RESEARCH ARTICLE

Journal of Vegetation Science IAVS

Diversity and distribution of Raunkiær's life forms in European vegetation

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Abstract

Aims: The Raunkiær's system classifies vascular plants into life forms based on the position of renewal buds during periods unfavourable for plant growth. Despite the importance of Raunkiær's system for ecological research, a study exploring the diversity and distribution of life forms on a continental scale is missing. We aim to (i) map the diversity and distribution of life forms in European vegetation and (ii) test for effects of bioclimatic variables while controlling for habitat-specific responses.

Location: Europe.

Methods: We used data on life forms of 8883 species recorded in 546,501 vegetation plots of different habitats (forest, grassland, scrub and wetland). For each plot, we calculated: (i) the proportion of species of each life form and (ii) the richness and evenness of life forms. We mapped these plot-level metrics averaged across 50 km × 50 km grid cells and modelled their response to bioclimatic variables.

Results: Hemicryptophytes were the most widespread life form, especially in the temperate zone of Central Europe. Conversely, therophyte and chamaephyte species were more common in the Mediterranean as well as in the dry temperate regions. Moreover, chamaephytes were also more common in the boreal and arctic zones. Higher proportions of phanerophytes were found in the Mediterranean. Overall, a higher richness of life forms was found at lower latitudes while evenness showed

more spatially heterogeneous patterns. Habitat type was the main discriminator for most of the responses analysed, but several moisture-related predictors still showed a marked effect on the diversity of therophytes and chamaephytes.

Conclusions: Our maps can be used as a tool for future biogeographic and macro-ecological research at a continental scale. Habitat type and bioclimatic conditions are key for regulating the diversity and distribution of plant life forms, with concomitant consequences for the response of functional diversity in European vegetation to global environmental changes.

1 | INTRODUCTION

Christen Christiansen Raunkiær (1934) proposed a classification system of vascular plant life forms based on the position and the degree of protection of the renewal buds during periods unfavourable for plant growth (i.e., cold and/or dry seasons). The system is based on the theory that the strategy for protecting the perennating organs reflects plant adaptation to cope with (micro)climatic conditions — particularly extremes, such as frost and drought. Despite various updates and advancements in the classification system and the addition of several subcategories within each life form (see e.g., Mueller-Dombois & Ellenberg, 1974; Galán de Mera et al., 1999), six main Raunkiær's life forms are most commonly used to classify vascular plants: therophytes, hydrophytes, geophytes, hemicryptophytes, chamaephytes and phanerophytes (Cain, 1950) (see Box 1 for further details on each life form).

Over several decades, the Raunkiær's system became one of the most commonly used life-form classification systems due to its simplicity and adaptability to various types of vegetation (Adamson, 1939; Cain, 1950). For these reasons, it has been widely applied to study the impacts of environmental change on vegetation (Harrison et al., 2010; Marini et al., 2011) and to study biogeographic patterns in plants (Danin & Orshan, 1990; Pignatti, 1994; Pavón et al., 2000; Irl et al., 2020). More recently, Raunkiær's life forms have also been proposed as indicators of plant trait syndrome driving local persistence strategies, particularly in insular systems (Ottaviani et al., 2020; Conti et al., 2022).

The Raunkiær's system is especially useful for classifying floras in seasonal climates where the growing season is determined by frost occurrence and/or water scarcity. Consequently, the diversity and distribution of life forms in European plant communities are expected to be strongly determined by climatic conditions. For example, the flora of continental temperate Europe is largely composed of hemicryptophytes with perennating buds at the ground surface (Leuschner & Ellenberg, 2017). This represents an effective adaptation to survive in herbaceous vegetation types characterised by winters with persistent snow cover and disturbed by mowing and grazing. Conversely, the strategy of chamaephytes (with buds rarely

higher than 25 cm above the ground surface) is well adapted to take advantage of the higher surface temperatures as well as high wind speeds and little snow cover (Bliss, 1962). As a result, it is expected that they will occur more frequently in alpine/tundra zones, where their morphology can provide an insulating microclimate that protects them from frost (e.g., in cushion-like plants) (Matteodo et al., 2013), as well as in the Mediterranean regions, where they can survive dry periods thanks to the high heteromorphism of transpiring organs (Montserrat-Martí et al., 2011).

At the same time, there is a strong association between the distribution of Raunkiær's life forms and specific habitat types since the latter can be defined based on the dominance of certain life forms (such as phanerophytes in forests and chamaephytes in heathlands; Chytrý et al., 2020) and because some habitats themselves are in turn largely driven by climate. Consequently, human impacts on European vegetation have strongly shaped life-form distribution, leading to a shift from mostly forest-dominated landscapes to open habitat types (Dengler et al., 2020). For this reason, assessing the response of the diversity of Raunkiær life forms to environmental factors necessitates accounting for different habitat types to control for potential dependence between certain habitats and life forms. Indeed, controlling for differences among major habitat types is key to better identifying patterns of functional trait variation along bioclimatic gradients (Kambach et al., 2023).

Understanding the diversity and distribution of plant functional traits and life forms has a broad appeal in macro-ecological and biogeographical research (Violle et al., 2014). The link between Raunkiær's life forms and vegetation type has been widely explored in the past century (Raunkiær, 1934; Adamson, 1939; Cain, 1950) and their variation along climatic gradients have been described in spatially-constrained areas (e.g., in elevational gradient studies; Irl et al., 2020; Pavón et al., 2000; Matteodo et al., 2013). Previous studies have also shown the large-scale distribution of plant traits associated with plant growth forms along climatic gradients (such as plant height; Moles et al., 2009; Olson et al., 2018) and how these changes are influenced, in part, by the differentiation between growth habits (Zanne et al., 2014). Nevertheless, to our knowledge, there have been only a few studies explicitly analysing large-scale

> **BOX 1   Overview of the main Raunkiær's life forms**
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> *Therophytes*. Annual plants, in which perennating organs correspond to the embryo contained in the seeds since no other organ survives the unfavourable season. Such life form is often associated with semi-arid and desert climates as the best effective adaptation to the driest conditions for plant growth or, more generally, to habitats with short windows of opportunity, either due to short growing seasons (e.g., steppe) or frequent disturbance events (e.g., arable land).
>
> *Hydrophytes*. Aquatic or semi-aquatic plants. They were originally classified by Raunkiær as a subgroup of cryptophytes ('hidden plants'; including also geophytes and helophytes). Hydrophytes include plants with free-floating buds at the water surface (e.g., *Lemna* spp.) as well as plants whose perennating organs are rooted in the soil (e.g., *Nymphaea* spp.). Helophytes—namely plants with submerged perennating organs but with emergent stems (e.g., *Typha* spp.)—are also included in the hydrophyte category in the present study.
>
> *Geophytes*. Herbaceous perennial plants bearing underground buds during the unfavourable season. Buds are borne by underground perennating organs such as rhizomes, tubers, bulbs or corms. These organs serve as a food supply enabling geophytes to have a rapid vegetative development compared to many other life forms when the adverse season ends. This life form is therefore more successful in Mediterranean climates and in temperate forest understories, where they can quickly sprout before canopy leaves are formed in the early spring. Geophytes can overlap with hemicryptophytes if the perennating buds are located at the base of the stem but still placed belowground (e.g., *Elytrigia repens*).
>
> *Hemicryptophytes*. Herbaceous perennial plants with buds located at the ground surface. Raunkiær's system further distinguishes between (1) non-rosette plants with absent basal leaves (e.g., *Silene dioica*); (2) partial rosette plants with both stem and basal leaves (e.g., *Ajuga reptans*); and (3) plants with basal leaves only (e.g., *Primula veris*). The hemicryptophytes are a very diverse group and constitute the most widespread life form in floras of humid temperate climates.
>
> *Chamaephytes*. Woody perennial plants with buds above the ground surface but lower than approximately 25 cm. Thus, buds of such plants are often protected by snow or by above-ground plant biomass present in the vegetation (including dead leaves on forest floors) during unfavourable conditions. The chamaephytes have a positive relationship with latitude and elevation proposed by Raunkiær, although they are widely representative of the subtropical evergreen and Mediterranean vegetation as well.
>
> *Phanerophytes*. Woody perennial plants with buds placed higher than 25 cm above the ground surface. Phanerophytes include large trees (e.g., *Fagus sylvatica*), shrubs (e.g., *Rhododendron* spp., *Viburnum* spp.) and woody lianas (e.g., *Hedera* spp.). Subcategories described by Raunkiær span from small shrubs (=nanophanerophytes) to very tall trees (=megaphanerophytes). The geographical distribution of such variants is linked to bioclimatic determinants of plant stature in the vegetation and within-species variability.

patterns of plant life forms within single biogeographical regions (Taylor et al., 2023) and habitat types (Blasi et al., 1990; Loidi et al., 2021).

As a result, we currently lack substantial knowledge about the geographic distribution of diversity in Raunkiær's life forms in Europe and how bioclimatic factors contribute to this distribution across different habitat types. Under the assumption that the Raunkiær's life forms represent life-history traits maximising organisms' performance under a given set of environmental conditions (Violle et al., 2007), we expect life forms to respond to both temperature and moisture gradients in various habitat types. Likewise, previous studies have shown that (continuous) trait syndromes follow considerable geographic variation at large spatial scales (e.g., Bruelheide et al., 2018) and that environmental conditions explain some of these patterns when accounting for responses within individual habitat types (Padullés Cubino et al., 2021; Kambach et al., 2023).

The recently assembled vegetation-plot databases covering large areas (Chytrý et al., 2016; Bruelheide et al., 2019; Sabatini et al., 2021) are an excellent means of exploring such patterns at the pan-European scale. They allowed us to check, for the first time, the distribution and diversity of plant life forms within and among different habitat types across a wide range of bioclimatic conditions and biogeographic regions located on the European continent. Here, we calculated the proportion of species for the six Raunkiær's life forms and the diversity (richness and evenness) of life forms in about half a million vegetation plots of forest, grassland, scrub and wetland habitats across Europe. We present maps of various metrics measuring life-form diversity at a resolution of 50 km × 50 km and modelled their response to climate while controlling for the main habitat categories.

2 | MATERIALS AND METHODS

2.1 | Vegetation data selection

The initial data set consisted of 1,508,375 vegetation plots from the European Vegetation Archive (EVA; Project 163; Chytrý et al., 2016; data retrieved 28 November 2022). Most plots were georeferenced with coordinate uncertainty of less than 5 km, while only 188,035

plots did not contain coordinate uncertainty information but were retained. We focused only on plots in Europe and excluded 1664 plots from Armenia, Azerbaijan, Cyprus, Georgia, Russia, Turkey and the Arctic Ocean islands.

The vegetation plots were then classified into four major habitat types based on species composition and cover: forest, grassland, scrub and wetland using the European Nature Information System (EUNIS) Habitat Classification expert system (Chytrý et al., 2020; ver. 2021-06-01). We excluded 549,238 plots that did not correspond to any of these four habitat types. Regarding the size of plots, we selected only plots in the range of 100–1000 m^2 for forests and 1–100 m^2 for the other habitat types and excluded 46,620 plots outside these ranges. However, we retained plots of unknown size because otherwise an important part of the geographic coverage would have been lost (see Večeřa et al., 2021).

To avoid oversampling of specific vegetation types, we stratified vegetation plots by geographic location and habitat. To this end, plots for each habitat type (at hierarchical level 3 of the EUNIS Habitat Classification system) were randomly selected with a minimum threshold distance of 8.6×10^{-4} degrees (corresponding to a resolution of approximately 100 m) using the 'clean_dup' function of the R package *ntbox* (Osorio-Olvera et al., 2020). This approach allowed us to maintain sufficient spatial variability in species composition across different level-3 EUNIS habitats while reducing the potential for pseudoreplication originating from spatially close vegetation plots with potentially similar composition. After spatial thinning, a total of 353,297 plots were excluded. In addition, 11,055 plots with less than 90% of the total number of species that could not be assigned to life forms were discarded. Finally, we obtained 546,501 vegetation plots used in our analysis (173,190 forests, 260,884 grasslands, 52,517 scrubs and 59,910 wetlands).

2.2 | Plant nomenclature and life-form data

Our vegetation data included a total of 10,281 taxa (hereafter referred to as species) classified as species, subspecies, hybrids and aggregates, excluding non-vascular plants and taxa identified at the genus level only. The taxonomy and plant nomenclature was unified according to the Euro+Med PlantBase (2023). We used species aggregates following the EUNIS-ESy expert system, which merges some related and similar species that are often not distinguished or misidentified (Chytrý et al., 2020). These species aggregates include some from the Euro+Med PlantBase and others defined in EUNIS-ESy. Information regarding species merging and the content of these aggregates can be found in the EUNIS-ESy repository (https://doi.org/10.5281/zenodo.4812736). Cover values belonging to the same species following nomenclature corrections were summed within the same plot and vegetation layer, while covers of the same species within different vegetation layers were merged using the formula proposed by Fischer (2015). This formula combines cover values of the same species occurring at different vegetation strata within the same

plot, assuming random overlap while ensuring that the combined cover values do not exceed 100% (Fischer, 2015). We used data on Raunkiær's life forms by Dřevojan et al. (2023) available at https://floraveg.eu. These data were compiled using several databases and floras (Săvulescu, 1952–1976; Horváth et al., 1995; Klotz et al., 2002; Tavşanoğlu & Pausas, 2018; Guarino et al., 2019; Kaplan et al., 2019), European broad-scale vegetation studies (Wagner et al., 2017; Giulio et al., 2020) and different online sources (e.g., CATMINAT, 2020, http://philippe.julve.pagesperso-orange.fr/catminat.htm; GreekFlora.gr, 2020, www.greekflora.gr). In the case of different assessments in original data sources, Dřevojan et al. (2023) critically revised them using additional sources and their knowledge.

The database covered 8883 species present across our vegetation data, including non-native species. Thus, we did not consider 1398 vascular plant species for which life-form data were not available. However, these species were very rare in our dataset, with a frequency ranging from 1 to 232 occurrences (mean = 8.3; SD = 17.1). Our final selection resulted in the following number of species categorised in one or more of the following life forms: therophytes (1816 species), hydrophytes (153 species), geophytes (959 species), hemicryptophytes (5006 species), chamaephytes (1020 species) and phanerophytes (909 species). We excluded epiphytes, represented by seven species only in our data. Each species was assigned to one (7916 species), two (954 species), or three (13 species) life-form categories, since plants of the same species can develop different life forms depending on site conditions (e.g., Médail et al., 2019).

2.3 | Calculating and mapping life-form diversity

We calculated two diversity metrics of plant life forms for each plot: (i) the proportion of species of each life form and (ii) the diversity of life forms, namely richness and evenness. Species assigned to more than one life form were counted as separate life forms at the plot level, dividing their cover by the number of life forms assigned to that species. Following Večeřa et al. (2021), we calculated the proportion of species of each life form as the number of species belonging to this life form divided by the total number of species recorded in the plot. Using proportions rather than the absolute species number decreases the effect of changes in species richness related to different plot sizes of sampled vegetation (Večeřa et al., 2021).

The community-level richness of plant life forms was defined as the count of life forms present in each plot. To calculate life-form evenness, we summed the cover of species belonging to the same life form in each plot and applied Pielou's evenness index using the 'diversity' function of the *vegan* R package (Oksanen et al., 2020). Pielou's index was calculated by dividing the Shannon index by the log-transformed number of life forms present in the plot. We then omitted from this analysis 7477 plots in which evenness could not be calculated because only one life form was present in the plot. Evenness was poorly correlated with richness (Pearson's $r = 0.21$). We used life-form richness and evenness rather than multidimensional

functional diversity metrics (such as functional evenness and divergence; see Villéger et al., 2008) as the latter are commonly applied when multiple traits are involved. Thus, since we only look at life forms as a single trait dimension, we consider the richness and evenness of life forms more intuitive metrics.

We prepared maps for the entire data set to visualise the geographical distribution patterns of life forms across Europe. Additionally, we generated habitat-specific maps by dividing the data set to examine patterns unique to each habitat type (Appendix S1). We assigned vegetation plots to a UTM grid ('EPSG:32633') of 50 km × 50 km resolution and calculated, for each metric, the arithmetic mean of the values from all the plots located in a given grid cell. Such spatial resolution, although coarse, accounts for poorly-sampled areas of Europe in our data (see e.g., Padullés Cubino et al., 2021; Večeřa et al., 2021), since single or few plots cannot properly represent vegetation data of one area. To deal with different sampling densities in the data set, we only displayed grid cells containing at least five plots for each metric analysed. We established the colour scale for each metric by grouping its values using *k*-means clustering. To better interpret the biogeographic distribution of values within each map, we assigned each cell to the European biogeographical regions (European Environment Agency, 2022) based on its geographical location and calculated arithmetic means and standard deviations of cell values across each region (see Appendix S2).

The patterns observed in our maps can be influenced by the species richness of vegetation plots. Thus, we prepared additional maps based on standardised effect sizes (SES) of the analysed metrics (Appendix S3). In each plot, we shuffled species identity 500 times without replacement for those species that contained life-form data by randomly sampling habitat type-specific species pools. Thus, we retained the same number of species and their abundances in each plot but with a different life-form composition at each repetition. We then re-calculated the expected values for all metrics at each repetition. We calculated SES as (observed value – mean of the expected values)/standard deviation of the expected values (Gotelli & McCabe, 2002). Thus, SES < −1.96 or >1.96 indicate significantly lower and higher values of a given metric than expected at random, respectively. We report maps obtained this way in Appendix S3. We also prepared alternative maps for the proportion of life forms by selecting the list of species found across all plots located in each 50 km × 50 km grid cell and calculating the proportion of each life form of species found in that cell (Appendix S3).

To better interpret the patterns found and to check for potential bias related to low overall richness in the plots, we further assessed which life form prevails in plots with low richness and evenness (see Appendix S4). To do so, we selected plots with richness and evenness equal to or lower than the 10th quantile of the diversity values in our data (10th quantile richness = 2; 10th quantile evenness = 0.2). This resulted in a subset of 69,585 and 54,178 plots for richness and evenness, respectively. Then, we summed the total relative cover of Raunkiær's life forms in each plot and selected the life form with the highest cover value in each plot. We plotted the maps with cells

of the grid containing at least five plots with low richness (≤ 2) and evenness (≤ 0.2) and highlighted separately those containing at least five plots where a given life form is dominant.

Spatial analyses were performed in R version 4.1.3 (R Core Team, 2022) using the *sf* package (Pebesma, 2018). Maps were drawn using the *ggplot2* package (Wickham, 2016).

2.4 | Statistical analyses

We modelled the effect of habitat types and bioclimatic variables on the response variables of the plot-level proportion of life forms and life-form diversity (richness and evenness). To reduce potential bias due to oversampled geographic areas, we subdivided our data set by further thinning plots to a minimum distance of ~2.5 km for each habitat type separately. The threshold distance of 2.5 km was selected to achieve a balance between data comparability and computation time in boosted regression trees (BRTs). This resulted in 143,426 plots used for modelling.

We utilised bioclimatic variables as continuous predictors. As we expected that some of the modelled response variables may change substantially across habitat types, we included habitat type (i.e., forest, grassland, scrub and wetland) as a single factor variable (with four levels) to control for the different proportions of life forms associated with different habitats. This allowed us to make separate predictions for each habitat type with respect to specific continuous bioclimatic predictors. We retrieved bioclimatic variables from the CHELSA data (version 2.1) at a resolution of 1 km. We considered bioclimatic variables available from CHELSA (Karger et al., 2017) and CHELSA-BIOCLIM+ (Brun et al., 2022). We used the variance inflation factor test for multicollinearity (with a maximum threshold of 10 for variable selection) using the 'vifstep' function of the R package *usdm* (Naimi et al., 2014). Finally, we included the following 13 bioclimatic variables as predictors: aridity index, mean winter temperature (BIO11), precipitation seasonality (BIO15), mean summer precipitation (BIO18), temperature seasonality (BIO4), mean climate moisture index, range of climate moisture index, growing-season length, growing-season temperature, potential net primary productivity, potential evapotranspiration and vapour pressure deficit. To account for potential inaccuracy in the coordinates and to match the minimum distance of the selected plots, we extracted bioclimatic variables at each plot by aggregating the 1-km rasters to 2.5-km resolution.

We fitted BRTs using the *dismo* R package (Hijmans et al., 2022). Decision trees are often used to model large-scale vegetation data because they can handle complex relationships and potential collinearities between predictors (Divíšek & Chytrý, 2018; Večeřa et al., 2019; Padullés Cubino et al., 2021). We used the Bernoulli distribution for modelling the proportion of life forms using the total number of species in each plot as a weighting factor to account for proportional data ranging between 0 and 1. We used the Poisson distribution for life-form richness to account for count data of life-form diversity (ranging between 1 and 6), while

evenness was modelled with a Gaussian distribution. Following Elith et al. (2008), we fitted BRT models and determined their optimal number of regression trees using a 10-fold cross-validation procedure using the 'gbm.step' function of the *dismo* package. We allowed the fitting of each regression tree on 50% of the data randomly sampled from the full training data set to avoid overfitting and improve the speed and accuracy of the model. Regression trees were gradually added to the model with a learning rate of 0.001. We set up a maximum of 10,000 regression trees with a complexity equal to 5 before stopping the cross-validation. Appendix S5 provides the plots displaying the average holdout residual deviance and its standard error as a function of the number of regression trees for each model.

We used the comparisons between fitted and observed values as evaluation statistics (=mean and standard error of the correlation and deviance at each fold) using the independent set of validation data (Hijmans & Elith, 2023). The relative influence (or 'contribution') of the predictor variables in each BRT model was estimated based on the number of times a predictor was selected for splitting, weighted by the squared improvement in the model resulting from each split and averaged across all trees (Elith et al., 2008). The relative influence of each variable was scaled to sum up to 100, with larger values indicating a stronger influence on the response.

We assessed spatial autocorrelation of model residuals by plotting correlograms of Moran's I using the 'eco.correlog' function of the *EcoGenetics* R package (Roser et al., 2017). Because we were interested in spatial autocorrelation at short spatial distances, for each model we randomly selected 250 plots that were at least 50 km apart from each other and calculated the spatial correlogram for all plots located within 250 km of the focal plot (Padullés Cubino et al., 2021). We allowed up to 2000 plots and selected at least 30 plots around each focal plot. The resulting correlograms were then summarised using loess (local polynomial regression fitting) with a span of 0.75. We detected a small positive signal of spatial autocorrelation at a distance of approx. 0.5 degrees in all of our models' residuals (see Appendix S5).

3 | RESULTS

3.1 | Maps of the proportion and diversity of life forms

Across Europe, the proportion of hemicryptophytes in vegetation plots was much higher than the proportion of other life forms, reflecting their dominance in the European flora (Figure 1). Hemicryptophytes represented, on average, more than two-thirds of the plot-level proportion of life forms across all plots analysed (mean=69.4%; SD=24.2%), followed by phanerophytes (mean=15.4%; SD=21%), geophytes (mean=15.2%; SD=13.2%), therophytes (mean=8.4%; SD=13.9%), chamaephytes (mean=7.3%; SD=11.5%) and hydrophytes (mean=2.3%; SD=9.5%). In some

cases, these proportions showed considerable variation across various European biogeographic regions (see Appendix S2).

The highest proportions of hemicryptophyte species were concentrated in continental temperate Europe and on the British Isles. Chamaephytes showed higher proportions in the Mediterranean as well as in the boreal region. Phanerophytes had the highest proportions in the Mediterranean and some Atlantic regions (e.g., in France). Patterns found for phanerophytes and chamaephytes were more pronounced in forest and scrub habitat types (Appendix S1), reflecting the more frequent occurrence of these life forms in such habitats. The proportion of therophytes was higher in the Mediterranean and in the temperate-dry zones of Europe (e.g., in the Pannonian region). Such a geographical pattern was more pronounced in grasslands than in other habitat types (Appendix S1). Geophytes had higher proportions at higher latitudes but did not show clear geographical patterns within each habitat (Appendix S1). Hydrophytes were more evenly distributed across European regions with no distinctive patterns, but clear hotspots were visible due to higher sampling intensity of wetland vegetation in some countries (e.g., Czech Republic, Lithuania and western Ukraine).

When analysing the geographical patterns of life-form diversity (Figure 2), we observed a gradient of increasing life-form richness from the northwest to the southeast of Europe. The median value of life-form richness across grid cells was 3.7 (range 2.2–5). Such a pattern was fairly consistent when analysed across different habitat types, especially in forests and grasslands (Appendix S1). The map of life-form evenness showed a less clear geographical pattern, with some of the lowest values located in parts of central and eastern Europe and the highest values in northern Europe, with an overall median of 0.55 (range 0.16–0.88). However, different habitat types displayed distinct geographic patterns of life-form evenness (Appendix S1). Specifically, forests and grasslands showed contrasting gradients, with evenness generally increasing with latitude in forests but decreasing in grasslands.

The observed geographical patterns in the maps were similar to the ones obtained with the null-model approach (Appendix S3) with averaged SES showing values correlated to those presented here (Pearson's $r > 0.5$) except for life-form richness (see Appendix S3). We also observed similar results in maps of the proportion of life forms when using the species pool of the individual grid cells (Appendix S3).

### 3.2 | Responses to bioclimatic predictors across habitat types

Habitat type was the predictor with the highest relative influence in the models for all the life forms, except therophytes (Figure 3), reflecting the distinction of life-form diversity compositions in the main habitat types. Consequently, many bioclimatic predictors analysed had a lower relative importance in the models. For example, for the proportion of hydrophytes, geophytes and phanerophytes, the habitat type had a relative influence exceeding 70%, strongly
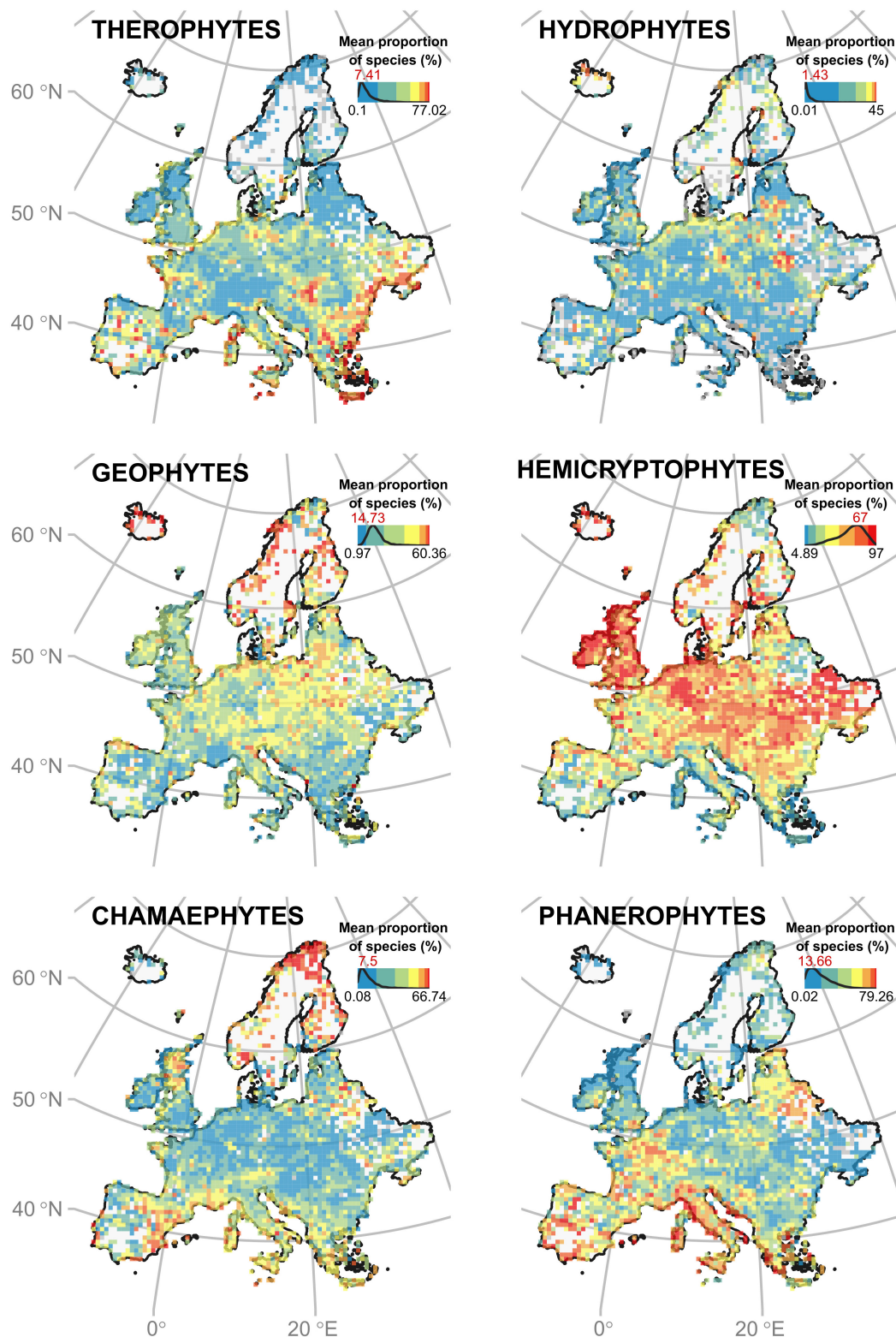
FIGURE 1 Maps of the mean proportion of Raunkiær's life forms (%) per spatial unit in European vegetation plots (including forest, grassland, scrub and wetland habitat types). The colour gradient ranges from low to high values (blue to red) of the proportion of species number averaged across vegetation plots in each 50 km × 50 km grid cell. The colour scale is obtained based on *k*-means clustering of mapped values. Only cells with at least five plots used for the calculation are displayed on the map. Grey cells correspond to cells where no plots containing a given life form were present (mean value equal to zero). The legend reports the distribution of values across the data set (black curve). The numbers below the legend represent the minimum and maximum values, while the number in red on top of the legend corresponds to the median across Europe.
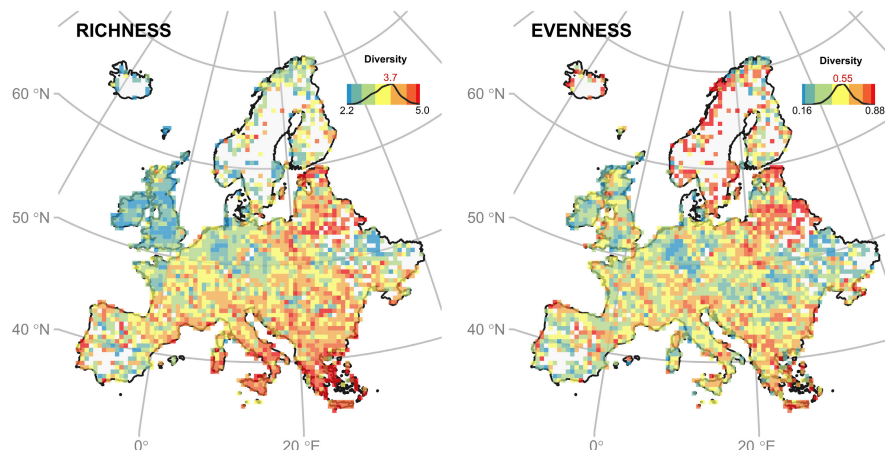
FIGURE 2 Maps of the mean richness and evenness of life forms per spatial unit of 50 km × 50 km in European vegetation plots (including forest, grassland, scrub and wetland habitat types). See the caption of Figure 1 for additional details.
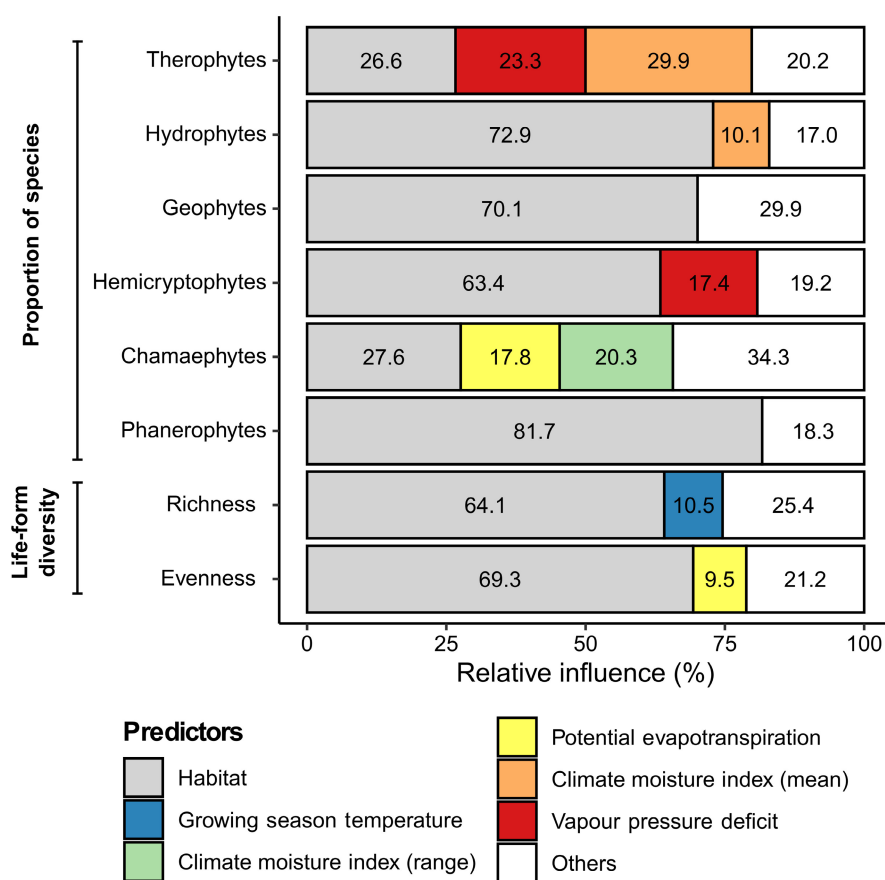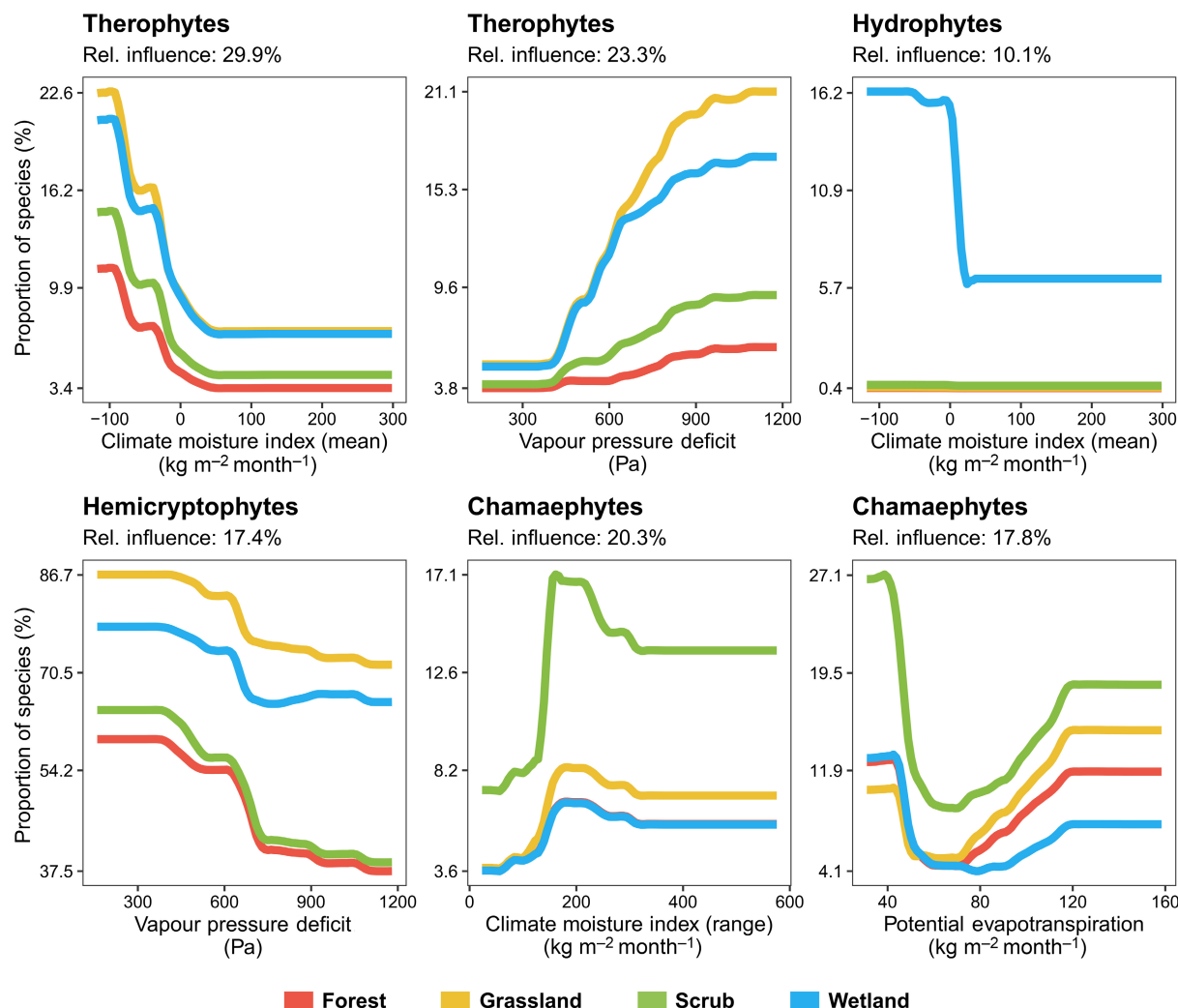

FIGURE 3 Relative influence of most relevant predictors in boosted regression trees (BRT) models. The score values of each model are scaled so that they sum up to 100%. Habitat type (either forest, grassland, scrub or wetland habitat type; in grey) was nearly always the most influential predictor across analysed models. Continuous predictors are represented with non-neutral colours. Only those variables whose relative influence was >9% for each model are shown. The remaining predictors are not shown (='other'; in white)

determining the proportion of life forms in the plots, independently from bioclimatic conditions (see Appendix S5). Habitat type was also key to distinguishing life-form diversity, with higher estimated richness in forests and scrub than in grasslands and wetlands and with lower evenness in grasslands than in other habitat types (see Appendix S5).

Nevertheless, some climatic predictors played a key role in shaping the distribution of some analysed metrics (Figure 4). The proportion of therophytes generally decreased with climatic moisture index and increased with vapour pressure deficit. In contrast, hemicryptophytes decreased with increasing vapour pressure deficit. Hydrophytes were also relatively less frequent in wetlands with a higher climate moisture index, indicating potentially higher diversity of aquatic plants under drier conditions. The proportion of chamaephytes was highest at intermediate values of the climatic moisture index (hump-shaped relationship) and it was lowest at intermediate values of potential evapotranspiration. Life-form richness and evenness were positively linked to growing-season temperature and

FIGURE 4 Results of the boosted regression trees (BRT) models showing the effect of most relevant bioclimatic predictors (relative influence >10%) on the proportions of species belonging to different life forms in European vegetation. Lines represent smoothed curves of the fitted functions based on local polynomial regression for the focal variable. Lines are predicted for each habitat separately by keeping constant other continuous variables present in the model using their average across the data. The values on the y-axis are back-transformed to the original values following logit transformation. Appendix S5 reports partial dependence plots across all life forms, the evaluation statistics and the number of observations used to fit each model.

potential evapotranspiration, respectively (see Appendix S5), but such climatic variables showed low relative influence on the prediction of these metrics (<11%).

4 | DISCUSSION

4.1 | Proportion of life forms in European vegetation

We identified distinct geographical patterns showing how local species richness (i.e., alpha diversity) in vascular plants in European vegetation is subdivided between different Raunkiær's life forms. We suggest that suitable conditions for a given plant life form are associated with higher species numbers of that life form and this mechanism links local adaptation to plant diversity within single life forms. Hemicryptophytes, for

example, are the group with the highest number of species in European vegetation. This success is attributed to the remarkable taxonomic and functional diversity within this group. It includes plants with renewal buds protected by cauline foliage at one end to those with rosette foliage protection at the other, with considerable variation in between (Cain, 1950). Indeed, the northern, central and eastern European climate (characterised by cold winters) supports the strategy of perennial herbs with renewal buds located at the soil surface (Leuschner & Ellenberg, 2017).

Our results overall highlighted the importance of habitats in determining the distribution of life forms in Europe. The diversity of phanerophyte and hydrophyte species, for example, was mostly driven by the presence or absence of forests and wetlands, respectively, while climatic variables showed lower importance. The direct effect of the bioclimatic drivers had a minor importance for most life forms compared to habitat types. Potentially, this is

because habitats: (i) may depend upon the dominance and presence of specific growth forms (e.g., trees in forests); (ii) may be influenced by climate themselves; and (iii) indirectly capture key factors neglected in our models that likely contribute to explaining the occurrence of life forms in the vegetation, such as disturbance (Midolo et al., 2023) and microclimate (see e.g., De Frenne et al., 2021).

We acknowledge that modelling life-form proportions (and potentially other trait dimensions) within vegetation presents a challenge due to the non-independence of certain habitat types and plant strategies. However, we still revealed that the diversity of life forms responds significantly to climatic variables within different habitat types. Our results overall indicate that moisture-related variables contribute more than temperature to the life-form distribution at the continental level across Europe. Consistently, Lancaster and Humphreys (2020) showed that growth forms in general explain very little of the thermal tolerance variability of plants worldwide, suggesting that life-form distribution might be more influenced by other factors than temperature. Therophytes specifically represented an exception in our results as they were more related to climatic factors than habitat type. We found a larger proportion of therophytes with increasing vapour pressure deficit and decreasing climatic moisture index, which represent key bioclimatic factors for drought-induced mortality in plants (Grossiord et al., 2020). Therophytes represent indeed the most extreme adaptation to long summer droughts in Mediterranean climates. Short-lived plants completing their life cycle during brief seasonal windows of opportunity also represent the best strategy in more disturbed habitats (Midolo et al., 2023). Conversely, more stable systems with higher moisture and productivity become more favourable for other life forms, such as hemicryptophytes. Such a pattern is consistent with studies addressing variation in life-form composition along environmental gradients at smaller spatial extents (Danin & Orshan, 1990; Giménez et al., 2004; Irl et al., 2020).

Although the current distribution of life forms is affected by local climatic conditions and distribution of habitat types, we argue that historical factors can also interact with climate to explain the variation in species number within life forms. The European flora is characterised by a much larger proportion of herbaceous (mostly hemicryptophytes) than woody (phanerophytes) species, which is, to a large extent, a consequence of the impoverishment of the woody flora during Pleistocene glaciations (Huntley, 1993; Eiserhardt et al., 2015). For instance, the higher number of phanerophyte species found in southern Europe might reflect the role of the last glacial period limiting the current distribution and diversity of tree and shrub species at higher latitudes in European forests (Svenning & Sandel, 2013; Médail et al., 2019; Loidi et al., 2021). Other historical factors can also include past dispersal events from different biogeographic regions. For example, the strong influence of sub-Mediterranean floristic elements in the Pannonian Basin (Fekete et al., 2016; Chytrý et al., 2022) can explain the large number of therophyte species we observed in this region. Yet, Pannonian vegetation specifically is also characterised by grasslands with many

open patches/gaps due to droughts and sandy soils favouring therophytes, which makes it difficult to disentangle historical factors from present-day bioclimatic drivers.

4.2 | Life-form diversity

Our maps identified clustered, yet irregularly distributed, life-form diversity values in the geographic space, with overall similar values across the main biogeographic regions (see Appendix S2), suggesting that several unaccounted factors could affect their distribution. Randomness in the distribution of life-form diversity appeared especially in the maps based on null models (Appendix S3). Nevertheless, the results of our model suggest that both life-form richness and evenness strongly depend on the habitat type under consideration. Forest and scrub habitat types had a slightly higher richness of life forms, mostly because of the presence of trees and shrubs, which are rarer in herbaceous habitats (grasslands and wetlands). We also found positive relationships between the temperature of the growing season and temperature seasonality with life-form richness (Appendix S5). This result is consistent with the positive coupling between functional diversity and climate seasonality observed by Boonman et al. (2021) in European grasslands and with the general role of warmer temperatures and seasonality in supporting higher plant diversity globally (Scheiner & Rey-Benayas, 1994). We argue that this is a consequence of greater seasonality supporting different life forms coping with different temperatures over the year and allowing the coexistence of life forms that can exploit different temporal niches at the same site without outcompeting each other.

Evenness exhibited a more random spatial distribution than richness. In most vegetation plots analysed, across Europe low evenness was nearly always associated with plots dominated by hemicryptophyte species (see Appendix S3), highlighting the prevailing role of hemicryptophytes in shaping life-form diversity. Evenness of life forms was generally lower in grassland than in other habitat types—and this potentially reflects the dominance of single life forms (mostly hemicryptophytes) in this habitat type. In addition, evenness was positively coupled with potential evapotranspiration. We expected evenness to decrease with potential evapotranspiration given the environmental filtering role of climate on plant trait evenness (Le Bagousse-Pinguet et al., 2017), but our results suggest instead that drier areas with higher evapotranspiration can harbour more life forms (therophytes, chamaephytes) other than hemicryptophytes, potentially allowing the formation of more even communities following niche partitioning by different life forms.

5 | CONCLUSIONS

Our study represents, to our knowledge, the first work to explore the distribution of Raunkiær's life forms at the community level across

Europe. Previous studies have mostly used the Raunkiær's system at local or regional levels (e.g., Blasi et al., 1990; Irl et al., 2020; Loidi et al., 2021), but never studied the distribution of plant life forms at a continental extent. Our maps depict a large variation in the proportions of species and life-form diversity across Europe and within the four major habitat types considered.

The results of our statistical models highlight the complex interplay between habitat types and bioclimatic predictors, particularly those related to humidity. In general, our maps revealed a considerable variation in analysed patterns when comparing the habitat types. This result is consistent with habitat specificity of community-level functional and phylogenetic differentiation (Padullés Cubino et al., 2021; Večeřa et al., 2021, 2023; Kambach et al., 2023), highlighting the need to account for habitat-specific responses when projecting models of the European vegetation in time and space. We also provided an assessment of how different environmental variables predict such patterns. Our models confirmed the key role of humidity in shaping the distribution of Raunkiær's life forms at the continental extent, as this is one of the main determinants for the growing season in most diverse European biogeographical regions (i.e. the Mediterranean and temperate-dry regions).

By identifying geographic patterns and environmental drivers of the diversity of plant life forms, we provided new insights into previous endeavours mapping functional diversity on continental or global scales (see e.g., Butler et al., 2017; Šímová et al., 2018). We believe these maps will support the interpretation of results obtained in studies focussing on large-scale patterns of taxonomic and functional diversity of European plants. In addition, the modelled relationships we obtained with environmental predictors open new questions on how the distribution of life forms is responding to global environmental changes and how these would scale up at the regional and landscape level. Finally, the metrics of life-form diversity used here can be applied to predict general trends of biodiversity change focusing on Raunkiær's system (or more complex functional groups) as modelling units for various modelling approaches, such as bioclimatic envelopes (Broennimann et al., 2006) and dynamic vegetation models (Boulangeat et al., 2012).

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DATA AVAILABILITY STATEMENT

The maps are freely available in the raster format at the Zenodo data repository (https://doi.org/10.5281/zenodo.10441454). The Raunkiær's life-form data for species of the European flora are available at the FloraVeg.EU website (https://floraveg.eu/download).

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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. Maps of habitat types.

Appendix S2. Average values of grid cells for different biogeographic regions.

Appendix S3. Alternative maps for life forms.

Appendix S4. Dominant life forms in plots with low diversity of life forms.

Appendix S5. Additional information on BRT models.