf.de), ORCID: https://orcid.org/0000-0002-6506-1889
Bärbel Gerowitt (baerbel.gerowitt@uni-rostock.de), ORCID: https://orcid.org/0000-0001-9435-3453
José Luis González-Andújar (andujar@ias.csic.es), ORCID: https://orcid.org/0000-0003-2356-4098
Eva Hernández Plaza (evahernandezplaza@gmail.com), ORCID: https://orcid.org/0000-0002-2378-2602
Jordi Izquierdo (jordi.izquierdo@upc.edu), ORCID: https://orcid.org/0000-0002-3949-1295
Michaela Kolářová (mkolarova@af.czu.cz), ORCID: https://orcid.org/0000-0002-9817-1195
Jevgenija Ņečajeva (jevgenija.necajeva@lu.lv), ORCID: https://orcid.org/0000-0002-0828-9721
Sandrine Petit (sandrine.petit-michaut@inrae.fr), ORCID: https://orcid.org/0000-0001-8781-8873
Gyula Pinke (pinke.gyula@sze.hu), ORCID: https://orcid.org/0000-0002-9956-1363
Matthias Schumacher (matthias.schumacher@uni-hohenheim.de), ORCID: https://orcid.org/0000-0002-5256-1673
Lena Ulber (lena.ulber@julius-kuehn.de), ORCID: https://orcid.org/0000-0003-2829-1527
Francesco Vidotto (francesco.vidotto@unito.it), ORCID: https://orcid.org/0000-0002-0971-1445

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 171–172
doi: 10.3897/VCS/2020/61660

SHORT DATABASE REPORT

ECOINFORMATICS

SIVIM Floodplain Forests – Database of riverine forests and scrubs from the Iberian Peninsula

Idoia Biurrun[1], Xavier Font[2]

1 *Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain*
2 *Department of Plant Biology, University of Barcelona, Barcelona, Spain*

Corresponding author: Idoia Biurrun (idoia.biurrun@ehu.es)

Academic editor: Jürgen Dengler ♦ **Received** 4 December 2020 ♦ **Accepted** 5 December 2020 ♦ **Published** 21 December 2020

Abstract

"SIVIM Floodplain Forests" (GIVD ID: EU-00-024) is a thematic database focused on vegetation plots of riverine forests and scrubs from the Iberian Peninsula and the Pyrenees (Spain, Portugal and southern France). It was registered in the GIVD in February 2016. The data are available both from EVA and sPlot in semi-restricted regime. The database includes both digitized relevés from the literature and unpublished data. Many digitized relevés were derived from SIVIM (GIVD ID EU-00-004) and BIOVEG (GIVD ID EU-00-011), with which SIVIM Floodplain Forests thus partly overlaps. Currently it contains 4,736 vegetation plots of floodplain forests, alder carrs, willow scrubs, and tamarisk and oleander thickets, 99% of them classified at association level. Plot size is available for 94.6% of the relevés. Plant taxonomy is standardized to Flora Iberica. The database has been used for studies on vegetation classification at Iberian and European level, as well as studies on plant invasion, fine-grain plant diversity and macroecological analyses, most of them via EVA.

Abbreviations: BIOVEG = Vegetation-Plot Database of the University of the Basque Country; EVA = European Vegetation Archive; GIVD = Global Index of Vegetation-Plot Databases; SIVIM = Iberian and Macaronesian Vegetation Information System.

Keywords

Alnetea glutinosae, *Alno glutinosae-Populetea albae*, floodplain forest, Iberian Peninsula, *Nerio-Tamaricetea*, Portugal, Pyrenees, relevé, *Salicetea purpureae*, Spain, vegetation-plot database, willow scrub

PENSOFT.

Copyright *Idoia Biurrun, Xavier Font*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

GIVD Fact Sheet

GIVD Database ID: EU-00-024			**Last update:** 2020-12-04
Iberian and Macaronesian Vegetation Information System (SIVIM) – Floodplain Forests		**Web address:**	
Database manager(s): Idoia Biurrun (idoia.biurrun@ehu.es); Xavier Font (xfont@ub.edu)			
Owner: Idoia Biurrun			
Scope: Phytosociological relevés of floodplain forests, alder carrs, willow scrubs and tamarisk and oleander thickets in the Iberian Peninsula			
Abstract:			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): TURBOVEG, MS Access, Excel, other, XML from B-VegAna		**Export format(s):** TURBOVEG, MS Access, Excel, XML from B-VegAna	
Plot type(s): normal plots		**Plot-size range:** 4 to 800	
Non-overlapping plots: 4736	**Estimate of existing plots:** 6000	**Completeness:** 79%	**Status:** ongoing capture
Total no. of plot observations: 4736	**Number of sources (biblioreferences, data collectors):** 275		**Valid taxa:** 2407
Countries (%): ES: 84; PT: 15; FR: 1			
Formations: Forest: 75% = Terrestrial: 75% // Non Forest: 25% = Terrestrial: 25% (Non arctic-alpin: 25% [Natural: 25%])			
Guilds: all vascular plants: 100%			
Environmental data (%): altitude: 97			
Performance measure(s): presence/absence only: <1%; cover: >99%			
Geographic localisation: GPS coordinates (precision 25 m or less): 10%; point coordinates less precise than GPS, up to 1 km: 76%; small grid (not coarser than 10 km): 14%; political units or only on a coarser scale (above 10 km): 0.2%			
Sampling periods: before 1920: 0%; 1920-1929: 0%; 1930-1939: <0.1%; 1940-1949: 0.4%; 1950-1959: 1.6%; 1960-1969: 2.1%; 1970-1979: 3.7%; 1980-1989: 22.3%; 1990-1999: 34.2%; 2000-2009: 26.0%; 2010-2019: 9.4%; unknown: 0.2%			
Information as of 2020-12-04 further details and future updates available from http://www.givd.info/ID/EU-00-024			

Acknowledgements

The development of the Iberian and Macaronesian Vegetation Information System (SIVIM) was supported by the Spanish Ministry of Education and Science (Projects CGL2006-13421-C04 and CGL2009-13317-C03). Idoia Biurrun was supported by the Basque Government (IT936-16).

E-mail and ORCID

Idoia Biurrun (Corresponding author, idoia.biurrun@ehu.es), ORCID: https://orcid.org/0000-0002-1454-0433
Xavier Font (xfont@ub.edu), ORCID: https://orcid.org/0000-0002-7253-8905

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 173–174
doi: 10.3897/VCS/2020/61776

SHORT DATABASE REPORT

ECOINFORMATICS

SIVIM Deciduous Forests – Database of deciduous forests from the Iberian Peninsula

Juan Antonio Campos[1], Arnau Mercadé[2], Xavier Font[2]

1 *Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, Bilbao, Spain*

2 *Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Spain*

Corresponding author: Juan Antonio Campos (juanan.campos@ehu.eus)

Academic editor: Jürgen Dengler ♦ **Received** 7 December 2020 ♦ **Accepted** 10 December 2020 ♦ **Published** 21 December 2020

Abstract

"SIVIM Deciduous Forests" is a thematic database established in 2015, focused on forest vegetation from the Iberian Peninsula and southern France. It was registered in the Global Index of Vegetation Databases (GIVD ID: EU-00-023) in January 2016. All types of temperate and submediterranean non-riparian deciduous forests of the phytosociological classes *Carpino-Fagetea sylvaticae*, *Quercetea pubescentis* and *Quercetea robori-petraeae* (formerly combined in the class *Querco-Fagetea*) are represented in the database. Currently, it contains 6,642 published vegetation plots of beech, birch, ash, lime and other deciduous mixed forests, as well as forests dominated by different species of deciduous and marcescent oaks, 100% of them classified at association level. Data are stored in TURBOVEG format, and are available upon request from the international vegetation-plot databases EVA and sPlot in semi-restricted regime. The relevés have also been included in SIVIM database, and thus they are freely available online. However, in SIVIM Deciduous Forests geolocation accuracy has been improved and the taxonomy and syntaxonomy unified. Plot size is available for 73% of the relevés, of which 82% are between 100 and 400 m^2. Plant taxonomy is standardized to Flora iberica. During the last four years, data of SIVIM Deciduous Forests were requested via EVA and sPlot for different projects, and have been used for several studies with various objectives, from floristic, vegetation and habitat-related topics to macroecological studies, and from local to global scales.

Abbreviations: EVA = European Vegetation Archive; GIVD = Global Index of Vegetation-Plot Databases; SIVIM = Iberian and Macaronesian Vegetation Information System.

Keywords

Deciduous forest, Iberian Peninsula, Pyrenees, *Querco-Fagetea*, relevé, secondary forest, submediterranean forest, temperate forest, vegetation-plot database

PENSOFT.

Copyright *Juan Antonio Campos et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

GIVD Fact Sheet

GIVD Database ID: EU-00-023			**Last update:** 2020-12-07
SIVIM Deciduous Forests		**Web address:**	
Database manager(s): Juan Antonio Campos (juanan.campos@ehu.eus)			
Owner: Juan Antonio Campos, Arnau Mercadé & Xavier Font			
Scope: Phytosociological relevés of deciduous forest (*Carpino-Fagetea sylvaticae*, *Quercetea pubescentis* and *Quercetea robori-petraeae* classes) in the Iberian Peninsula and southern France.			
Abstract:			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): TURBOVEG		**Export format(s):** TURBOVEG, MS Access, Excel	
Plot type(s): normal plots		**Plot-size range:** 1 to 3000 m^2	
Non-overlapping plots: 6642	**Estimate of existing plots:** 7000	**Completeness:** 100%	**Status:** completed and continuing
Total no. of plot observations: 6642	**Number of sources (biblioreferences, data collectors):** 308		**Valid taxa:** 2647
Countries (%): Spain: 71; France: 22; Portugal: 1.9; Andorra: 0.42			
Formations: Forest: 100%. Terrestrial: 100%			
Guilds: all vascular plants: 100%			
Environmental data (%): altitude: 98; slope aspect: 73; slope inclination: 68			
Performance measure(s): cover: 100%			
Geographic localisation: GPS coordinates (precision 25 m or less): 0%; point coordinates less precise than GPS, up to 1 km:42.7%; small grid (not coarser than 10 km): 52.3%; political units or only on a coarser scale (above 10 km): 5%			
Sampling periods: before 1920: 0%; 1920-1929: 0%; 1930-1939: 0.34%; 1940-1949: 1%; 1950-1959: 2.5%; 1960-1969: 6.2%; 1970-1979: 8.3%; 1980-1989: 35.2%; 1990-1999: 29.16%; 2000-2009: 14%; 2010-2019: 3.3%; unknown: 0%			
Information as of 2020-12-07 further details and future updates available from http://www.givd.info/ID/EU-00-023			

Acknowledgements

The development of the Information System of the Iberian and Macaronesian Vegetation (SIVIM) was supported by the Spanish Ministry of Education and Science (Projects CGL2006-13421-C04 and CGL2009-13317-C03). Juan Antonio Campos was supported by the Basque Government (projects IT299-10 and IT936-16).

E-mail and ORCID

Juan Antonio Campos (Corresponding author, juanan.campos@ehu.eus), ORCID: https://orcid.org/0000-0001-5992-2753
Arnau Mercadé (arnaumerc77@hotmail.com), ORCID: https://orcid.org/0000-0002-1817-1559
Xavier Font (xfont@ub.edu), ORCID: https://orcid.org/0000-0002-7253-8905

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 175–189
doi: 10.3897/VCS/2020/54942

RESEARCH PAPER

Phytosociological overview of the *Fagus* and *Corylus* forests in Albania

Giuliano Fanelli[1], Petrit Hoda[2], Mersin Mersinllari[3], Ermelinda Mahmutaj[2], Fabio Attorre[1], Alessio Farcomeni[4], Vito Emanuele Cambria[5], Michele De Sanctis[1]

1 *Department of Environmental Biology, Sapienza University of Rome, Rome, Italy*
2 *Research Center for Flora and Fauna, Faculty of Natural Sciences, U.T., Tirana, Albania*
3 *Departamenti Shkencave të Shëndetit dhe Mirëqenies sociale, Fakulteti Shkencave të aplikuara, K.U "Logos", Tirana, Albania*
4 *Department of Economics and Finance, University of Rome "Tor Vergata", Rome, Italy*
5 *Department of Land, Environment, Agriculture and Forestry, University of Padova, Legnaro, Italy*

Corresponding author: Michele De Sanctis (michele.desanctis@uniroma1.it)

Academic editor: Wolfgang Willner ♦ **Received** 2 June 2020 ♦ **Accepted** 30 November 2020 ♦ **Published** 30 December 2020

Abstract

Aim: The aim of this study is to analyze the mesophilous forests of Albania including *Fagus sylvatica* and submontane *Corylus avellana* forests. Mesophilous Albanian forests are poorly known and were not included in the recent syntaxonomic revisions at the European scale. **Study area:** Albania. **Methods:** We used a dataset of 284 published and unpublished relevés. They were classified using the Ward's minimum variance. NMDS ordination was conducted, with over-laying of climatic and geological variables, to analyze the ecological gradients along which these forests develop and segregate. Random Forest was used to define the potential distribution of the identified forest groups in Albania. **Results:** The study identified seven groups of forests in Albania: *Corylus avellana* forests, *Ostrya carpinifolia-Fagus sylvatica* forests, lower montane mesophytic *Fagus sylvatica* forests, middle montane mesophytic *Fagus sylvatica* forests, middle montane basiphytic *Fagus sylvatica* forests, upper montane basiphytic *Fagus sylvatica* forests, upper montane acidophytic *Fagus sylvatica* forests. These can be grouped into four main types: *Corylus avellana* and *Ostrya carpinifolia-Fagus sylvatica* forests, thermo-basiphytic *Fagus sylvatica* forest, meso-basiphytic *Fagus sylvatica* forest and acidophytic *Fagus sylvatica* forests. This scheme corresponds to the ecological classification recently proposed in a European revision for *Fagus sylvatica* forests **Conclusion:** Our study supports an ecological classification of mesophilous forests of Albania at the level of suballiance. Analysis is still preliminary at the level of association, but it shows a high diversity of forest types.

Taxonomic reference: Euro+Med PlantBase (http://ww2.bgbm.org/EuroPlusMed/) [accessed 25 Novemeber 2019].

Syntaxonomic references: Mucina et al. (2016) for alliances, orders and classes; Willner et al. (2017) for suballiances.

Keywords

Albania, *Corylus avellana*, *Fagetalia sylvaticae*, *Fagus sylvatica*, *Fraxino orni-Ostryion*, phytosociology, Random Forest

Introduction

Fagus sylvatica forests are among the most studied vegetation types in Europe (Braun-Blanquet 1932; Moor 1938; Soó 1964; Dierschke 2004). However, notwithstanding decades of research, the syntaxonomy of *Fagus sylvatica* forests is still problematic, particularly in Southern Europe. Locally, it is possible to encounter species which are endemic or with restricted range (Willner et al. 2009), which has led to the description of regional alliances such as *Aremonio-Fagion*, *Geranio striati-Fagion*, etc. (Gentile 1964; Marinček et al. 1992, Mucina et

PENSOFT.

Copyright *Giuliano Fanelli et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

al. 2016), but the diagnostic species are usually rare and do not occur in the whole geographical range of the alliances, which are therefore not easily identifiable floristically. A recent broad-scale revision of *Fagus sylvatica* forests (Willner et al. 2017) supported a multidimensional classification that recognizes the traditional geographical alliances, but also classifies most of the variability of *Fagus sylvatica* forests at the level of suballiance. This classification groups *Fagus sylvatica* forests into three main informal groups: acidophytic, meso-basiphytic and thermo-basiphytic *Fagus sylvatica* forests, which in turn are divided into a number of geographical and floristically well-defined suballiances. This classification cuts across the geographical range of *Fagus sylvatica*, but the authors also proposed an alternative classification into six geographically defined alliances, e.g. *Aremonio-Fagion*, *Geranio striati-Fagion* and *Fagion moesiacae*. Even though Southern European forests have been extensively studied (Bergmeier and Dimopoulos 2001; Di Pietro 2009), they are still under-sampled with respect to Central Europe or the Dinarides. In Albania, very few vegetation relevés have been published (Mersinllari 1989; Kalajnxhiu et al. 2012; Mahmutaj 2015) and this country is a blank in the maps of Willner et al. (2017).

Mesophilous forests, including *Fagus sylvatica* and *Corylus avellana* forests, cover a large area in Albania: 171.000 ha, about 17% of the total forested area (Albanian Forest Cadastre of 2017, INSTAT 2019). The widespread cloud belt at an altitude of 1000–1800 m in most mountain ranges, due to the condensation of humidity coming from the sea (Markgraf 1927), can explain such a wide distribution.

The aim of this study is to analyze the Albanian mesophilous forests, and contribute to the syntaxonomic knowledge of these forests in Southern Europe, in particular at the higher ranks of the phytosociological system. This is particularly important from a conservation point of view, as there are many relicts of pristine or ancient *Fagus sylvatica* forests in Albania, that have been declared World Heritage sites recently (Knapp et al. 2014; Diku and Shuka 2018). A better knowledge of the ecological and floristic composition of these forests would greatly enhance their effective and appropriate management and conservation.

Methods

Study area

Despite its small area (28. 748 km^2), Albania is a diverse country with a quite distinct and rich flora and vegetation (Dring et al. 2002; Barina et al. 2018). The geological formations are very diverse. They include, ranging from Palaeozoic to Quaternary, mainly sedimentary, magmatic, metamorphic and ultrabasic rocks (Xhomo et al. 2002). Along the coast, Albania has a Mediterranean climate (Pumo et al. 1990), with humid winters and dry summers, whereas inland the climate becomes temperate (Rivas-Martinez et al. 2004).

Mesophilous *Fagus sylvatica* forests are most widespread on the western slopes of the mountain ranges (Figure 1) stretching all the way from Shkodër to Nemërçkë (Mersinllari 1989). They occur from the northernmost zone of the Albanian Alps (Vermosh, Lekbibaj, Valbonë, Fushëzezë, Theth), that are dominated by calcareous rocks, southwards along the central-eastern part of Albania (Arrën, Livadh-Kabash, Lurë, Dejë, Qafështamë, Bizë, Steblevë, Shebenik, Stravaj, Zavalinë, Polis, Valamarë, Tomorr), to the south-eastern areas (Moravë, Rovje, Gërmenj, and few very small stands at Nemërçka mountain). Generally, they occur at altitudes of 800–1800 m, between the deciduous oak belt and the alpine meadows. They are missing in southern Albania, where climate becomes too warm, with higher temperatures and longer summer aridity.

Within the *Fagus sylvatica* distribution area, as seen in the Vegetation Map of Europe (Bohn et al. 2000, 2004; Figure 1), the annual mean temperature is 8.9 °C (minimum: 7 °C, max: 14.7 °C), with the maximum temperature of the warmest month reaching on average 24.2 °C (minimum: 13.8 °C, max: 30.3 °C) and minimum temperature of the coldest month -4.1 °C (minimum: -10.1 °C, max: 1.5 °C) (CHELSA data; Karger et al. 2017). The mean annual precipitation is about 1046.6 mm. The average, minimum, maximum and standard deviation of all bioclimatic CHELSA variables are presented in Suppl. material 1. The geological substrata are the same for the whole of Albania, except for the absence of alluvial sediments (see Suppl. material 2 for the complete list).

Dataset

We used 284 relevés of mesophilous forests obtained from the "Vegetation database of Albania" (De Sanctis et al. 2017), stored in EVA (Chytrý et al. 2016). They have been collected by the authors between 2002 and 2016 within the framework of international projects (see Acknowledgments) or during personal field investigations. All the relevés were carried out according to the Braun-Blanquet approach (Braun-Blanquet 1964; Dengler et al. 2008). The plot sizes range from 30 to 500 m^2, with an average of 174 m^2 (further details about site and layer data of the relevés are presented in Suppl. material 3). Bryophytes have been collected and identified where they were abundant.

To analyze the ecological features of these forests and model their potential distribution we selected a set of environmental variables we consider ecologically relevant for mesophilous forests. Bioclimatic variables were obtained from CHELSA (Karger et al. 2017): annual mean temperature (Bio1); temperature seasonality (Bio4); minimum temperature of coldest month (Bio6); temperature annual range (Bio7); annual precipitation (Bio12); precipitation of warmest quarter (Bio18). Geological substrata were obtained by grouping of the geological categories provided by the Geological Map of Albania (Xhomo et al. 2002) (see Suppl. material 2 for further details). The resulting types

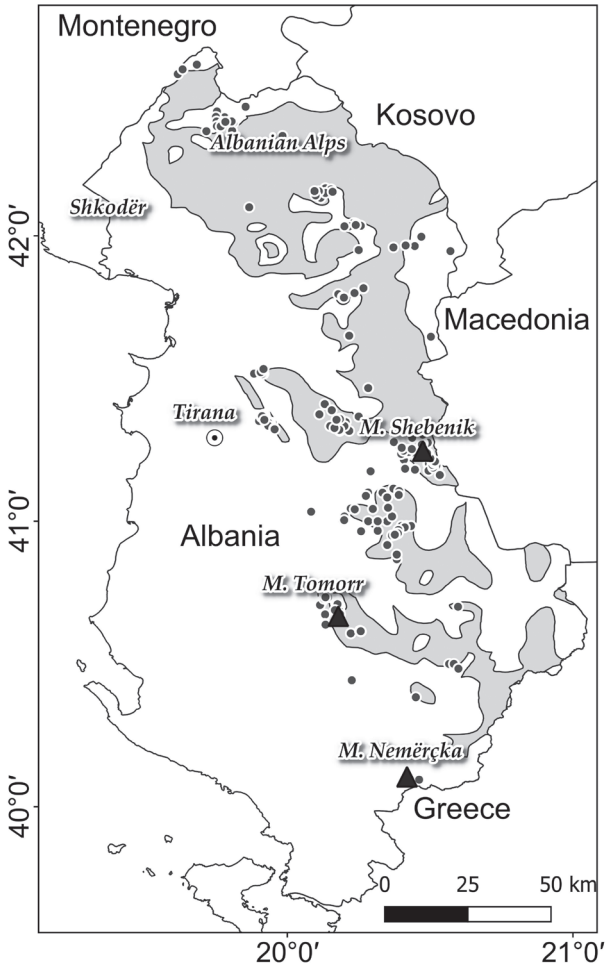

Figure 1. Study area. The black dots represent the relevés used in the analysis and the grey polygons represent the area of *Fagus sylvatica* forests according the Vegetation Map of Europe (Bohn et al. 2000, 2004).

were limestone, flysch, ophiolite and alluvion. Altitude was derived from the GTOPO30 digital elevation model (https://dds.cr.usgs.gov/ee-data/coveragemaps/shp/ee/gtopo30/; accessed 20 November 2019).

Data analysis

To identify the mesophilous forest types of Albania, we performed a hierarchical clustering using the *cluster* package (Maechler et al. 2019) of R software (http://www.R-project.org/). The Ward's minimum variance clustering (Murtagh and Legendre 2014) was used. It is a special case of the objective function approach originally presented by Ward (1963), with Euclidean distance as the similarity coefficient. The fidelity coefficient of Tichý and Chytrý (2006) was used to identify the diagnostic species of the resulting clusters (phi coefficient × 100). We performed a simultaneous calculation of Fisher's exact test in the JUICE software (Tichý 2002) to exclude species with non-significant fidelity. Group size was standardized to the average size of all groups present in the dataset (Tichý and Chytrý 2006) to avoid the phi coefficient being dependent on the size of the target group.

Ordination analysis was performed to analyze the ecological gradients underlying the distribution and floristic differentiation of the identified clusters. We adopted the Non-Metric Multidimensional Scaling (NMDS) analysis using the *vegan* package (Oksanen et al. 2016) of R. The NMDS procedure was applied with default options, which include use of the Bray-Curtis dissimilarity index and a maximum of 20 random starts in search of the stable solution. We used the Bray-Curtis dissimilarity, instead of the Euclidean distance, for ordination, because we were interested in the compositional dissimilarity between the sites, rather than in the raw differences in abundance of one species or another (Legendre and Legendre 1998; Bray and Curtis 1957). To identify the ecological variables involved in the identified NMDS gradients, we overlaid environmental vectors onto the ordination using the *envfit* function of the *vegan* package (Oksanen et al. 2016).

The interpretation of the forest types was supported by the construction of a map of their potential distribution. The map was obtained by modelling the spatial distribution of classified relevés and the environmental variables (Franklin 1995). Random Forests (RF) (Breiman 2001) was used as modeling method (see Suppl. material 4 for procedure and validation details) because of its widely recognized efficacy in similar vegetation studies (Brzeziecki et al. 1993; Maggini et al. 2006; Scarnati et al. 2009; Attorre et al. 2014).

Results

The dendrogram (Figure 2) splits the dataset into two main clusters. The first on the left includes groups A1 and A2 and represents the vegetation of lower altitudes (*Corylus avellana* and *Ostrya carpinifolia-Fagus sylvatica* forests). The second cluster was further split into a sub-cluster including the groups B and C, characterized by thermo-basiphytic *Fagus sylvatica* forests, and a second sub-cluster with groups D, E and F including the mesophytic *Fagus sylvatica* forests. Mesophytic *Fagus sylvatica* forests are finally divided into meso-basiphytic (D, E) and acidophytic (F) *Fagus sylvatica* forests.

The NMDS diagram (Figure 3) shows that the seven clusters have minimum overlap (stress 0.24). The first axis is correlated with a climatic gradient which includes all the climatic variables (precipitation of the driest quarter, mean annual temperature, mean temperature of the coldest month, temperature seasonality). The second axis separates the different lithologies, with acidic lithologies such as serpentines on the negative side and alluvions and limestones, with neutral to alkaline reaction, on the positive side.

The seven clusters are ordered mainly according the first axis, representing the different altitudinal belts. Although the second axis is strongly correlated with lithology, it is probably also in part correlated with summer drought since it separates clusters B and C, which show some influence of the Mediterranean climate (see Figure

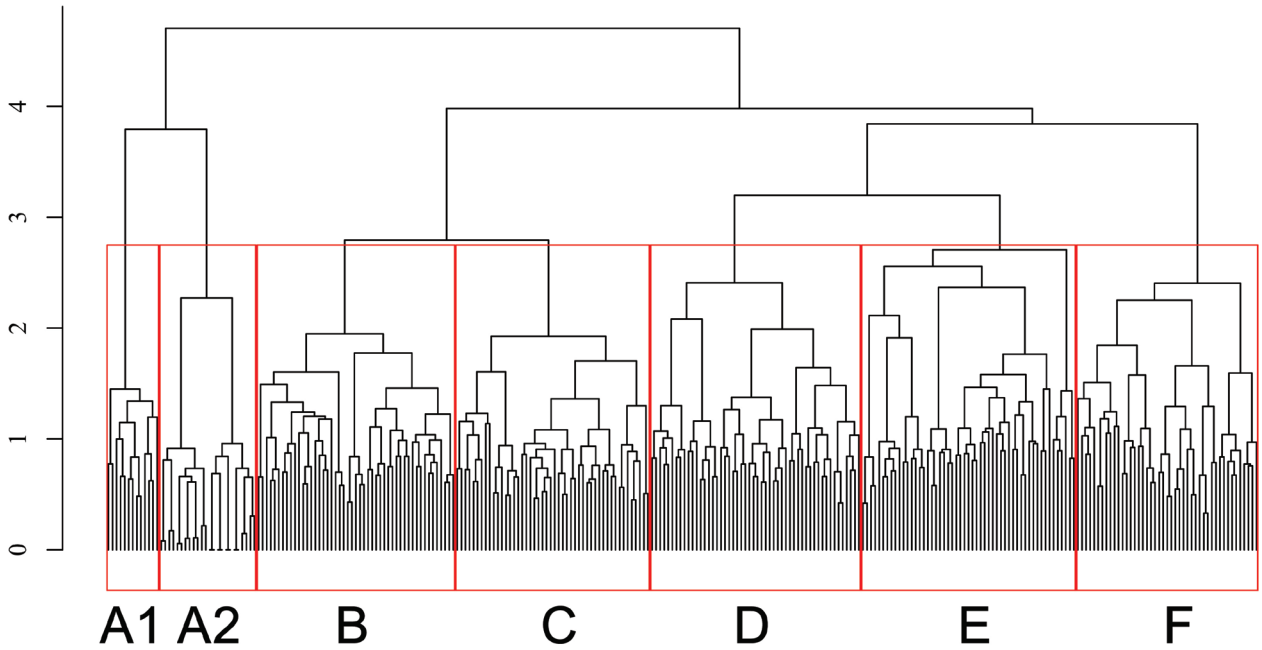

Figure 2. Dendrogram of relevés resulting from Ward's minimum variance clustering, with Euclidean distance as the similarity coefficient. Cluster **A1** *Corylus avellana* forests. Cluster **A2** *Ostrya carpinifolia-Fagus sylvatica* forests.Cluster **B** lower montane thermophytic *Fagus sylvatica* forests. Cluster **C** Middle montane, slightly acidic *Fagus sylvatica* forests. Cluster **D** upper montane basiphytic *Fagus sylvatica* forests. Cluster **E** middle montane basiphytic *Fagus sylvatica* forests. Cluster **F** upper-montane acidophytic *Fagus sylvatica* forests.

3) and are rich in thermophilous species, from clusters D and E, which are rich in mesophilous species.

We also analyzed lower cut levels of the dendrogram to see if it was possible to identify floristically and ecologically well-characterized sub-groups. Cutting the dendrogram at level 0.16 we obtained 17 sub-groups of *Fagus sylvatica* forests, two of *Corylus avellana*, while the *Ostrya carpinifolia-Fagus sylvatica* cluster remained undivided. This seemed to be the level at which the differentiation of the plant communities was maximum, as shown in the NMDS we performed separately on each of the seven main clusters with the same methods as above (Suppl. material 5).

The geographical distribution of the clusters (Figure 4) and of the potential vegetation of mesophilous forests in Albania (Figure 5; results of the validation analysis are presented in Suppl. material 4) showed a main gradient from the coast towards inland; along this gradient the thermophytic types are substituted by mesophytic types, in accordance with decreasing water stress, diminishing temperatures and rising altitudes.

Description of clusters and communities

We present each cluster together with a list containing the species with fidelity values higher than 30 (values are given after the species names). The synoptic table of the clusters is given in Table 1, and average, minimum and maximum of stational data of the relevés of each cluster are provided in Suppl. material 6. Within each cluster, we describe the included sub-groups (plant communities), which are coded by the letter of the cluster and a progressive number. The number corresponds with that given in the ordered table of relevés in Suppl. material 7. The syntaxonomic scheme is presented in Appendix 1.

Cluster A1: *Corylus avellana* forests

Diagnostic species: *Teucrium polium 67.6*, *Corylus avellana 66.1*, *Cerastium brachypetalum 55.3*, *Polygala vulgaris 52.5*, *Euphorbia helioscopia 52.5*, *Dorycnium pentaphyllum 52.5*, *Rosa canina 49.1*, *Helianthemum nummularium 48.6*, *Bituminaria bituminosa 45.2*, *Capsella bursa-pastoris 45.2*, *Euphorbia myrsinites 44.5*, *Bellis perennis 43.1*, *Lotus corniculatus 42.8*, *Helleborus odorus 41.9*, *Juglans regia 40.9*, *Dorycnium hirsutum 36.9*, *Stellaria holostea 36.7*, *Poa annua 36.7*, *Oenanthe pimpinelloides 36.7*, *Medicago sativa 36.7*, *Linum usitatissimum 36.7*, *Campanula glomerata 36.7*, *Blackstonia perfoliata 36.7*, *Carpinus orientalis 35.9*, *Saponaria calabrica 33.8*, *Primula vulgaris 33.7*, *Origanum vulgare 33.7*, *Juniperus oxycedrus subsp. oxycedrus 33.0*, *Potentilla reptans 31.3*, *Thymus longicaulis 30.7*

The relevés of this cluster represent a stage of degradation, as indicated by the great number of grassland species and the limited number of nemoral species. Among the nemoral species the most remarkable are *Anemone ranunculoides*, *Carpinus orientalis* and *Primula vulgaris*, which

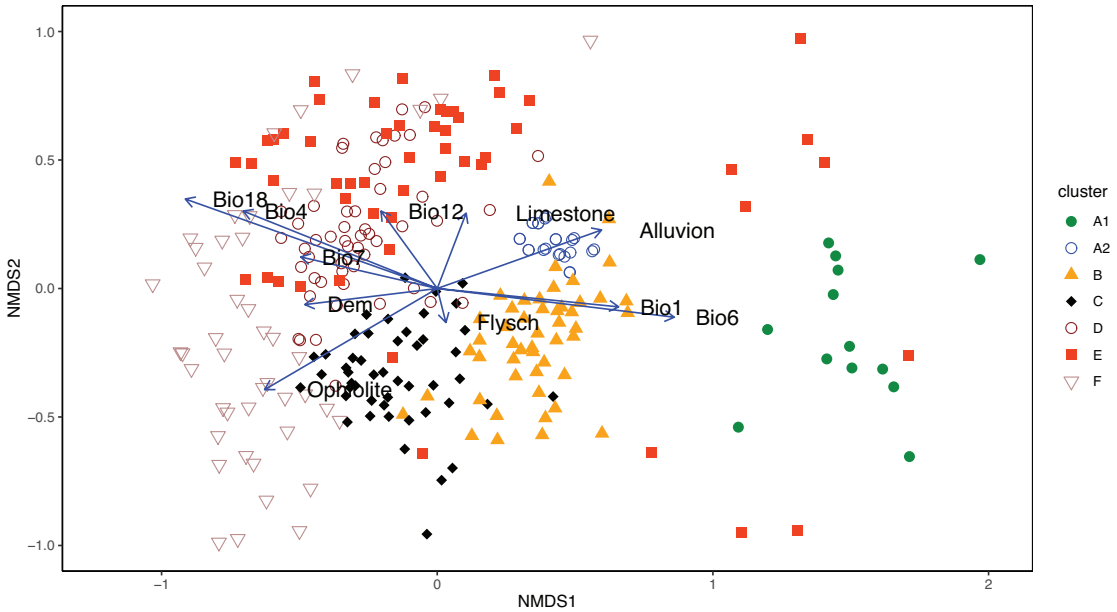

Figure 3. Non-Metric Multidimensional Scaling (NMDS) of relevés using Bray-Curtis dissimilarity index and a maximum of 20 random starts in search of the stable solution. Overlaid vectors represent the following environmental variables: Bio1: annual mean temperature; Bio4 Temperature Seasonality (standard deviation *100); Bio7: temperature annual range; Bio12: annual precipitation; Bio18: precipitation of warmest quarter; geological substrata include Ophiolite, Limestone, Flysch, Alluvion. Cluster **A1** *Corylus avellana* forests. Cluster **A2** *Ostrya carpinifolia-Fagus sylvatica* forests. Cluster **B** lower montane thermophytic *Fagus sylvatica* forests. Cluster **C** middle montane, slightly acidic *Fagus sylvatica* forests. Cluster **D** upper montane basiphytic *Fagus sylvatica* forests. Cluster **E** Middle montane basiphytic *Fagus sylvatica* forests. Cluster **F** Upper-montane acidophytic *Fagus sylvatica* forests.

point to an affinity with forests of the *Carpinion orientalis* (Fanelli et al. 2015; Mucina et al. 2016).

The forests of cluster A1 might be referred to the *Astrantio-Corylion avellanae*, an alliance including the *Corylus* thickets in the Alps and Southern Europe (Mucina et al. 2016). This alliance is usually classified in the class *Crataego-Prunetea*.

These forests occur in Southern Albania (Figures 4, 5) and in the Korab-Koritnik National Park at an altitude of 900–1200 m (average altitude: 1034 m), in a narrow belt below the *Fagus sylvatica* forests. Their restricted occurrence is probably a relict of a more widespread past distribution, that was largely destroyed by human activity.

Cluster A2: *Ostrya carpinifolia–Fagus sylvatica* forests

Diagnostic species: *Carpinus betulus 92.5*, *Galium sylvaticum 83.6*, *Crataegus monogyna 82.1*, *Ajuga reptans 82.1*, *Juniperus communis 80.0*, *Melica uniflora 78.3*, *Ostrya carpinifolia 73.9*, *Clinopodium vulgare 72.6*, *Dactylis glomerata 70.2*, *Brachypodium sylvaticum 66.5*, *Myosotis sylvatica 62.9*, *Acer campestre 59.4*, *Pteridium aquilinum 59.3*, *Rubus idaeus 59.0*, *Anemone nemorosa 58.9*, *Melittis melissophyllum 56.9*, *Daphne mezereum 56.5*, *Asperula taurina 56.3*, *Anthoxanthum odoratum 54.8*, *Ilex aquifolium 53.5*, *Teucrium chamaedrys 51.0*, *Galium odoratum 51.0*, *Lathyrus niger 50.5*, *Hedera helix 50.2*, *Euphorbia amygdaloides 49.7*, *Cornus mas 48.7*, *Geranium robertianum 47.6*, *Daphne laureola 47.1*, *Galium lucidum 44.9*, *Epilobium montanum 43.7*, *Lathyrus venetus 43.3*, *Corylus avellana 43.3*, *Acer obtusatum 43.2*, *Sorbus torminalis 43.0*, *Populus tremula 42.6*, *Veronica chamaedrys 42.3*, *Knautia drymeia 40.7*, *Poa nemoralis 40.4*, *Fraxinus ornus 38.4*, *Galium aparine 38.3*, *Luzula sylvatica 38.2*, *Silene vulgaris 37.3*, *Viburnum lantana 35.4*, *Carex sylvatica 35.4*, *Scilla bifolia 33.4*, *Prunella vulgaris 33.4*, *Pilosella cymosa 33.2*, *Lonicera xylosteum 33.0*, *Aremonia agrimonoides 32.9*, *Dryopteris filix-mas 32.8*, *Athyrium filix-femina 32.4*, *Campanula persicifolia 30.7*

These forests can be found at an altitude of 1000–1400 m (average altitude: 1210 m) in Central Albania (Figures 4, 5), mainly in the surroundings of Tirana. This cluster includes forests with dominance of *Ostrya carpinifolia* and *Fagus sylvatica* and is characterized by several thermophilous species of the *Quercetalia pubescenti-petraeae*. The species of the *Ostryo-Fagenion* are scarce, and thus this cluster probably represents an ecotone between *Ostrya carpinifolia* forests (referable to *Fraxino orni-Ostryion*), which are widespread near Tirana, and beech forests.

The dendrogram divides A2 into two communities, but their floristic differentiation is very poor and based on the frequency of common species rather than on diagnostic species. The distinction is probably due to a higher level of disturbance in one on the two communities.

Table 1. Synoptic table of relevés. The values shown in the table represent the constancy values of the species as percentage frequency. Dark grey species with fidelity >15 and frequency >35; light grey species with fidelity >15 and frequency <35. Non-diagnostic species with frequency <20 are not shown. Cluster A1: *Corylus avellana* forests; Cluster A2: *Ostrya carpinifolia-Fagus sylvatica* forests; Cluster B: lower montane thermophytic *Fagus sylvatica* forests; Cluster C: middle montane, slightly acidic *Fagus sylvatica* forests; Cluster D: upper montane basiphytic *Fagus sylvatica* forests; Cluster E: middle montane basiphytic *Fagus sylvatica* forests; Cluster F: upper-montane acidophytic *Fagus sylvatica* forests. The syntaxonomic reference (diagnostic value) of species follows Table 1 in Willner et al. (2017).

Cluster code	**A1**	**A2**	**B**	**C**	**D**	**E**	**F**	**Syntaxonomic reference**
Number of relevés	**13**	**24**	**49**	**48**	**52**	**53**	**45**	
Salvia glutinosa	8	33	24	2	15	32	2	*Aremonio-Fagion*
Cardamine enneaphyllos	–	–	–	19	13	4	–	*Aremonio-Fagion*
Knautia drymeia	–	25	2	–	–	2	2	*Ostryo-Fagenion*
Polystichum lonchitis	–	–	–	2	15	2	11	*Lonicero alpigenae-Fagenion*
Lonicera alpigena	–	–	4	–	–	9	7	*Lonicero alpigenae-Fagenion*
Laburnum alpinum	–	–	10	–	2	–	–	*Aremonio-Fagion*
Epimedium alpinum	–	–	–	10	2	4	–	*Ostryo-Fagenion*
Sesleria autumnalis	–	–	8	2	–	–	–	*Ostryo-Fagenion*
Asplenium viride	–	–	–	–	4	–	–	*Lonicero alpigenae-Fagenion*
Euonymus verrucosus	–	–	2	–	–	–	–	*Ostryo-Fagenion*
Gentiana asclepiadea	–	–	–	–	–	–	2	*Aremonio-Fagion*
sum Aremonio-Fagion	**8**	**58**	**50**	**35**	**51**	**53**	**24**	
Lathyrus laxiflorus	8	–	–	–	4	21	2	*Fagion moesiacae*
Physospermum cornubiense	15	–	2	13	–	6	4	*Fagion moesiacae*
Digitalis viridiflora	–	–	–	–	–	6	7	*Fagion moesiacae*
Lathyrus alpestris	–	–	–	10	2	–	–	*Fagion moesiacae*
Campanula sparsa	–	–	6	–	–	2	–	*Fagion moesiacae*
sum Fagion moesiacae	**23**	**0**	**8**	**23**	**6**	**35**	**13**	
Campanula pichleri	–	–	–	4	4	32	29	*Geranio versicoloris-Fagion*
Anemone apennina	15	–	20	6	–	–	–	*Geranio versicoloris-Fagion*
Cyclamen hederifolium	–	–	2	–	–	8	–	*Geranio versicoloris-Fagion*
sum Geranio-Fagion	**15**	**0**	**22**	**10**	**4**	**40**	**29**	
Ostrya carpinifolia	23	100	39	–	–	2	–	thermo-basiphytic beech forests
Clinopodium vulgare	31	100	16	4	–	17	–	thermo-basiphytic beech forests
Crataegus monogyna	–	83	6	–	–	8	–	thermo-basiphytic beech forests
Primula vulgaris	54	50	22	2	2	13	–	thermo-basiphytic beech forests
Festuca heterophylla	23	33	51	10	–	4	7	thermo-basiphytic beech forests
Cornus mas	8	50	20	–	–	4	–	thermo-basiphytic beech forests
Fraxinus ornus	8	50	37	4	–	9	2	thermo-basiphytic beech forests
Acer campestre	8	50	2	–	–	2	–	thermo-basiphytic beech forests
Cephalanthera rubra	–	25	22	8	8	11	–	thermo-basiphytic beech forests
Sorbus torminalis	–	25	–	–	–	4	–	thermo-basiphytic beech forests
Melittis melissophyllum	8	50	4	–	2	2	–	thermo-basiphytic beech forests
Primula veris	–	–	20	–	–	4	–	thermo-basiphytic beech forests
Cephalanthera damasonium	–	–	20	6	8	17	7	thermo-basiphytic beech forests
Viburnum lantana	–	17	2	–	–	–	–	thermo-basiphytic beech forests
Campanula persicifolia	–	17	4	–	–	–	2	thermo-basiphytic beech forests
Campanula trachelium	8	–	8	2	–	–	–	thermo-basiphytic beech forests
Hippocrepis emerus	8	–	4	–	–	6	–	thermo-basiphytic beech forests
Rosa arvensis	8	–	–	2	–	2	–	thermo-basiphytic beech forests
Carex digitata	–	–	–	–	–	–	4	thermo-basiphytic beech forests
Polygonatum odoratum	–	–	2	–	4	–	–	thermo-basiphytic beech forests
Galium odoratum	8	100	10	44	75	32	4	meso-basiphytic beech forest
Lamiastrum galeobdolon	–	50	8	23	62	38	9	meso-basiphytic beech forest
Geranium robertianum	15	83	14	6	42	42	7	meso-basiphytic beech forest
Cardamine bulbifera	8	33	29	27	46	15	2	meso-basiphytic beech forest
Actaea spicata	–	–	–	8	19	–	–	meso-basiphytic beech forest
Carex sylvatica	–	17	2	–	–	–	–	meso-basiphytic beech forest
Polystichum aculeatum	–	–	2	10	2	25	4	meso-basiphytic beech forest
Urtica dioica	8	–	8	–	2	9	–	meso-basiphytic beech forest
Paris quadrifolia	–	–	–	4	4	6	–	meso-basiphytic beech forest
Stachys sylvatica	–	–	–	–	2	–	–	meso-basiphytic beech forest
Vaccinium myrtillus	–	–	–	6	4	6	78	acidophytic beech forests
Calamagrostis arundinacea	–	–	–	–	–	–	11	acidophytic beech forests
Fagus sylvatica	15	100	100	100	100	89	100	
Lactuca muralis	8	75	65	33	63	75	24	
Euphorbia amygdaloides	62	100	24	38	13	34	11	
Fragaria vesca	69	42	78	25	17	28	7	
Aremonia agrimonoides	23	75	61	23	6	42	24	
Helleborus odorus	85	50	78	4	4	28	–	
Anemone nemorosa	–	100	29	10	60	2	27	
Rubus idaeus	23	100	29	25	13	21	16	
Pteridium aquilinum	15	100	29	17	19	32	13	
Acer pseudoplatanus	31	42	59	10	23	40	9	
Veronica chamaedrys	38	75	41	4	13	26	–	
Corylus avellana	100	75	14	–	4	–	–	

Cluster code	A1	A2	B	C	D	E	F	Syntaxonomic reference
Number of relevés	**13**	**24**	**49**	**48**	**52**	**53**	**45**	
Brachypodium sylvaticum	23	100	24	4	–	26	13	
Hedera helix	31	75	47	–	2	8	–	
Saxifraga rotundifolia	–	42	20	4	27	38	31	
Lathyrus venetus	15	67	31	4	15	11	13	
Dactylis glomerata	15	92	27	–	–	13	2	
Melica uniflora	23	100	18	2	2	2	2	
Doronicum columnae	8	50	37	8	4	23	18	
Abies alba	–	–	6	38	38	11	53	
Juniperus communis	15	100	12	8	–	2	7	
Ajuga reptans	31	100	6	–	–	2	–	
Prenanthes purpurea	–	–	2	27	46	6	53	
Prunella vulgaris	38	50	6	4	–	8	22	
Myosotis sylvatica	31	75	2	–	12	–	–	
Carpinus betulus	–	100	12	–	–	2	–	
Symphytum tuberosum	8	33	35	10	13	6	9	
Daphne mezereum	–	67	12	2	6	9	16	
Luzula sylvatica	8	50	18	13	10	4	9	
Calamintha grandiflora	–	–	18	10	25	47	11	
Asplenium trichomanes	8	25	12	2	17	30	11	
Sanicula europaea	15	–	12	15	38	17	2	
Oxalis acetosella	–	–	–	23	52	21	2	
Orthilia secunda	–	–	2	17	12	13	42	
Juniperus oxycedrus s. oxycedrus	38	–	35	2	–	9	–	
Viola reichenbachiana	–	–	20	23	–	32	7	
Potentilla micrantha	15	25	12	4	8	2	11	
Galium sylvaticum	–	75	–	–	–	2	–	
Teucrium chamaedrys	23	50	–	–	–	4	–	
Poa nemoralis	–	42	10	–	–	13	11	
Ceterach officinarum	8	–	24	2	10	25	7	
Neottia nidus-avis	–	–	18	13	27	15	–	
Rosa species	8	8	41	2	–	4	7	
Dryopteris filix-mas	–	33	6	8	10	6	4	
Bellis perennis	38	–	22	–	–	–	–	
Carex species	–	–	4	–	–	23	31	
Festuca species	–	–	4	–	–	23	31	
Euphorbia myrsinites	38	–	12	–	–	8	–	
Teucrium polium	54	–	2	–	–	2	–	
Carpinus orientalis	31	–	16	–	–	6	–	
Ilex aquifolium	–	42	8	–	–	2	–	
Rosa canina	38	–	10	2	–	–	–	
Viola species	–	–	–	2	42	4	2	
Asperula taurina	–	42	2	4	–	–	–	
Acer obtusatum	–	33	2	6	–	6	–	
Epilobium montanum	–	33	–	–	–	13	–	
Geum urbanum	–	–	14	–	6	26	–	
Athyrium filix-femina	–	25	2	2	10	4	2	
Viola odorata	23	–	12	6	–	2	–	
Cerastium brachypetalum	38	–	4	–	–	–	–	
Pilosella cymosa	–	25	14	–	–	2	–	
Scilla bifolia	–	25	6	–	10	–	–	
Pinus nigra	–	–	2	–	–	–	38	
Thymus longicaulis	23	–	2	–	–	6	9	
Erica carnea	–	–	–	2	–	–	36	
Lathyrus niger	–	33	–	–	–	–	4	
Acer platanoides	–	8	20	–	6	2	–	
Helianthemum nummularium	31	–	2	–	–	2	–	
Origanum vulgare	23	–	10	–	–	2	–	
Silene vulgaris	–	25	2	–	–	4	4	
Anthoxanthum odoratum	–	33	–	–	–	–	–	
Dorycnium pentaphyllum	31	–	–	–	–	–	–	
Euphorbia helioscopia	31	–	–	–	–	–	–	
Polygala vulgaris	31	–	–	–	–	–	–	
Pinus peuce	–	–	–	2	–	–	29	
Dorycnium hirsutum	23	–	6	–	–	2	–	
Rhamnus alpina s. fallax	–	–	6	–	2	21	2	
Sorbus aucuparia	–	–	6	–	2	–	22	
Populus tremula	–	25	–	–	–	2	2	
Galium lucidum	–	25	–	–	–	2	–	
Juglans regia	23	–	–	–	–	4	–	
Daphne laureola	–	25	–	–	–	–	–	
Lotus corniculatus	23	–	2	–	–	–	–	
Capsella bursa-pastoris	23	–	–	–	–	–	–	
Bituminaria bituminosa	23	–	–	–	–	–	–	
Hepatica nobilis	–	–	–	2	–	–	20	
Milium effusum	–	–	–	21	–	–	–	
Primula elatior	–	–	20	–	–	–	–	

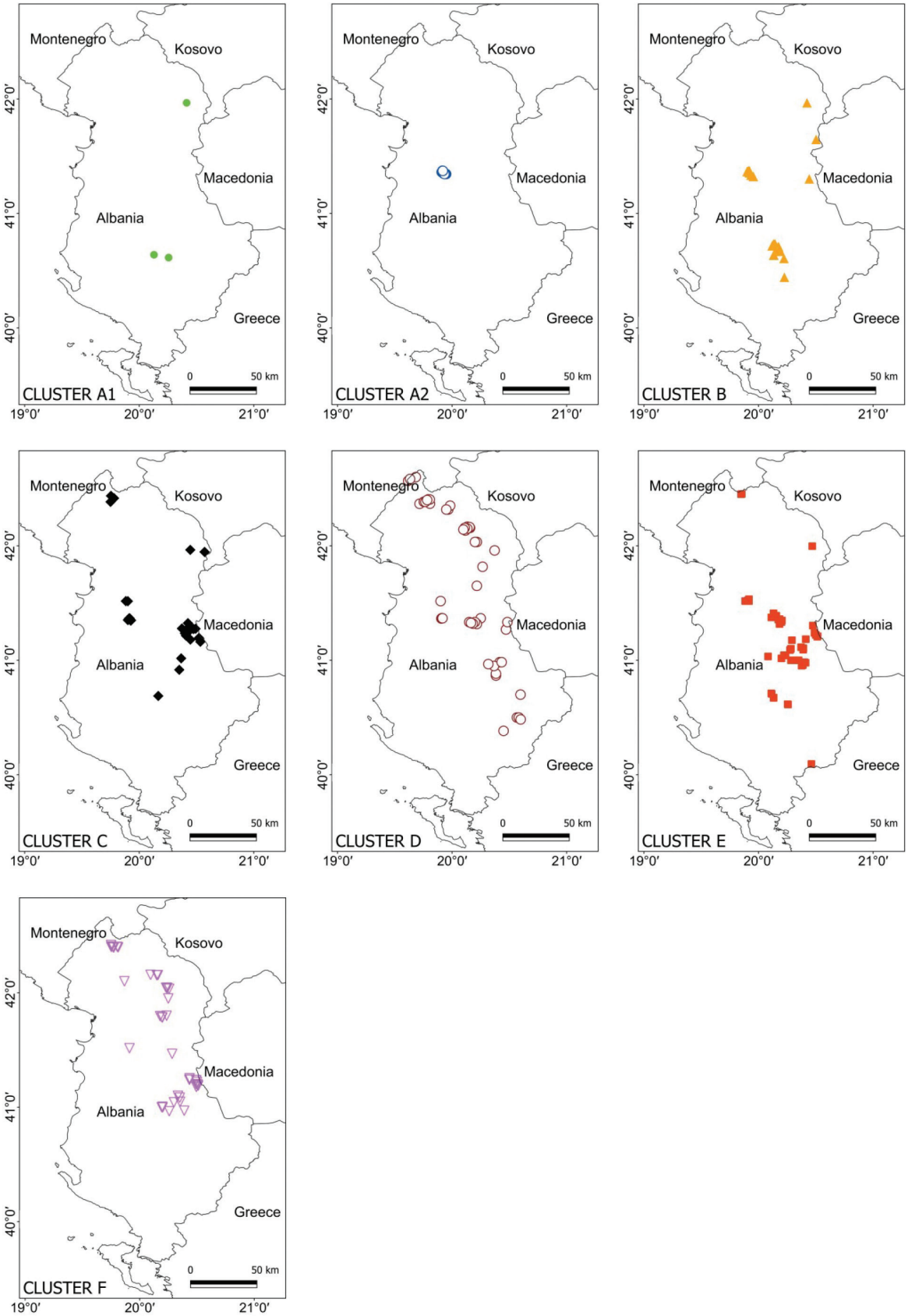

Figure 4. Distribution maps of the seven clusters of relevés. Symbols in the maps represent the sampling locations. Cluster **A1** *Corylus avellana* forests. Cluster **A2** *Ostrya carpinifolia-Fagus sylvatica* forests. Cluster **B** lower montane thermophytic *Fagus sylvatica* forests. Cluster **C** middle montane, slightly acidic *Fagus sylvatica* forests. Cluster **D** upper montane basiphytic *Fagus sylvatica* forests. Cluster **E** middle montane basiphytic *Fagus sylvatica* forests. Cluster **F** upper-montane acidophytic *Fagus sylvatica* forests.

Cluster B: lower montane thermophytic *Fagus sylvatica* forests

Diagnostic species: *Primula elatior 42.4*, *Rosa species 42.2*, *Primula veris 37.9*, *Crocus veluchensis 37.9*, *Helleborus odorus 35.9*, *Festuca heterophylla 34.5*, *Fragaria vesca 33.3*, *Geranium aristatum 32.9*, *Polygala nicaeensis 32.7*, *Erythronium dens-canis 32.7*, *Doronicum austriacum 31.1*

This cluster is among the best differentiated in the dataset, with many important diagnostic species. This forest type occurs in a belt with a strong maritime influence in Central and Southern Albania, but it is also present in the mountains of Northern Albania. The position in the NMDS diagram indicates that cluster B occupies the lower belt (lower montane; the average altitude of distribution is 1187 m).

The cluster includes many species of the suballiance *Lathyro veneti-Fagenion* (*Acer obtusatum*, *Cyclamen hederifolium*, *Lilium chalcedonicum*) although with very low frequency; also a few species of *Aremonio-Fagion* s.l. (*Laburnum alpinum*, *Salvia glutinosa*) and *Geranio striati-Fagion* (*Anemone apennina*) are present with high frequency. These species suggest that this cluster is related to the suballiance *Lathyro veneti-Fagenion*. The diagnostic species of this suballiance are numerous but rare. However, the geographical position and overall floristic composition rather suggests an assignment to the *Doronico orientalis-Fagenion moesiacae*.

Cluster B can be differentiated into two communities: B/1 occurs from 900 to 1200 m in the area of Dajti, in central Albania. It is well characterized by the presence of *Cephalanthera rubra*, *Neottia nidus-avis* and *Rhamnus alpina* subsp. *fallax*. All these species also occur in other clusters but show a clear optimum here.

B/2 is characterized by the presence of *Ilex aquifolium* that is widespread also in the *Fagus sylvatica* forests of Southern Italy. The species is present with low frequency, but it was probably more common in the past, having been selectively destroyed by humans. Other diagnostic species are *Doronicum columnae*, *Hedera helix*, *Euphorbia amygdaloides*, *Sanicula europaea*, *Poa nemoralis*, *Festuca heterophylla*, and *Erythronium dens-canis*. *Ostrya carpinifolia* is also present, but this is probably due to catenal contact with *O. carpinifolia* communities present on steeper slopes. This community occurs from 900 to 1500 m in Dajti and Tomorr but also in Northern Albania. One of the relevés that was previously referred to the *Calamintho grandiflorae-Fagetum* Rizovski & Džekov ex Matevski et al. 2011 (De Sanctis et al. 2018) belongs here. Another distinction between cluster B/1 and B/2 is the presence of *Pteridium aquilinum* and *Fragaria vesca* in B/2, indicating an intense disturbance by fire.

Cluster C: middle montane, slightly acidic *Fagus sylvatica* forests

Diagnostic species: *Milium effusum 42.9*

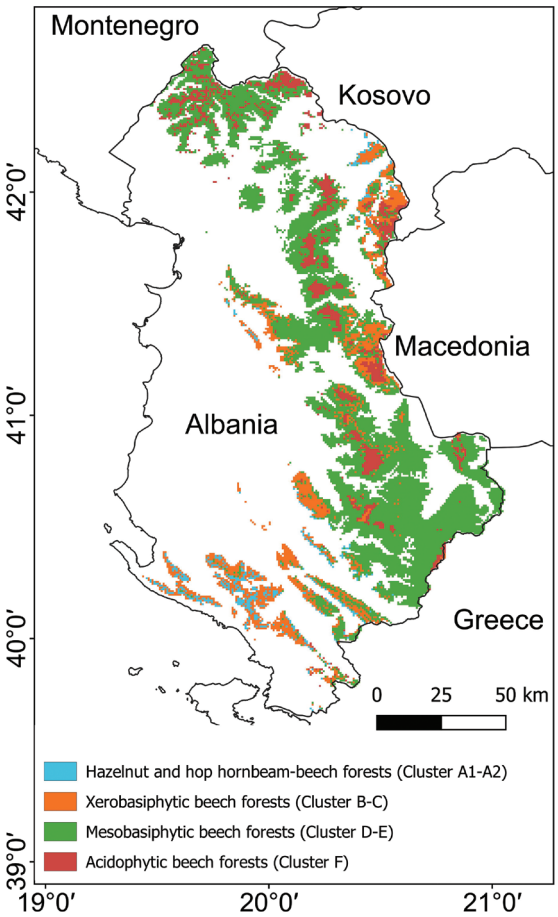

Figure 5. Map of the potential distribution of the four main groups of relevés resulting from random forest procedure. Cluster **A1** *Corylus avellana* forests. Cluster **A2** *Ostrya carpinifolia-Fagus sylvatica* forests. Cluster **B** lower montane thermophytic *Fagus sylvatica* forests. Cluster **C** middle montane, slightly acidic *Fagus sylvatica* forests. Cluster **D** upper montane basiphytic *Fagus sylvatica* forests. Cluster **E** middle montane basiphytic *Fagus sylvatica* forests. Cluster **F** upper-montane acidophytic *Fagus sylvatica* forests.

Cluster C occurs on average at higher altitudes than cluster B (1300–1600 m; average altitude: 1412 m) but occupies more or less the same Northern-Central sector of Albania (Figures 4, 5). The cluster contains some species of thermo-basiphytic *Fagus sylvatica* forests, which, however, do not have high frequency (*Cephalanthera damasonium*, *Hepatica nobilis*, *Primula vulgaris* etc.). A few species of *Geranio striati-Fagion* and *Lathyro veneti-Fagenion* are present (*Lathyrus venetus*, *Anemone apennina*, *Laburnum anagyroides*, *Lilium chalcedonicum*) but with lower frequency than in cluster B. The most characteristic species are diagnostic of the *Doronico orientalis-Fagenion moesiacae* (*Physospermum cornubiense*, *Lathyrus alpestris*).

Cluster C can be differentiated into four communities, some of which correspond to associations identified in the *Fagus sylvatica* forests of Shebenik-Jabllanice National Park by De Sanctis et al. (2018).

C/1 is characterized by *Epimedium alpinum*, *Allium ursinum*, *Viola odorata*, *Symphytum tuberosum*, and *Milium effusum*. It was previously described as *Epimedio alpini-Fagetum sylvaticae* Fanelli (De Sanctis et al. 2018), and it occurs in Shebenik, but also in Korab, at an altitude of 1100–1300 m We checked the herbarium material and we can confirm that *Epimedium alpinum* belongs to the subsp. *alpinum* and not to the recently described subspecies *albanicum* (Shuka et al. 2019).

C/2 is characterized by *Milium effusum* (which is shared with the previous cluster), *Lathraea squamaria*, *Abies alba* and *Orthilia secunda*. This community was referred to the *Orthilio secundae-Fagetum* in De Sanctis et al. (2018), but it probably represents a distinct type that can be described after more material is collected to assess its variability and its relationship with other associations. It shows many affinities with cluster D/3. This cluster occurs at 1300–1600 m and only in Shebenik area.

C/3 is well characterized by *Cardamine bulbifera*, *Cardamine enneaphyllos*, *Dryopteris carthusiana* and *Neottia nidus-avis*. *Orthilia secunda* is also present. This community was identified with the *Calamintho grandiflorae-Fagetum* due to its similarity with a stand of this community in Galicicia mountains (Matevski et al. 2011; De Sanctis et al. 2018). The community occurs at Shebenik, Korab and the Dajtj range at an altitude varying from 1200 to 1900 m, but in general in an alti-montane belt.

C/4 is poorly characterized by *Lilium martagon*. It occurs in Dajtj at an altitude of 1500–1600 m, and probably represents only a variant of B/2 at higher altitudes.

Cluster D: upper montane basiphytic *Fagus sylvatica* forests

Diagnostic species: *Oxalis acetosella 44.7*, *Actaea spicata 32.1*, *Lamium galeobdolon 31.7*, *Galium odoratum 30.1*

A high number of meso-basiphytic *Fagus sylvatica* forest species is present in cluster D (*Actaea spicata*, *Cardamine bulbifera*, *Galium odoratum*, *Lamium galeobdolon* etc.) and a few ferns of *Lonicero alpigenae-Fagenion*, but with low frequency (*Polystichum lonchitis*, *Asplenium viridis*, *Gymnocarpium dryopteris*).

This cluster is widespread throughout Albania (Figures 4, 5). It usually occurs at altitudes from 950 to 1500 m, but in general these forests are more common in the range 1400–1500 m (average altitude: 1447 m).

Cluster D can be differentiated into four communities: D/1 is characterized by *Luzula sylvatica*, *Gymnocarpium dryopteris*, *Euphorbia amygdaloides*, *Calamintha grandiflora*, *Epipactis helleborine*, *Scilla bifolia*, *Dryopteris filix-mas*, *Daphne mezereum* and *Salvia glutinosa*. It is related to the associations usually referred to *Aremonio-Fagion* or to *Lonicero alpigenae-Fagenion* in the Dinarides (Marincek et al. 1992). The forests of this type can be found in the Shebenik range at an altitude of 1000–1800 m and in the Albanian Alps.

D/2 is diagnosed by *Potentilla micrantha*, *Lathyrus venetus*, *Paris quadrifolia*, *Cephalanthera damasonium* and *Lathyrus laxiflorus*. It is similar to the *Lathyro alpestri-Fagetum* Bergmeier 1990 (in particular for the presence of *Lathyrus venetus* and *Cephalanthera damasonium*) which occurs in Central Eastern Greece in moderately warm habitats (Bergmeier and Dimopoulos 2001).

D/3 is mainly characterized by the abundance of *Abies alba*, a species which is present in other clusters but reaches its optimum here. Other species such as *Orthilia secunda* and *Cardamine enneaphyllos* are frequent in this cluster. In summary this community represents an "Abieti-Fagetum" but is clearly different from the *Fagus sylvatica-Abies alba* forests of the Dinarides and Alps and probably deserves recognition as a distinct association. It thrives in all the mountains of Albania, but it is particularly well represented in SE Albania. It generally occurs at an altitude from 1500 to 1700 m but can extend down to 950 m.

D/4 is characterized by *Aremonia agrimonioides*, *Calamintha grandiflora* and *Lathyrus venetus*. These species are present also in other communities and are widespread in the southern Balkans (Willner et al. 2017; Dzwonko and Loster 2000) but are particularly well represented here. The first 3 relevés of this cluster are very well characterized by a set of species (*Hesperis matronalis*, *Aquilegia vulgaris*, *Moehringia muscosa*, *Selaginella helvetica*) which are typical of ravines and shaded situations and probably are transgressive from some other community (perhaps related to *Tilio-Acerion*). This community is present in the Albanian Alps and in the Dajtj range in central Albania at an altitude varying from 1000 to 1800 m.

Cluster E: middle montane basiphytic *Fagus sylvatica* forests

Diagnostic species: *Calamintha grandiflora 34.7*, *Geranium macrorrhizum 34.0*, *Rhamnus alpina subsp. fallax 32.4*, *Geum urbanum 32.4*, *Polystichum aculeatum 31.1*, *Campanula pichleri 30.4*, *Allium ursinum 30.0*

This cluster clearly belongs to the suballiance *Doronico columnae-Fagenion*. Willner et al. (2017) recognized this suballiance in the meso-basiphytic *Fagus sylvatica* forests, but they could not identify any characteristic species for it. Marinšek et al. (2013) identified several diagnostic species for SE Europe, many of which are present in our plots, although with relatively low frequency: *Abies borisii-regis*, *Potentilla micrantha*, *Campanula sparsa*. Several species of mesophytic forests are also present (*Geranium robertianum*, *Cardamine bulbifera*, *Polystichum aculeatum*, *Galium odoratum*, *Lamium galeobdolon* etc.). A few species of *Doronico orientalis-Fagenion moesiacae* are present with high frequency (*Geum urbanum*, *Lathyrus laxiflorus*). The suballiance is referred to the *Fagion moesiacae* in Marinšek et al. (2013) and in Willner et al. (2017).

This cluster is mainly distributed in central Albania but is also present in the North and South (Figures 4, 5). It

spans a wide altitudinal range from 1100 to 1900 m (average altitude: 1390 m).

In Cluster E four communities can be identified: E/1 is diagnosed by a set of species (*Sorbus graeca*, *Epipactis helleborine*, *Lilium martagon*) that is also present in community C/4, and by *Bromus ramosus*, *Cardamine enneaphyllos*, and *Brachypodium sylvaticum*, which are also present in cluster C. The community is therefore relatively well characterized but shows some affinities to cluster C that possibly represents an altitudinal variant. The community occurs usually at 1300–1900 m, but can extend down to 1100 m. The community occurs near Librazhd and near Tirana in central Albania.

E/2 is well characterized among Albanian *Fagus sylvatica* woods by *Allium ursinum*, *Epilobium montanum*, and *Hesperis matronalis* (which is also present in a few relevés of cluster D/4). *Abies alba* is also present, but with low frequency. The community occurs in a wide altitudinal range from 1100 to 1900 m It occurs in Central Albania near Tirana.

E/3 is well characterized by *Oxalis acetosella*, *Sanicula europaea*, *Luzula forsteri*, *Euphorbia amygdaloides*, *Daphne mezereum*, *Urtica dioica*, and *Polystichum aculeatum*. *Cephalanthera rubra* is also present, but more typical of community B/2. The community is very close and possibly identical to the *Lamiastro montani-Fagetum* described from a limited area in Northern Greece (Bergmeier and Dimopoulus 2001) due to the presence of *Oxalis acetosella*, *Hordelymus europaeus*, *Lathyrus laxiflorus*, but a few important species of the latter (*Anemone ranunculoides*, *Paris quadrifolia*) are lacking. The community generally grows at an altitude of 1300–1500 m particularly in central Albania near Tirana and in the Shebenik range.

E/4 is a poorly characterized community distinct particularly because of the presence of *Euphorbia amygdaloides* and *Pinus heldreichii*. It occurs in Korab and Tomorr on limestones at an altitude of about 1800 m.

Cluster F: upper-montane acidophytic *Fagus sylvatica* forests

Diagnostic species: *Vaccinium myrtillus 77.3*, *Pinus nigra 56.6*, *Erica carnea 54.6*, *Pinus peuce 48.6*, *Hepatica nobilis 39.3*, *Orthilia secunda 37.3*, *Sorbus aucuparia 35.9*, *Prenanthes purpurea 35.4*, *Buxus sempervirens 34.1*, *Carex species 33.9*, *Abies alba 32.5*, *Calamagrostis arundinacea 31.1*

This cluster includes several species of acidophytic *Fagus sylvatica* forests with high frequency and abundance (*Calamagrostis arundinacea*, *Vaccinium myrtillus*). At the same time, some species of *Lonicero alpigenae-Fagenion* have their optimum in or are restricted to this cluster, even though with low frequency (*Polystichum lonchitis*, *Lonicera alpigena*, *Luzula multiflora*, *Gymnocarpium dryopteris*). Another interesting acidophilous species is *Erica carnea*. The forests corresponding to this cluster usually develop on acidic soils, so we are inclined to refer to the cluster as acidophytic beech forests. This cluster occurs at an altitude of 1000–1890 m (average altitude: 1470 m) and is restricted to Northern and Central Albania (Figures 4, 5).

Cluster F can be differentiated into three communities: F/1 is characterized by mesophytic species with thermophytic affinity such as *Sanicula europaea*, *Euphorbia amygdaloides*, *Doronicum columnae*, *Calamintha grandiflora* and *Anemone nemorosa*. These species are probably transgressive from other community. This community develops at an altitude of 800–1100 m and therefore represents the lowest forests among the acidophytic ones. The cluster occurs mainly in the Shebenik range.

F/2 is differentiated mainly by *Pinus peuce*, which transgresses from communities of the *Pinion peucis* (De Sanctis et al. 2018), whereas F/3 is characterized by the presence of *Pinus nigra* which again transgresses from communities of the *Erico-Pinetea*. F/2 generally occurs at altitude of 1500–1800 m and F/3 at 900–1000 m.

All three communities are similar to the *Orthilio secundae-Fagetum* (Bergmeier and Dimopoulos 2001). However, the Albanian communities are also floristically distinct, showing some affinities to the communities of the Dinarides, as suggested by the presence of some species of the *Lonicero alpigenae-Fagenion*.

Discussion

Three alliances are traditionally recognized among the basiphytic *Fagus sylvatica* forests of the Balkans: *Aremonio-Fagion*, *Fagion moesiacae* and *Geranio striati-Fagion* (Marinšek et al. 2013). The alliances are recognized based on regional endemics and of species with narrow ranges. Our relevés show some influence from all three alliances, with the thermo-basiphytic forests (B, C) having affinities to the *Geranio striati-Fagion*, the meso-basiphytic forests to the *Aremonio-Fagion* (D, E) and the acidophytic (F) forests to the *Luzulo-Fagion sylvaticae*. However, the floristic characterization is poor, with only few species from these alliances occurring in our data set. Moreover, the delimitation and floristic definition of these alliances provided in the revisions covering different geographical contexts (Marinček et al. 1992; Dzwonko and Loster 2000; Bergmeier and Dimopoulos 2001) is contradictory and therefore difficult to apply to the Albanian forests.

The system of Albanian forests fits better with the ecological classification in Willner et al. (2017). We found two main clusters corresponding to thermo-basiphytic and mesophytic *Fagus sylvatica* forests, respectively. Mesophytic *Fagus sylvatica* forests were in turn divided into acidophytic (cluster F) and meso-basiphytic *Fagus sylvatica* forests (clusters E and D). These three main clusters could be further divided into seven clusters corresponding to narrower ecological groups. The attribution to existing suballiances is relatively straightforward using the diagnostic species indicated in Willner et al. (2017) and in Marinšek et al. (2013) and leads to the classification presented in the syntaxonomic scheme at the end of the pa-

per, with meso-basiphytic *Fagus sylvatica* forests referred to as *Fagion moesiacae* and acidophytic *Fagus sylvatica* forests presumably to *Luzulo-Fagion*.

Ecologically, the seven units (A–F) are well characterized, with each forest type occupying a different section of the ecological space with minimal overlap (see Figure 3). We have a main climatic gradient corresponding to the altitudinal belts and a second gradient separating forests according to substrata. The system is very similar to that of Willner (2002) for Southern Central European forests, where also a main division in altitudinal belt and a secondary division according to substrata has been proposed. In our case, however, the second gradient seems to be a combination of soil properties and Mediterranean influence. It separates cluster B and C, which show some Mediterranean influence, from D and E, that are not influenced by Mediterranean climate.

We identified 17 communities of *Fagus sylvatica* forest. Considering the limited area of the study, this is a very high diversity, which is similar to most of the Dinarides and Eastern Alps (Horvat et al. 1974; Willner 2002). *Fagus sylvatica* probably has an ecological optimum in this part of Europe, due to high rainfall and suitable soils. This results not only in the high number of communities but also in a high number of higher syntaxonomic units. The variety of mesophilous forests and the local coexistence of many different types is well represented in the map (Figure 5) of the four main groups of mesophilous forests of Albania.

In contrast to *Fagus sylvatica* forest, the *Corylus avellana* forests are relatively homogenous and easy to interpret. In our opinion the closest relationship can be found to the *Astrantio-Corylion* Passarge 1978. However, there are differences with the thickets of Central Europe, since the Albanian *Corylion* occupies a specific ecological position, in a belt below the *Fagus sylvatica* forests in both Central and Southern Albania, in relatively oceanic conditions. The climate of this belt is probably very similar to the microclimate of ravines, cool and oceanic, and this climatic similarity might explain the apparently contradictory geomorphological context. Nonetheless our relevés are from very disturbed (mainly fires) *Corylus avellana* forests, and we defer a more detailed account of this type of forest to a future study.

Scrutiny of the map of potential vegetation of mesophilous forests in Albania (Figure 5) shows a few clear patterns. From the coast inwards, thermophytic types are substituted by mesophytic types, in accordance with decreasing water stress, diminishing temperatures and rising altitudes. Nonetheless, since the morphology of the Albanian ranges is quite corrugated, different forest types can occur in close proximity to each other.

Another interesting pattern is the absolute dominance of thermophytic types in the south. Southern Albania is, in fact, phytogeographically distinct from the rest of the country and transitional towards northern Greece as already highlighted in previous studies (Markgraf 1932).

Conclusion

The mesophilous vegetation of Albania presents a high diversity, with seven groups of forest and many communities. This diversity is partly related to the variety of climates and substrates, but also to the optimal conditions for mesophilous species in the Western Balkans due to the high rainfall and relatively warm climate.

Our material fits nicely in the ecological system of Willner et al. (2017), with the suballiances *Doronico orientalis-Fagenion moesiacae*, *Doronico columnae-Fagenion* and the alliance *Luzulo-Fagion*.

Although we were able to fit the majority of data analyzed in this study into existing syntaxa, we must not forget that Albanian mesophilous forests present a relevant degree of originality. The reason lies most likely in the climate of Albania, which is a unique combination of features belonging to both Central European and Mediterranean climate: it is warm like Southern Italy and Greece, but is characterized by a relatively high humidity, like the Dinarides. This uniqueness is reflected in the striking percentage of endemics of the Albanian flora (Barina et al. 2018).

If the issue of higher units of Albanian *Fagus sylvatica* forests is relatively straightforward, the identification of the associations is still in need of further studies. In fact, the clusters that we considered at the level of association are characterized usually not by character species but by combinations of differential species. This is a situation that occurs frequently in *Fagus sylvatica* forests (see for instance Willner 2002). Nonetheless, many of our clusters are well characterized, and we refrain from a formal description of undescribed associations only because we defer such a step to further local studies analyzing in depth the ecological characterization and the catenal relationships of these forest types.

Data availability

Plot data are included in the Suppl. material 7.

Author contributions

G.F., P.H. and M.D.S. conceived the study, A.F. and M.D.S. run the statistical analysis, and M.M, E.M., F.A. and V.E.C. contributed to the interpretation of results.

Acknowledgements

This study was carried out within the framework of the IUCN Project "Institutional Support to the Albanian Ministry of Environment, Forest and Water Administration (MoEFWA) for Sustainable Biodiversity Conservation and Use in Protected Areas and the Management of Waste" funded by the IDC (Italian Development Cooperation) and of the NaturAL Project – IPA 2013 "Strength-

ening national capacity in nature protection – preparation for Natura 2000 network" funded by the European Union. We thank the Linguistic Editor Lynda Weekes for the accurate language revision.

References

Attorre F, Francesconi F, De Sanctis M, Alfò M, Martella F, Valenti R, Vitale M (2014) Classifying and mapping potential distribution of forest types using a finite mixture model. Folia Geobotanica 49: 313–335. https://doi.org/10.1007/s12224-012-9139-8

Barina Z, Somogyi G, Pifkó D, Rakaj M (2018) Checklist of vascular plants of Albania. Phytotaxa 378: 1–339. https://doi.org/10.11646/phytotaxa.378.1.1

Bergmeier E, Dimopoulos P (2001) Fagus sylvatica forest vegetation in Greece: syntaxonomy and gradient analysis. Journal of Vegetation Science 12: 109–126. https://doi.org/10.1111/j.1654-1103.2001.tb02622.x

Bohn U, Neuhäusl R, Gollub G, Hettwer C, Neuhäuslová Z, Schlüter H, Weber H (2000) Map of the Natural Vegetation of Europe, Scale 1:2.500.000, German Federal Agency for Nature Conservation, Bonn, DE.

Bohn U, Gollub G, Hettwer C, Neuhäuslová Z, Raus T, Schlüter H, Weber H (2004) Map of the Natural Vegetation of Europe, Scale 1:2.500.000, Explanatory text with CD-ROM, German Federal Agency for Nature Conservation, Bonn, DE.

Braun-Blanquet J (1964) Pflanzensoziologie. 3 Auflage. Springer, Wien, AT, 865 pp. https://doi.org/10.1007/978-3-7091-8110-2

Braun-Blanquet J (1932) Zur Kenntnis nordschweizerischer Waldgesellschaften. Beihefte zum Botanischen Centralblatt, Ergänzungsband 49: 7–42.

Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. Ecological Monographs 27: 325–349. https://doi.org/10.2307/1942268

Breiman L (2001) Random forests. Machine Learning 45: 5–32. https://doi.org/10.1023/A:1010933404324 [accessed 7 Dec 2019]

Brullo S, Scelsi F, Spampinato G (2001) La vegetazione dell'Aspromonte [The vegetation of Aspromonte]. Laruffa Editore, Reggio Calabria, IT, 368 pp.

Brzeziecki B, Kienast F, Wildi O (1993) A simulated map of the potential natural forest vegetation of Switzerland. Journal of Vegetation Science 4: 499–508. https://doi.org/10.2307/3236077

Chytrý M, Hennekens S, Jiménez-Alfaro B, Knollová I, Dengler J, Jansen F, Landucci F, Schaminée HJJ, Aćić S, … Yamalov S (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. Applied Vegetation Science 19: 173–180. https://doi.org/10.1111/avsc.12191

De Sanctis M, Fanelli G, Mullaj A, Attorre F (2017) Vegetation database of Albania. Phytocoenologia 47: 107–108. https://doi.org/10.1127/phyto/2017/0178

De Sanctis M, Fanelli G, Gjeta E, Mullaj A, Attorre F (2018) The forest communities of Shebenik-Jabllanicë National Park (Central Albania). Phytocoenologia 48: 51–76. https://doi.org/10.1127/phyto/2017/0205

Dengler J, Chytrý M, Ewald J (2008) Phytosociology. In: Jørgensen SE, Fath BD (Eds) Encyclopedia of ecology, Vol. 4. Elsevier, Oxford, 2767–2779. https://doi.org/10.1016/B978-008045405-4.00533-4

Di Pietro R (2009) Observations on the Fagus sylvatica woodlands of the Apennines (peninsular Italy): an intricate biogeographical and syntaxonomical issue. Lazaroa 30: 89–97.

Dierschke H (2004) Sommergrüne Laubwälder (*Querco-Fagetea* s.lat.) in Europa – Einführung und Übersicht. Tuexenia 24: 3–17.

Diku A, Shuka L (2018) Old Fagus sylvatica forests in Albania. ILIRIA organisation [Report no. 978-9928-202-93-2], Tirana, AL, 26 pp.

Dring J, Hoda P, Mersinllari M, Mullaj A, Pignatti S (2002) Plant communities of Albania-A preliminary overview. Annali di botanica 2: 7–30.

Dzwonko Z, Loster S (2000) Syntaxonomy and phytogeographical differentiation of the Fagus woods in the Southwest Balkan Peninsula. Journal of Vegetation Science 11: 667–678. https://doi.org/10.2307/3236574

Euro+Med (2019) Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed/ [accessed 2 Nov 2019]

Fanelli G, De Sanctis M, Gjeta E, Mullaj A, Attorre F (2015) The vegetation of the Buna river protected landscape (Albania). Hacquetia 14: 129–174. https://doi.org/10.1515/hacq-2015-0008

Feoli E, Lagonegro M (1982) Syntaxonomic analysis of Fagus sylvatica woods in the Apennines (Italy) using the program package IAHOPA. Vegetatio 50: 129–173. https://doi.org/10.1007/BF00364109

Franklin J (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in physical geography 19: 474–499. https://doi.org/10.1177/030913339501900403

Gentile S (1964) Notizie preliminari sulle faggete dell'Appennino calabro. Delpinoa 4: 305–317.

Horvat I, Glavač V, Ellenberg H (1974) Vegetation Südosteuropas. Geobotanica selecta 4. Gustav Fischer Verlag, Stuttgart, DE, 768 pp.

INSTAT (2019) Forest statistics 2017. Institue of Statistics, Tirana, AL, 22 pp.

Kalajnxhiu A, Tsiripidis I, Bergmeier E (2012) The diversity of woodland vegetation in Central Albania along an altitudinal gradient of 1300 m. Plant Biosystems 146: 954–969. https://doi.org/10.1080/11263504.2011.634446

Knapp H. D, Schroeder C, Schwaderer G (2014) Report of the Excursion to Ancient Fagus sylvatica Forests in Albania and Macedonia. EuroNatur Stiftung, Radolfzel, DE, 20 pp.

Košir P, Čarni A, Di Pietro R (2008) Classification and phytogeographical differentiation of broad-leaved ravine forests in southeastern Europe. Journal of Vegetation Science 19: 331–342. https://doi.org/10.3170/2008-8-18372

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Scientific Data 4: e170122. https://doi.org/10.1038/sdata.2017.122

Landucci F, Tichý L, Šumberová K, Chytrý M (2015) Formalized classification of species-poor vegetation: a proposal of a consistent protocol for aquatic vegetation. Journal of Vegetation Science 26: 791–803. https://doi.org/10.1111/jvs.12277

Legendre P, Legendre L (1998) Numerical ecology. 2nd English edition. Elsevier Science BV, Amsterdam, NL, 853 pp.

Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K (2019) cluster: Cluster Analysis Basics and Extensions. R package version 2.1.0. https://cran.r-project.org/web/packages/cluster/index.html [accessed 10 October 2019]

Maggini R, Lehmann A, Zimmermann NE, Guisan A (2006) Improving generalised regression analysis for the spatial prediction of forest communities. Journal of Biogeography 33: 1729–1749. https://doi.org/10.1111/j.1365-2699.2006.01465.x

Mahmutaj E (2015) Studimi dhe kartografimi i Habitateve dhe Florës së Parkut Kombëtar Tomorr-Kulmak, me fokus kryesor ata prioritarë (sipas Natura 2000), të rrallë e të kërcënuar [Studying and mapping the Habitats and Flora of Tomorr-Kulmak National Park, with the main focus on those of priority (according to Natura 2000), rare and threatened]. Ph.D. thesis, Tirana University, Tirana, AL.

Marinček L, Mucina L, Zupančič M, Poldini L, Dakskobler I, Accetto M (1992) Nomenklatorische Revision der illyrischen Buchenwälder (Verbano Aremonio-Fagion). Studia Geobotanica 12: 121–135.

Marinšek A, Šilc U, Čarni A (2013) Geographical and ecological differentiation of Fagus forest vegetation in SE Europe. Applied Vegetation Science 16: 131–147.

Markgraf F (1927) An den Grenzen des Mittelmeergebietes. Pflanzengeographie von Albanien. Repertorium Specerum Novarum Regni vegetabili Beih 45: 1–99.

Markgraf, F (1932) Pflanzengeographie von Albanien. Ihre Bedeutung für Vegetation und Flora der Mittelmeerländer. Bibliotheca Botanica 105: 1–132.

Matevski V, Carni A, Avramovski O, Juvan N, Kostadinovski M, Košir P, Marinšek A, Paušic A, Šilc U (2011) Forest Vegetation of the Galicica Mountain Range in Macedonia. Založba ZRC Publishing House, Ljubljana, SI, 200 pp. https://doi.org/10.3986/9789610502906

Mersinllari M (1989) Studime gjeobotanike te pyjeve tea hut ne Shiperi [Geobotanical study of Fagus sylvatica forest in Albania]. Ph.D. thesis, Tirana University, Tirana, AL.

Moor M (1938) Zur Systematik der Fagetalia. Berichte der Schweizerischen Botanischen Gesellschaft 48: 417–469.

Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, … Tichý L (2016) Vegetation of Europe: Hierarchical floristic classification system of plant, lichen, and algal communities. Applied Vegetation Science 19 (Supplement 1): 3–264. https://doi.org/10.1111/avsc.12257

Murtagh F, Legendre P (2014) Ward's hierarchical agglomerative clustering method: which algorithms implement Ward's criterion? Journal of classification 31: 274–295. https://doi.org/10.1007/s00357-014-9161-z

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2016) vegan: Community Ecology Package. R package version 2.4–2. https://cran.r-project.org/web/packages/vegan/index.html [accessed 26 October 2019]

Pumo E, Krutaj F, Lamani F, Gruda GJ, Kabo M, Demiri M, Mecaj N, Pano N, Qirijazi P, ... Melo V (1990) Gjeografia Fizike e Shqipërisë [Physical geography of Albania]. Qëndra e studimeve gjeografike 1: 1–285.

Rivas-Martínez S, Penas A, Díaz TE (2004) Bioclimatic and biogeographic maps of Europe. https://www.globalbioclimatics.org/form/maps.htm [accessed 30 October 2019].

Scarnati L, Attorre F, Farcomeni A, Francesconi F, De Sanctis M (2009) Modelling the spatial distribution of tree species with fragmented populations from abundance data. Community Ecology 10: 215–224. https://doi.org/10.1556/ComEc.10.2009.2.12

Shuka L, Tan K, Hallaçi B (2019) Report 129. In: Vladimirov V, Aybeke M, Tan K (Eds) New Floristic records in the Balkans: 40. Phytologia Balcanica 25: 295–335.

Soó R (1964) Die regionalen *Fagion*-Verbände und Gesellschaften Südosteuropas. Acta Agronomica Academiae Scientiarum Hungaricae 1: 1–104.

Tichý L (2002) JUICE, software for vegetation classification. Journal Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal Vegetation Science 17: 809–818. https://doi.org/10.1111/j.1654-1103.2006.tb02504.x

Török K, Podani J, Borhidi A (1989) A numerical revision of *Fagion Illyricum.* Vegetatio 81: 1269–180. https://doi.org/10.1007/BF00045522

Ward Jr, Joe H (1963) Hierarchical grouping to optimize an objective function. Journal of the American statistical association 58: 236–244. https://doi.org/10.1080/01621459.1963.10500845

Willner W (2002) Syntaxonomische Revision der südmitteleuropäischen Buchenwälder. Phytocoenologia 32: 337–453. https://doi.org/10.1127/0340-269X/2002/0032-0337

Willner W, Di Pietro R, Bergmeier E (2009) Phytogeographical evidence for post-glacial dispersal limitation of European Fagus sylvatica forest species. Ecography 32: 1011–1018. https://doi.org/10.1111/j.1600-0587.2009.05957.x

Willner W, Solomeshch A, Carni A, Bergmeier E, Ermakov N, Mucina L (2016) Description and validation of some European forest syntaxa – a supplement to the EuroVegChecklist. Hacquetia 15: 15–25. https://doi.org/10.1515/hacq-2016-0005

Willner W, Jiménez-Alfaro B, Agrillo E, Biurrun I, Campos JA, Čarni A, Casella L, Csiky J, Ćušterevska R, … Chytrý M (2017) Classification of European Fagus sylvatica forests: a Gordian Knot? Applied Vegetation Science 20: 494–512. https://doi.org/10.1111/avsc.12299

Xhomo A, Kodra A, Dimo LL, Xhafa Z, Nazaj Sh, Nakuci V, Yzeiraj D, Lula F, Sadushi P, … Melo V (2002) Geological Map of Albania 1: 200 000 scale. Republika e Shqipërisë: Ministria e Industrisë dhe Energjitikës, Ministria e Arsimit dhe Shkencës, Shërbimi Gjeologjik Shqiptar, Albpetroli, Universiteti Politeknik i Tiranës, Tirana, AL.

E-mail and ORCID

Giuliano Fanelli (giuliano.fanelli@gmail.com), ORCID: https://orcid.org/0000-0002-3143-1212
Petrit Hoda (hodapetrit@yahoo.com)
Mersin Mersinllari (mersin.mersinllari@yahoo.com)
Ermelinda Mahmutaj (mahmutaje@yahoo.com)
Fabio Attorre (fabio.attorre@uniroma1.it), ORCID: http://orcid.org/0000-0002-7744-2195
Alessio Farcomeni (alessio.farcomeni@uniroma2.it), ORCID: https://orcid.org/0000-0002-7104-5826
Vito Emanuele Cambria (vitoemanuele.cambria@phd.unipd.it), ORCID: http://orcid.org/0000-0003-0481-6368
Michele De Sanctis (Corresponding author, michele.desanctis@uniroma1.it), ORCID: http://orcid.org/0000-0002-7280-6199

Supplementary material

Supplementary material 1
The average, minimum, maximum and standard deviation of the 19 bioclimatic CHELSA variables related to the *Fagus sylvatica* area of distribution in Albania according the Vegetation Map of Europe
Link: https://doi.org/10.3897/VCS/2020/54942.suppl1

Supplementary material 2
Lithological substrata of Albania obtained through our grouping of the geological substrata provided by the Geological Map of Albania
Link: https://doi.org/10.3897/VCS/2020/54942.suppl2

Supplementary material 3
The average, minimum, maximum of site and layer data of all relevés
Link: https://doi.org/10.3897/VCS/2020/54942.suppl3

Supplementary material 4
Random Forest validation: Cramer's V index for cross-classification table and out-of-bag classification error
Link: https://doi.org/10.3897/VCS/2020/54942.suppl4

Supplementary material 5
Non-Metric Multidimensional Scaling (NMDS) ordination of relevés for each cluster
Link: https://doi.org/10.3897/VCS/2020/54942.suppl5

Supplementary material 6
The average, minimum, maximum of site and layer data of the relevés of each cluster
Link: https://doi.org/10.3897/VCS/2020/54942.suppl6

Supplementary material 7
Ordered relevés table
Link: https://doi.org/10.3897/VCS/2020/54942.suppl7

Appendix 1

Syntaxonomic scheme. Corresponding clusters are given in brackets.

Crataego-Prunetea Tx. 1962 nom. conserv. propos.
- ***Prunetalia spinosae*** Tx. 1952
  - ***Astrantio-Corylion avellanae*** Passarge 1978 (**A1**)

Quercetea pubescentis Doing-Kraft ex Scamoni et Passarge 1959
- ***Quercetalia pubescenti-petraeae*** Klika 1933
  - ***Fraxino orni-Ostryion*** Tomažič 1940 (**A2**)

Carpino-Fagetea sylvaticae Jakucs ex Passarge 1968
- ***Fagetalia sylvaticae*** Pawlowski 1928
  - ***Fagion moesiacae*** Blecic et Lakusic 1970
    - *Doronico orientalis-Fagenion moesiacae* Marinšek, Čarni et Šilc 2013 (**B**)
    - *Doronico columnae-Fagenion moesiacae* Dzwonko, Loster, Dubiel et Drenkovski 1999 (**C**, **D, E**)

- ***Luzulo-Fagetalia sylvaticae*** Scamoni et Passarge 1959
  - ***Luzulo-Fagion sylvaticae*** Lohmeyer et Tx. in Tx. 1954 (**F**)

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 191–217
doi: 10.3897/VCS/2020/60848

RESEARCH PAPER

GRASSLANDS AND OPEN VEGETATION IN THE PALAEARCTIC

Classification of tall-forb vegetation in the Pamir-Alai and western Tian Shan Mountains (Tajikistan and Kyrgyzstan, Middle Asia)

Arkadiusz Nowak[1,2], Sebastian Świerszcz[1,3], Sylwia Nowak[1], Marcin Nobis[4,5]

1 *Botanical Garden, Center for Biological Diversity Conservation, Polish Academy of Sciences, Warszawa, Poland*
2 *Institute of Biology, University of Opole, Opole, Poland*
3 *The Franciszek Górski Institute of Plant Physiology, Polish Academy of Sciences, Kraków, Poland*
4 *Department of Taxonomy, Phytogeography and Palaeobotany, Institute of Botany, Jagiellonian University, Kraków, Poland*
5 *Research laboratory 'Herbarium', National Research Tomsk State University, Tomsk, Russia*

Corresponding author: Sebastian Świerszcz (s.swierszcz@obpan.pl)

Academic editor: Jürgen Dengler ♦ **Received** 17 November 2020 ♦ **Accepted** 8 December 2020 ♦ **Published** 30 December 2020

Abstract

Aims: To complete the syntaxonomic scheme for tall-forb vegetation of the montane and alpine belts in the Pamir-Alai and western Tian Shan Mountains in Tajikistan and Kyrgyzstan with some remarks on its environmental predictors. **Study area**: Middle Asia: Tajikistan and Kyrgyzstan. **Methods**: A total of 244 relevés were sampled in 2013–2019 using the seven-degree cover-abundance scale of the Braun-Blanquet approach. These were classified with a modified TWINSPAN algorithm with pseudospecies cut-levels 0%, 5% and 25%, and total inertia as a measure of cluster heterogeneity. Diagnostic species were identified using the phi coefficient as a fidelity measure. NMDS was used to explore the relationships between the distinguished groups. **Results**: Our classification revealed 19 clusters of tall-forb vegetation in Middle Asia. Among others we found forb communities typical for Tian Shan, western Pamir-Alai, forb-scree vegetation of Pamir-Alai, dry tall-forbs and typical forbs of the alpine belt. A total of eight new tall-forb associations and five communities were distinguished. The forb vegetation of Middle Asia has been assigned to the class *Prangetea ulopterae* Klein. The main factors differentiating the species composition of the researched vegetation are elevation, mean annual temperature, sum of annual precipitation and inclination of the slope. **Conclusions**: The paper presents the first insight into the comprehensive classification of the alpine forb vegetation in Middle Asia and fosters progress in explaining the relationship of boreo-temperate and Mediterranean-like (Irano-Turanian) vegetation in western Asian and central Asian subregions of the Irano-Turanian phytogeographical region.

Taxonomic references: The nomenclature of the vascular plants follows generally Cherepanov (1995) and for *Bromus* spp. The Plant List (2020) Version 1.1. http://www.theplantlist.org/.

Syntaxonomic references: The names of syntaxa are used in accordance with Ermakov (2012), Gadghiev et al. (2002) and Nowak et al. (2018).

Abbreviation: NMDS = Non-metric Multidimensional Scaling.

Keywords

Alpine vegetation, forb, Middle Asia, Pamir-Alai, phytogeography, *Prangetea ulopterae*, shiblyak, syntaxonomy

PENSOFT.

Copyright *Arkadiusz Nowak et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Tall-forb vegetation is known to be one of the most prominent and species-rich communities, particularly in mountainous landscape (Kočí 2001). The communities of the class *Mulgedio-Aconitetea* are natural tall-grass, tall-forb, or krummholz (shrubberies) vegetation with a well developed, often luxuriant herb layer. In the newest classification, the shrubby krummholz is excluded and incorporated into *Betulo carpaticae-Alnetea viridis* (Mucina et al. 2016). All these prominent vegetation types of the mountainous landscapes occur at varying elevations, mainly from lower montane to the high alpine belt. Its range covers a vast area from western and northern Europe to southern Siberia (Hilbig 1995; Ermakov et al. 2000). However, towards the south such hygrophilous vegetation gradually gives way to the more thermophilous and drought-tolerant tall-forb communities of the Irano-Turanian region. Middle Asia, as in the case of chasmophytic, steppe and forest vegetation (Nowak et al. 2017a, 2018, 2020a), stretches on the borderland of these different, although closely related, types of vegetation. Distinct communities are formed here, particularly in the relatively moist and nutrient rich habitats of the Afghano-Turanian subregion *sensu* Kamelin (2010). This subregion supports a species rich and abundant vegetation with a dominance of tall forbs, mainly from the *Apiaceae* (*Ferula*, *Mediasia*, *Prangos*) and *Polygonaceae* (*Aponogeton*, *Polygonum*, *Rheum*) families. For this type of tall-forb vegetation, in the northern Iran, the class *Prangetea ulopterae* was coined (Klein 1987).

In the long history of research on the vegetation of Middle Asia, mainly in Tajikistan, vegetation similar to the *Prangetea* class was defined in very different ways. Firstly, it was recognized as "forb meadows" (Korovin 1934), subtropical steppes or semi-savannas (Rubtsov 1952; Ovchinnikov 1957), communities of *Prangos* and *Ferula* (Golovkova 1959) or the "ephemeroid" vegetation (Agakhanyanz and Yusufbekov 1975). Ovchinnikov (1971) proposed the name "yuganniki" for *Prangos pabularia* communities (*Prangos* in Tajik language is *yugan*) and kamolniki (scree forbs) for *Ferula* spp. vegetation. Additionally, Pavlov (1967, 1980) introduced the term "umbeliferniki" for *Apiaceae* species (alternative name *Umbelliferae*) dominated vegetation.

In the Pamir-Alai, in central Tajikistan, the first notes on the composition and distribution of *Apiaceae* dominated communities were published by Goncharov (1936). His research was focused on the vegetation of *Feruleto-Prangosetum*, *Polygoneto-Prangosetum* and *Artemisio-Feruletum* with prominent contribution of *Ferula kokanica*, *F. jaeschkeana*, *P. pabularia*, *Polygonum coriarium* and *Artemisia persica*. Additionally, from the Hissar Mountains, namely the Varzob River Valley, the community of *Prangos pabularia-Ferula jeaschkeana* was mentioned (Ovchinnikov 1971). Less frequently, the communities of *Prangetea ulopterae* were noted from the Eastern Pamir, some of which may be scree vegetation. It is also worth mentioning the works of Agakhanyanz (1966) who reported the vegetation of *Ferula grigoriewii* (as *Feruleta grigorjewii*) and *Prangos pabularia* (as *Prangoseta pabulariae*).

Representation of *Prangetea ulopterae* can be observed not only in Pamir-Alai but also in western Tian Shan. These areas are in close proximity to juniper groves and occur as a forb rich undergrowth dominated by *Prangos pabularia*, *Ferula tenuisecta*, *F. tschimganica*, *F. pallida*, *F. prangifolia* and *Rheum maximowiczii*. This vegetation occurs mainly in upper montane and alpine belts at an elevation of 1,500–2,800 m a.s.l. (Pavlov 1980). Recently, the work of Wagner (2009) gives some important insights and shows nine distinct plant communities belonging to meadow-forb vegetation (e.g. *Dactylis glomerata-Karatavia kultiassovii* and *Nepeta mariae-Aconogonon coriarium*) in the Aksu-Jabagly Nature Reserve in the western Tian Shan. Other pasture vegetation communities were revealed in the research of Borchardt et al. (2011), where they proposed a variation of tall-forb communities (*Aconogono coriarium-Prangos pabularia-Galium aparine* and *Ligularia thomsoni-Dactylis glomerata* communities). However, these studies did not aggregate the communities into higher-level units and rationalise them with the known orders and classes. Understandably, the hierarchical system of all Middle Asian grasslands is challenging to the vegetation ecologist, despite being crucial for communication and application in conservation (De Cáceres et al. 2018).

This paper presents the first attempt to classify the tall-forb vegetation in the Pamir-Alai and south-western Tian Shan Mountains and to relate it to steppe and alpine meadow communities. We aimed at addressing the following questions during our study: (1) What is the diversity of tall-forb vegetation of the montane and alpine zones in the Pamir-Alai and south-western Tian Shan Mountains? (2) What are the environmental and habitat requirenments of the described plant communities? (3) What is the species composition and structure of the vegetation plots? and (4) Which species have important diagnostic value for the described communities?

Study area

The vegetation survey was conducted in an area of ca. 350,000 km^2 located in the central part of Middle Asia (the Pamir-Alai in Tajikistan, and western and central Tian Shan in Kyrgyzstan, Figure 1). Due to the considerable phytogeographical differences between Pamir-Alai and Tian Shan Mountains, the research aimed at examining the tall-forb vegetation of both areas, including Alai, Transalaian, Alichurian, Shachdarian, Shugnan, Sarikol, Yazgulem and Peter the First Ranges in Pamir-Alai and Trans-Ili Alatau, Kyungey Ala-Too, Terskey Ala-Too, Songkol, Fergana, Kyrgyz and the Chatkal Mountains in Kyrgyzstan. The mountainous character of the highland landscapes of Middle Asia makes this territory particularly suitable for different types of tall-forb communities.

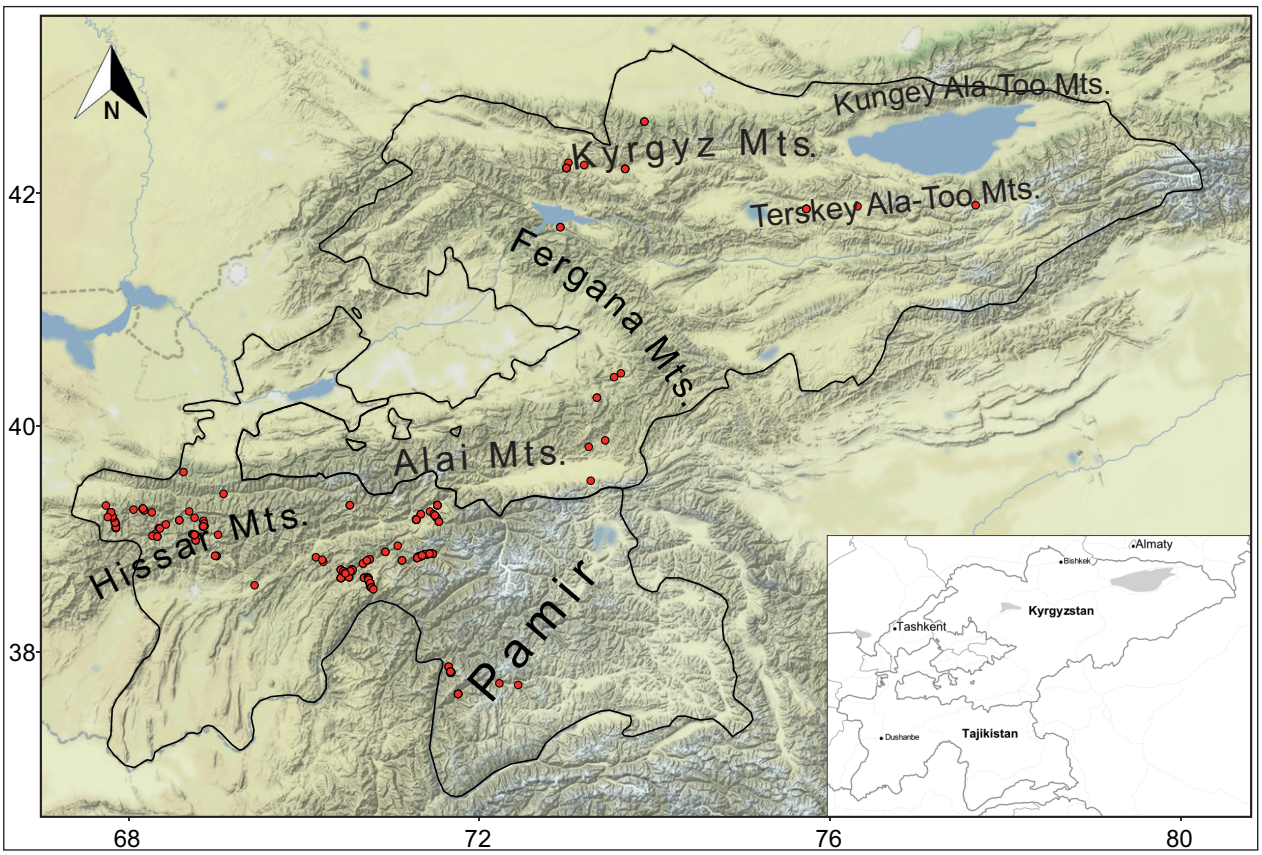

Figure 1. Study area and distribution of the vegetation plots (n = 244).

The vast alpine habitats of Middle Asia extend across a long elevational gradient. The studied sites were located between 1,300 and 3,500 m a.s.l. (mean 2,270) and within habitats that differ in terms of aspect, inclination, bedrock and particle size.

The study area is located between two main bioclimatic zones (the Irano-Turanian and Central Asiatic) and is additionally influenced by the Indo-Indochinese climate from the south and Euro-Siberian from the north. It is difficult to characterize the climatic conditions of the region, as it stretches across a transition zone between the Temperate and Irano-Turanian macrobioclimates. The first zone is characterized by a summer precipitation peak, whereas a winter precipitation peak and higher continentality are typical of the latter (Djamali et al. 2012). There are four main climatic regions within the research area (Latipova 1968; Narzikulov and Stanyukovich 1968; Safarov 2003):

(1) The warm, continental, Irano-Turanian region that includes the Fergana Valley. The surroundings of Jalalabad and Osh are characterized by winter precipitation that in March achieves its peak of 80 mm and an annual average of ca. 200–250 mm. The temperatures reach 20 °C in April and 34 °C from June to August. During these months, the precipitation is scarce, with 0–10 mm of rainfall per month. Snow and frost occur from December to February, with an average no lower than -3 °C and extreme values reaching -27 °C in some years.

(2) The warm, humid, continental region that includes the Tian Shan and Pamir-Alai ranges. Average temperature in June in the colline and montane belts within this region is around 22 °C. In the alpine belt, the temperature drops to 10 °C. Annual precipitation ranges from about 500 mm on the northern slopes up to ca. 1000 mm on the southern.

(3) The cold semi-arid region that includes the Issyk-Kul basin, central and western parts of the Alai Valley, and foothills and plateaus on the colline, montane and subalpine belts. These areas are clearly distinguished by lower precipitation, with an average ca. 200–400 mm per year. The distribution of rainfall during the year is similar to that in the temperate climate, with a maximum of 70 mm between May and July. The temperature exceeds 20 °C only in summer, and the annual average temperature is ca. 10 °C.

(4) The cold desert climate region that includes the easternmost sections of the Alai Valley and the eastern Pamirian Plateau. This area is distinguished by significant aridity with less than 100 mm mean annual precipitation. Only in May and August does the average monthly precipitation exceed 20 mm. The yearly annual temperature is slightly above 0 °C, with the minimum falling below -30 °C in January – February.

It is important to note that a multitude of local anomalies caused by orography, wind conditions and altitudinal differences occur within each of these regions (Figure 1).

Methods

Data sampling and data analyses

In total, 244 relevés were collected in tall-forb vegetation of Tajikistan and southern Kyrgyzstan in all vertical belts of Pamir-Alai and the Tian Shan Ranges during seven successive vegetation seasons (2013–2019). The size of each sampled vegetation plot ranged from 4 m^2 to 50 m^2, but most were 10 m^2. In each plot, all vascular plant and cryptogam species were recorded using the seven-degree Braun-Blanquet cover-abundance scale (Westhoff and van der Maarel 1973). The sampled data represent broad ranges of habitats, elevations, aspects, and inclination. For each plot, geographical coordinates were measured using a GPSMAP 60CSx device with an accuracy of ±5 m and a WGS84 reference frame.

In the tables containing plot data (Suppl. material 1), both latitude and longitude are given in decimal scale.

Data were stored in the Vegetation of Middle Asia database (Nowak et al. 2017b) and analyzed in R (R Core Team 2020) and JUICE software (Tichý 2002). A modified TWlNSPAN analysis (Hill 1979; Roleček et al. 2009) provided an initial understanding of the data structure and resolution. The cover-abundance scale was transformed using the three-step interval scale with cut-off levels at 0%, 5% and 25%. As the plots were selected fairly objectively, we downweighted rare species using chord distance as a measure of cluster heterogeneity (Roleček et al. 2009). Taxa identified only at the genus level were omitted during the analysis. Diagnostic species were identified using the phi coefficient as a fidelity measure (Chytrý and Tichý 2003). Group size was standardised and the Fisher exact test ($p < 0.05$) applied. Species with a phi coefficient higher than 0.20 were considered diagnostic for a particular cluster (except that for communities of *Phlomoides oreophila* and *Inula macrophylla* where we show only those with phi >0.30 to shorten the list for the first twelve clusters, which seem to have outlier positions in the data. Diagnostic taxa for alliances were defined as those with a phi coefficient ≥ 0.15 in at least two clusters within this alliance (with the exception of one very distinct cluster). Species with a higher frequency than 40% were defined as constant, and those with a maximum cover value exceeding 20% as the dominant species of an individual cluster (plant community). For translation of the TWINSPAN results into phytosociological associations, we chose the highest division that still yielded floristically well-characterized terminal clusters with their own diagnostic species (Dengler et al. 2005, Michl et al. 2010). These terminal clusters were considered as associations or plant communities, depending on the geographical range, certainty of taxonomic status of the diagnostic species, and recommendations of the International Code of Phytosociological Nomenclature (ICPN). The habitat profile and authors' field experience were used during the division to find comprehensive and ecologically interpretable results of classification.

To check the floristic-sociological classification and highlight the relationships between relevés and species, non-metric multidimensional scaling (NMDS) was performed (with downweighting of rare species, response data were log-transformed). Species cover values on the 7-degree Braun-Blanquet scale were transformed to a percentage scale (r, +, 1, 2, 3, 4, 5 to 0.1, 1, 5, 15, 37.5, 62.5 and 87.5 respectively). Differences in environmental factors (elevation, temperature, precipitation, inclination) and vegetation variables (cover herb and moss layer, species richness and Shannon diversity index) between groups were assessed using the Kruskal–Wallis rank sum test (function *kruskal.test*) with multiple comparison based on Dunn's test using the *dunnTest* function in the 'FSA' package (Ogle et al. 2018) in R. Climatic data were extracted from the Chelsa database version 1.2 (http://chelsa-climate.org; Karger et al. 2017).

The shortened synoptic table with the constancy of all diagnostic species is presented in Table 1. The full synoptic table is given in Supplementary material 2. All mentioned plant communities are arranged into an overview at the beginning of the description in the results section. We considered the spatial structure and environmental characteristics – mainly the elevation and precipitation – to be the habitats' most significant attributes.

The species nomenclature mainly followed Cherepanov (1995) and, in some exceptional cases (e.g. *Bromus* spp.), according to The Plant List (2020). The plant material collected during field studies was deposited in the Herbarium of Middle Asia Mountains, hosted in OPUN (University of Opole, Poland) and KRA (Jagiellonian University, Poland).

Results

General floristic features and relations between plant communities

The total number of taxa recorded in the whole data set (244 relevés) was 810 with only 18 exceeding 5% of constancy. The group of species with the highest frequencies includes plants typical of tall-forbs such as *Prangos pabularia* (99 occurrences), *Polygonum coriarium* (68), *Ferula kuhistanica* (65), *Scabiosa songarica* (60), *Ligularia thomsonii* (58), *Elaeosticta hirtula* (54), *Geranium regelii* (48), *Eremurus comosus* (45) and *Phlomoides lehmanniana* (41). However, the most frequent species was *Poa bulbosa* (132), considered a typical steppe plant, but apparently having a wider ecological amplitude. Other typically grassland species were *Carex turkestanica* (73), *Plantago lanceolata* (53) and *Arenaria serpyllifolia* (52). The group of most frequent species includes also scree plants like *Galium spurium* subsp. *spurium* (84) and *Hypericum scabrum* (41). Despite the close similarity between tall-forbs and xeric shrubs, the latter group includes only few taxa in the data set, such as *Ephedra gerardiana*, *E. glauca*, *Rosa beggeriana*, *R. corymbifera* or *R. divina* which occur with low frequency. Much richer is the flora of screes with fre-

Table 1. Shortened synoptic table with percentage frequency and fidelity values. Only diagnostic species are given. See Supplementary material 2 for the full version of this table. Group No.: 1 – Community of *Phlomoides oreophila*; 2 – Community of *Allium hymenorhizum*; 3 – *Feruletum sumbuli*; 4 – *Heracleetum lehmannianii*; 5 – *Eremuretum kaufmannii*; 6 – *Anthriscidetum glacialis*; 7 – Community of *Cousinia batalinii* and *Euphorbia pamirica*; 8 – *Phlomoidetum kaufmannianae*; 9 – *Phlomoidetum tadshikistanicae*; 10 – Community of *Senecio saposhnikovii*; 11 – *Eremuretum stenophyllido-comosi*; 12 – Community of *Inula macrophylla*; 13 – *Stipetum margelanicae*; 14 – *Lathyretum mulkaki*; 15 – *Potentillo orientalis-Eremuretum fusci*; 16 – *Hordeo bulbosi-Astragaletum retamocarpi*; 17 – Community of *Ferula kuhistanica*; 18 – *Eremuretum robusti*; 19 – *Phlomoido lehmannianae-Onobrychidetum grandis*.

Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	29	
	Poion alpinae	*Ligulario thomsonii-Geranion regelii*						*Rheion maximowiczii*					*Scabioso songaricae-Phlomoidion lehmannianae*							
Community of *Phlomoides oreophila*																				
Phlomoides oreophila	50 47.4	. ---	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	8
Cerastium tianschanicum	36 37.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Festuca alatavica	29 36.1	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Alchemilla bungei	21 36	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Caragana jubata	14 35.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Astragalus alpinus	29 34.8	. ---	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Pedicularis ludwigii	36 33.2	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	6
Aulacospermum simplex	36 32.1	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Thalictrum foetidum	36 32.1	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Poa alpina	29 32	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Myosotis asiatica	57 31.5	25 ---	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	10
Valeriana dubia	36 31.1	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Veronica porphyriana	21 30.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Polygonum ellipticum	50 29.3	. ---	. ---	. ---	. ---	29 9.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	12
Ligularia narynensis	29 28.4	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Gentiana karelinii	29 28.4	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Palustriella decipiens	14 28.1	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Aconogonon songaricum	14 27.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Galium tianschanicum	14 27.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Dracocephalum nutans	14 27.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Potentilla stanjukoviczii	29 27.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Cortusa turkestanica	14 27.2	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Dracocephalum heterophyllum	21 26.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Silene graminifolia	43 25.9	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	6
Kobresia pamiroalaica	21 25.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Leontopodium ochroleucum	21 25.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Hordeum turkestanicum	29 25.3	. ---	. ---	12 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	6
Helictotrichon pubescens	36 25.1	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Aquilegia vicaria	14 24.6	. ---	. ---	12 4.2	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Primula olgae	29 24.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Aster serpentimontanus	29 24.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Phleum alpinum	43 23.5	. ---	. ---	. ---	. ---	18 10	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	9
Agrostis canina	29 23	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Linum atricalyx	29 21.6	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4

Group No.	1		2		3		4		5		6		7		8		9		10		11		12		13		14		15		16		17		18		19		Frequency
No. of relevés	14		4		17		17		10		17		17		7		2		1		36		4		17		14		13		4		4		17		29		
	Poion alpinae		*Ligulario thomsonii-Geranion regelii*												*Rheion maximowiczii*										*Scabioso songaricae-Phlomoidion lehmannianae*														
Koeleria macrantha	29	21.6	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	4
Ceratodon purpureus	57	21.5	.	---	.	---	24	5.8	.	---	.	---	29	7.3	29	---	.	---	.	---	.	---	.	---	.	---	.	---	8	---	.	---	.	---	6	---	.	---	21
Euphorbia alatavica	21	20.6	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Adenophora himalayana	21	20.6	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Kobresia capilliformis	14	20.5	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Community of *Allium hymenorhizum*																																							
Allium hymenorhizum	7	---	75	77.5	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	4
Euphorbia jaxartica	.	---	75	47.6	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Pedicularis grigorjevii	.	---	100	44.8	.	---	.	---	30	6.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	14	---	.	---	.	---	.	---	.	---	7	---	11
Eremogone griffithii	.	---	75	44	.	---	.	---	.	---	.	---	18	7	.	---	.	---	.	---	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	7
Nepeta podostachys	.	---	75	33	.	---	6	---	40	7.1	.	---	18	---	29	---	.	---	.	---	.	---	.	---	.	---	21	---	.	---	.	---	.	---	18	---	10	---	22
Astragalus saratagius	.	---	75	32.8	.	---	.	---	10	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	4
Asyneuma argutum	.	---	75	31.3	24	5.8	.	---	20	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	7	---	8	---	.	---	.	---	6	---	.	---	12
Ferula ovina	.	---	50	30.1	6	---	.	---	20	---	.	---	.	---	57	15.4	.	---	.	---	.	---	.	---	.	---	.	---	8	---	.	---	.	---	.	---	3	---	11
Phlomoides seravschanica	.	---	50	25.6	.	---	.	---	10	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	8	---	.	---	.	---	.	---	.	---	4
Rosa divina	.	---	50	24	6	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	7	---	.	---	.	---	.	---	.	---	10	4.8	7
Astragalus skorniakowii	.	---	25	23.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1
Angelica ternata	.	---	25	23.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1
Gypsophila cephalotes	.	---	25	23.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1
Asperula pamirica	.	---	25	23.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1
Polygonum coriarium	.	---	100	22.4	59	7.4	18	---	70	10.7	71	9.1	59	7	.	---	.	---	.	---	.	---	.	---	12	---	43	---	23	---	.	---	.	---	29	---	21	---	68
Cousinia pannosa	.	---	25	21.7	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	7	---	.	---	.	---	.	---	.	---	.	---	2
Cousinia outichaschensis	.	---	25	20.6	12	5	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Lomatocarpa albomarginata	.	---	25	20.6	6	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Ass. *Feruletum sumbuli*																																							
Ferula sumbul	.	---	.	---	59	66.7	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	10
Hedysarum flavescens	21	13.8	.	---	29	37.9	.	---	10	---	.	---	.	---	.	---	.	---	.	---	3	---	.	---	.	---	7	---	.	---	.	---	.	---	.	---	7	---	13
Ephedra intermedia	.	---	.	---	41	34	.	---	.	---	.	---	6	---	.	---	.	---	.	---	3	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	9
Thalictrum kuhistanicum	.	---	.	---	65	32.3	12	---	10	---	24	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	21	---	15	---	.	---	.	---	.	---	3	---	24
Asyneuma attenuatum	.	---	.	---	24	22	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	4
Euphorbia transoxana	.	---	.	---	29	21.7	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	5
Astragalus kabadianus	.	---	.	---	12	21.1	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Ass. *Heracleetum lehmannianii*																																							
Heracleum lehmannianum	7	---	.	---	6	---	65	58.7	.	---	18	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	10
Euphorbia lamprocarpa	.	---	.	---	.	---	24	38.9	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	4
Ranunculus brevirostris	7	---	.	---	.	---	41	36.4	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	9
Mentha asiatica	7	---	.	---	.	---	47	36	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	6	---	.	---	10
Trifolium pratense	.	---	.	---	6	---	71	34.3	.	---	18	---	.	---	.	---	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	12	---	.	---	20
Carum carvi	7	---	.	---	.	---	47	29.3	.	---	24	5.5	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	8	---	.	---	.	---	6	---	.	---	15
Cousinia pseudarctium	.	---	.	---	.	---	59	29.2	20	---	18	---	29	---	.	---	.	---	.	---	.	---	.	---	.	---	71	19.3	.	---	.	---	25	---	41	8.7	.	---	38
Nepeta cataria	.	---	.	---	.	---	18	27.5	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Convolvulus arvensis	.	---	.	---	.	---	35	26	.	---	6	---	.	---	43	---	.	---	.	---	31	---	.	---	.	---	.	---	15	---	.	---	25	---	65	---	7	---	37
Dactylis glomerata	.	---	.	---	6	---	59	25.3	.	---	71	19.9	.	---	.	---	.	---	.	---	.	---	.	---	.	---	7	---	.	---	50	---	.	---	53	5.8	10	---	38

Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	29	
	Poion alpinae	*Ligulario thomsonii-Geranion regelii*						*Rheion maximowiczii*					*Scabioso songaricae-Phlomoidion lehmannianae*							
Allium elatum	. ---	. ---	. ---	24 23	. ---	. ---	. ---	. ---	. ---	. ---	3 ---	. ---	. ---	7 ---	. ---	. ---	. ---	6 ---	. ---	7
Cynoglossum viridiflorum	. ---	. ---	. ---	18 23	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Lithospermum officinale	. ---	. ---	. ---	18 21.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	8 ---	. ---	. ---	. ---	10 ---	7
Poa pratensis	43 ---	. ---	. ---	76 20.3	40 ---	65 9.6	. ---	. ---	100 ---	. ---	11 ---	. ---	. ---	7 ---	23 ---	50 ---	75 ---	35 ---	3 ---	56
Ass. *Eremuretum kaufmannii*																				
Eremurus kaufmannii	. ---	. ---	. ---	. ---	40 47.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	3 ---	6
Dictamnus angustifolius	. ---	. ---	. ---	. ---	50 33.5	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	. ---	14 ---	8 ---	. ---	. ---	. ---	. ---	10
Lonicera nummulariifolia	. ---	. ---	. ---	. ---	20 30.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	8 ---	. ---	. ---	. ---	. ---	3
Restella albertii	. ---	. ---	. ---	. ---	20 27.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Poa urssulensis	. ---	25 ---	. ---	. ---	80 26.9	71 12.9	6 ---	. ---	. ---	. ---	3 ---	. ---	24 ---	14 ---	8 ---	. ---	. ---	6 ---	14 ---	35
Artemisia dracunculus	29 ---	25 ---	24 ---	6 ---	80 26.9	12 ---	. ---	. ---	. ---	100 ---	. ---	. ---	6 ---	. ---	31 ---	. ---	. ---	12 ---	3 ---	29
Paeonia intermedia	. ---	. ---	. ---	. ---	40 25.7	29 19.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	23 4.4	. ---	. ---	. ---	. ---	12
Iris hoogiana	. ---	. ---	. ---	. ---	30 24.4	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	4
Astragalus nuciferus	. ---	. ---	. ---	. ---	30 23.2	. ---	. ---	. ---	. ---	. ---	3 ---	. ---	. ---	. ---	8 ---	. ---	. ---	. ---	. ---	5
Ass. *Anthriscidetum glacialis*																				
Anthriscus glacialis	. ---	. ---	. ---	. ---	. ---	59 64.1	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	10
Elytrigia repens	. ---	. ---	. ---	12 ---	. ---	47 51.4	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 ---	. ---	16
Draba huetii	7 ---	. ---	. ---	. ---	. ---	29 40.1	. ---	. ---	. ---	. ---	14 ---	. ---	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	12
Picris nuristanica	. ---	. ---	12 ---	6 ---	. ---	35 38.9	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	7 ---	11
Crepis darvazica	. ---	. ---	. ---	. ---	. ---	53 35.1	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	9
Leonurus turkestanicus	. ---	. ---	. ---	. ---	. ---	41 30.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	14 ---	. ---	. ---	. ---	6 ---	. ---	10
Oberna wallichiana	. ---	. ---	. ---	6 ---	. ---	65 30.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	7 ---	. ---	. ---	. ---	6 ---	. ---	14
Tanacetum pseudachillea	. ---	. ---	6 ---	. ---	. ---	35 26.8	. ---	. ---	. ---	. ---	14 ---	. ---	. ---	. ---	. ---	. ---	. ---	18 ---	. ---	15
Euphorbia sarawschanica	. ---	. ---	. ---	. ---	. ---	53 25.4	. ---	. ---	. ---	. ---	3 ---	. ---	. ---	14 ---	8 ---	. ---	. ---	18 ---	7 ---	18
Astragalus aksuensis	. ---	. ---	. ---	. ---	. ---	41 25.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	7
Anemonastrum protractum	7 ---	. ---	. ---	. ---	. ---	24 24.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Rumex nepalensis	. ---	. ---	. ---	. ---	. ---	35 24.6	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	6
Asyneuma baldshuanicum	. ---	. ---	. ---	. ---	. ---	29 23.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Phleum pratense	. ---	. ---	. ---	12 ---	. ---	41 21.9	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	9
Pedicularis olgae	. ---	. ---	6 ---	. ---	. ---	53 21.1	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	15 ---	. ---	. ---	6 ---	. ---	13
Polygonum hissaricum	. ---	. ---	. ---	. ---	. ---	18 20.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	12 5	. ---	5
Ligularia alpigena	21 9.5	. ---	. ---	. ---	10 ---	29 20.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	7 ---	. ---	. ---	. ---	. ---	. ---	10
Nepeta formosa	. ---	. ---	. ---	. ---	. ---	35 20.4	. ---	. ---	. ---	. ---	. ---	. ---	. ---	7 ---	. ---	. ---	. ---	. ---	. ---	7
Community of *Cousinia batalinii* and *Euphorbia pamirica*																				
Euphorbia pamirica	. ---	. ---	. ---	6 ---	. ---	. ---	29 100.7	. ---	. ---	. ---	. ---	. ---	. ---	21 ---	. ---	. ---	. ---	. ---	7 ---	11
Cousinia batalinii	. ---	. ---	. ---	. ---	. ---	. ---	71 43.6	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	12
Eremopoa persica	. ---	. ---	. ---	12 ---	. ---	. ---	41 43.3	14 ---	. ---	. ---	. ---	. ---	. ---	14 ---	. ---	. ---	50 14.9	12 ---	3 ---	17
Tulipa dasystemon	. ---	. ---	. ---	. ---	. ---	. ---	12 29.1	. ---	. ---	. ---	3 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Astragalus lasiosemius	. ---	. ---	. ---	. ---	. ---	. ---	24 26.7	. ---	. ---	. ---	. ---	. ---	. ---	14 ---	. ---	. ---	. ---	. ---	14 ---	10
Piptatherum sogdianum	. ---	. ---	. ---	. ---	. ---	. ---	47 26.4	. ---	. ---	. ---	. ---	. ---	. ---	14 ---	. ---	. ---	. ---	. ---	3 ---	11
Ephedra gerardiana	. ---	. ---	. ---	. ---	. ---	. ---	24 24.7	. ---	. ---	. ---	. ---	. ---	. ---	7 ---	. ---	. ---	. ---	. ---	14 ---	9
Lappula badachschanica	. ---	. ---	. ---	. ---	. ---	. ---	41 24.3	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	7
Artemisia rutifolia	. ---	50 8.6	6 ---	. ---	. ---	. ---	41 23.6	29 ---	. ---	. ---	. ---	. ---	. ---	. ---	15 ---	. ---	. ---	6 ---	3 ---	16

Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	29	
	Poion alpinae	*Ligularia thomsonii-Geranion regelii*						*Rheion maximowiczii*					*Scabioso songaricae-Phlomoidion lehmannianae*							
Acantholimon parviflorum	. ---	. ---	. ---	. ---	. ---	. ---	29 22.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Tetrataenium olgae	. ---	. ---	. ---	. ---	. ---	. ---	18 21.9	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Scariola orientalis	. ---	. ---	29 8.5	. ---	. ---	. ---	41 21.6	. ---	. ---	. ---	. ---	. ---	. ---	14 ---	. ---	. ---	. ---	6 ---	. ---	15
Linaria sessilis	. ---	. ---	. ---	. ---	. ---	. ---	24 20.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Kudrjaschevia allotricha	. ---	. ---	. ---	. ---	. ---	. ---	29 20.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Ass. *Phlomoidetum kaufmannianae*																				
Phlomoides kaufmanniana	. ---	. ---	. ---	. ---	. ---	. ---	. ---	86 80.6	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	6
Bryum caespiticium	. ---	. ---	. ---	. ---	. ---	. ---	. ---	100 63.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	7
Perovskia virgata	. ---	. ---	. ---	. ---	. ---	. ---	. ---	71 56.2	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Neurotropis kotschyana	. ---	. ---	. ---	. ---	10 ---	. ---	. ---	29 47.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	12 ---	21 ---	11
Pohlia nutans	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	57 46.4	. ---	. ---	. ---	. ---	. ---	. ---	8 ---	. ---	. ---	6 ---	. ---	7
Encalypta vulgaris	. ---	. ---	. ---	6 ---	. ---	6 ---	. ---	86 45.8	. ---	. ---	. ---	. ---	. ---	. ---	8 ---	. ---	. ---	12 ---	. ---	11
Crambe kotschyana	. ---	. ---	. ---	. ---	. ---	. ---	. ---	57 37	. ---	. ---	. ---	. ---	. ---	14 4.1	. ---	. ---	. ---	. ---	. ---	6
Eremurus soogdianus	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 35.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Scandix stellata	. ---	. ---	. ---	. ---	. ---	. ---	. ---	57 34.4	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Piptatherum kokanicum	. ---	. ---	. ---	. ---	. ---	. ---	. ---	57 33.4	. ---	. ---	8 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	7 ---	9
Papaver pavoninum	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	71 33.4	. ---	. ---	. ---	50 11.4	. ---	. ---	. ---	. ---	. ---	. ---	10 ---	11
Lindelofia macrostyla	. ---	. ---	. ---	12 ---	. ---	. ---	18 ---	57 33.1	. ---	. ---	11 ---	. ---	. ---	. ---	. ---	50 12	25 ---	6 ---	10 ---	20
Alcea nudiflora	. ---	. ---	. ---	. ---	. ---	. ---	. ---	57 30.5	. ---	. ---	25 ---	25 ---	. ---	7 ---	8 ---	. ---	. ---	12 ---	. ---	18
Crepis pulchra	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	57 28.9	. ---	100 ---	17 ---	. ---	. ---	7 ---	. ---	. ---	. ---	. ---	3 ---	14
Tortula muralis	. ---	. ---	. ---	. ---	. ---	. ---	35 15.1	57 27.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	10
Boissiera squarrosa	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 25.5	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Taeniatherum crinitum	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 25.5	. ---	. ---	3 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Erodium cicutarium	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 25	. ---	. ---	8 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Bunium persicum	. ---	. ---	12 ---	6 ---	. ---	. ---	. ---	71 23.2	. ---	. ---	44 ---	. ---	. ---	21 ---	. ---	50 ---	. ---	12 ---	3 ---	32
Nardurus krausei	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 23	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Bromus danthoniae	. ---	. ---	. ---	. ---	. ---	. ---	. ---	57 22.5	50 16.7	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3 ---	6
Anisantha tectorum	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	43 21.1	. ---	. ---	. ---	25 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Scrophularia scabiosifolia	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 20.2	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Valerianella ovczinnikovii	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 20.2	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Ass. *Phlomoidetum tadschikistanicae*																				
Phlomoides tadshikistanica	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	100 92	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Amoria repens	36 10.4	. ---	12 ---	41 ---	30 ---	24 ---	. ---	. ---	100 52.3	. ---	8 ---	. ---	. ---	. ---	8 ---	. ---	25 ---	6 ---	. ---	29
Ranunculus muricatus	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	100 47.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Phlomoides canescens	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	100 37.9	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	2
Medicago sativa	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	100 33.1	. ---	25 ---	. ---	6 ---	. ---	. ---	50 15.3	. ---	35 3.6	7 ---	22
Trichodesma incanum	. ---	. ---	. ---	. ---	. ---	. ---	6 ---	14 ---	100 30.7	. ---	. ---	. ---	. ---	. ---	. ---	25 ---	. ---	. ---	. ---	5
Achillea biebersteinii	. ---	. ---	. ---	. ---	10 ---	. ---	. ---	. ---	100 25.1	. ---	33 ---	. ---	6 ---	7 ---	15 ---	50 ---	. ---	12 ---	14 ---	27
Hedysarum denticulatum	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	50 23.6	. ---	3 ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	4
Geranium divaricatum	. ---	. ---	. ---	. ---	. ---	. ---	6 ---	29 11.3	50 21.2	. ---	3 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	5
Community of *Senecio saposhnikovii*																				
Senecio saposhnikovii	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	100 88.4	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	1
Anaphalis racemifera	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	100 47.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	1

Group No.	1		2		3		4		5		6		7		8		9		10		11		12		13		14		15		16		17		18		19		Frequency
No. of relevés	14		4		17		17		10		17		17		7		2		1		36		4		17		14		13		4		4		17		29		
	Poion alpinae		*Ligularia thomsonii-Geranion regelii*												*Rheion maximowiczii*										*Scabioso songaricae-Phlomoidion lehmannianae*														
Cirsium badakhschanicum	.	---	.	---	.	---	18	---	.	---	12	---	.	---	.	---	.	---	100	47.2	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	6
Dracocephalum diversifolium	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	100	37.9	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1
Thalictrum isopyroides	.	---	.	---	.	---	.	---	.	---	.	---	6	---	.	---	.	---	100	35.3	.	---	.	---	.	---	.	---	8	---	.	---	.	---	.	---	.	---	3
Gentianella turkestanorum	21	6.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	100	33.4	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	4
Cotoneaster nummularioides	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	100	33.3	14	2.8	.	---	.	---	7	---	.	---	.	---	.	---	.	---	.	---	7
Berberis heterobotrys	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	100	32.5	.	---	25	---	.	---	.	---	.	---	.	---	.	---	.	---	7	---	4
Thymus proximus	14	11.6	.	---	.	---	.	---	10	---	.	---	.	---	.	---	.	---	100	26.7	.	---	.	---	.	---	.	---	15	3	.	---	.	---	.	---	.	---	6
Artemisia santolinifolia	.	---	.	---	6	---	.	---	.	---	.	---	6	---	14	---	.	---	100	23.2	.	---	50	17.7	.	---	.	---	.	---	.	---	.	---	.	---	14	1.5	10
Ass. *Eremuretum stenophyllido-comosi*																																							
Exochorda korolkowii	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	28	39.9	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	10
Eremurus comosus	.	---	50	---	.	---	.	---	.	---	6	---	.	---	57	6.4	100	15.3	.	---	69	34.9	.	---	6	---	7	---	.	---	50	---	.	---	12	---	17	---	45
Rosa ovczinnikovii	.	---	.	---	24	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	56	29.7	.	---	6	---	57	---	.	---	25	---	.	---	29	---	45	12.7	53
Ferula transiliensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	33	27.6	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	12
Colutea paulsenii	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	25	26.2	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	9
Rosa popovii	.	---	.	---	.	---	.	---	10	---	.	---	.	---	.	---	.	---	.	---	39	26.2	.	---	12	---	.	---	.	---	.	---	.	---	.	---	14	---	21
Berberis nummularia	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	19	24.3	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	8
Eremurus stenophyllus	.	---	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	64	22.3	.	---	.	---	.	---	.	---	25	---	.	---	6	---	.	---	26
Community of *Inula macrophylla*																																							
Inula macrophylla	.	---	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	100	87.6	.	---	.	---	.	---	.	---	.	---	.	---	3	---	7
Microthlaspi perfoliatum	.	---	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	39	---	50	62.1	.	---	.	---	8	---	25	---	.	---	.	---	.	---	19
Convolvulus pseudocantabrica	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	100	60.6	.	---	.	---	.	---	.	---	.	---	.	---	.	---	5
Bromus oxyodon	.	---	.	---	12	---	.	---	10	---	12	---	6	---	.	---	.	---	100	---	.	---	100	56.4	6	---	36	1.8	.	---	.	---	.	---	12	---	.	---	19
Stubendorffia orientalis	.	---	.	---	.	---	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	50	55.4	.	---	.	---	.	---	.	---	.	---	6	---	.	---	4
Serratula lyratifolia	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	75	55.2	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Delphinium biternatum	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	47.4	.	---	.	---	8	---	.	---	.	---	.	---	14	---	7
Eremurus tianschanicus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	43.6	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Galium pamiroalaicum	36	14.8	.	---	6	---	.	---	10	---	6	---	.	---	.	---	.	---	.	---	.	---	50	36.1	12	---	.	---	.	---	.	---	.	---	6	---	7	---	15
Stipa caucasica	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	6	---	50	34.8	6	---	21	---	.	---	.	---	.	---	.	---	7	---	11
Astragalus sieversianus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	75	34.5	6	---	.	---	8	---	25	---	.	---	6	---	3	---	9
Carex turkestanica	21	---	.	---	.	---	.	---	40	---	6	---	.	---	14	---	.	---	.	---	39	---	100	33.8	71	11.3	14	---	23	---	50	---	.	---	18	---	83	12.1	73
Eremurus turkestanicus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	33.7	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Artemisia ferganensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	33.7	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Eulophus ferganensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	33.7	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Astragalus alopecias	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	30.4	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Perovskia abrotanoides	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	30.4	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Artemisia glanduligera	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	30.4	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Spiraea hypericifolia	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	30.1	.	---	.	---	8	---	.	---	.	---	.	---	3	---	4
Haplophyllum acutifolium	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	28.2	6	---	.	---	.	---	.	---	.	---	.	---	.	---	3
Silene brahuica	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	27.4	18	8.7	14	---	.	---	.	---	.	---	.	---	14	---	12
Stipa kazachstanica	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	26.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Spiraea pilosa	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	26.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Tulipa bifloriformis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	26.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2
Achnatherum caragana	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	26.6	18	5.9	.	---	.	---	.	---	.	---	.	---	.	---	5

Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	29	
	Poion alpinae	*Ligulario thomsonii-Geranion regelii*						*Rheion maximowiczii*					*Scabioso songaricae-Phlomoidion lehmannianae*							
Alyssum calycinum	. ---	. ---	. ---	. ---	. ---	. ---	. ---	57 16	. ---	. ---	3 ---	75 26.5	. ---	. ---	. ---	50 13.7	. ---	12 ---	24 ---	19
Carex pachystylis	. ---	. ---	. ---	. ---	. ---	. ---	. ---	14 ---	. ---	. ---	6 ---	50 25.3	29 9.2	. ---	15 ---	. ---	. ---	18 ---	17 ---	20
Scutellaria przewalskii	7 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	50 24.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3
Dianthus tetralepis	. ---	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	50 24.3	. ---	7 ---	8 ---	. ---	. ---	. ---	3 ---	6
Hyalolaena trichophylla	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	25 23.8	. ---	. ---	. ---	. ---	. ---	. ---	. ---	1
Leptorhabdos parviflora	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	8 ---	50 22.5	29 13	14 ---	. ---	. ---	. ---	. ---	10 ---	15
Impatiens parviflora	. ---	. ---	. ---	12 ---	10 ---	. ---	. ---	14 ---	. ---	. ---	19 ---	50 21.6	. ---	. ---	15 ---	. ---	. ---	. ---	. ---	15
Ass. *Stipetum margelanicae*																				
Carex dimorphotheca	7 ---	. ---	. ---	. ---	. ---	35 17.6	12 ---	. ---	. ---	. ---	. ---	. ---	59 69.6	. ---	8 ---	. ---	50 ---	. ---	. ---	22
Stipa margelanica	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	65 61.1	. ---	. ---	. ---	. ---	. ---	. ---	11
Astragalus mucidus	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	76 47.1	. ---	. ---	. ---	. ---	. ---	10 ---	16
Scabiosa songarica	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	25 ---	75 7.4	94 33.9	43 ---	. ---	25 ---	. ---	29 ---	66 19.6	60
Allium barsczewskii	. ---	. ---	12 ---	. ---	. ---	6 ---	18 ---	. ---	. ---	. ---	22 ---	25 ---	53 31.2	29 ---	8 ---	25 ---	. ---	18 ---	17 ---	38
Astragalus krauseanus	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	59 28.8	. ---	. ---	. ---	. ---	12 ---	. ---	12
Cousinia mulgediifolia	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	41 22.3	. ---	. ---	. ---	. ---	6 ---	7 ---	10
Ferula violacea	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	18 21.8	. ---	8 ---	. ---	. ---	. ---	. ---	4
Astragalus filicaulis	. ---	. ---	. ---	. ---	10 ---	. ---	. ---	. ---	. ---	. ---	8 ---	. ---	24 20.5	. ---	. ---	. ---	. ---	. ---	3 ---	9
Poa bulbosa	. ---	. ---	24 ---	47 ---	50 ---	35 ---	29 ---	29 ---	100 ---	. ---	64 ---	75 ---	100 20.3	43 ---	69 ---	100 ---	100 ---	76 6.3	72 8.8	132
Ass. *Lathyretum mulkaki*																				
Lathyrus mulkak	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	29 44.7	. ---	. ---	. ---	. ---	. ---	4
Lophanthus elegans	. ---	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	. ---	. ---	. ---	. ---	. ---	21 24.8	. ---	. ---	. ---	. ---	. ---	4
Iris darwasica	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	3 ---	. ---	. ---	36 22.6	. ---	. ---	. ---	. ---	. ---	6
Nepeta olgae	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	14 20.9	8 ---	. ---	. ---	. ---	. ---	3
Ass. *Potentillo orientalis-Eremuretum fusci*																				
Eremurus fuscus	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	54 66.4	. ---	. ---	. ---	. ---	7
Veronica arguteserrata	. ---	. ---	. ---	12 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	38 39.3	. ---	. ---	. ---	. ---	7
Eremurus brachystemon	. ---	. ---	. ---	. ---	10 ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	31 37.3	. ---	. ---	. ---	. ---	5
Scorzonera tadshikorum	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	15 35.1	. ---	. ---	. ---	7 ---	4
Gymnospermium albertii	. ---	. ---	. ---	. ---	40 30.3	. ---	. ---	. ---	. ---	. ---	3 ---	. ---	. ---	7 ---	54 31.3	. ---	. ---	. ---	. ---	13
Ass. *Hordeo bulbosi-Astragaletum retamocarpi*																				
Astragalus retamocarpus	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	6 ---	. ---	. ---	100 89.7	. ---	. ---	. ---	5
Hypericum perforatum	. ---	. ---	. ---	29 19.2	. ---	6 ---	. ---	. ---	. ---	. ---	36 ---	. ---	. ---	7 ---	. ---	100 55.5	25 ---	24 ---	3 ---	30
Medicago rigidula	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	17 4.3	. ---	. ---	. ---	. ---	100 47.6	. ---	. ---	. ---	10
Hordeum bulbosum	. ---	. ---	. ---	18 ---	. ---	. ---	. ---	. ---	. ---	. ---	31 ---	25 ---	. ---	. ---	. ---	100 42	. ---	29 11.8	. ---	24
Aegilops triuncialis	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	75 41.4	. ---	. ---	. ---	3
Crupina vulgaris	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	19 ---	. ---	. ---	7 ---	. ---	75 39.1	. ---	6 ---	3 ---	13
Buglossoides arvensis	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	25 ---	. ---	. ---	. ---	. ---	50 34.3	. ---	. ---	. ---	11
Ferula gigantea	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	50 33.7	. ---	. ---	. ---	2
Medicago orbicularis	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	50 33.7	. ---	. ---	. ---	2
Rochelia cardiosepala	. ---	. ---	. ---	6 ---	10 ---	12 ---	. ---	. ---	. ---	. ---	17 ---	. ---	18 ---	14 ---	. ---	100 32.8	50 ---	18 ---	48 ---	38
Elaeosticta allioides	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	14 ---	. ---	41 10	7 ---	. ---	100 32.1	. ---	. ---	14 ---	21
Vicia angustifolia	. ---	. ---	. ---	12 ---	. ---	. ---	. ---	. ---	. ---	. ---	11 ---	. ---	. ---	. ---	. ---	50 29.2	. ---	12 ---	. ---	10
Tragopogon capitatus	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	. ---	50 26.8	. ---	. ---	. ---	2

Group No.	1		2		3		4		5		6		7		8		9		10		11		12		13		14		15		16		17		18		19		Frequency
No. of relevés	14		4		17		17		10		17		17		7		2		1		36		4		17		14		13		4		4		17		29		
	Poion alpinae		*Ligulario thomsonii-Geranion regelii*												*Rheion maximowiczii*										*Scabioso songaricae-Phlomoidion lehmannianae*														
Tulipa subquinquefolia	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	.	---	.	---	.	---	.	---	50	26	.	---	.	---	.	---	3
Pseudohandelia umbellifera	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	25.8	.	---	.	---	3	---	3
Elaeosticta hirtula	.	---	.	---	.	---	24	---	10	---	18	---	12	---	.	---	.	---	.	---	33	---	.	---	24	---	14	---	.	---	100	25.7	.	---	59	9.5	41	---	54
Echium biebersteinii	.	---	.	---	.	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	24.3	.	---	.	---	.	---	3
Medicago denticulata	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	.	---	.	---	.	---	.	---	25	21.9	.	---	.	---	.	---	2
Ass. *Eremuretum robusti*																																							
Eremurus robustus	.	---	.	---	.	---	.	---	.	---	24	2.3	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	15	---	.	---	.	---	53	46.4	10	---	18
Phlomoides arctifolia	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	7	---	.	---	.	---	.	---	29	31.6	14	12.1	10
Vicia tenuifolia	.	---	.	---	29	---	35	12.7	.	---	24	---	.	---	.	---	.	---	.	---	.	---	25	---	.	---	.	---	8	---	25	---	25	---	41	30.5	21	---	32
Cousinia umbrosa	.	---	.	---	.	---	.	---	30	6.8	18	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	15	---	25	---	.	---	41	26.1	17	---	21
Ass. *Phlomoido lehmannianae-Onobrychidetum grandis*																																							
Phlomoides lehmanniana	.	---	.	---	.	---	.	---	10	---	12	---	.	---	.	---	.	---	.	---	28	---	.	---	12	---	14	---	.	---	50	---	.	---	24	---	62	37.3	41
Onobrychis grandis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	.	---	12	---	21	---	.	---	.	---	.	---	.	---	45	34.8	19
All. *Ligulario thomsonii-Geranion regelii*																																							
Ligularia thomsonii	29	---	.	---	65	8.2	59	---	70	22.5	94	24.9	.	---	.	---	100	---	100	---	.	---	.	---	.	---	7	---	.	---	.	---	.	---	24	---	7	---	58
Geranium regelii	86	32.3	50	---	47	1.1	41	3.6	40	---	59	19.4	.	---	.	---	100	6.3	.	---	.	---	.	---	.	---	.	---	15	---	.	---	.	---	6	---	.	---	48
Centaurea ruthenica	.	---	25	---	35	13.7	.	---	10	---	6	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	64	---	15	---	.	---	.	---	12	---	28	2.4	30
Galium turkestanicum	43	21.5	.	---	.	---	29	9.7	20	---	6	---	.	---	.	---	.	---	100	---	8	---	.	---	.	---	.	---	.	---	.	---	.	---	6	---	.	---	19
Myosotis alpestris	.	---	.	---	.	---	.	---	30	21.9	53	27.1	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	12
Potentilla sericea	.	---	75	20.3	.	---	.	---	.	---	53	26.5	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	12
Linum olgae	21	18.8	25	---	.	---	.	---	10	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	6
Fritillaria regelii	.	---	.	---	.	---	.	---	.	---	24	16.5	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	15	7.7	.	---	.	---	.	---	.	---	6
All. *Rheion maximowiczii*																																							
Plantago lanceolata	.	---	.	---	.	---	59	7.1	.	---	18	---	.	---	.	---	100	37.9	.	---	56	---	.	---	.	---	.	---	31	---	75	20.3	25	---	53	4	3	---	53
Ferula kokanica	.	---	.	---	.	---	.	---	.	---	.	---	53	24.7	29	---	.	---	.	---	.	---	.	---	.	---	71	32.8	46	16.2	.	---	.	---	6	---	28	8.7	36
Rheum maximowiczii	.	---	.	---	.	---	.	---	10	---	.	---	35	29.1	.	---	.	---	.	---	14	---	25	---	.	---	43	2.4	.	---	.	---	.	---	.	---	14	---	23
Poterium polygamum	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	50	22.1	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	18
Bunium badachschanicum	.	---	.	---	.	---	.	---	.	---	.	---	24	20.8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	4
All. *Scabioso songaricae-Phlomoidion lehmannianae*																																							
Ferula kuhistanica	.	---	.	---	.	---	18	---	.	---	53	11.8	.	---	.	---	.	---	.	---	22	---	.	---	18	---	43	---	15	---	50	---	75	---	59	14.4	66	19.8	65
Gentiana olivieri	.	---	.	---	.	---	.	---	10	---	24	---	.	---	.	---	.	---	.	---	25	---	.	---	35	13.7	14	---	.	---	50	---	.	---	12	---	34	6.3	36
Rumex paulsenianus	.	---	.	---	6	---	12	---	10	---	6	---	.	---	.	---	100	22	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	41	21	7	---	16
Solenanthus circinnatus	.	---	.	---	6	---	12	---	10	---	24	3.9	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	29	6.6	3	---	14
Poterium lasiocarpum	.	---	.	---	.	---	24	9.2	.	---	.	---	.	---	29	13.3	.	---	.	---	3	---	.	---	.	---	.	---	.	---	.	---	.	---	18	8.2	.	---	10
Rochelia peduncularis	.	---	.	---	.	---	.	---	.	---	.	---	12	---	.	---	.	---	.	---	.	---	.	---	6	---	7	---	.	---	.	---	25	---	.	---	17	2.8	10
Onobrychis baldshuanica	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	8	---	.	---	12	14.2	.	---	.	---	.	---	.	---	.	---	.	---	5
O. *Ferulo kuhistanicae-Prangetalia pabulariae*																																							
Prangos pabularia	.	---	.	---	.	---	.	---	50	---	6	---	35	---	.	---	.	---	.	---	47	---	50	---	100	24.6	71	---	23	---	100	5	25	---	53	---	83	20.9	99
Origanum tyttanthum	.	---	.	---	.	---	18	---	.	---	.	---	.	---	.	---	50	---	.	---	64	---	50	---	.	---	21	---	38	---	.	---	.	---	6	---	14	---	42
Potentilla transcaspia	.	---	.	---	.	---	12	---	10	---	29	---	.	---	.	---	.	---	.	---	3	---	.	---	6	---	.	---	8	---	50	---	50	---	35	---	7	---	23

quent representatives including *Rochelia cardiosepala*, *Polygonum paronychioides*, *P. polycnemoides*, *Rheum maximowiczii* or *Poterium polygamum*. Additionally, a number of thermophilous shrubs were detected with *Lonicera nummulariifolia*, *Cousinia batalinii*, *Cerasus verrucosa* or *Crataegus remotilobata* as the most frequent. There are also species originating in juniper woods, such as *Juniperus seravschanica* or *Lonicera olgae*. It is worth noticing that the species list of the tall-forb vegetation of Middle Asia also includes a number of taxa of open, ruderal habitats (e.g. *Convolvulus arvensis*, *Potentilla orientalis*), mesophilous forests (*Impatiens parviflora*, *Asyneuma argutum*, *A. baldshuanicum*) or steppes (*Gentiana olivierii*, *Bunium persicum* or *Hordeum bulbosum*).

As a result of the TWINSPAN classification, three main groups at the alliance level have been distinguished within the tall-forb vegetation (Figure 2). Additionally, one group was assigned to alpine meadows and left rankless for further studies (comm. *Phlomoides oreophila*). The NMDS diagram clearly showed a distinction between three main tall-forb types and vegetation classified as alpine meadows (Figure 3). The most diverse alliance includes dry tall-forb communities of the subhumid zone of the eastern Irano-Turanian region, which occur within the complex of vast pasturelands (steppes and pseudosteppes). This group (*Scabioso songaricae-Phlomoidion lehmannianae*) includes the highest number of distinct communities with typical tall-forbs (e.g. *Eremuretum robusti* or *Phlomoido lehmannianae-Onobrychidetum grandis*) or communities transitional towards grasslands (e.g. *Stipetum margelanicae* or *Potentillo orientalis-Eremuretum fusci*). A very distinguishable type of tall-forb vegetation in Middle Asia are the communities on scree-like habitats. They inhabit gentle slopes with deep, nutrient-rich soil, but are covered by rock debris. In this type of tall-forb vegetation, representative of the *Prangetea ulopterae* known from Iran, we defined five communities (e.g. *Phlomoidetum kaufmannianae* and *Eremuretum stenophyllido-comosi*) and include them in the newly coined alliance *Rheion maximowiczii*. The last group, shown on the left part of the TWINSPAN diagram, covers the mesophilous tall-forb communities of the western Pamir-Alai Mountains with very distinct communities such as *Feruletum sumbuli*, *Heracleetum lehmannianii*, *Eremuretum kaufmannii* and *Anthriscidetum glacialis*. They are included in the new alliance *Ligulario thomsonii-Geranion regelii*.

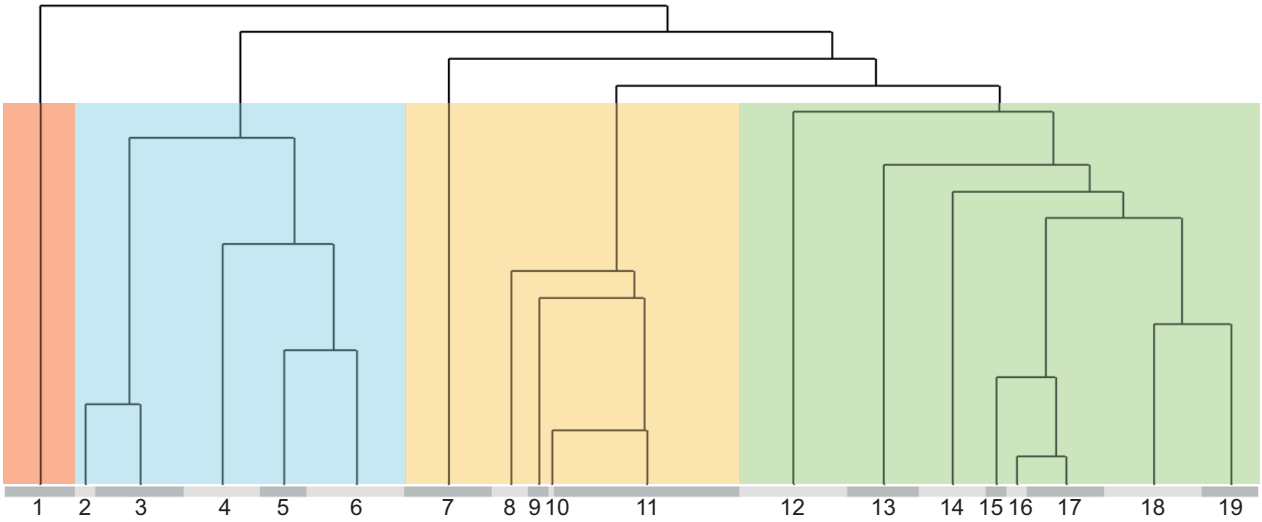

Figure 2. Dendrogram illustrating the assigment of relevé groups identified by TWINSPAN to particular syntaxonomic units (see Syntaxonomic synopsis). The different background colors refer to alliances: red – *Poion alpinae*, blue – *Ligulario thomsonii-Geranion regelii*, orange – *Rheion maximowiczii* and green – *Scabioso songaricae-Phlomoidion lehmannianae*.

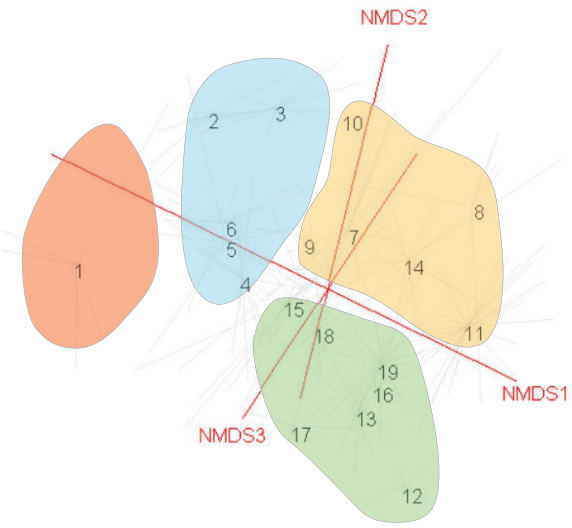

Figure 3. NMDS ordination of tall-forb communities in the Pamir-Alai and western Tian-Shan Mountains. The different envelopes colors refer to alliances: red – *Poion alpinae*, blue – *Ligulario thomsonii-Geranion regelii*, orange – *Rheion maximowiczii* and green – *Scabioso songaricae-Phlomoidion lehmannianae*. Numbers on ordination refer to centroids of clusters (see Syntaxonomic synopsis).

Classification of the vegetation units

As a result of our classification analysis, 19 well-defined plant communities were distinguished according to species composition (Figure 2). As our study pioneers research in the area, we chose not to apply any refinements in the classification by moving some relevés between clusters using iterative relocation methods or deletion of any outliers. With insufficient field experience to identify atypical or fragmentary stands, we believe that our approach is the most justified. Distribution maps of all tall-forb types within the study area are presented in Figure 4. Environmental and vegetation parameters are presented in Figure 5 and photographs of selected communities are presented on Figures 6 and 7.

Syntaxonomic synopsis

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* (cluster 1)

Irano-Turanian thermophilous, mesic tall-forb communities of the western Pamir-Alai and Tian Shan Mountains

Class: *Prangetea ulopterae* Klein 1987
2. Order: to be described

Forb rich mesophilious tall-forb communities of the western Pamir-Alai Mountains

2.1. Alliance: *Ligulario thomsonii-Geranion regelii* Nowak et al. all. nov. prov.
   2.1.1. Community of *Allium hymenorhizum* (cluster 2)
   2.1.2. *Feruletum sumbuli* Nowak et al. 2015 (cluster 3)
   2.1.3. *Heracleetum lehmannianii* Nowak et al. ass. nov. prov. (cluster 4)
   2.1.4. *Eremuretum kaufmannii* Nowak et al. ass. nov. prov. (cluster 5)
   2.1.5. *Anthriscidetum glacialis* Nowak et al. 2020 ass. nov. prov. (cluster 6)

Scree-like tall-forb communities of the eastern Irano-Turanian region

2.2. Alliance: *Rheion maximowiczii* Nowak et al. all. nov. prov.
   2.2.1. Community of *Cousinia batalinii* and *Euphorbia pamirica* (cluster 7)
   2.2.2. *Phlomoidetum kaufmannianae* Nowak et al. ass. nov. prov. (cluster 8)
   2.2.3. *Eremostachyetum tadshikistanicae* Nowak et al. 2016 (cluster 9)
   2.2.4. Community of *Senecio saposhnikovii* (cluster 10)
   2.2.5. *Eremuretum stenophyllido-comosi* Nowak et al. ass. nov. prov. (cluster 11)

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. prov.
   2.3.1. Community of *Inula macrophylla* (cluster 12)
   2.3.2. *Stipetum margelanicae* Nowak et al. 2016 (cluster 13)
   2.3.3. *Lathyretum mulkaki* Nowak et al. ass. nov. prov. (cluster 14)
   2.3.4. *Potentillo orientalis-Eremuretum fusci* S. Świerszcz et al. 2020 (cluster 15)
   2.3.5. *Hordeo bulbosi-Astragaletum retamocarpi* S. Świerszcz et al. 2020 (cluster 16)
   2.3.6. Community of *Ferula kuhistanica* (cluster 17)
   2.3.7. *Eremuretum robusti* Nowak et al. ass. nov. prov. (cluster 18)
   2.3.8. *Phlomoido lehmannianae-Onobrychidetum grandis* Nowak et al. ass. nov. prov. (cluster 19)

Mesic mown and grazed subalpine meadows and pastures on fertile soils

1.1.1. Community of *Phlomoides oreophila* (cluster 1)

Diagnostic species: *Alchemilla bungei*, *Astragalus alpinus*, *Aulacospermum simplex*, *Caragana jubata*, *Cerastium tianschanicum*, *Festuca alatavica*, *Geranium regelii*, *Myosotis asiatica*, *Pedicularis ludwigii*, *Phlomoides oreophila*, *Poa alpina*, *Thalictrum foetidum*, *Valeriana dubia*, *Veronica porphyriana*
Constant species: *Geranium regelii*, *Phlomoides oreophila*
Dominant species: *Phlomoides oreophila*
Floristic and habitat characteristics: We recorded plots of this association in the alpine belt of Kyrgyz and Talas Ranges in Kyrgyzstan (Figure 4). It was found between 2,100 and 3,500 m a.s.l. (mean approx. 2,750, Figure 5a). It occupies gently sloping mountains on a vast territory making up the sheep pastures. It grows on fertile, deep and well hydrated soils, often with a close relationship to mire vegetation with *Primula auriculata*, *P. olgae*, or the alpine windswept matts of *Kobresia pamiroalaica*. The plots have dense cover and a typical forb luxuriance with the average vegetation cover over 90% (Figure 5d). The association is fairly species rich, with a mean of 26 species per plot (ranging from 13 to 37; Figure 5f). The community is intensively grazed by sheep and sporadically goats. Due to scarse sampling we left this community rankless and plan to collect supplementary data from pasturelands of Kyrgyzstan.

Irano-Turanian thermophilous, mesic tall-forb communities of the Pamir-Alai and Tian Shan Mountains

For the eastern territories of the Irano-Turanian region, a distinct group of communities within the forb vege-

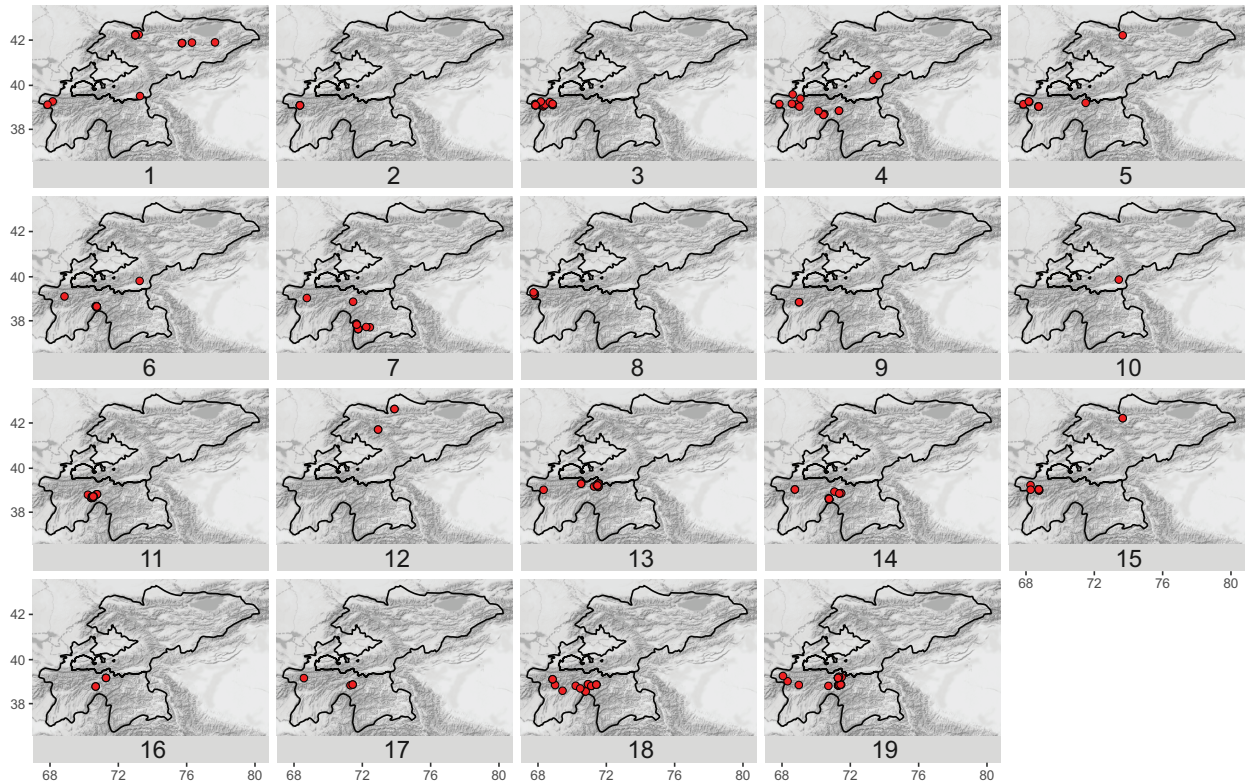

Figure 4. Distribution of relevés assigned to the particular vegetation units (n = 244). The name of syntaxon (1–19) are written in the Syntaxonomic synopsis.

tation of *Prangetea ulopterae* Klein 1978 dominated by typical Middle Asian species such as *Prangos pabularia*, *Ferula kuhistanica*, *F. kokanica*, *Aponogeton coriarium* and *A. songaricum* should be defined. This type of vegetation occurs throughout the Pamiro-Alai and the western and southern Tian Shan. It inhabits fertile soils, mainly in the alpine belt. They vary according to the type of habitat, in particular the inclination of the slope and the presence of stones in the substrate. In particular, the forb vegetation of the *Rheion* alliance occupies places with the topsoil covered with unstable rocks, creating a characteristic "fertile scree" vegetation. This tall-forb vegetation is most often used extensively as pastures for sheep and goats, less often for horses and yaks.

Forb rich mesophilious tall-forb communities of the western Pamir-Alai Mountains

2.1. Alliance: *Ligulario thomsonii-Geranion regelii* Nowak et al. all. nov. prov.

These tall-forb communities grow mainly in the alpine belt of the western Pamir-Alai ranges on deep and humid fertile soils with calcareous bedrock. They form a luxuriant vegetation on slopes and flat lands. Only *Heracleetum lehmannianii* is apparently restricted to river sides and occasionally slope water outflows. The composition of this vegetation is clearly determined by large forbs, with the high share of *Geranium* sp., *Phlomoides* sp., *Polygonum* sp., *Eremurus* sp., *Anthriscus* sp. and *Nepeta* sp.

Diagnostic taxa: *Ligularia thomsonii*, *Centaurea ruthenica*, *Fritillaria regelii*, *Geranium regelii*, *Galium turkestanicum*, *Myosotis alpestris*, *Potentilla sericea*

2.1.1. Community of *Allium hymenorhizum* (cluster 2)

Diagnostic species: *Allium hymenorhizum*, *Lomatocarpa albomarginata*, *Angelica ternata*, *Asperula pamirica*, *Astragalus saratagius*, *A. skorniakowii*, *Asyneuma argutum*, *Cousinia outichaschensis*, *C. pannosa*, *Eremogone griffithii*, *Euphorbia jaxartica*, *Ferula ovina*, *Gypsophila cephalotes*, *Nepeta podostachys*, *Pedicularis grigorjevii*, *Phlomoides seravschanica*, *Polygonum coriarium*, *Rosa divina*
Constant species: *Allium hymenorhizum*, *Eremogone griffithii*, *Nepeta podostachys*, *Pedicularis grigorjevii*, *Polygonum coriarium*
Dominant species: *Allium hymenorhizum*, *Linum olgae*
Floristic and habitat characteristics: The stands of *Allium hymenorhizum* occur in different habitats in terms of environmental conditions, particularly humidity. It generally prefers organic, well watered soils, sometimes in contact with typical fens, but generally inhabits slopes with typical tall-forb, meadow-like or even grassy vegetation across the whole Tajikistan. Due to this uncertainty and the small sample number, we leave this community rankless. Patches of this vegetation were found in the alpine belt at the average elevation of ca. 2,800 m a.s.l. (between 2,700 – 2,850 m a.s.l., Figure 5a). It inhabits gently slopes with 5° to 15° inclination (average 11°) and northern aspects. The plots were moderately rich in species with the average of

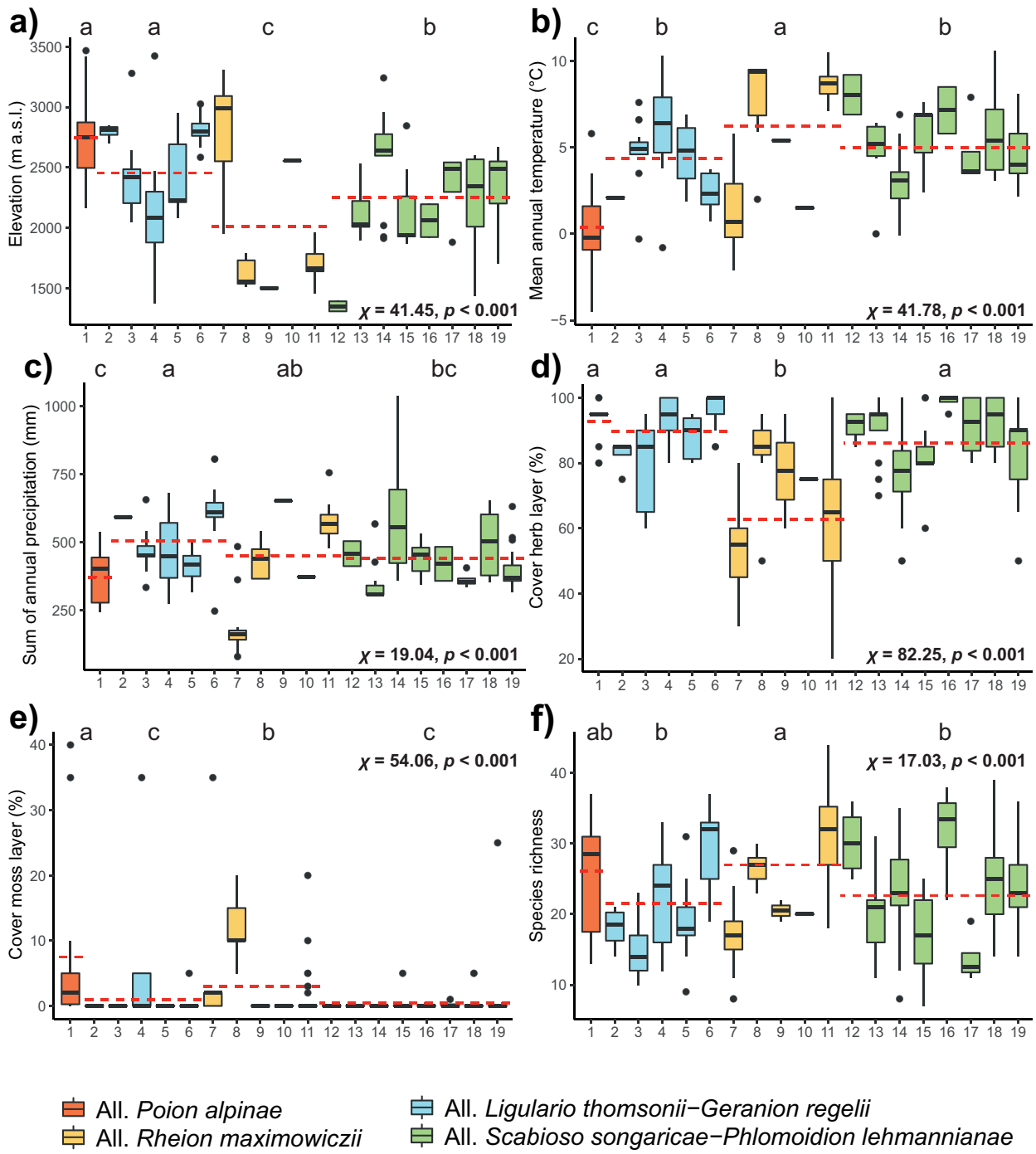

Figure 5. Boxplots showing median (line), quartiles, outliers and the range of (a) elevation, (b) mean annual temperature, (c) sum of annual precipitation, (d) cover of herb layer, (e) cover of moss layer and (f) species richness for particular syntaxonomic units. Red line indicates mean values of alliances. The values of χ^2 and p for statistical tests for vegetation groups are shown. Different letters indicate significant differences among the alliances. The abbreviations of the syntaxonomic units are explained in the Syntaxonomic synopsis.

ca. 18 taxa per plot (ranging from 14 to 21; Figure 5f). The community has high vegetation cover reaching up to 85% (Figure 5d). This tall-forb vegetation is extensively grazed by sheep and, sporadically, goats.

2.1.2. *Feruletum sumbuli* Nowak et al. 2015 (cluster 3)

Diagnostic species: *Astragalus kabadianus*, *Asyneuma attenuatum*, *Ephedra intermedia*, *Euphorbia transoxana*, *Ferula sumbul*, *Hedysarum flavescens*, *Thalictrum kuhistanicum*

Constant species: *Ferula sumbul*, *Hedysarum flavescens*

Dominant species: *Ferula sumbul*, *Hedysarum flavescens*

Floristic and habitat characteristics: *Ferula sumbul* is an endemic plant of the western Pamir-Alai occurring in Tajikistan preferably in the Zeravshan and Funn Ranges (Nowak et al. 2020a). Occasionally, it occurs in forest openings and alpine meadows, but forms the com-

munity in the valley bottoms, particularly often in sites with coarse blocks of rocks from eroded rock walls (Figure 6a). The association was described as the forb community from scree aprons in Fann Mountains (Nowak et al. 2015; Figure 4). Its stands are distributed in the alpine belt within the range of elevations from 2,050 to 3,300 m a.s.l. (Figure 5a). It prefers limestone bedrock and alkaline soil substrates. Patches of this association were found on relatively gentle slopes (foothills of large block screes) with a mean inclination of approx. 10°. The association inhabits different slopes with northern, southern and western aspects. It is characterized by a dense forb cover up to 95% (mean close to 80%, Figure 5d) and a negligible moss contribution. The richness of vascular plant species is moderate, with an average of 15 species and a maximum of 23 per plot (Figure 5f).

2.1.3. *Heracleetum lehmannianii* Nowak et al. ass. nov. prov. (cluster 4)

Diagnostic species: *Allium elatum*, *Carum carvi*, *Convolvulus arvensis*, *Cousinia pseudarctium*, *Cynoglossum viridiflorum*, *Dactylis glomerata*, *Euphorbia lamprocarpa*, *Heracleum lehmannianum*, *Lithospermum officinale*, *Mentha asiatica*, *Nepeta cataria*, *Poa pratensis*, *Ranunculus brevirostris*, *Trifolium pratense*
Constant species: *Cousinia pseudarctium*, *Heracleum lehmannianum*
Dominant species: *Cousinia pseudarctium*, *Heracleum lehmannianum*
Floristic and habitat characteristics: This distinct association is formed by the endemic *Heracleum lehmannianum* of Middle Asia distributed across all of Pamir-Alai and western Tian Shan (Nowak et al. 2020a). *Heracleetum lehmannianii* mainly occurs along mountain rivers and streams, rarely inhabiting water outflows on slopes (Figure 6b). The vegetation has been recorded in the Zeravshan, Hissar, Hazratishoh and Western Pamir Ranges (Figure 4). The association prefers deep, well watered soils with small gravel ingredients. The phytocoenosis has a fairly wide altitudinal amplitude across montane and alpine belts and inhabits the range between 1,500 and 3,500 m a.s.l. (mean approx. 2,000; Figure 5a). Patches of this vegetation inhabit mainly flat land, but sometimes they can be found on relatively steep slopes, up to 30° (mean approx. 15°), where it prefers the northern aspects. Total cover of the herb layer is very high, often reaching 100% (Figure 5d). Only occasionally, whether in *Heracleum lehmannianum* or *Cousinia pseudarctium* stands, does it have sparser cover, but never below 80%. The vegetation is moderately rich in species relative to the average of 22 species per plot. However, some patches can consist of up to 33 or have as few as 12 species per plot (Figure 5f). The moss layer has inconsiderable value, however in some sites close to fen vegetation it can reach up to 35% (Figure 5e). The association is clearly a vicariant one of the Caucasian stands of *Heracleum mantegazzianum* or *H. sosnovskyi* and Alborz hogweeds like *H. persicum*.

2.1.4. *Eremuretum kaufmannii* Nowak et al. ass. nov. prov. (cluster 5)

Diagnostic species: *Artemisia dracunculus*, *Astragalus nuciferus*, *Dictamnus angustifolius*, *Eremurus kaufmannii*, *Iris hoogiana*, *Lonicera nummulariifolia*, *Paeonia intermedia*, *Poa urssulensis*, *Restella albertii*
Constant species: *Artemisia dracunculus*, *Ligularia thomsonii*, *Prangos pabularia*
Dominant species: *Eremurus kaufmannii*, *Prangos pabularia*
Floristic and habitat characteristics: This is typical alpine tall-forb vegetation of the Pamir-Alai Range. *Eremurus kaufmannii* occurs in northern Tajikistan and northern Afghanistan forming its own association on gentle slopes in the alpine pastureland zone (Ovchinnikov 1963). The patches of this remarkable vegetation were noted in the Zeravshan and Hissar Mountains (Figure 4) at the elevation of ca. 2,400 m a.s.l. (ranging between 2,100 and 2,850; Figure 5a). They occur on gentle slopes from 10° to 40° (mean ca. 20°) inclination and preferably at a northern aspect. The total cover of the vegetation was approx. 90% on average (ranging between 80 and 95%; Figure 5d). This tall-forb vegetation is moderately rich in species having from 9 to 31 species per plot (mean ca. 19; Figure 5f). This type of forb, dominated by the decorative *Eremurus kaufmannii*, is very spectacular in the pasture landscape of alpine meadows (the plant itself is poisonous to stock animals, Figure 6c). The tall, ornamental *Eremurus* is a prominent feature in the landscape of the high Pamir-Alai mountains, especially after the first passage of sheep herds.

2.1.5. *Anthriscidetum glacialis* Nowak et al. ass. nov. prov. (cluster 6)

Diagnostic species: *Anemonastrum protractum*, *Anthriscus glacialis*, *Astragalus aksuensis*, *Asyneuma baldshuanicum*, *Crepis darvazica*, *Draba huetii*, *Elytrigia repens*, *Euphorbia sarawschanica*, *Leonurus turkestanicus*, *Ligularia alpigena*, *Oberna wallichiana*, *Pedicularis olgae*, *Phleum pratense*, *Picris nuristanica*, *Polygonum hissaricum*, *Rumex nepalensis*, *Tanacetum pseudachillea*
Constant species: *Anthriscus glacialis*, *Ferula kuhistanica*, *Geranium regelii*, *Ligularia thomsonii*
Dominant species: *Anthriscus glacialis*, *Ferula kuhistanica*
Floristic and habitat characteristics: *Anthriscus glacialis* is a widely distributed alpine species across the whole Pamir-Alai and western Tian Shan Ranges (Chukavina 1984). We recorded the stands of this species mainly in the central section of the Darvaz Range around the Hoburobot Pass (Figure 4). It grows on nutrient rich, deep, nitrophilous soils within a pastureland complex with intensive grazing (Figure 6d). Stands of this vegetation were recorded in the upper alpine belt between 2,500 and 3,000 m a.s.l. elevation (mean ca. 2,800 m; Figure 5a). The association prefers gentle slopes or flat plots in the vast pasturelands, sometimes in close vicinity to villages (so called "letovki" – summer huts) with mean inclination of approx. 12° (ranging from

5° to 25°. It occurs preferably at western and south-western aspects. The herb layer is particularly luxuriant and reaches on average close to 100% cover (Figure 5d). *Anthriscidetum glacialis* includes from 19 to 37 species, approx. 30 per plot (Figure 5f). It is intensively grazed and very sporadically mowed (patches in villages neighbourhood).

Scree like tall-forb communities of the eastern Irano-Turanian region

Alliance: *Rheion maximowiczii* Nowak et al. all. nov. prov.

This tall-forb vegetation mainly grows in the montane and subalpine belts on gravelly scree-like slopes, with the soil often covered by coarse rocky debris. Therefore, apart from the typical tall-forb species, there are many scree plants such as *Tetrataenium olgae* or *Senecio saposchnikovii*. The soil profile is relatively deep and nutrient rich, however in some cases it is almost completely covered with unstable rock debris. In Middle Asia, communities of this type occur across the Pamir-Alai and western Tian Shan Ranges, and is particularly frequent in Zeravshan, Vanch, Rushan, Hissar, Alai and Fergana Mountains. Plots of the phytocoenoses were sampled at elevation between 1,500 and 3,300 m a.s.l. (mean approx. 2,000; Figure 5a). They inhabit slopes with an inclination of 3°-45° (average 25°). This tall-forb alliance is rich in species with an average of 27 per plot (ranging from 8 to 44; Figure 5f). The herbaceous layer varies from 20% to 100%, with an average of ca. 65% (Figure 5d). The vegetation forms luxuriant stands (Figures 6e, 7e, f) with a number of dominant species that are endemic to Middle Asia (e.g. *Rheum maximowiczii*, *Bunium badachschanicum*, *Phlomoides tadschikistanica*). As in other *Prangetea ulopterae* vegetation, large *Apiaceae* species are highly represented (e.g. *Ferula kokanica* or *F. transiliensis*). Patches of this vegetation can withstand periodic drought of habitats during hot summer.
Diagnostic taxa: *Bunium persicum*, *B. badachschaniucum*, *Eremurus stenophyllus*, *Ferula kokanica*, *Plantago lanceolata*, *Poterium polygamum*, *Rheum maximowiczii*

2.2.1. Community of *Cousinia batalinii* and *Euphorbia pamirica* (cluster 7)

Diagnostic species: *Acantholimon parviflorum*, *Artemisia rutifolia*, *Astragalus lasiosemius*, *Bunium badachschanicum*, *Cousinia batalinii*, *Ephedra gerardiana*, *Eremopoa persica*, *Euphorbia pamirica*, *Kudrjaschevia allotricha*, *Lappula badachschanica*, *Linaria sessilis*, *Piptatherum sogdianum*, *Rheum maximowiczii*, *Scariola orientalis*, *Tetrataenium olgae*, *Tulipa dasystemon*
Constant species: *Ferula kokanica*
Dominant species: *Cousinia pseudarctium*, *Ferula kokanica*
Floristic and habitat characteristics: *Cousinia batalini* is an endemic plant of the Hissar and Darvaz Ranges, and occurs only sporadically in the Western Pamir (Rasulova 1991). The second of the two main diagnostic species, *Euphorbia pamirica*, is distributed almost across the same area. It grows in the Hissaro-Darvaz geobotanical region, but is also rarely found in the West and East Pamirs (Ovchinnikov 1981). The community forms a scree-like vegetation, however is rich in species with considerable cover in the herb layer. Plots of this vegetation were noted in the alpine belt at an elevation of 1,950 to 3,300 (average approx. 2,850 m a.s.l.; Figure 5a). The patches were recorded on slopes with an inclination of 10°-45° (average 35°), preferably at south-western and southern aspects. The total cover of herbs was approx. 55% (ranging from 30% to 80%; Figure 5d) and the plots consisted of 8 to 29 species per plot (mean approx. 17; Figure 5f). This is one of the most scree-like vegetation types of *Prangetea ulopterae*, and because of its internal heterogeneity we decide to leave it rankless.

2.2.2. *Phlomoidetum kaufmannianae* Nowak et al. ass. nov. prov. (cluster 8)

Diagnostic species: *Alcea nudiflora*, *Anisantha tectorum*, *Boissiera squarrosa*, *Bromus danthoniae*, *Bunium persicum*, *Crambe kotschyana*, *Crepis pulchra*, *Eremurus soogdianus*, *Erodium cicutarium*, *Lindelofia macrostyla*, *Nardurus krausei*, *Neurotropis kotschyana*, *Papaver pavoninum*, *Perovskia virgata*, *Phlomoides kaufmanniana*, *Piptatherum kokanicum*, *Scandix stellata*, *Scrophularia scabiosifolia*, *Taeniatherum crinitum*, *Valerianella ovczinnikovii*, *Bryum caespiticium*, *Encalypta vulgaris*, *Pohlia nutans*, *Tortula muralis*
Constant species: *Perovskia virgata*, *Phlomoides kaufmanniana*; *Bryum caespiticium*, *Encalypta vulgaris*, *Pohlia nutans*
Dominant species: *Phlomoides kaufmanniana*
Floristic and habitat characteristics: *Phlomoides kaufmanniana* is a narrowly distributed forb species of the western Pamir-Alai. Its stands were found only in a few valleys in the Zeravshan and Turkestan Mountains in Tajikistan (Kochkareva 1986). It has been noted in the montane belt at an elevation of approx. 1,500 – 1,800 m a.s.l. (average approx. 1,630; Figure 5a). This vegetation prefers western aspects with a moderate inclination of about 5°-35° (average approx. 15°, Figure 7e). The cover of the herb layer ranges from 50 to 95%, with a mean of 80% (Figure 5d). Mosses were observed within plots with a mean cover of ca. 12% (Figure 5e). Plots include from 23 to 30 species, with an average of approx. 26 per plot (Figure 5f).

2.2.3. *Eremostachyetum tadshikistanicae* Nowak et al. 2016 (cluster 9)

Diagnostic species: *Achillea biebersteinii*, *Amoria repens*, *Geranium divaricatum*, *Hedysarum denticulatum*, *Medicago sativa*, *Phlomoides canescens*, *P. tadshikistanica* (*Eremostachys tadshikistanica*), *Ranunculus muricatus*, *Trichodesma incanum*
Constant species: *Amoria repens*, *Phlomoides tadshikistanica*, *Plantago lanceolata*
Dominant species: *Phlomoides tadshikistanica*

Floristic and habitat characteristics: *Phlomoides tadshikistanica* is an endemic species of the Hissar, Darvaz and Ak-tau ranges in the western Pamir-Alai (Kochkareva 1986). This community has been characterised in our previous work devoted to scree vegetation on montane and colline belts (Nowak et al. 2016b), but it is also presented here as we found two additional plots representing this association in the Darvaz Mountains (Figure 4). They were located at an elevation of 1,500 m a.s.l. (Figure 5a) on a steep scree exposed to the south and with an inclination of 45° (Figures 5a, 7f). The average herb layer cover was approx. 80%. Plots were moderately rich with 19 or 22 species per plot (Figure 5f).

2.2.4. Community of *Senecio saposhnikovii* (cluster 10)

Diagnostic species: *Anaphalis racemifera*, *Artemisia santolinifolia*, *Berberis heterobotrys*, *Cirsium badakhschanicum*, *Cotoneaster nummularioides*, *Dracocephalum diversifolium*, *Gentianella turkestanorum*, *Senecio saposhnikovii*, *Thalictrum isopyroides*, *Thymus proximus*
Constant species: *Senecio saposhnikovii*
Dominant species: *Senecio saposhnikovii*
Floristic and habitat characteristics: The only patch of vegetation supporting *Senecio saposchnikovii* was noted in the Alai range close to the Uch-tube village (Figure 4). It occurs on steep, loose scree at an elevation of approx. 2,500 m a.s.l. (Figure 5a), with the soil underlying gravel. The community grows on the exposed western slopes with an inclination of approx. 35°. The vegetation was relatively abundant with 75% cover of the herb layer (Figure 5d) and was composed of 20 plant species (Figure 5f). This very distinct community is left rankless until additional patches are surveyed.

2.2.5. *Eremuretum stenophyllido-comosi* Nowak et al. ass. nov. prov. (cluster 11)

Diagnostic species: *Berberis nummularia*, *Colutea paulsenii*, *Exochorda korolkowii*, *Rosa ovczinnikovii*, *R. popovii*, *Eremurus comosus*, *E. stenophyllus*, *Ferula transiliensis*, *Poterium polygamum*
Constant species: *Eremurus comosus*
Dominant species: *Rosa ovczinnikovii*; *Eremurus comosus*
Floristic and habitat characteristics: This is one of the most frequent communities of the scree-like forbs of the Eastern Irano-Turanian subregion, however it can also occur in gentle sloping or flat pastures with negligible rock debris. The association has been recorded mainly in the Hissar Mountains (e.g. Mayhura Valey) and Darvaz Mountains (e.g. Obikhingou Valley; Figure 4). *Eremurus stenophyllus* is a typical Irano-Turanian element distributed from Iran to Central Asia, but *E. comosus* is considered an endemic plant of the western Pamir-Alai Mountains (Ovchinnikov 1963). The community forms distinct stands on large areas within the montane belt (Figure 6e). The association's plots have been found at an elevation between 1,450 and 2,000 m a.s.l. (average approx. 1,700 m; Figure 5a). They mainly inhabit south-eastern and southern slopes, with varying inclinations from 5° to 40° (average approx. 23°). The association is characterized by a varied herb cover, ranging between 20 and 100% (approx. 60% on average, Figure 5d). Between 18 and 44 vascular plant species were recorded in each relevé, with an average of 32, which positioned this tall-forb association as one of the most speciose (Figure 5f).

Tall-forb communities of the subhumid zone of the eastern Irano-Turanian region

2.3.2. Alliance: *Scabioso songaricae-Phlomoidion lehmannianae* Nowak et al. all. nov. prov.

This tall-forb vegetation forms luxuriant stands mainly in montane and subalpine belts on gentle slopes with nutrient rich soil and negligible rock debris. The only exception is the association of *Lathyretum mulkaki* growing occasionally almost on pure screes, but then creating species impoverished stands. Patches of this vegetation are found in micromosaic situations with other vegetation, mainly thermophilous shrubs (shiblyak) or scree vegetation and alpine pastures. In Middle Asia, the communities of this type occur across all of Pamir-Alai and western Tian Shan Mountains, and are particularly frequent in the Darvaz, Hissar, Peter the First, Vanch, Alai and Fergana Mountains. The plots comprising this phytocoenoses were sampled at an elevation between 1,300 and 3,250 m a.s.l. (mean approx. 2,200; 5a). They inhabited slopes with an inclination of up to 55° (average approx. 20°). This tall-forb vegetation is rich in species with an average of 23 per plot (ranging from 7 to 39; Figure 5f). The cover of herbaceous layer is much higher than in the previous alliance (*Ligulario thomsonii-Geranion regelii*) and differs from 50% to 100% reaching the average of ca. 85% (Figure 5d). The vegetation forms dense stands (Figures 6f, 7a-d, g) with a number of distinct, prominent Middle Asian species (e.g. *Eremurus robustus*, *E. fuscus*, *E. brachystemon*, *Lathyrus mulkak*, *Phlomoides lehmanniana*, *P. tadshikistanica*). As in other *Prangetea ulopterae* vegetation the large *Apiaceae* species have considerable representation, e.g. *Prangos pabularia*, *Ferula gigantea*, *F. kuhistanica* or *F. violacea*.
Diagnostic taxa: *Gentiana olivieri*, *Onobrychis baldshuanica*, *Phlomoides lehmanniana*, *Poterium lasiocarpum*, *Rumex paulsenianus*, *Inula macrophylla*, *Rochelia peduncularis*, *Soleanthus circinnatus*

2.3.1. Community of *Inula macrophylla* (cluster 12)

Diagnostic species: *Artemisia ferganensis*, *A. glanduligera*, *Astragalus alopecias*, *A. sieversianus*, *Bromus oxyodon*, *Carex turkestanica*, *Convolvulus pseudocantabrica*, *Delphinium biternatum*, *Eremurus tianschanicus*, *E. turkestanicus*, *Eulophus ferganensis*, *Galium pamiroalaicum*, *Inula macrophylla*, *Microthlaspi perfoliatum*, *Perovskia abrotanoides*, *Serratula lyratifolia*, *Spiraea hypericifolia*, *Stipa caucasica*, *Stubendorffia orientalis*
Constant species: *Bromus oxyodon*, *Carex turkestanica*, *Convolvulus pseudocantabrica*, *Galium pamiroalaicum*,

Inula macrophylla, *Prangos pabularia*, *Serratula lyratifolia*, *Stubendorffia orientalis*
Dominant species: *Bromus oxyodon*, *Carex turkestanica*, *Inula macrophylla*, *Prangos pabularia*, *Stubendorffia orientalis*
Floristic and habitat characteristics: Stands of *Inula macrophylla* are relatively common in the Pamir-Alai, however it seems that the species is only a contributor to other vegetation types. It is widespread in the whole of Middle Asia and occurs also in the Tarbagatai Mountains in Kazkhstan (Kinzikaeva 1988). We recorded only a few plots dominated by this plant in the Fergana and Talas in Kyrgyzstan (Figure 4) at the elevation of 1,300 to 1,400 m a.s.l. (average 1,350 m, Figure 5a) on deep, nutrient rich soil overlying limestone bedrock (Figure 6f). This community inhabits relatively steeply descending slopes with a mean inclination of approx. 30°, with a preference for northern aspects. It is characterized by a very dense herb cover which often reaches 100% (average close to 90%, Figure 5d). The richness of vascular plant species was high, with an average of 30 species and a maximum of 36 per plot (Figure 5f).

2.3.2. *Stipetum margelanicae* Nowak et al. 2016 (cluster 13)

Diagnostic species: *Allium barsczewskii*, *Astragalus filicaulis*, *A. krauseanus*, *A. mucidus*, *Carex dimorphotheca*, *Cousinia mulgediifolia*, *Ferula violacea*, *Poa bulbosa*, *Scabiosa songarica*, *Stipa margelanica*
Constant species: *Artemisia persica*, *Carex dimorphotheca*, *Poa bulbosa*, *Prangos pabularia*, *Scabiosa songarica*, *Stipa margelanica*
Dominant species: *Prangos pabularia*, *Stipa margelanica*
Floristic and habitat characteristics: This association was previously proposed after field studies conducted in the northern Pamir-Alai (Nowak et al. 2016a), but with additional data it is presented again here. *Stipetum margelanicae* has the intermediate character and is a kind of steppe vegetation with a significant share of forb plants. It has been found in the alpine belt within an altitudinal range between 1,900 and 2,200 m a.s.l. (mean approx. 2,100; Figure 5a). Patches of this vegetation inhabit gentle slopes (average inclination of approx. 15°) and only sporadically were found on steeper descents of up to 40°. It prefers south-eastern and eastern aspects. The total cover of herb layer is relatively high and ranges from 70% to 100% (mean approx. 90%; Figure 5d). The vegetation is moderately rich, with 13 to 31 species per plot (mean ca. 20; Figure 5f).

2.3.3. *Lathyretum mulkaki* Nowak et al. ass. nov. prov. (cluster 14)

Diagnostic species: *Iris darwasica*, *Lathyrus mulkak*, *Lophanthus elegans*, *Nepeta olgae*
Constant species: *Cousinia pseudarctium*, *Ferula kokanica*
Dominant species: *Cousinia pseudarctium*, *Ferula kokanica*, *Lathyrus mulkak*
Floristic and habitat characteristics: This tall-forb vegetation (Figure 7a) occurs mainly in the Darvaz and Hissar Mountains in the alpine belt with relatively high precipitation (up to 1,000 mm yearly). It is closely related to scree communities in terms of habitat conditions, however the floristic composition positioned it within the *Scabioso songaricae-Phlomoidion lehmannianae* alliance. Documented plots occupied steep slopes at the alpine elevations in the Western Pamir-Alai Mountains (Figure 4). They were noted at ca. 1,900 to 3,250 m a.s.l. with a mean of ca. 2,600 m (Figure 5a), mainly at southern and southwestern aspects with an inclination of 10° to 55° (mean approx. 30°). The number of vascular plant species ranges from 8 to 35 with a mean of 23 (Figure 5f). The average cover of the herb layer was moderate when compared to other forb vegetation of Middle Asia, ranging from 50 to 100%, average approx. 75%. (Figure 5d).

2.3.4. *Potentillo orientalis-Eremuretum fusci* S. Świerszcz et al. 2020 (cluster 15)

Diagnostic species: *Eremurus brachystemon*, *E. fuscus*, *Gymnospermium albertii*, *Scorzonera tadshikorum*, *Veronica arguteserrata*
Constant species: *Eremurus fuscus*
Dominant species: *Eremurus brachystemon*, *E. fuscus*, *Ferula kokanica*, *Gymnospermium albertii*
Floristic and habitat characteristics: This association was described from the alpine belt of the western Pamir-Alai as intensively grazed grassland vegetation (Świerszcz et al. 2020). During the current research, additional plots of this vegetation were found in Central Tajikistan as well as in the Kyrgyz and Talass Mountains in Kyrgyzstan (Figure 4). This association prefers vast open habitats in the alpine pastureland zone between 1,850 and 2,500 m a.s.l. (mean approx. 2,100; Figure 5a). It develops on gentle slopes with an average inclination of approx. 20°. *Potentillo orientalis-Eremuretum fusci* appears indifferent to slope or exposure, but often occurs at southern or north-western aspects (Figure 7d). The total cover of the herb layer is high and ranges between 80 and 100% (average approx. 83%; Figure 5d). The species richness is moderate with 7 to 25 species per plot (average 17; Figure 5f).

2.3.5. *Hordeo bulbosi-Astragaletum retamocarpi* S. Świerszcz et al. 2020 (cluster 16)

Diagnostic species: *Aegilops triuncialis*, *Astragalus retamocarpus*, *Buglossoides arvensis*, *Crupina vulgaris*, *Echium biebersteinii*, *Elaeosticta allioides*, *E. hirtula*, *Ferula gigantea*, *Hordeum bulbosum*, *Hypericum perforatum*, *Medicago denticulata*, *M. orbicularis*, *M. rigidula*, *Pseudohandelia umbellifera*, *Rochelia cardiosepala*, *Tragopogon capitatus*, *Tulipa subquinquefolia*, *Vicia angustifolia*
Constant species: *Astragalus retamocarpus*, *Carex turkestanica*, *Ferula kuhistanica*, *Medicago rigidula*, *Poa bulbosa*
Dominant species: *Astragalus retamocarpus*, *Ferula kuhistanica*, *Poa bulbosa*

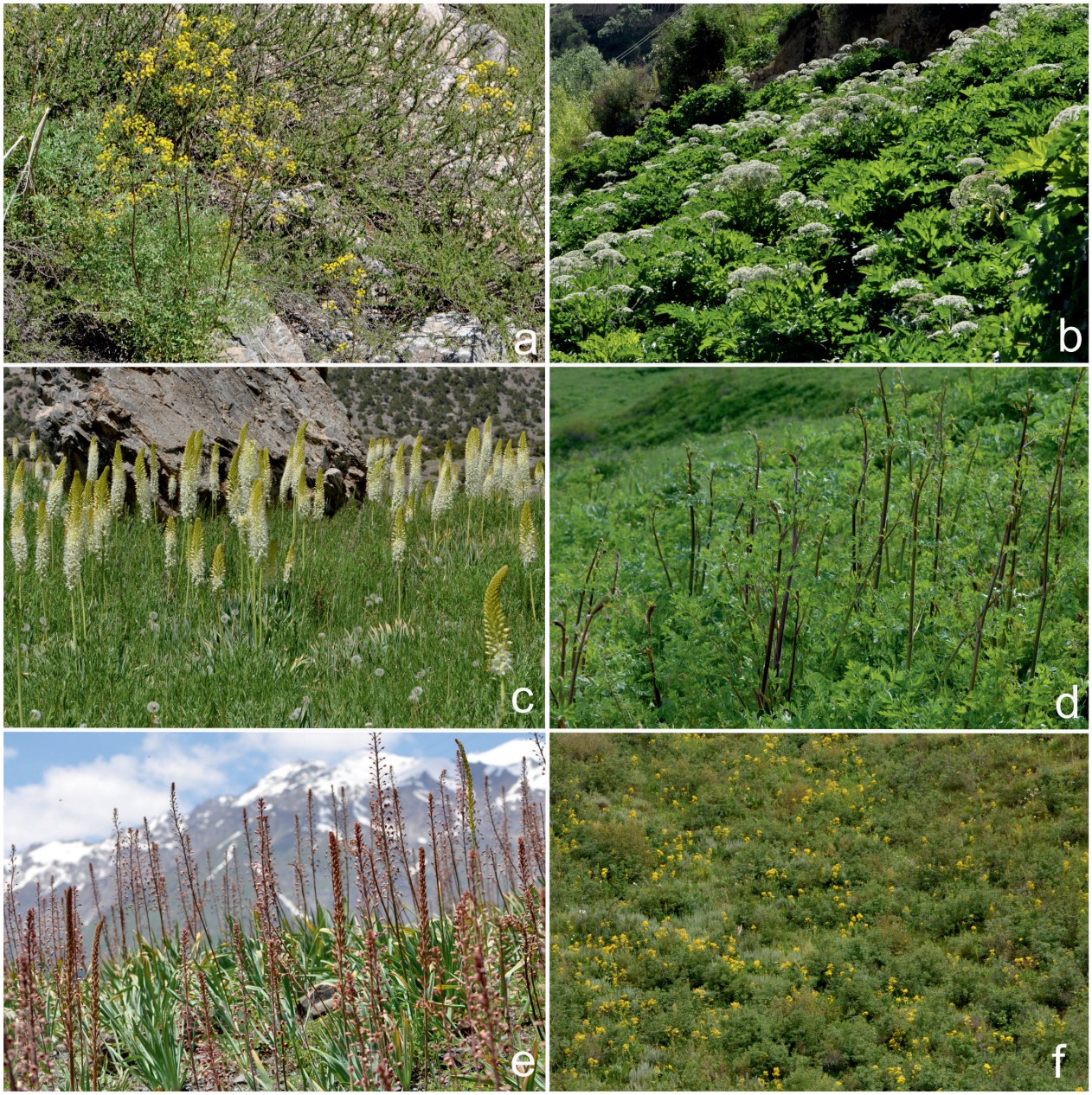

Figure 6. Photographs of the tall-forb vegetation belonging to: a – *Feruletum sumbuli* in the Haf-kul Valley in the Funn Mts, Western Pamir-Alai; b – *Heracleetum lehmannianii* on the slope water outflow in Haf-kul Valley, Western Pamir-Alai, approx. 1,850 m a.s.l.; c – *Eremuretum kaufmannii* in the Kuli-kalon Plateau in Funn Mountains, approx. 3,400 m a.s.l.; d – *Anthriscidetum glacialis* near the Hoburobot Pass in Darvaz Mountains, approx. 3,500 m a.s.l.; e – *Eremuretum stenophyllido-comosi* in Mayhura Valley in Hissar Mountains, approx. 2,650 m a.s.l.; f – community of *Inula macrophylla* near Chilishtak Village in Darvaz Mountains, approx. 1,450 m a.s.l.

Floristic and habitat characteristics: This is another association that was described from the montane belt of south-western Pamir-Alai as the pseudosteppe vegetation (Świerszcz et al. 2020). A few additional plots of this vegetation were found in Peter the First Range (Figure 4) in the alpine pastureland zone between 1,900 and 2,200 m a.s.l. (mean approx. 2,050; Figure 5a). It was recorded on gentle slopes with an average inclination of approx. 14° at western or southern aspects. As in other grasslands or forb-dominated vegetation, the density of vegetation was very high and the noted cover of herbs was close to 100% (Figure 5d). The average species richness was also one of the highest, with 30 species per plot (ranging from 22 to 38, Figure 5f).

2.3.6. Community of *Ferula kuhistanica* (cluster 17)

Diagnostic species: -
Constant species: *Ferula kuhistanica*
Dominant species: *Cousinia pseudarctium*, *Ferula kuhistanica*, *Potentilla orientalis*, *Rochelia cardiosepala*
Floristic and habitat characteristics: *Ferula kuhistanica* is one of the most frequent species in tall-forb vegetation

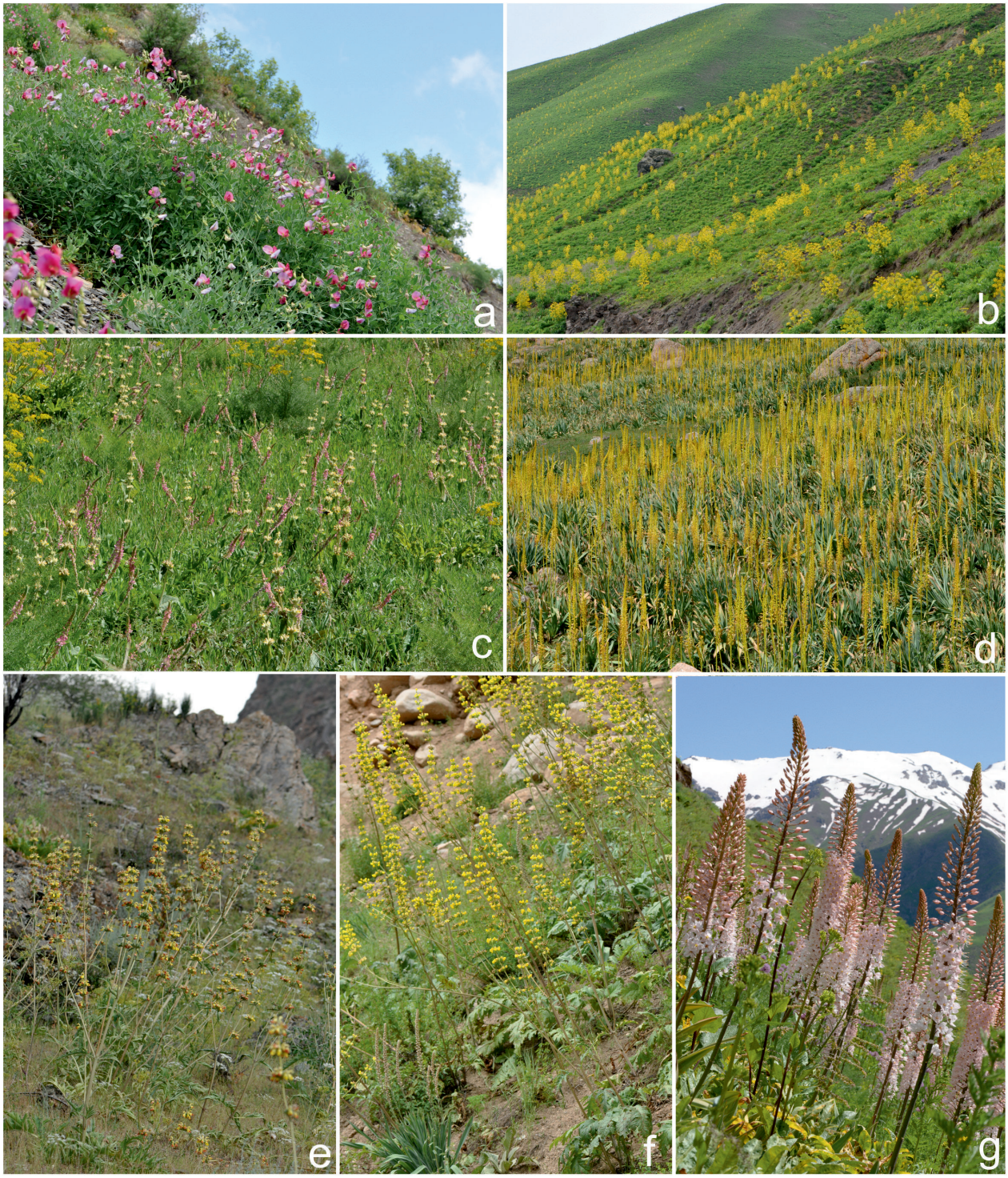

Figure 7. Photographs of the tall-forb vegetation belonging to: a **–** *Lathyretum mulkaki* near the Anzob Pass in Hissar Mountains, approx. 3,100 m a.s.l.; b – community of *Ferula kuhistanica* near the Hoburobot Pass in Darvaz Mountains, approx. 3,600 m a.s.l.; c – *Phlomoido lehmannianae-Onobrychidetum grandis* in the Obikhingou River Valley near Roha, approx. 3,200 m a.s.l.; d – *Potentillo orientalis-Eremuretum fusci* in Talas Mts, Kyrgyzstan, approx. 2,700 m a.s.l.; e – *Phlomoidetum kaufmannianae* near Mogien in Funn Mountains, approx. 1,600 m a.s.l.; f – *Eremostachyetum tadshikistanicae* in Darvaz Mountains, approx. 1,500 m a.s.l.; g – *Eremuretum robusti* near Rabot, Darvaz Mountains, approx. 2,750 m a.s.l.

in the Pamir-Alai, contributing to almost all communities growing on nutrient rich, deep soils of higher montane and alpine belts. Cluster 17 was separated by the algorithm as probably the central community within the alliance with no diagnostic species. A few plots of the community were found in the Darvaz and Peter the First ranges (Figure 4)

in heavily grazed pasturelands which possibly impoverished the community affecting floristic composition (Figure 7b). Thus, we only mention this group for consistency without giving a detailed floristic description.

2.3.7. *Eremuretum robusti* Nowak et al. ass. nov. prov. (cluster 18)

Diagnostic species: *Cousinia umbrosa*, *Eremurus robustus*, *Phlomoides arctifolia*, *Vicia tenuifolia*
Constant species: *Eremurus robustus*, *Ferula kuhistanica*, *Prangos pabularia*
Dominant species: *Cousinia pseudarctium*, *Eremurus robustus*, *Phlomoides arctifolia*, *Prangos pabularia*
Floristic and habitat characteristics: This is one of the most spectacular tall-forb vegetation types in Pamir-Alai (Figure 7g), with the main occurrence on the humid slopes of the Hissar, Darvaz, Hazratishoh and Peter the First Ranges (Figure 4). It forms tall stands in the upper montane and alpine belts within an altitudinal range between 1,500 and 2,600 m a.s.l. (average approx. 2,250 m; Figure 5a). It grows on flat, deep, well-watered soils in wide river valleys or occasionally, on gentle slopes with an inclination up to 25°. However, it always occurs in a moist, deep and fertile soil substrate, at no particular aspect. *Eremuretum robusti* is a luxuriant, rich vegetation with between 14 and 39 species within the sampled plots (average approx. 25, Figure 5f). The association is characterized by a relatively high total cover of herb layer. In many cases it reached 100%, with the average over 90% (Figure 5d). It is one of the most eminent tall-forb vegetation types of Middle Asia.

2.3.8. *Phlomoido lehmannianae-Onobrychidetum grandis* Nowak et al. ass. nov. prov. (cluster 19)

Diagnostic species: *Onobrychis grandis*, *Phlomoides lehmanniana*
Constant species: *Ferula kuhistanica*, *Phlomoides lehmanniana*, *Poa bulbosa*, *Prangos pabularia*
Dominant species: *Ferula kuhistanica*, *Phlomoides lehmanniana*, *Prangos pabularia*
Floristic and habitat characteristics: This association is one of the most widespread in Central Tajikistan, mainly in the Darvaz, Peter the First and Hissar Ranges (Figure 4). It also has some outliers in the Zeravshan, Turkestan and western Pamirian Mountains. The Pamir-Alai is an exclusive occupancy area of *Phlomoides lehmanniana*, an endemic of these mountains (Figure 7c). The association patches inhabit moderately fertile slopes within the upper montane and alpine belts, between ca. 1,700–2,700 m a.s.l. (mean ca. 2,400 m; Figure 5a). Phytocoenoses were noticed on flat lands in a wide valley, as well as on relatively steep slopes, up to 45° (average approx. 17°) and southerly aspects. The particular plot of *Phlomoido lehmannianae-Onobrychidetum grandis* consisted of 14 to 36 species (average 24, Figure 5f). The total herb cover ranged from 50% to 100% (average 84%) (Figure 5d) in a particular plot.

Discussion

The origin of the tall-forb vegetation in Middle Asia

Because paleoecological and palynological data are limited and incomplete for Middle Asia, the history of vegetation is insufficiently explained and due to past misunderstandings (see Zhilin 1989) can be misleading. However, based on palaeoflora data from the Turan (Turgay flora) region, the Russian palaeoecologists presented interesting hypotheses about the development of vegetation of large umbel communities (see Klein 1988). From the lower Miocene, significant variations in climate caused the replacement of broadleaf turgay forests (ancestor of today's chernoles – *Juglans regia* and *Platanus orientalis* stands), first by the paleoshiblyak (= preshiblyak) and later by steppes and deserts. In vast areas the dense broadleaf forests gave way to sclerophyllous and xerophytic formations often with patchy physiognomy. Preshiblyak was a sparse tree and shrub "paleoformation", very xerophilic, considered to be the ancestral to the current thermophilous shiblyak and juniper grooves. Besides numerous woody species, there was a luxuriant herb layer that included representatives of today's typical tall-forb taxa such as *Prangos*, *Ferula*, *Rheum* and *Polygonum*. Due to strong climatic stress, preshiblyak became a stage of prompt radiation for many genera like e.g. *Malus*, *Rosa*, *Crataegus*, *Amygdalus*, *Ficus* etc. One prominent taxon that has benefited from these changes was *Ferula*, particularly species from the subtribe *Ferulinae* (*Ferula*, *Dorema*, *Leutea*; Panahi 2019). During the Pliocene-Pleistocene transition, not only was there a progressive reduction of broad-leaf forests, but also further fragmentation of the shiblyak for the benefit of ephemeroid formations of umbels. Kamelin (1967) suggests that, during the Pleistocene, the complex of semi-savannas with high grass (Himalayan-type prairies introduced by Korovin) spread widely and adapted perfectly to the post-Pliocene xerothermic period, with an ephemeroid-type development rhythm. This complex was derived from the preshiblyak, which reduced further in the Pleistocene and transformed in its upper limits into thermophilic forests of *Junipers*. The latter, after their felling and thinning by man, gave way to communities of large umbellifers. The natural species composition of this vegetation was poor and the structure sparse, which in the gaps allowed room for the development of a rich undergrowth. Moreover, it is supposed that the vegetation of large umbels evolved after the anthropogenic impact of the pastoral culture in Central Asia which replaced juniper groves and shiblyak orchards (Klein 1988). As the pastoralism in Tajikistan and Kyrgyzstan has a very long tradition (Dakhshleyger 1980; Mirzabaev et al. 2016), the species pool and surface of the pastures and meadows is fairly high. The impacted, loose character of both descendant vegetation types of preshiblyak harbor in the gaps more than 1,300 typical tall-forb species only in the territory of Tajikistan, including ca. 30 *Ferulas*, four *Pran-*

gos and many other *Apiaceae* (Nowak et al. 2020b). Many of these are endemic plants of the country (Nowak et al. 2011) and at the same time due to considerable changes in agriculture economy of Tajikistan, are facing serious threat (Nowak et al. 2020b).

When analyzing the origin of tall-forb vegetation in Middle Asia, it is worth noting the ecological affiliation of species that they share with closely related vegetation types. It is clearly evident that in terms of floristic similarity, the closest vegetation type is xerophytic shrubs (so called Rosaria and Efedrovniki – 185 common species), followed by thermophilous shrubland (so called shiblyak – 161 species), broad-leaved forests (141), Juniper grooves (127) and screes (104). These commonalities imply that the most important process for the formation of the species composition was aridization and the formation of xeric and thermophilous shrub and thicket vegetation.

It can therefore be summarized that after development of the main genera and species in the Eocene, the increase in occupancy area during the forest transition into sparse forb-forest vegetation of preshiblyak achieved compositional stability and allowed further expansion in shiblyak and juniper forest gaps during the Oligocene and Pliocene. This, along with progressive aridization and cooling of the climate, further developed the tall-forb communities dominated by umbels to reach their probable peak in the Holocene. It was only the intensive pastoral economy in the 20th century that initiated the process of degeneration of this vegetation and its change into intensively managed pastures or pseudosteppes. This should be one of the important concerns in regard to grazed tall-forb vegetation, as the long history of pastoralism (reaching 8000 years) and the grassland management in the region is no longer beneficial, but currently strongly impacting the vegetation cover in Middle Asia, including forbs (Mirzabaev et al. 2016). Sheep, goats, horses, yaks, cows and camels increase in numbers and combined with climate changes are an increasing threat to plant cover (Dakhshleyger 1980, Mirzabaev et al. 2016).

Comparisons of the Middle Asian tall-forb vegetation to the sourrounding areas

Due to the high rate of Pamir-Alai endemism, the very distinct and typically Irano-Turanian vegetation of *Prangetea ulopterae* does not share many taxa with the plots documented in Iran. The only common species occurring in Middle Asia that were defined as diagnostic for the class are *Hypericum scabrum*, *Ferula ovina*, *Lappula microcarpa* and *Scariola* (=*Lactuca*) *orientalis* (Klein 1987, 1988), the last being more characteristic for scree vegetation rather than tall-forb. However, the list of other species known to have the ecological optimum in this vegetation and occurring in both areas (Iran and Middle Asia) is longer. Examples are e.g.: *Cotoneaster nummularia*, *Berberis integerrima*, *Lonicera numulariifolia*, *Thalictrum sultanbadense*. Additionally, there are many genera common in both regions with the most prominent *Cousinia*, *Geranium*, *Helichrysum*, *Isatis*, *Eryngium*, *Crepis*, *Cephalaria*, *Onosma*, *Rheum* and the richest *Astragalus* (Klein 1987). Despite this, all plant communities that were defined from Iran apparently have a different set of species and distinct habitat requirements (*Nepetetum fissae*, *Salvietum hypoleucae* and *Helichrysetum oligocephali*).

Furthermore, the ancient Babylon territory lies in a former area of ancient Mediterranean vegetation. In the mountains of Helgurd-dagh in eastern Iraq, Hadač and Agnew (1963) described a number of pasture communities, including *Corydaleto-Prangetum ferulaceae* in the cones and aprons of rocky walls, *Prangeto-Astragaletum tragacanthae*, *Aethionemeto-Astragaletum tragacanthae* and *Rheetum ribis*. They were documented only by few relevés and sometimes not all taxa were identified at the species level. Nevertheless, it is clear that this type of vegetation is closely related to its physiognomy and species composition of dominating plants of *Prangetea* known from Iran and Middle Asia. However, also in this case there are no common species and closer habitat similarities. The same holds true for the vegetation dominated by *Prangos pabularia* found in the mountains of Kopet-Dagh in southern Turkmenistan (Herrnstadt and Heyn 1977).

The overlap between Irano-Turanian tall-forb and scree vegetation and its relation to Juniper grooves

In this dry, semi-arid zone, the distinction between tall-forb vegetation dominated by *Apiaceae* and the scree vegetation, which can also be dominated by species of *Ferula*, *Prangos* or *Tetrataenium*, is not clear (Nowak et al. 2020a). Despite physiognomic similarities, the vegetation with the domination of *Apiaceae* species can be significantly different in species composition, abundance and habitat preferences. Only in Tajikistan do many *Apiaceae* species inhabit areas other than tall-forb habitats. Examples include meadows and pastures (e.g. *Ferula foetida*, *F. tadshikorum*, *F. karatavica*), screes (e.g. *Ferula giorgiewii*, *F. ovina*, *F. foetidissima*, *F. koso-polianskyi*, *Tetrataenium olgae*) or rock habitats (e.g. *Ferula bucharica*, *F. botschanzevii*, *F. lithophila*, *F. tschimganica*, *F. ugamica*, *Kafirnighania hissarica*, *Zeravshania regeliana*; see Nowak et al. 2020a). Thus, the separation of the nutrient poor scree, fertile pasture and meadow and nutrient rich habitats of tall-forb vegetation in Middle Asia requires thorough analyses, a large data base and fine resolution in this complex of phytogeographical boundaries. The Miocene aridization did not only influence the nutrient rich woody or shrubby vegetation but also left its mark on rock, scree and grassland communities. Species of the genus *Ferula* entered various habitats and are still found there today. Therefore, the name "umbeliferniki" for all tall-forb vegetation is inappropriate. In our case, out of 19 communities, only 5 are dominated by large umbels.

The suggested close relationship between tall-forb vegetation of Middle Asia to juniper groves also requires a detailed analysis as it is questionable when considering the

share of common species. As mentioned above, Klein (1988) suggests after Ovchinnikov (1971) that *Prangetea ulopterae* in Middle Asia originated from the Turgay flora and the ancient Mediterranean vegetation. At the beginning of the lower Miocene, significant variations in climate and gradual aridization caused the replacement of broad-leaf turgay forests by the paleoshiblyak. Palaoshiblyak is considered to be the ancestor formation for *Apiaceae* dominated stands as well as juniper groves (Kamelin 1967; Ovchinnikov 1967, 1971; Pavlov 1980). Additionally, Kamelin's (1967) opinion is that in the upper limits of prashiblyak, due to natural (xerophitysation, climate changes in Pleistocene) and anthropogenic (pastoral culture) factors, the shrubby formation was fragmented and in the patchy mosaic the *Apiaceae* began to expand and developed into today's thermophilous tall-forb communities. However, the number of common species, which may reveal the relationship of the two plant formations, is relatively small. Even typical deciduous forests (*Juglans regia* and *Platanus orientalis* stands) share more common taxa with tall-forb vegetation, not to mention the xerophytic and thermophilous shrubs. It is also worth noting that juniper forests themselves are not a homogenous formation. Apart from the typically thermophilic ones dominated by *Juniperus seravschanica*, there is also a zonal belt in the upper montane (sometimes up to 3,500 m a.s.l.) of *J. turkestanica* and *J. semiglobosa*. These two distinct belts have relatively different species composition and supposedly dissimilar relationship to tall-forb vegetation. It is still questionable whether the thermophilous *J. seravshanica* groves are more closely related to typical *Prangetea ulopterae* than they are to *J. turkestanica* stands, which themselves may be closer to alpine tall-forbs with *Anthriscus glacialis* or *Eremurus* spp.

The vegetation complex of xerotermophilous scrubs and Irano-Turanian tall-forbs extends far west, into the mountains of Armenia, the Caucasus and the mountains of Turkey. The recognition of links between the *Prangetea* vegetation and other thermophilous vegetation, e.g. the fringe vegetation of *Geranietea sanguinei* known from south-eastern Europe and Western Asia needs to be resolved. Particularly interesting is the relationship to xerophilous fringe and tall-forb vegetation of the Illyrian, Dinaric and Balkan Peninsula zone, which include a number of *Apiaceae* species (e.g. *Ferulago campestris*, *Laserpitium siler*, *Selinum silaifolium*) and reflects apparent habitat similarities (in *Dictamno albi-Ferulagion galbaniferae* and *Lathyro laxiflori-Trifolion velenovskyi*; Mucina et al. 2016). As the tall-forb vegetation of the Irano-Turanian region are less hygrophilous and occupy not so fertile deep soils (as compared to the *Mulgedio-Aconitetea* vegetation known from the temperate zone), it is likely that there are also relationships and similarities to the steppe vegetation of *Festuco-Brometea* (e.g. *Stipion korshinskyi* Toman, 1969) and also with Middle Asian steppes (*Cleistogenetea squarrosae* Mirkin et al. ex Korotkov et al. 1991). In our data set, several plots were classified into the steppe vegetation with a high share of forb species (*Stipetum margelanicae*, *Hordeo-Astragaletum retamocarpi*). Additionally, some relationship to mesic mown and grazed meadows and pastures on fertile soils supporting *Poo alpinae-Trisetetalia* Ellmauer et Mucina 1993 should be investigated, especially if we considered the northern territories of Middle and particularly Central Asia. Towards the Altay and Siberia, the share of boreal species increases and the typical *Mulgedio-Aconitetea* vegetation prevails (Ermakov et al. 2000; Zibzeev and Nedovesova 2017; Heim and Chepinoga 2019). The definitive classification and characterization of the tall-forb communities require additional detailed survey in the montane and alpine belt of the whole Middle and Central Asia, particularly in the Tian Shan and Altay Mountains. Additionally, resolution of the Hindukush and Kopet-Dagh Mountains in relation to Middle Asian steppes and pseudosteppes (*Vulpio persicae-Caricion pachystylidis* Świerszcz et al. 2020; see Nowak et al. 2017b; Świerszcz et al. 2020), alpine swards and hay meadows (*Poo alpinae-Trisetalia*), and boreo-temperate grasslands of *Molinio-Arrhenatheretea* meadows (mainly the steppe meadows of *Galietalia veri* or mesic meadows of the continental forest-steppe zone *Carici macrourae-Crepidetalia sibiricae*), is required.

Environmental features determining the floristic composition of communities

Despite considerable compositional differences between communities due to the great phytogeographic distinctiveness and high floristic richness of forb vegetation across Middle Asia, there are also other factors controlling its diversity. The longest gradient (NMDS1, Figure 3) of the tall-forb variability is apparently related to elevation. It clearly distinguishes communities from the highest locations, such as patches of *Phlomoides oreophila*, *Allium hymenorhizum* and *Anthriscidetum glacialis*, which prefers high-mountain habitats with cold and humid conditions. At the other extreme the vegetation of *Phlomoidetum kaufmannianae*, *Eremuretum stenophyllido-comosi* and community of *Inula macrophylla* are grouped. They prefer well drained substrates, warm and dry sites at colline and lower montane elevations. The pattern of vegetation types along the second ordination axis is less obvious. However, looking at its extremes it can be attributed to the fertility of the habitat. At one end (upper part of Figure 3), the communities of *Allium hymenorhizum*, *Cousinia batalinii* and *Euphorbia pamirica* and the association of *Feruletum sumbuli* are placed. They occupy less fertile, shallow, often stony soil substrates. The opposite extreme is occupied by phytocoenoses that prefer deep, fertile soils, rich in mineral and organic content. The examples of tall-forb associations that thrive in this habitat are luxuriant *Heracleetum lehmannianii*, *Hordeo bulbosi-Astragaletum retamocarpi*, *Eremuretum robusti* and the community of *Ferula kuhistanica*. Although hardly detectable, the third gradient is most likely related to the compactness and stability of the substrate. Vegetation of *Phlomoides oreophila* and *Ferula kuhistanica* as well as *Stipetum margelanicae* and *Phlomoido lehmannianae-Onobrychidetum grandis* grow on the stable, compact soils mainly on flatland or gentle slopes in the high alpine belt. The typical scree habitats are mainly occupied by communities such as *Phlomoidetum tadshikistanicae* or *Eremuretum stenophyllido-comosi* that occur in lower elevations mainly on southern slopes

with loose, unstable top soil. This vegetation is composed of species adapted to frequent disturbances caused by rolling stones and landslides, and to periodical drought. Disturbances due to land runoff are a critical factor for plant competitiveness and growing abilities and seem to be one of the most important drivers of vegetation variability in the stony landscapes of Middle Asia (Nowak et al. 2016b).

Conclusions

Our study has expanded the knowledge of the open habitat vegetation in the Pamir-Alai and western Tian Shan Mountains and contributed to the consistent hierarchical classification of tall-forb communities in the Irano-Turanian region (Nowak et al., 2020). The syntaxonomic position of some of the distinguished communities is still unclear, hence further research into floristic composition and habitat requirements for the vegetation of Middle Asia is required, especially in the communities originating from preshiblyak, i.e. thermophilous shrubs, xeric thickets and juniper woods.

Substantial areas of shrubby vegetation (both shiblyak and *Rosa-Ephedra* stands) in Middle Asia have been already degraded, and both climate warming and intensification of land use are serious threats for the biodiversity of grasslands in this region (Mirzabaev et al. 2016). This would also include the extremely species rich tall-forb.

Data availability

All relevant data are within the paper and its Supporting Information files.

Author contributions

A.N., M.N. and S.Ś. planned the research, conducted the field sampling and identified the plant species. A.N.. and S.Ś. performed statistical analyses. S.N. prepared the analytical tables, while all the authors participated in the writing of the manuscript and verification of plants in herbarium.

Acknowledgements

The authors would like to thank Firuza Illarionova from the Dushanbe Nature Protection Team for assistance and help in organising the expeditions. We are indebted to reviewers of the manuscript who helped considerably in improving it. Additionally, we would like to thank Stephen Bell for language proofreading that significantly improved the manuscript. The project was partially supported by the National Science Centre, Poland, no. 2017/25/B/NZ8/00572.

References

Agakhanyanz OE (1966) Basic problems of the physical geography of the Pamirs (Vol. 2). Akademia Nauk Tadzhikskoi SSR, Dushanbe, TJ, 245 pp. [In Russian with English summary]

Agakhanyanz OE, Yusufbekov KY (1975) Rastitel 'nost zapadnogo Pamira i opyt ee Rekonstruktsii [Vegetation of the Western Pamirs and the Experience of Its Reconstruction]. Akademia Nauk Tadzhikskoi SSR, Dushanbe, TJ, 311 pp. [In Russian]

Borchardt P, Schickhoff U, Scheitweiler S, Kulikov M (2011) Mountain pastures and grasslands in the SW Tien Shan, Kyrgyzstan – Floristic patterns, environmental gradients, phytogeography, and grazing impact. Journal of Mountain Science 8: 363–373. https://doi.org/10.1007/s11629-011-2121-8

De Cáceres M, Franklin SB, Hunter JT, Landucci F, Dengler J, Roberts DW (2018) Global overview of plot-based vegetation classification approaches. Phytocoenologia 48: 101–112. https://doi.org/10.1127/phyto/2018/0256

Carrapa B, DeCelles PG, Wang X, Clementz MT, Mancin N, Stoica M, Kraatz B, Meng J, Abdulov S, Chen F (2015) Tectono-climatic implications of Eocene Paratethys regression in the Tajik basin of central Asia. Earth and Planetary Science Letters 424: 168–178. https://doi.org/10.1016/j.epsl.2015.05.034

Cherepanov SK (1995) Plantae Vasculares URSS [Vascular plants of the Soviet Union]. Nauka, Leningrad, RU, 532 pp. [In Russian]

Chukavina AP (1984) Flora Tadzhikskoi SSR. T. VII. Zontichnye – Verbenovye [Flora of the Tajik SSR. T. VII. *Umbelliferae – Verbenaceae*]. Izdatelstvo Nauka, Leningrad, RU. [In Russian]

Chytrý M, Tichý L (2003) Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic: a statistical revision. Folia Sci. Nat. Univ. Masaryk. Brun. 108: 1–231. http://user.mendelu.cz/xfriedl/Fytocenologie pro ZF (KA, RSZ)/Literatura, zdroje ke studiu/Literatura, ebooky/Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic.pdf

Dakhshleyger GF (1980) Khozyaystvo Kazakhov na rubezhe XVIIII-XX vekov. [The economy of the Kazakh people at the turn ofthe 19–20th century]. AN Kaz. SSR, Alma-Ata, KA. [In Russian]

Dengler J, Berg C, Jansen F (2005) New ideas for modern phytosociological monographs. Annali di Botanica Nuova Serie 5: 193–210.

Djamali M, Brewer S, Breckle SW, Jackson ST (2012) Climatic determinism in phytogeographic regionalization: A test from the Irano-Turanian region, SW and Central Asia. Flora 207: 237–249. https://doi.org/10.1016/j.flora.2012.01.009

Ermakov N, Shaulo D, Maltseva T (2000) The class *Mulgedio-Aconitetea* in Siberia. Phytocoenologia 30: 145–192. https://doi.org/10.1127/phyto/30/2000/145

Ermakov NB (2012) Vysshie sintaksony nastajaschich opustinnenych stepey juzhnoy Sibirii i Mongolii. [Higher syntaxa of genuine deserted steppes of southern Siberia and Mongolia]. Vestnik NGU 10: 5–15. [In Russian]

Gadghiev IM, Korolyuk AY, Tytlyanova AA, Andievsky VS, Bayartogtokh B, Grishina LG, Kosykh NP, Kyrgys CO, …, Smelyansky IE (2002) Stepi Centralnoi Azii. [Steppes of Central Asia]. SB RAS Publisher, Novosibirsk, RU, 299 pp. [In Russian]

Golovkova AG (1959) Rastitel'nost tsentral'nogo Tyan-Shanya [Vegetation of the central Tian Shan]. Kirg. Gosud. Universitet, Frunze, KG, 457 pp. [In Russian]

Goncharov NF (1936) Ocherk rostilel'nosti Tsentral'nogo Tadzhikistana, Tadzhisko-Pamirskaya ekhspeditsiya 1932 [Essay on vegetation of Central Tajikistan, Tajik-Pamir Expedition 1932]. Izd. Akademii Nauk SSSR, Moskva-Leningrad, RU, 236 pp. [In Russian]

Hadač E, Agnew ADQ (1963) Plant communities of Helgurd mountain, Iraq. Bull. Iraq Nat. Hist. Inst. 2: 1–16.

Heim RJ, Chepinoga VV (2019) Subalpine tall-herb vegetation patterns: A case study from the Khamar-Daban Range (southern Baikal region, Eastern Siberia). Botanica Pacifica 8: 39–49. https://doi.org/10.17581/bp.2019.08111

Herrnstadt I, Heyn CC (1977) Monographic study of the genus *Prangos* (*Umbelliferae*). Boissiera. Conservatoir et Jardin botaniques, Geneve, 91 pp.

Hilbig W (1995) The Vegetation of Mongolia. SPB Academic Publishing, Amsterdam, 258 pp.

Hill MO (1979) TWINSPAN: A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University, Ithaca.

Kamelin RV (1967) About some remarkable anomalies in the flora of Mountainous Middle Asian province. Botanicheskii Zhurnal 52: 447–460.

Kamelin RV (2010) Oreocryophytic elements of the Montane Middle Asian flora. Botanicheskii Zhurnal 95: 730–757.

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Scientific Data 4: e170122. https://doi.org/10.1038/sdata.2017.122

Kinzikaeva GK (1988) Flora Tadzhikskoi SSR. T. IX. Marenovye – Slozhnotsvetnye [Flora of the Tajik SSR. T. IX. *Rubiaceae – Compositae*]. Izdatelstvo Nauka, Leningrad, RU, 568 pp. [In Russian]

Klein JC (1987) Les pelouses xérophiles d'altitude du flanc sud de l'Alborz central (Iran) [The high xerophilic lawns of the southern part of the central Alborz (Iran)]. Phytocoenologia 15: 253–280. https://doi.org/10.1127/phyto/15/1987/253 [In French]

Klein JC (1988) Les groupements à grandes ombellifères et à xérophytes orophiles: Essai de synthèse à l'échelle de la région irano-touranienne [Groups with large umbellifers and xerophilic xerophytes: Synthesis on the scale of the Iranian-Turanian region]. Phytocoenologia 16: 1–36. https://doi.org/10.1127/phyto/16/1988/1 [In French]

Kochkareva TF (1986) Flora Tadzhikskoi SSR. T. VIII. Kermekovye – Podorozhnikovye [Flora of the Tajik SSR. T. VIII. *Limoniaceae – Plantaginaceae*]. Izdatelstvo Nauka, Leningrad, RU, 520 pp. [In Russian]

Kočí M (2001) Subalpine tall-forb vegetation (*Mulgedio-Aconitetea*) in the Czech Republic: Syntaxonomical revision. Preslia 73: 289–331.

Korovin EP (1934) Rastitelnost' Srednei Azii i Yuzhnogo Kazakhstana [Vegetation of Middle Asia and South Kazakhstan]. SAGIZ, Tashkent, UZ, 480 pp. [In Russian]

Latipova WA (1968) Kolichestvo osadkov [Precipitation]. In: Narzikulov IK, Stanyukovich KW (Eds) Atlas Tajikskoi SSR [Atlas of the Tajik SSR]. Akademia Nauk Tajikskoi SSR, Dushanbe-Moskva, TJ, 68–69. [In Russian]

Li Q, Zhou X, Ni X, Fu B, Deng T (2020) Latest Middle Miocene fauna and flora from Kumkol Basin of northern Qinghai-Xizang Plateau and paleoenvironment. Science China Earth Sciences 63: 188–201. https://doi.org/10.1007/s11430-019-9521-8

Michl T, Dengler J, Huck S (2010) Montane-subalpine tall-herb vegetation (*Mulgedio-Aconitetea*) in central Europe: Large-scale synthesis and comparison with northern Europe. Phytocoenologia 40: 117–154. https://doi.org/10.1127/0340-269X/2010/0040-0377

Mirzabaev A, Ahmed M, Werner J, Pender J, Louhaichi M (2016) Rangelands of Central Asia: challenges and opportunities. Journal of Arid Land 8: 93–108. https://doi.org/10.1007/s40333-015-0057-5

Mucina L, Bültmann H, Dierßen K, Theurillat JP, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, ..., Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (Suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Narzikulov IK, Stanyukovich KW (1968) Atlas Tajikskoi SSR [Atlas of the Tajik SSR]. Akademia Nauk Tajikskoi SSR, Dushanbe, TJ. [In Russian]

Nowak A, Nowak S, Nobis M (2011) Distribution patterns, ecological characteristic and conservation status of endemic plants of Tadzhikistan – A global hotspot of diversity. Journal for Nature Conservation 19: 296–305. https://doi.org/10.1016/j.jnc.2011.05.003

Nowak A, Nowak S, Nobis M, Nobis A (2014) Vegetation of rock clefts and ledges in the Pamir Alai Mts, Tajikistan (Middle Asia). Central European Journal of Biology 9: 444–460. https://doi.org/10.2478/s11535-013-0274-x

Nowak A, Nowak S, Nobis M, Nobis A (2015) Vegetation of taluses and screes of the high montane and alpine zone in the Pamir Alai Mountains (Tajikistan, Middle Asia). Phytocoenologia 45: 299–324. https://doi.org/10.1127/phyto/2015/0048

Nowak A, Nowak S, Nobis A, Nobis M (2016a) Vegetation of feather grass steppes in the western Pamir Alai Mountains (Tajikistan, Middle Asia). Phytocoenologia 46: 295–315. https://doi.org/10.1127/phyto/2016/0145

Nowak A, Nowak S, Nobis M, Nobis A (2016b) Vegetation of screes of the montane and colline zones in the Pamir-Alai Mts in Tajikistan (Middle Asia). Tuexenia 36: 223–248. https://doi.org/10.14471/2016.36.001

Nowak A, Nobis M, Nowak S, Gębala M, Nobis A (2017a) Phytosociology and ecology of deciduous forests in Tajikistan (Middle Asia). Phytocoenologia 47: 67–94. https://doi.org/10.1127/phyto/2017/0084

Nowak A, Nobis M, Nowak S, Nobis A, Swacha G, Kącki Z (2017b) Vegetation of Middle Asia – the project state of art after ten years of survey and future perspectives. Phytocoenologia 47: 395–400. https://doi.org/10.1127/phyto/2017/0208

Nowak A, Nobis A, Nowak S, Nobis M (2018) Classification of steppe vegetation in the eastern Pamir Alai and southwestern Tian-Shan Mountains (Tajikistan, Kyrgyzstan). Phytocoenologia 48: 369–391. https://doi.org/10.1127/phyto/2018/0237

Nowak A, Nowak S, Nobis M (2020a) The Pamir-Alai Mountains (Middle Asia: Tajikistan). In: Noroozi J (Ed.) Plant biogeography and vegetation of high mountains of Central and South-West Asia. Plant and Vegetation (Vol. 17). Springer, Cham, 42 pp. https://doi.org/10.1007/978-3-030-45212-4_1

Nowak A, Świerszcz S, Nowak S, Hisorev H, Klichowska E, Wróbel A, Nobis A, Nobis M (2020b) Red List of vascular plants of Tajikistan – the core area of the Mountains of Central Asia global biodiversity hotspot. Scientific Reports 10: e6235. https://doi.org/10.1038/s41598-020-63333-9

Ogle DH, Wheeler P, Dinno A (2018) FSA: Fisheries Stock Analysis. R package version 0.8.22. https://github.com/droglenc/FSA

Ovchinnikov PN (1957) Flora Tadzhikskoi SSR. T. I, Paprotnikoobraznye – Zlaki [Flora of the Tajik SSR. T. I. *Polypodiophyta – Gramineae*]. Izdatelstvo Akademii Nauk SSSR, Moskva-Leningrad, RU, 546 pp. [In Russian]

Ovchinnikov PN (1963) Flora Tadzhikskoi SSR. T. II, Osokovye – Orkhidnye [Flora of the Tajik SSR. T. II. *Cyperaceae – Orchidaceae*]. Izdatelstvo Akademii Nauk SSSR, Moskva-Leningrad, RU, 456 pp. [In Russian]

Ovchinnikov PN (1967) Osnovnye cherty rastitelnosti i rajony flory Tajikistana. Flora Tajikskoy SSR, Vol. 1 [The main features of vegetation and areas of flora of Tajikistan. Flora of the Tajik SSR, Vol. 1]. Izdatelstvo Nauka, Moskva-Leningrad. [In Russian]

Ovchinnikov PN (1971) Vidovoy sostav rastitelnogo pokrova ushchelya reki Varzob. 1. Vyshe rastenya. [Species composition of the vegetation cover of the Varzob River valley. 1. Higher plants]. In: Ovchinnikov PN (Ed.) Flora i rastitelnost ushchelya reki Varzob [The flora and vegetation of the Varzob River Valley]. Izdatelstvo Nauka, Leningrad. [In Russian]

Ovchinnikov PN (1981) Flora Tadzhikskoi SSR. T. VI, Bobovye (rod Astragal) [Flora of the Tajik SSR. T. VI. *Fabaceae* (genus *Astragalus*)]. Izdatelstvo Nauka, Leningrad, 725 pp. [In Russian]

Panahi M (2019) Biogeographic reconstruction of the genus *Ferula* inferred from analyses of nrDNA and cpDNA sequences. Iranian Journal of Botany 25: 79–94. https://doi.org/10.22092/ijb.2019.126389.1241

Pavlov VN (1967) Formatsja *Prangos pabularia* Lind. v gorah Sredney Azii [*Prangos pabularia* Lind. formations in the mountains of Central Asia]. Botanicheskii Zhurnal 52: 1111–1123. [In Russian]

Pavlov VN (1980) Rastitelnyi pokrov zapadogo Tian-Shanya [Vegetation cover of the western Tian Shan]. Izdatelstvo Moskovskovo Univ., Moscow, 246 pp. [In Russian]

Popova S, Utescher T, Averyanova A, Tarasevich V, Tropina P, Xing Y (2019) Early Miocene flora of central Kazakhstan (Turgai Plateau) and its paleoenvironmental implications. Plant Diversity 41: 183–197. https://doi.org/10.1016/j.pld.2019.04.002

R Core Team (2020) R: A language and environment for statistical computing. https://www.r-project.org/

Rasulova MR (1991) Flora Tadzhikskoi SSR. T. X, Slozhnotsvetnye [Flora of the Tajik SSR. T. X. *Compositae*)]. Izdatelstvo Nauka, Leningrad, 620 pp. [In Russian]

Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. Journal of Vegetation Science 20: 596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x

Rubtsov N (1952) Vegetation cover in Kazakhstan. Essays on the physical geography of Kazakhstan. Publishing House of Academy of Sciences of the Kazakh SSR, Alma-Ata, 48–61.

Safarov N (2003) First National Report on Biodiversity Conservation. Dushanbe, 19 pp.

Świerszcz S, Nobis M, Swacha G, Kącki Z, Dembicz I, Waindzoch K, Nowak S, Nowak A (2020) Pseudosteppes and related grassland vegetation in the Pamir-Alai and western Tian Shan Mts – the borderland of the Irano-Turanian and Euro-Siberian regions. Tuexenia 40: 147–173. https://doi.org/10.14471/2020.40.004

The Plant List (2020) The Plant List. http://www.theplantlist.org/ [accessed 30 May 2020]

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Wagner V (2009) Eurosiberian meadows at their southern edge: Patterns and phytogeography in the NW Tien Shan. Journal of Vegetation Science 20: 199–208. https://doi.org/10.1111/j.1654-1103.2009.01032.x

Westhoff V, van der Maarel E (1973) The Braun-Blanquet approach. In: Whittaker RH (Ed.) Ordination and classification of communities. W. Junk, The Hague, 617–726. https://doi.org/10.1007/978-94-010-2701-4_20

Zhilin SG (1989) History of the development of the temperate forest flora in Kazakhstan, USSR from the Oligocene to the early Miocene. The Botanical Review 55: 205–330. https://doi.org/10.1007/BF02858522

Zibzeev EG, Nedovesova TA (2017) Coenotic diversity of the communities with *Duschekia fruticosa*. In the Altai-Sayan mountain system. Rastiteľnyj Mir Aziatskoj Rossii 4: 47–58. https://doi.org/10.21782/RMAR1995-2449-2017-4(47-58)

E-mail and ORCID

Arkadiusz Nowak (anowak@uni.opole.pl), ORCID: https://orcid.org/0000-0001-8638-0208
Sebastian Świerszcz (Corresponding author, s.swierszcz@obpan.pl), ORCID: https://orcid.org/0000-0003-2035-0035
Sylwia Nowak (snowak@uni.opole.pl), ORCID: https://orcid.org/0000-0003-2867-9839
Marcin Nobis (m.nobis@uj.edu.pl), ORCID: https://orcid.org/0000-0002-1594-2418

Supplementary material

Supplementary material 1
The analytic table of tall-herb vegetation in the Pamir-Alai and western Tian Shan Mts. (Tajikistan and Kyrgyzstan, Middle Asia).
Link: https://doi.org/10.3897/VCS/2020/60848.suppl1

Supplementary material 2
Full synoptic table with percentage frequency and fidelity values.
Link: https://doi.org/10.3897/VCS/2020/60848.suppl2

VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 219–220
doi: 10.3897/VCS/2020/62232

SHORT DATABASE REPORT

ECOINFORMATICS

SIVIM Alpine – Database of high-mountain grasslands in the Iberian Peninsula

Borja Jiménez-Alfaro[1], Xavier Font[2]

1 *Institute of Biodiversity (IMIB, CISC-UO-PA), University of Oviedo, Oviedo, Spain*

2 *University of Barcelona, Barcelona, Spain*

Corresponding author: Borja Jiménez-Alfaro (jimenezalfaro@uniovi.es)

Academic editor: Jürgen Dengler ♦ **Received** 18 December 2020 ♦ **Accepted** 18 December 2020 ♦ **Published** 30 December 2020

Abstract

SIVIM Alpine (GIVD ID: EU-00-034) is a thematic database focused on vegetation plots from alpine grasslands of the Iberian Peninsula. The main aim of the database is to centralize historical and new vegetation plots of grassland-like communities above the treeline from Spanish mountains, the Pyrenees (including France and Andorra) and Serra da Estrela (Portugal). The database was registered in GIVD in December 2020, and it is currently available in EVA under semi-restricted regime. SIVIM Alpine includes both digitized relevés from the literature and unpublished data. Most of digitized relevés overlap with SIVIM (GIVD ID EU-00-004) but the header data and the geographical coordinates of SIVIM Alpine have been improved when possible. The database is routinely updated with new surveys conducted with GPS and detailed ecological data. Nowadays, SIVIM Alpine contains 6,420 vegetation plots corresponding to all phytosociological alliances described in the Iberian Peninsula for high-mountain grassland vegetation, 85% of them also classified at the association level. Plot size is available for 80% of the relevés. Plant taxonomy keeps the names provided by the original authors of the relevés, with an additional correspondence to Euro+Med and The Plant List, when possible. The database is continuously updated by revisiting the original sources. Different versions of the database have been used to vegetation analysis at national at continental scales.

Abbreviations: EVA = European Vegeation Archive; GIVD = Global Index of Vegetation-Plot Databases; SIVIM = Iberian and Macaronesian Vegetation Information System.

Keywords

Alpine vegetation, *Festucetea indigestae, Festuco-Ononidetea*, Iberian Peninsula, *Kobresio-Seslerietea*, Mountains, *Nardetea*, Portugal, Pyrenees, relevé, Spain, vegetation-plot database

PENSOFT.

Copyright *Borja Jiménez-Alfaro et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

GIVD Fact Sheet

GIVD Database ID: EU-00-034			**Last update:** 2020-12-18
SIVIM Alpine		**Web address:**	
Database manager(s): Borja Jiménez-Alfaro (jimenezalfaro.borja@gmail.com); Xavier Font (xfont@ub.edu)			
Owner: Borja Jiménez-Alfaro			
Scope: SIVIM Alpine focuses on high-mountain (alpine) grassland-like communities of the Iberian Peninsula. All vegetation plots recording the co-occurrence of vascular plants (as a minimum) in areas typically between 1 and 200 m2 are included.			
Abstract:			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): TURBOVEG, MS Access, Excel		**Export format(s):** TURBOVEG, MS Access, Excel, CSV file	
Plot type(s): normal plots, time series		**Plot-size range:** 1 to 200	
Non-overlapping plots: 6420	**Estimate of existing plots:** 7000	**Completeness:** 92%	**Status:** completed and continuing
Total no. of plot observations: 6420	**Number of sources (biblioreferences, data collectors):** 100		**Valid taxa:** 2112
Countries (%): AD: 2; FR: 12; PT: 1; ES: 78			
Formations: Non Forest: 3% = Terrestrial: 3% (Arctic-alpin: 1%; Non arctic-alpin: 2% [Natural: 1%; Semi-natural: 0%])			
Guilds: all vascular plants: 100%; bryophytes (terricolous or aquatic): 5%; lichens (terricolous or aquatic): 5%			
Environmental data (%): altitude: 96; slope aspect: 69; slope inclination: 63; microrelief: 0; surface cover other than plants (open soil, litter, bare rock etc.): 50; other soil attributes: 2; soil pH: 2; land use categories: 2; soil depth: 2			
Performance measure(s): presence/absence only: 0%; cover: 100%; number of individuals: 0%; measurements like diameter or height of trees: 0%; biomass: 0%; other: 0%			
Geographic localisation: GPS coordinates (precision 25 m or less): 2%; point coordinates less precise than GPS, up to 1 km: 48%; small grid (not coarser than 10 km): 43%; political units or only on a coarser scale (above 10 km): 7%			
Sampling periods: before 1920: 0%; 1920-1929: 0%; 1930-1939: 0%; 1940-1949: 6%; 1950-1959: 2%; 1960-1969: 3%; 1970-1979: 9%; 1980-1989: 19%; 1990-1999: 24%; 2000-2009: 18%; 2010-2019: 14%; unknown: 5%			
Information as of 2020-12-18 further details and future updates available from http://www.givd.info/ID/EU-00-034			

Acknowledgements

SIVIM was supported by the Spanish Ministry of Education and Science (Projects CGL2006-13421-C04 and CGL2009-13317-C03). BJ-A was funded by the Marie Curie Clarín-COFUND program of the Principality of Asturias-EU (ACB17-26) and the Spanish Research Agency (grant AEI/ 10.13039/501100011033).

E-mail and ORCID

Borja Jiménez-Alfaro (Corresponding author, jimenezalfaro@uniovi.es), ORCID: https://orcid.org/0000-0001-6601-9597
Xavier Font (xfont@ub.edu), ORCID: https://orcid.org/0000-0002-7253-8905