Received: 4 September 2022 | Revised: 9 February 2023 | Accepted: 10 February 2023

DOI: 10.1111/jvs.13179

Journal of Vegetation Science IAVS

REPORT

Bryophytes of Europe Traits (BET) data set: A fundamental tool for ecological studies

Kristel van Zuijlen[1] | Michael P. Nobis[1] | Lars Hedenäs[2] | Nick Hodgetts[3] | Juan A. Calleja Alarcón[4,5] | Belén Albertos[6] | Markus Bernhardt-Römermann[7,8] | Rosalina Gabriel[9] | Ricardo Garilleti[6] | Francisco Lara[4,5] | Chris D. Preston[10] | Josef Simmel[11] | Edi Urmi[12] | Irene Bisang[1,2] | Ariel Bergamini[1]

[1]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[2]Swedish Museum of Natural History, Stockholm, Sweden

[3]Cuillin Views, Isle of Skye, UK

[4]Centro de Investigación en Biodiversidad y Cambio Global, Universidad Autónoma de Madrid, Madrid, Spain

[5]Departamento de Biología (Botánica), Universidad Autónoma de Madrid, Madrid, Spain

[6]Botánica y Geología, Facultad de Farmacia, Universidad de Valencia, Valencia, Spain

[7]Institute of Ecology and Evolution, Friedrich Schiller University Jena, Jena, Germany

[8]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Germany

[9]Centre for Ecology, Evolution and Environmental Changes (cE3c), Azorean Biodiversity Group (ABG); CHANGE – Global Change, University of the Azores, Azores, Portugal

[10]Cambridge, UK

[11]Büro für Botanik und Mykologie, Oberndorf, Germany

[12]Department of Systematic and Evolutionary Botany, University of Zurich, Zurich, Switzerland

Correspondence
Kristel van Zuijlen, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland.
Email: kristel.vanzuijlen@wsl.ch

Co-ordinating Editor: Rune Halvorsen

Abstract

Bryophytes are a diverse group of organisms with unique properties, yet they are severely underrepresented in plant trait databases. Building on the recently published European Red List of bryophytes and previous trait compilations, we present the Bryophytes of Europe Traits (BET) data set, including biological traits such as those related to life history, growth habit, sexual and vegetative reproduction; ecological traits such as indicator values, substrate and habitat; and bioclimatic variables based on the species' European range. The data set includes values for 65 traits and 25 bioclimatic variables, containing more than 135,000 trait values with a completeness of 82.7% on average. The data set will enable future studies in bryophyte biology, ecology and conservation, and may help to answer fundamental questions in bryology.

KEYWORDS
bioclimatic variables, ecological indicator values, hornworts, IUCN, life-history traits, liverworts, mosses, Red List

Irene Bisang and Ariel Bergamini contributed equally to this work.

1 | INTRODUCTION

Species' traits have become increasingly prevalent for studying diverse ecological processes occurring at organismal, community and ecosystem scales (Funk et al., 2017). Although global plant trait databases such as TRY (Kattge et al., 2020) and Tundra Trait Team (Bjorkman et al., 2018) have increased the accessibility to trait data substantially, these databases consist largely of trait values for vascular plants, and bryophytes are severely underrepresented. Yet, a comprehensive compilation of bryophyte traits would enable tackling a range of important questions as a recent horizon-scan of fundamental questions in bryology has pointed out (Patiño et al., 2022).

Bryophytes are a taxonomically and ecologically diverse group of organisms consisting of mosses, liverworts and hornworts, with about 20,000 species worldwide (Goffinet & Shaw, 2009). They possess unique properties that differ from all other green land plants: their life cycle is dominated by the haploid gametophyte (rather than the diploid sporophyte as in other land plants), they disperse by wind-borne spores and/or vegetative propagules, they are mostly poikilohydric (i.e., the water content of bryophyte tissues is largely determined by that of the environment), and they are generally very small in stature (Goffinet & Shaw, 2009). This combination of characteristics has allowed bryophytes to thrive under a wide range of environmental conditions from tropical to polar regions, where they are an essential part of the species diversity and play an important role in ecosystem processes such as moisture retention or biogeochemical cycling (Lindo & Gonzalez, 2010; Turetsky et al., 2012; Ah-Peng et al., 2017; Permin et al., 2022).

Despite bryophytes being insufficiently represented in global trait databases as well as in trait-based studies (St. Martin & Mallik, 2017), bryologists and ecologists have always measured functional properties of bryophytes and attempted to group them according to life-history characteristics and/or their adaptations to the environment (e.g., life and growth forms [Mägdefrau, 1982; La Farge-England, 1996], life strategies [During, 1979, 1992; Kürschner & Frey, 2012], and ecological indicator values [Düll, 1991]). Building on such classification systems and given the need for bryophyte trait data, several regional bryophyte trait data sets and publications have emerged over the past two decades (Dierssen, 2001; Hill et al., 2007; Urmi, 2010; Henriques et al., 2017; Bernhardt-Römermann et al., 2018; Simmel et al., 2021). With the publication of the European Red List of mosses, liverworts and hornworts (Hodgetts et al., 2019), the opportunity arose to scale up from regional trait compilations to a continental trait data set of bryophytes. Thus, we present here the Bryophytes of Europe Traits (BET) data set, consisting of a variety of biological and ecological species traits (using "traits" in a broad sense) and bioclimatic variables, compiled for all 1,816 European bryophyte species.

2 | TRAIT COMPILATION

We compiled traits for all 1,816 European bryophyte species considered for the European Red List (Hodgetts et al., 2019). Primary sources included data gathered for the European Red List and several existing bryophyte trait compilations and data sets from different parts of Europe: life strategies (following During, 1979, 1992, available from Dierssen, 2001), Ellenberg indicator values (Düll, 1991, available from Ellenberg & Leuschner, 2010), BRYOATT (Hill et al., 2007), BryForTrait (Bernhardt-Römermann et al., 2018), BRYOTRAIT-AZO (Henriques et al., 2017), Flora indicativa (Urmi, 2010), and Ellenberg N values by (Simmel et al., 2021). As a baseline, nomenclature followed the Red List (Hodgetts et al., 2019). Species names were matched with species names in each individual trait source in an automated process, using available checklists (Hodgetts & Lockhart, 2020) and R packages (Cayuela et al., 2012). The resulting matched species names were thoroughly checked and corrected through expert knowledge. Because of extensive taxonomic and phylogenetic analyses in the European bryoflora since publication of the above-mentioned primary trait sources which led to, for example, species splits, merges, and generic rearrangements, we used only exact matches and homotypic synonyms, except for the life strategies compiled by Dierssen (2001). The latter consist of broad categories and closely related species are considered to fit under the same category.

We selected biological and ecological species' traits (using "trait" in a broad sense, see for example Dawson et al., 2021) that were mostly available from multiple sources, which would result in good coverage of the traits across European species, or were relatively easy to complete using bryophyte floras, species-specific literature, or expert knowledge. Nevertheless, we also included some traits that were rather incomplete because they may prove useful for some applications. Our selection of traits relates to life history and growth habit, sexual and vegetative reproduction, ecological indicator values, substrate, and habitat. If necessary, we adjusted or simplified traits to allow merging across multiple trait sources. As such, we recoded frequency traits (e.g., sporophyte frequency) as "rare," "occasional," and "common". Ecological indicator values were only merged on the condition that the scaling system was the same across multiple sources; for example, levels 1–9. For continuous traits such as mean spore diameter and mean shoot size, values were scaled to the same units and averaged for species across multiple sources. For categorical traits, simpler classifications were preferred over more complex ones. Traits for which a species can have more than one value, such as substrate type, were split into several binary traits: presence/absence on soil, deadwood, and so on. After compiling the traits from the primary sources as described above, we filled gaps in the data as much as possible by complementing trait values manually, using multiple European (occasionally extra-European) bryophyte floras, species-specific literature and expert knowledge (unpublished author sources). A list of the literature used to fill the gaps is provided in Appendix S1.

In addition to biological and ecological traits, we calculated bioclimatic characteristics for the European range of each species by overlaying their European range maps from the International Union for Conservation of Nature (IUCN) Red List assessments (Hodgetts et al., 2019) and bioclimatic maps of CHELSA version 2.1 (Karger

et al., 2017, 2021) at a spatial resolution of 30 arc seconds. For species extinct (EX) or regionally extinct (RE) according to the European IUCN Red List, IUCN maps of the historical ranges were used. In addition to the 19 traditional bioclimatic variables (Hijmans et al., 2005; Xu & Hutchinson, 2013), we included 6 growing degree days variables from the CHELSA BIOCLIM+ data set (Brun et al., 2022a; 2022b). Median values of the extracted bioclimatic variables were calculated for all 25 variables. The number of extracted grid cells is reported as an indicator of range size.

We conducted manual trait completion and expert-based plausibility checks using spreadsheets, whereas automated name matching, trait merging, compiling, data organization and cleaning, map processing, extraction of bioclimatic variables and exploratory data analyses were performed in R (version 4.1.1; R Core Team, R Foundation for Statistical Computing Vienna, AT) (R Core Team, 2021), using the packages *dplyr* (version 1.0.9), *stringr* (version 1.4.0), *Taxonstand*, *sf*, *terra* (version 1.6-7), *FactoMineR* and *missMDA* (Lê et al., 2008; Josse & Husson, 2016; Pebesma, 2018; Wickham, 2019; Cayuela et al., 2021; Hijmans, 2022; Wickham et al., 2022).

3 | DESCRIPTION OF THE DATA SET

The BET data set (doi: 10.16904/envidat.348; van Zuijlen et al., 2023) consists of more than 135,000 values for 65 traits and 25 bioclimatic variables for all 1,816 European bryophyte species. This includes all native or naturalized species in Europe as considered in the European Red List of Bryophytes (Hodgetts et al., 2019), minus one species that is now considered to have been misreported for Europe (Hodgetts & Lockhart, 2020). Later additions to or taxonomic or nomenclatural changes in the European bryoflora were not considered. The variables are grouped into biological traits, ecological traits, and bioclimatic variables (Figure 1), which are briefly described below. Detailed descriptions of all traits and variables can be found in Appendix S2 and following the data set's doi in the EnviDat repository. Overall, the data set is 82.7% complete (17.3% missing values), with varying degrees of missingness among traits (Figure S3).

The 28 biological traits include classifications related to life history and growth habit; that is, shoot size (**size**), life strategy (**lstrat**, **lstrat_e**; according to During, 1979, 1992), life form (**lform**, simplified from Mägdefrau, 1982), growth form (Glime, 2017), generation length (**genl**, following Bergamini et al., 2019), r vs K strategy (**rK**), dominant species (**dmnt**); whether species have permanent protonema (**pprot**) and whether species have rhizoids (**rhiz**). Further, traits related to sexual reproduction are mating type or sexual condition (**sex**, monoicous or dioicous), minimum, mean and maximum spore diameter (**smind**, **smeand**, **smaxd**), sporophyte frequency (**sfreq**), length of the sporophyte season (**sseas**), maximum length of the seta (**setmaxl**), capsule position (**capspos**), whether species have a peristome (**peri**) and whether species have dwarf males (**dwarfm**). Traits related to vegetative reproduction include whether species produce vegetative propagules (**vp**), whether species produce gemmae (**vp_gem**), tubers (**vp_tub**), bulbils (**vp_bul**), deciduous leaves and leaf tips (**vp_lea**) and/or deciduous branches and shoot tips (**vp_bra**), and the frequency (**vpfreq**) and maximum size (**vpmaxs**) of vegetative propagules.

The 36 ecological traits consist of Ellenberg indicator values for light (**indL**), temperature (**indT**), continentality (**indK**), moisture (**indF**), acidity (**indR**) and nutrient availability (**indN**), and additional indicator values for salt (**indS**) and heavy metals (**indHM**). Further, traits related to distribution include major biome (**biome**), eastern limit category (**eastlim**), lower elevational limit (**lim_low**), upper elevational limit (**lim_up**), elevational range (**lim_range**), estimates of the extent of occurrence and area of occupancy (**EOO_est**, **AOO_est**) and their uncertainty range (**EOO_unc**, **AOO_unc**). Traits related to substrate type include whether species are found on soil (**sub_so**), rock (**sub_ro**), bark (**sub_ba**), deadwood (**sub_wo**), epiphytically on

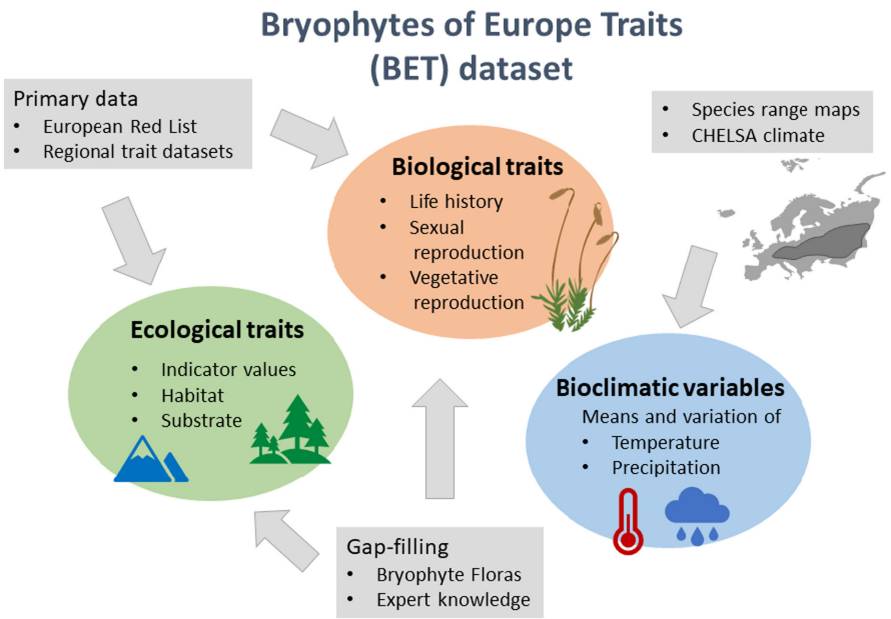

FIGURE 1 Schematic overview of the process of trait compilation for the Bryophytes of Europe Traits data set.

non-woody plant material (**sub_nw**; i.e., on leaves, other bryophytes or lichens) and on animal carcasses or dung (**sub_an**), on how many of these substrate classes species are found (**sub_sum**), and whether species are classified as epiphytes (**epiphyte**) or as aquatic species (**aquatic**). Traits related to habitats include whether species are found in wetlands (**hab_we**), forests (**hab_fo**), shrubland (**hab_sh**), grasslands (**hab_gr**), rocky areas (**hab_ro**) and artificial terrestrial habitats (**hab_ar**) (all derived from the IUCN habitat classification system), in how many of these habitat classes species are found (**hab_sum**), how strongly species are bound to forest habitats (**forest**), and two different scales of hemeroby (**hem_e**, **hemeroby**; i.e., whether a species is largely restricted to close-to-nature habitats, largely restricted to man-made habitats, or indifferent).

The 25 bioclimatic variables include the 19 traditional bio1 to bio19 variables (abbreviations renamed here): mean annual air temperature (**MAT**), mean diurnal air temperature range (**T_diurR**), isothermality (**T_iso**), temperature seasonality (**T_seas**), mean daily maximum air temperature of the warmest month (**Tmax_warmM**), mean daily minimum air temperature of the coldest month (**Tmin_coldM**), annual range of air temperature (**T_annualR**), mean air temperatures of the wettest, driest, warmest and coldest quarter (**T_wetQ**, **T_dryQ**, **T_warmQ**, **T_coldQ**), annual precipitation (**MAP**), precipitation of the wettest and the driest month (**P_wetM**, **P_dryM**), precipitation seasonality (**P_seas**) and mean monthly precipitation of the wettest, driest, warmest and coldest quarter (**P_wetQ**, **P_dryQ**, **P_warmQ**, **P_coldQ**). The six additional bioclimatic variables are number of growing degree days with daily mean air temperatures above 0°C, 5°C and 10°C (**ngd0, ngd5, ngd10**) and growing degree days heat sum above 0°C, 5°C and 10°C (**gdd0, gdd5, gdd10**). The number of extracted grid cells used to calculate each bioclimatic variable (**nc**) is reported as an indicator of range size.

To visualize how biological and ecological traits and bioclimatic variables relate to each other, we performed a principal component analysis (PCA) on continuous and ordinal categorical traits, with the bioclimatic variables and traits with more than 70% missing values added as supplementary variables. We imputed missing values using the regularized iterative PCA algorithm (Josse & Husson, 2012) and performed the final PCA on the completed data set of observed values for non-missing entries and predicted values for missing entries (Figure 2). The first and second dimensions, which together explain 36.74% of the variation, show that biome, indicator value for temperature (indT), upper elevational limit (lim_up), elevational range (lim_range), eastern limit (eastlim), extent of occurrence (EOO_est), forest, spore size (smind, smeand, smaxd) and hemeroby (including hem_e) contribute mostly to the multivariate trait space. Unsurprisingly, mean, minimum and maximum spore diameter are strongly related to each other but also to sporophyte frequency (sfreq) and sporophyte season length (sseas). Other traits that are closely associated to each other are biome and the indicator value for temperature, the two variables describing hemeroby, and elevational range, upper elevational limit and eastern limit. Mean annual temperature (MAT) and related variables (i.e., heat sum of growing degree days; gdd0, gdd5 and gdd10) are positively associated to indicator value for temperature and biome, and negatively associated to indicator value for continentality, while temperature seasonality is positively related to elevational range (Figure 2).

4 | DISCUSSION AND PERSPECTIVE

The BET data set contains categorical as well as continuous traits, provided as species averages for continuous traits and the most prevalent or only category for categorical traits in the European context. Except for some traits that act as measures of niche breadth, which are therefore indicative of some level of variation within a species (e.g., the number of substrate types on which a species is found), intraspecific variation is not included in this data set. Several studies have highlighted the importance of intraspecific variation in ecological studies (Des Roches et al., 2018). However, large-scale comparisons on intraspecific variation in bryophytes are mostly lacking, potentially because standardized protocols for measuring functional traits such as those that exist for vascular plants (Pérez-Harguindeguy et al., 2013) are not available for bryophytes this far. Nonetheless, because interspecific variation most likely overrides intraspecific variation, at least for categorical traits, the BET data set is useful for comparisons among species.

The data set is meant to stimulate and facilitate research on bryophyte biology, ecology, and conservation. Potential applications could be in finding answers to several of the fundamental questions in bryology, as highlighted by Patiño et al. (2022). Although the data set is limited to species occurring in Europe, it may be useful also for other regions of the northern hemisphere, since, for example, the majority of the North American bryophyte flora is identical to the European one (Frahm & Vitt, 1993; Ignatov, 2001). Furthermore, the data set may also be of help for ecologists who are less familiar with bryophytes; for example, to increase focus and functional resolution on the often-overlooked bryophytes in ecological studies (Lett et al., 2021).

The data set presented here provides an overview of the known traits and current status of all bryophyte species known to occur in Europe. Although many traits are completed for all or nearly all species, a few traits are highly incomplete (Figure S3). Depending on what the data set will be used for, problems with missing values could be solved by excluding traits with high proportions of missing values, or by using imputation algorithms to impute missing values (Penone et al., 2014; Johnson et al., 2021). Future work on this data set may include further completion of trait values, the addition of traits that are currently lacking (for example, more detailed morphological and physiological traits), and updating the status of species with unresolved taxonomic issues. Likewise, more accurate species distributions may be used instead of current range maps for improving bioclimate characterization, because the level of detail and completeness of current range maps varies among species. It is easily possible to track potential future changes in and additions to the data set. These can be made available in an uncomplicated way by publishing an updated

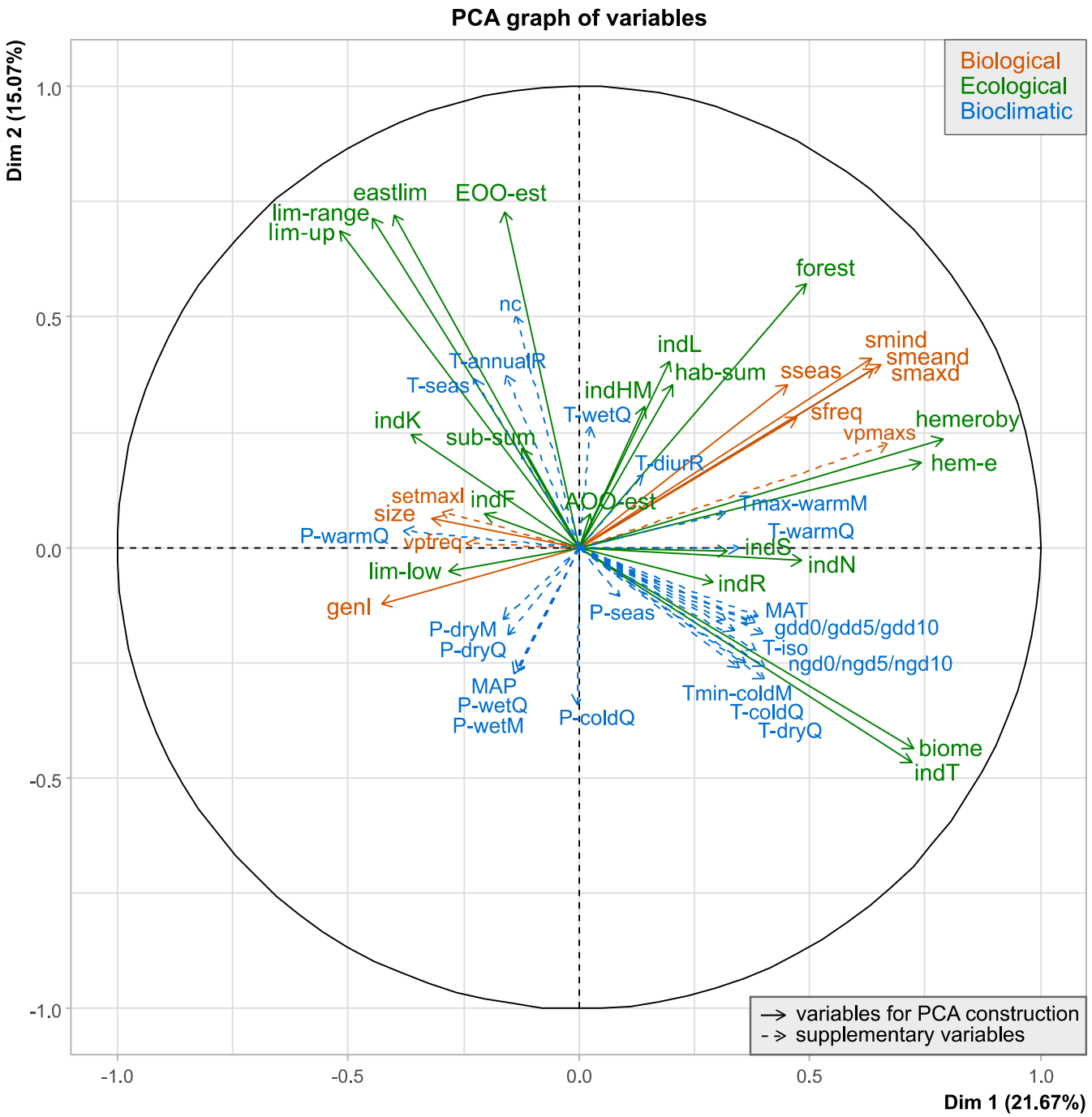

FIGURE 2 Results of a principal component analysis (PCA) showing the correlation circle for the continuous and ordinal categorical traits and bioclimatic variables for the first and second dimension, with imputed values for any missing values. The PCA is performed on biological and ecological traits that are more than 30% complete; with traits that are less than 30% complete and the bioclimatic variables added as supplementary variables. Trait and bioclimate abbreviations are explained in the Section 3 "Description of the data set"; underscores in the names are replaced with hyphens to improve readability.

version of the BET data set in the EnviDat repository, while also keeping the original data set available.

AUTHOR CONTRIBUTIONS

AB, IB and MPN conceived the idea; KvZ compiled the trait data with support from AB, IB and MPN; LH and NH verified the name matching across data sets; KvZ, AB, IB, LH and NH complemented gaps in the compiled trait data; AB, IB, LH and NH performed plausibility checks; MPN extracted the range maps and calculated the bioclimatic variables; all other coauthors contributed data and/or approved the final traits table; KvZ led the writing of the manuscript with support from all coauthors.

ACKNOWLEDGEMENTS

We thank Lars Söderström for checking and complementing trait values for liverworts, Markus Meier for providing a checklist of species names, IUCN for providing the species range maps, and the European Committee for the Conservation of Bryophytes (ECCB) for their invaluable contribution to the publication of the European Red List. Open access funding provided by ETH-Bereich Forschungsanstalten.

FUNDING INFORMATION

Funding was received from an internal grant of the Swiss Federal Research Institute WSL (project number: 202101N2105).

DATA AVAILABILITY STATEMENT

The data set presented here is available through the EnviDat repository at doi: 10.16904/envidat.348 (van Zuijlen et al., 2023).

ORCID

Kristel van Zuijlen https://orcid.org/0000-0001-6476-1982
Michael P. Nobis https://orcid.org/0000-0003-3285-1590
Lars Hedenäs https://orcid.org/0000-0003-1763-1696
Juan A. Calleja Alarcón https://orcid.org/0000-0002-6586-0939
Belén Albertos https://orcid.org/0000-0002-2116-5600
Markus Bernhardt-Römermann https://orcid.org/0000-0002-2740-2304
Rosalina Gabriel https://orcid.org/0000-0002-3550-8010
Ricardo Garilleti https://orcid.org/0000-0002-5977-2908
Francisco Lara https://orcid.org/0000-0002-1665-5277
Josef Simmel https://orcid.org/0000-0003-1483-2126
Irene Bisang https://orcid.org/0000-0002-0403-6196
Ariel Bergamini https://orcid.org/0000-0001-8816-1420

REFERENCES

Ah-Peng, C., Cardosa, A.W., Flores, O., West, A., Wilding, N., Strasberg, D. & Hedderson, T.A.J. (2017) The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. *Journal of Hydrology*, 548, 665–673. Available from: https://doi.org/10.1016/j.jhydrol.2017.03.043

Bergamini, A., Bisang, I., Hodgetts, N., Lockhart, N., Van Rooy, J. & Hallingbäck, T. (2019) Recommendations for the use of critical terms when applying IUCN red-listing criteria to bryophytes. *Lindbergia*, 2019(1), 1–6. Available from: https://doi.org/10.25227/linbg.01117

Bernhardt-Römermann, M., Poschlod, P. & Hentschel, J. (2018) BryForTrait – A life-history trait database of forest bryophytes. *Journal of Vegetation Science*, 29(4), 798–800. Available from: https://doi.org/10.1111/jvs.12646

Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Thomas, H.J.D., Alatalo, J.M. et al. (2018) Tundra trait team: a database of plant traits spanning the tundra biome. *Global Ecology and Biogeography*, 27(12), 1402–1411. Available from: https://doi.org/10.1111/geb.12821

Brun, P., Zimmermann, N.E., Hari, C., Pellissier, L. & Karger, D.N. (2022a) CHELSA-BIOCLIM+ a novel set of global climate-related predictors at kilometre-resolution. *EnviDat [Dataset]*. Available from: https://doi.org/10.16904/envidat.332

Brun, P., Zimmermann, N.E., Hari, C., Pellissier, L. & Karger, D.N. (2022b) Global climate-related predictors at kilometre resolution for the past and future. *Earth System Science Data*, 14(12), 5573–5603. Available from: https://doi.org/10.5194/essd-14-5573-2022

Cayuela, L., Granzow-de la Cerda, Í., Albuquerque, F.S. & Golicher, D.J. (2012) Taxonstand: An r package for species names standardisation in vegetation databases. *Methods in Ecology and Evolution*, 3(6), 1078–1083. Available from: https://doi.org/10.1111/j.2041-210X.2012.00232.x

Cayuela, L., Macarro, I., Stein, A. & Oksanen, J. (2021) Taxonstand: Taxonomic standardization of plant species names'.

Dawson, S.K., Carmona, C.P., González-Suárez, M., Jönsson, M., Chichorro, F., Mallen-Cooper, M. et al. (2021) The traits of "trait ecologists": An analysis of the use of trait and functional trait terminology. *Ecology and Evolution*, 11(23), 16434–16445. Available from: https://doi.org/10.1002/ece3.8321

Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T. et al. (2018) The ecological importance of intraspecific variation. *Nature Ecology and Evolution*, 2(1), 57–64. Available from: https://doi.org/10.1038/s41559-017-0402-5

Dierssen, K. (2001) Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophytorum Bibliotheca*, 56, 1–289.

Düll, R. (1991) Zeigerwerte von Laub- und Lebermoosen. In: Ellenberg, H., Weber, H., Düll, R., Wirth, V., Werner, W. & Paulissen, D. (Eds.) *Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica (Vol. 18)*, 3rd edition. Göttingen: Goltze, pp. 9–166.

During, H.J. (1979) Life strategies of bryophytes: A preliminary review. *Lindbergia*, 5(1), 2–18.

During, H.J. (1992) Ecological classification of bryophytes and lichens. In: Bates, J.W. & Farmer, A.M. (Eds.) *Bryophytes and lichens in a changing environment*. Oxford: Clarendon Press, pp. 1–31.

Ellenberg, H. & Leuschner, C. (2010) Zeigerwerte der Pflanzen Mitteleuropas. In: *Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht*, 6th edition. Stuttgart: Eugen Ulmer. Available from: https://doi.org/10.1111/j.1654-1103.2012.01443.x

Frahm, J.-P. & Vitt, D.H. (1993) Comparisons between the mossfloras of North America and Europe. *Nova Hedwigia*, 56(3–4), 307–333.

Funk, J.L., Larsen, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J. et al. (2017) Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews*, 92(2), 1156–1173. Available from: https://doi.org/10.1111/brv.12275

Glime, J.M. (2017) Adaptive strategies: growth and life forms. In: Glime, J.M. (Ed.) *Bryophyte ecology*. Michigan Technological University and the International Association of Bryologists, pp. 1–18. Available from: https://digitalcommons.mtu.edu/bryophyte-ecology/

Goffinet, B. & Shaw, A.J. (2009) In: Goffinet, B. & Shaw, J.A. (Eds.) *Bryophyte biology*, 2nd edition. Cambridge: Cambridge University Press.

Henriques, D.S.G., Ah-Peng, C. & Gabriel, R. (2017) Structure and applications of BRYOTRAIT-AZO, a trait database for Azorean bryophytes. *Cryptogamie Bryologie*, 38(2), 137–152. Available from: https://doi.org/10.7872/cryb/v38.iss2.2017.137

Hijmans, R.J. (2022) terra: Spatial data analysis. R package version 1.6-7.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. Available from: https://doi.org/10.1002/joc.1276

Hill, M.O., Preston, C.D., Bosanquet, S.D.S. & Roy, D.B. (2007) BRYOATT – Attributes of British and Irish mosses, Liverworts and hornworts.

Hodgetts, N. & Lockhart, N. (2020) Checklist and country status of European bryophytes – Update 2020. *Irish Wildlife Manuals* No. 123, 1–214.

Hodgetts, N., Cálix, M., Englefield, E., Fettes, N., Criado, M.G., Patin, L. et al. (2019) *A miniature world in decline: European Red List of mosses, liverworts and hornworts*. Brussels: IUCN, International Union for Conservation of Nature. Available from: https://doi.org/10.2305/IUCN.CH.2019.ERL.2.en

Ignatov, M.S. (2001) Moss diversity in the Western and northern Palearctic. *Arctoa*, 10(1), 219–236. Available from: https://doi.org/10.15298/arctoa.10.23

Johnson, T.F., Isaac, N.J.B., Paviolo, A. & González-Suárez, M. (2021) Handling missing values in trait data. *Global Ecology and Biogeography*, 30(1), 51–62. Available from: https://doi.org/10.1111/geb.13185

Josse, J. & Husson, F. (2012) Handling missing values in exploratory multivariate data analysis methods. *Journal de la Société Française de Statistique*, 153(2), 79–99.

Josse, J. & Husson, F. (2016) missMDA: A package for handling missing values in multivariate data analysis. *Journal of Statistical Software*, 70(1), 1–26. Available from: https://doi.org/10.18637/jss.v070.i01

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2017) Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 1–20. Available from: https://doi.org/10.1038/sdata.2017.122

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2021) Data from: Climatologies at high resolution for the earth's land surface areas. *EnviDat [Dataset]*. Available from: https://doi.org/10.16904/envidat.228.v2.1

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. et al. (2020) TRY plant trait database – Enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188. Available from: https://doi.org/10.1111/gcb.14904

Kürschner, H. & Frey, W. (2012) Life strategies in bryophytes – A prime example for the evolution of functional types. *Nova Hedwigia*, 96(1–2), 83–116. Available from: https://doi.org/10.1127/0029-5035/2012/0071

La Farge-England, C. (1996) Growth form, branching pattern, and perichaetial position in mosses: cladocarpy and pleurocarpy redefined. *The Bryologist*, 99(2), 170. Available from: https://doi.org/10.2307/3244546

Lê, S., Josse, J. & Husson, F. (2008) FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, 25(1), 1–18. Available from: https://doi.org/10.18637/jss.v025.i01

Lett, S., Jónsdottir, I.S., Becker-Scarpitta, A., Christiansen, C.T., During, H., Ekelund, F. et al. (2021) Can bryophyte groups increase functional resolution in tundra ecosystems? *Arctic Science*, 8(3), 609–637. Available from: https://doi.org/10.1139/as-2020-0057

Lindo, Z. & Gonzalez, A. (2010) The Bryosphere: an integral and influential component of the Earth's biosphere. *Ecosystems*, 13(4), 612–627. Available from: https://doi.org/10.1007/s10021-010-9336-3

Mägdefrau, K. (1982) Life-forms of bryophytes. In: Smith, A.J.E. (Ed.) *Bryophyte ecology*. Springer Netherlands: Dordrecht, pp. 45–58 10.1007/978-94-009-5891-3_2

Patiño, J., Bisang, I., Goffinet, B., Hedenäs, L., McDaniel, S., Pressel, S. et al. (2022) Unveiling the nature of a miniature world: A horizon scan of fundamental questions in bryology. *Journal of Bryology*, 44(1), 1–34. Available from: https://doi.org/10.1080/03736687.2022.2054615

Pebesma, E. (2018) Simple features for R: standardized support for spatial vector data. *The R Journal*, 10(1), 439–446. Available from: https://doi.org/10.32614/RJ-2018-009

Penone, C., Davidson, A.D., Shoemaker, K.T., di Marco, M., Rondinini, C., Brooks, T.M. et al. (2014) Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in ecology and evolution*, 5(9), 961–970. Available from: https://doi.org/10.1111/2041-210X.12232

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2013) New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(34), 167–234. Available from: https://doi.org/10.1071/BT12225

Permin, A., Horwath, A.B., Metcalfe, D.B., Priemé, A. & Rousk, K. (2022) High nitrogen-fixing rates associated with ground-covering mosses in a tropical mountain cloud forest will decrease drastically in a future climate. *Functional Ecology*, 36(7), 1772–1781. Available from: https://doi.org/10.1111/1365-2435.14088

R Core Team. (2021) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.r-project.org/

Simmel, J., Ahrens, M. & Poschlod, P. (2021) Ellenberg N values of bryophytes in Central Europe'. *Journal of Vegetation Science*. Edited by R. Halvorsen, 32, 1–20. Available from: https://doi.org/10.1111/jvs.12957

St. Martin, P. & Mallik, A.U. (2017) The status of non-vascular plants in trait-based ecosystem function studies. *Perspectives in Plant Ecology, Evolution and Systematics*, 27, 1–8. Available from: https://doi.org/10.1016/j.ppees.2017.04.002

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D. & Tuittila, E.-S. (2012) The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, 196(1), 49–67. Available from: https://doi.org/10.1111/j.1469-8137.2012.04254.x

Urmi, E. (2010) Bryophyta (Moose). In: Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W. et al. (Eds.) *Flora indicativa – Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*, 2nd edition. Bern: Haupt, pp. 283–310.

van Zuijlen, K., Nobis, M.P., Hedenäs, L., Hodgetts, N., Calleja Alarcón, J.A., Albertos, B. et al. (2023) Bryophytes of Europe traits (BET) dataset. *EnviDat [Dataset]*. Available from: https://doi.org/10.16904/envidat.348

Wickham, H. (2019) stringr: Simple, consistent wrappers for common string operations. R package version 1.4.0.

Wickham, H., François, R., Henry, L. & Müller, K. (2022) dplyr: A grammar of data manipulation. R package version 1.0.9.

Xu, T. & Hutchinson, M.F. (2013) New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. *Environmental Modelling and Software*, 40, 267–279. Available from: https://doi.org/10.1016/j.envsoft.2012.10.003

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Reference list of secondary sources from which trait data were compiled.

Appendix S2. Detailed explanations of traits and variables in the BET data set.

Appendix S3. Traits and bioclimatic variables ordered by completeness of trait values.

How to cite this article: van Zuijlen, K., Nobis, M.P., Hedenäs, L., Hodgetts, N., Calleja Alarcón, J.A., Albertos, B. et al. (2023) Bryophytes of Europe Traits (BET) data set: A fundamental tool for ecological studies. *Journal of Vegetation Science*, 34, e13179. Available from: https://doi.org/10.1111/jvs.13179