

REPORT

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

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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.

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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 (**dwarfsm**). 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

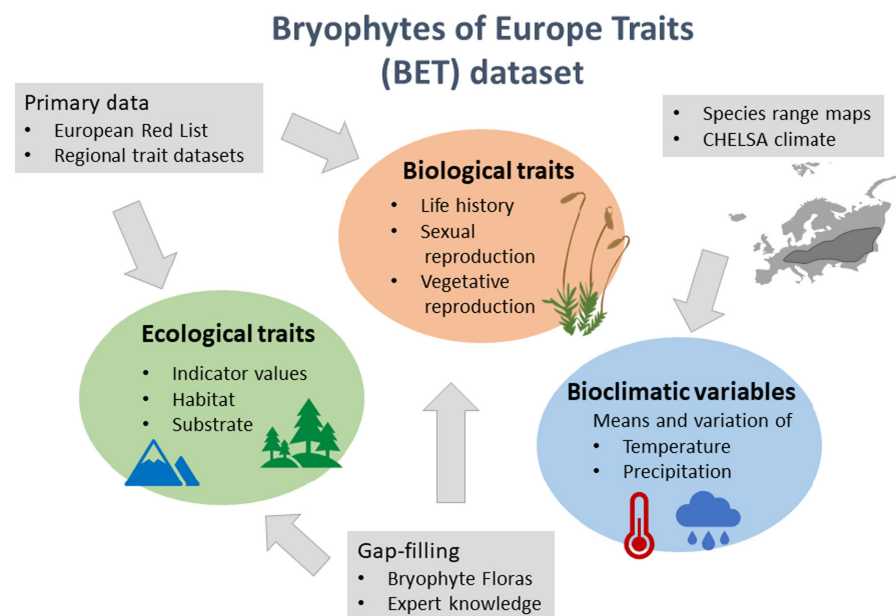


FIGURE 1 Schematic overview of the process of trait compilation for the Bryophytes of Europe Traits data set.



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 (**smin**, **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

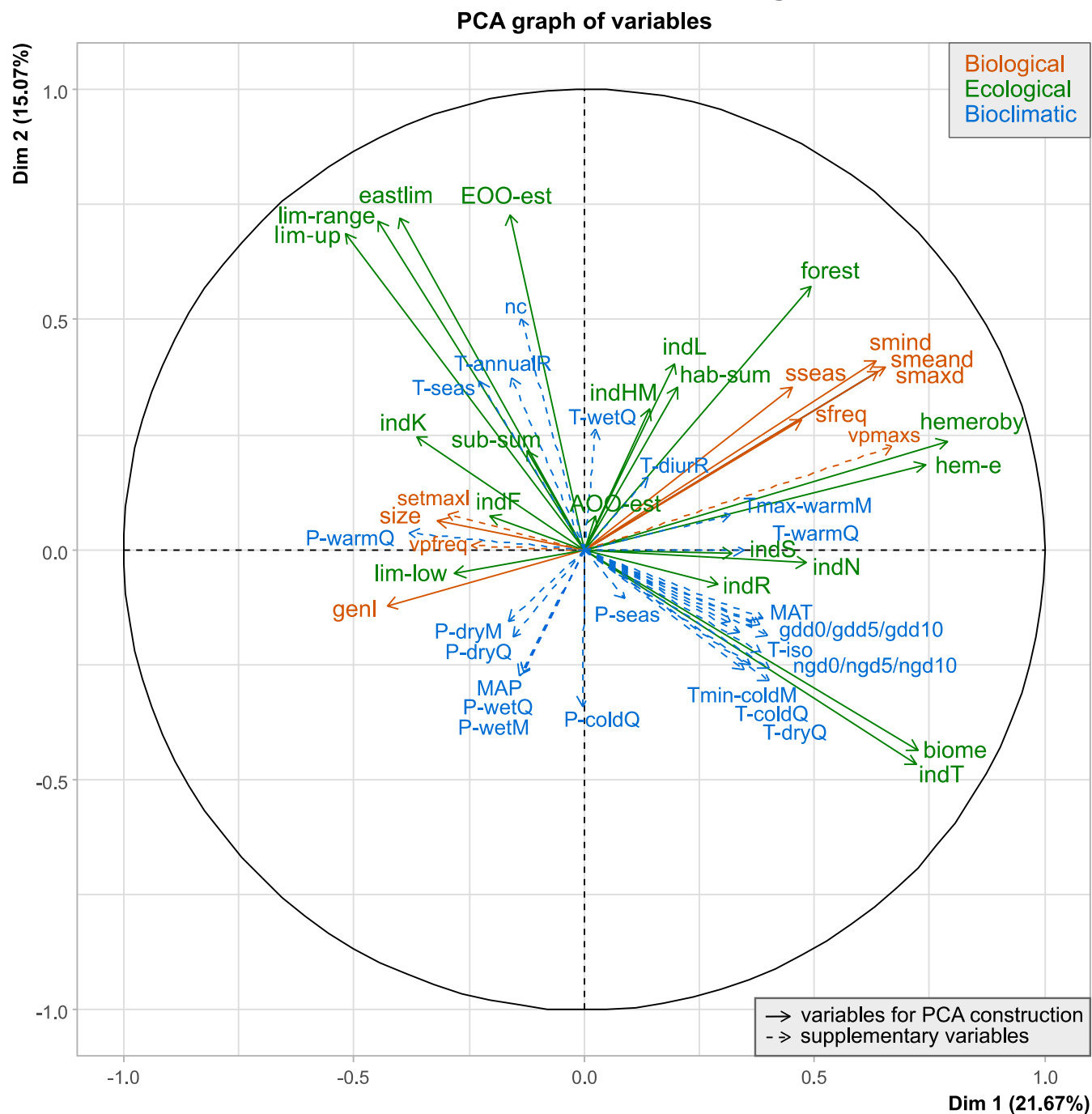


FIGURE 2 Results of a principal component analysis (PCA) showing the correlation circle for the continuous and ordinal categorical traits and bioclimatic variables for the first and second dimension, with imputed values for any missing values. The PCA is performed on biological and ecological traits 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.

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DATA AVAILABILITY STATEMENT

The data set presented here is available through the EnviDat repository at doi: [10.16904/envi.dat.348](https://doi.org/10.16904/envi.dat.348) (van Zuijlen et al., 2023).

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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.

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