Extinction risk of European bryophytes predicted by bioclimate and traits

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1. Introduction

The earth is facing a global biodiversity crisis, with 75 % of the land surface significantly altered by human impacts and more species threatened by global extinction than ever before (IPBES, 2019), the latter being referred to as the sixth mass extinction (Ceballos et al., 2015; Chichorro et al., 2022). However, extinction risk, the quantification of how likely a species is to go extinct in the foreseeable future, is not randomly distributed among species, space and phylogeny (Davies, 2019; Tanentzap et al., 2020). Multiple studies have shown that species threatened with extinction are characterised by certain traits (Chichorro et al., 2022; Foden et al., 2013; Hagge et al., 2021; Pearson et al., 2014), and extrinsic factors such as habitat alterations, biological invasions, and climate change have been shown to threaten species (Fréville et al., 2007; Murray et al., 2011). For instance, certain geographical regions and life forms are linked to ongoing extinction in seed plants (Humphreys et al., 2019) and species with a small geographic range and narrow habitat breadth are generally more vulnerable to extinction (Chichorro et al., 2019). Understanding why and how species are threatened is crucial for nature conservation and to prevent further extinctions from happening. Furthermore, modelling approaches using traits and extrinsic factors can be used to predict the extinction risk of data-deficient species in Red List assessments (Bland et al., 2015; Davidson et al., 2012; Luiz et al., 2016).

To address this, we used random forest models to study which bioclimatic variables and ecological traits are important predictors for extinction risk in European bryophytes. We hypothesized that species with a high extinction risk have a short life span, low dispersal capacities, and are more likely specialists than generalists in terms of ecological traits and bioclimate. Overall, we found bioclimatic variables to be the most important predictors for extinction risk, most notably precipitation seasonality, and related ecological traits such as continentality and elevational range. Important biological traits were plant size, life strategy and sporophyte production. In general, species living at climatic extremes and/or those with a narrow environmental range are more likely to be threatened. In addition, small-sized species and/or species with low reproductive effort and/or larger spore size are more likely to be threatened. Our findings imply that climate change may become an important driver of bryophytes extinction risk and that biological and ecological traits will be most relevant for species in coping with future threats.

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the risk assessments (Chichorro et al., 2019; Hernández-Yáñez et al., 2022).

Recently, the complete European bryophyte flora, i.e., mosses, liverworts, and hornworts, has been assessed against the IUCN criteria to produce a Red List of all European bryophyte species (Hodgetts et al., 2019). Bryophytes are small in size but constitute a large and diverse lineage of land plants that are present in all terrestrial and freshwater habitats and possess unique traits that distinguish them from other green land plants (Shaw et al., 2011; Stanton and Coe, 2021). Their life cycle is dominated by the haploid gametophyte phase (as opposed to seed plants that are dominated by the diploid sporophyte phase) and they disperse often easily by small wind-borne spores and/or through vegetative propagules. Most species are poikilohydric, i.e., they lack a conductive system to transport water and assimilates and therefore depend on water availability in their environment (Goffinet and Shaw, 2009; Brodribb et al., 2020). As a result, many species are desiccation-tolerant and can withstand extreme stresses when desiccated (Proctor et al., 2007; Stark, 2017). All these characteristics allow them to inhabit places where vascular plants often cannot grow such as rock surfaces or the bark of trees. Despite their stress tolerance and versatility, 22.5% of the bryophyte species assessed for the European Red List are considered threatened by extinction (382 species; listed as Vulnerable, Endangered or Critically Endangered) and another 10.1% (173 species) are considered Near Threatened (Hodgetts et al., 2019). Furthermore, not included in these numbers are 93 species listed as Data Deficient (5.2% of the assessed species), indicating that the actual number of threatened species is likely higher.

Important aspects of bryophyte life-history strategies that may be related to extinction risk include trade-offs between different reproductive modes (sexual vs asexual), in the production of few, large sporophytes vs many, small spores, in the survival of harsh conditions through avoidance (as diaspores) vs tolerance, and in the potential life span, which is negatively correlated to reproductive effort (During, 1992, 1997; Kürschner and Frey, 2012). For example, previous works have shown that there is a tendency of species with a relatively short life span to be rare (Longton and Heddderson, 2000; Söderström and During, 2005). Despite their generally high dispersal capacities (Patioño and Vanderpoorten, 2018), bryophytes are predicted to lag behind in coping with current and future climate change (Zanatta et al., 2020) and there is evidence that dispersal and/or establishment limitation does occur, at least in some species (Kimmerer, 2005; Laaka-Lindberg et al., 2000; Lölbel et al., 2006). Within bryophytes, as much as 50–60% of species are dioecious, i.e., sexes on separate individuals (gametophytes), which is unique among land plants as only 6% of flowering plants are sporophytically dioecious (Glime and Bisang, 2017; Haig, 2016; Renner and Ricklefs, 1995). As female and male reproductive organs need to be relatively close to each other for successful fertilization, the dioecious mating type hampers sexual reproduction and eventually spore dispersal (McDaniel and Perroud, 2012; Villarreal and Renner, 2013), affecting rarity patterns (Laaka-Lindberg et al., 2000; Longton, 1992) and potentially extinction risk. Yet, also vegetative reproduction seems to be an important trait, as formation of vegetative propagules are more common among dioicus bryophytes (During, 2007), and non-endemic species are more likely to produce asexual propagules (Carter et al., 2016).

With increasing global change pressures, it has become clear that across taxa, specialist species are declining and being replaced by generalist species, resulting in biotic homogenization such as functional homogenization (Clavel et al., 2011; Rolfe et al., 2023; Tordoni et al., 2019). This pattern arises from specialist species being highly adapted towards certain habitats that are under threat, while generalist species, i.e., species with broad ecological niches, can thrive across a range of environmental conditions. Competition between rare and common bryophytes could also play a role in the restriction of many rare species to specialized habitats (Cleavitt, 2005). In addition, climate change is causing changes in species distributions, with species expanding to higher elevations and latitudes (Bergamini et al., 2009; Chen et al., 2011; Vitasce et al., 2021) leading to known or predicted extinction risks (Foden et al., 2013; Patino et al., 2016; Thuiller et al., 2005). Bioclimatic variables provide an ecologically meaningful set of climate variables (Hijmans et al., 2005; Karger et al., 2017) widely used for such analyses.

In this study, we aim to disentangle which biological and ecological traits and bioclimatic variables relate to the extinction risk of the complete European bryophyte flora by means of Random Forest models. We hypothesize that threatened species, i.e. those that have a high extinction risk 1) have a life history strategy related to a short life span and low dispersal capacities, i.e. low spore or vegetative propagule production and/or large spore size, and 2) are more likely to be specialists than generalists, i.e. have strict habitat preferences and high or low (but not intermediate) indicator and bioclimatic values. Identifying the traits and bioclimate that make a bryophyte prone to extinction will increase our understanding of why species are threatened, thereby highlighting conservation needs, which may accelerate the design of adequate and efficient conservation actions.

2. Methods

2.1. Data preparation

We used the Bryophytes of Europe Traits (BET) dataset, a compilation of 65 biological and ecological traits and 25 bioclimatic variables for all 1816 bryophytes native or naturalized to Europe (Van Zuijlen et al., 2023a, 2023b). Biological traits in the dataset are related to life history, growth habit, sexual and vegetative reproduction; ecological traits include indicator values, substrate and habitat classifications; and the bioclimatic variables are based on the species’ European range. The extinction risk of these species was recently assessed following IUCN methodology (IUCN, 2022) in the European Red List (Hodgetts et al., 2019). The BET dataset follows the taxonomy, nomenclature, and Red List category from Hodgetts et al. (2019) and Hodgetts and Lockhart (2020). Here, we used a dichotomous response variable to represent extinction risk: species with category VU (vulnerable), EN (endangered), CR (critically endangered), RE (regionally extinct) or EX (globally extinct) were considered “threatened” (n = 389) while species with category LC (least concern) or NT (near threatened) were considered “non-threatened” (n = 1313) (IUCN, 2022). Species with category NA (not applicable) or DD (data deficient) were excluded from the data, resulting in a total of 1702 species included in the analysis.

We used Random Forest models to explore which traits are important in explaining extinction risk. Random Forest (RF) is a machine learning method that combines the predictions of a multitude of classification trees into a robust model (Breiman, 2001). Advantages of RF are high predictive accuracy and the ability to model complex interactions and non-linear relations (Cutler et al., 2007). RF starts with the selection of many bootstrap samples from the data to which single classification trees are fit. Observations that do not occur in a bootstrap sample are referred to as out-of-bag (OOB) observations. Each tree is used to predict the OOB observations, and the predicted class of an observation is calculated by majority vote of the OOB predictions. Error rates are computed for each observation using the OOB predictions and averaged over all observations. Since OOB observations are not used in the fitting of the trees, the OOB estimates are essentially cross-validated accuracy estimates (Cutler et al., 2007; Hastie et al., 2005). In addition, variable importance can be computed by permuting OOB data. For each tree, the prediction error on the OOB portion of the data is recorded and the same is done after permuting each predictor variable. The difference between the missclassification rate for the permuted and original OOB data, averaged over all trees and divided by the standard error, is a measure of the importance of the variable (Cutler et al., 2007; Liaw and Wiener, 2002). All data organization and analyses as described below were performed in R, version 4.3.2 (R Core Team, 2023).
2.2. Imputation procedure

As with many life-history trait datasets, the BET dataset contains gaps. Imputation of missing values has often been found to outperform complete-case analysis in ecological and evolutionary studies (Kim et al., 2018; Penone et al., 2014), although caution is required for severely biased datasets (Johnson et al., 2021). Generally, imputation results improve by adding phylogenetic information, and imputation errors decrease with lower numbers of missing values. To minimize potential bias, we excluded variables with >50 % missing values, resulting in a dataset with 10.5 % missing values (Supporting information S1.1). We followed an adapted version of a procedure that uses phylogenetic information to impute the remaining missing values (Debastiani et al., 2021; Penone et al., 2014). Since a complete phylogeny of European bryophytes is not available, we used taxonomy as a proxy for phylogenetic relatedness, as has been done in other studies (Borgelt et al., 2022; Davidson et al., 2017). We generated a pairwise distance matrix using the tax2dist function from the R package rdentity (Mitchell et al., 2022) and the complete taxonomy (i.e., species = 0, genus = 1, family = 2, order = 3, class = 4, phylum = 5). Next, we performed a principal coordinates analysis (PCoA) on the distance matrix. The resulting taxonomic eigenvectors (TVRs) were extracted and added to the trait dataset as additional variables. The missing trait values were imputed using the R package missForest (Stekhoven and Bühlmann, 2012), which has been shown to be particularly useful for datasets with different types of variables, complex interactions and nonlinear relations (Penone et al., 2014; Stekhoven and Bühlmann, 2012) and has the additional advantage of providing OOB imputation error estimates. To determine the number of TVRs to add to the dataset, we analysed the effect of different numbers of TVR on the OOB imputation error estimates (Supporting information S1.2). Based on this we selected the first seven eigenvectors, which cumulatively explained ca. 52 % of the taxonomic variation. For the imputation true continuous variables were coded as such, while ordinal and nominal categorical variables were coded as factors. All following analyses were performed on the imputed dataset.

2.3. Variable selection and Random Forest models

Variable selection and subsequent construction of RF models were performed using the imputed dataset for all trait groups combined, as well as for biological traits, ecological traits, and bioclimatic variables separately (from now on referred to as combined, biological, ecological, and bioclimatic). As geographic range size is an important determinant in several of the IUCN criteria (which in turn determine the extinction risk category; IUCN, 2022), we excluded variables estimating geographic range size to prevent circular reasoning (i.e., extent of occurrence (EOO, est), area of occupancy (AOO, est), and the number of extracted grid cells used for calculating bioclimate median values (nc)). For each RF model, we performed feature selection by means of the Boruta algorithm (Kursa and Rudnicki, 2010) and excluded variables that were rejected as important (i.e., deemed unimportant) in determining extinction risk (threatened vs non-threatened). Finally, for each RF model, we excluded variables that were highly correlated (absolute correlation coefficient > 0.7; Dormann et al., 2013) using Pearson’s correlation coefficient for continuous and Cramer’s V for categorical variables (correlation plots for the variables for the combined model are given in the supporting information; Figs. S2.1-S2.2). Taxonomic eigenvectors were not highly correlated to any of the continuous variables and were retained to account for phylogenetic relatedness within traits. The resulting selection of variables for each model is given in Table S2.1.

For each selection of variables (i.e., combined, biological, ecological and bioclimatic), we constructed RF models with the R package randomForest (Liaw and Wiener, 2002) using 500 trees and applying weights to balance out threatened vs non-threatened species in the sampling data for growing each tree. As the dataset is unbalanced with much less threatened species (22.2 %) than non-threatened species, increasing the weight helps to reduce the prediction error for the minority class (Zhu et al., 2018), i.e., for threatened species. As such, we calculated the weights as 1 divided by the proportion of threatened species and 1 divided by the proportion of non-threatened species and applied them to threatened and non-threatened species, respectively. For each RF model, we calculated the following performance metrics: accuracy (proportion of correctly classified species), specificity (proportion of non-threatened species correctly classified as non-threatened), sensitivity (proportion of threatened species correctly classified as threatened), precision (proportion of threatened species across species predicted to be threatened), and AUC (area under the receiver operating characteristic (ROC) curve for sensitivity vs false positive rate). A value of 1 denotes the highest performance for all of these metrics.

3. Results

The combined RF model explaining extinction risk in European bryophytes with biological and ecological traits and bioclimatic variables had an overall accuracy of 0.84 (i.e., the proportion of correctly predicted species) and a sensitivity of 0.65 (i.e., True Positive Rate, the proportion of species correctly predicted as threatened compared to the total number of threatened species) (Table 1). Bioclimatic variables had the highest variable importance in this model (Fig. S2.3), notably precipitation seasonality, precipitation during the warmest quarter (which is correlated with precipitation of the driest quarter and driest month; Fig. S2.1), diurnal temperature range, and mean annual precipitation (which is also correlated to precipitation of the driest quarter and month, as well as to precipitation of the wettest month, wettest quarter, and coldest quarter; Fig. S2.1). The ecological trait with the highest importance was the indicator value for continentality, followed by lower elevational limit, indicator for temperature, and elevational range (Fig. S2.3). The biological traits retained in the model, i.e., plant size, life strategy and spore size, were of lower importance and listed below all taxonomic eigenvectors (Fig. S2.3).

The RF model explaining extinction risk with biological traits had the lowest accuracy and sensitivity of all models (Table 1). The biological trait that best explained extinction risk in European bryophytes was plant size, followed by life strategy, the season length of sporophyte production, mean spore diameter, vegetative propagation, deciduous leaves or leaf fragments (a form of vegetative propagation), frequency of sporophyte production, and mating type (Fig. 1). Taxonomic eigenvectors were also important predictors in the model - only plant size had a

<table>
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<th>Performance metric</th>
<th>Combined RF</th>
<th>Biological RF</th>
<th>Ecological RF</th>
<th>Bioclimatic RF</th>
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<tr>
<td>OOB Accuracy</td>
<td>16.3 %</td>
<td>22.5 %</td>
<td>17.3 %</td>
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<td>Sensitivity</td>
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<td>Precision</td>
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<td>AUC</td>
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1 Out-of-bag estimate of error rate.
2 Proportion of correctly classified species.
3 Proportion of non-threatened species correctly classified as non-threatened.
4 Proportion of threatened species correctly classified as threatened.
5 Proportion of threatened species correctly classified across species predicted to be threatened.
6 Area under the receiver operating characteristic (ROC) curve for sensitivity vs false positive rate.
higher importance, indicating that taxonomic position (as a proxy for phylogenetic relatedness) is a strong indicator of extinction risk, and more important than most biological traits (Fig. S2.4). The proportion of threatened species decreases with increasing plant size, meaning that larger species are less likely to be threatened (Fig. 1a). Perennial and short-lived shuttle species are more likely to be threatened, while long-lived shuttle species are less likely to be threatened (Fig. 1b), which implies that there is no link with generation length. Bryophytes that do not produce sporophytes or only during one season have a higher proportion of threatened species than those that produce sporophytes rarely to frequently or over two or more seasons (Fig. 1c, h). Species with larger spores are more likely to be threatened (1d), and those that do not produce vegetative propagules have a higher proportion of threatened species (1e, f). *Sphagnum* species are less likely to be threatened compared to other growth forms (Fig. 1g). Finally, the proportion of threatened species is lower in species that exhibit both mating types, while the proportion of threatened species is higher for strictly monoicous species than for dioicous ones (Fig. 1h).

The ecological RF model had a higher accuracy and sensitivity than the biological RF meaning that the overall prediction and especially that of threatened species was better for the ecological RF (Table 1). The ecological trait with the highest importance in the model was lower elevational limit, followed by the indicator value for continentality, eastern limit category and elevational range (the latter being highly
correlated with upper elevational limit (see Fig. S2.1), which was therefore excluded before modelling) (Fig. S2.5). The high variable importance of taxonomic eigenvectors highlights the relevance of taxonomic position also in relation to ecological traits (Fig. S2.5). The proportion of threatened species increases with increasing lower elevational limit, meaning that species that do not occur in the lowlands are more likely to be threatened with extinction (Fig. 2a). Similarly, the proportion of threatened species decreases with increasing elevational range, meaning that species with a wider elevational range are less likely to be threatened (Fig. 2d). Species with high or low indicator values for continentality or temperature are more likely to be threatened than species with intermediate continentality values and those that are indifferent (Fig. 2b, f). Species with a hyper-oceanic distribution (eastern limit category = 0) are more likely to be threatened, while species with a circumpolar distribution are less likely to be threatened (eastern limit category = 6; Fig. 2c). Biome category followed a similar pattern as to indicator value for temperature, although less clear (Fig. 2e). Species that occur in habitats that are close to nature (i.e., not impacted by humans) are more likely to be threatened than those that occur in hemerobic (impacted/created by humans) habitats and species that occur in both types (Fig. 2g). Both shade-adapted species (light indicator value = 3) and those that are found in full light (indicator value = 9) have a higher proportion of threatened species than those that are indifferent or found under different light conditions. Finally,

![Fig. 2. Partial dependence plots for the Random Forest model using ecological traits as predictors and weights to balance out threatened vs non-threatened species. The y-axes are in logit scale: the higher the logit, the higher the proportion of threatened species (logit = 0 means that the proportion of threatened species is 0.5). Note that the scale of the y-axis differs among plots. In order of variable importance (excluding taxonomic eigenvectors and some traits with less informative responses; see Figs. S2.5-S2.6): a) lower elevational limit; b) indicator value K (continentality; 1 = extreme oceanic to 9 = extreme continental, x = indifferent); c) eastern limit category (0 = hyperoceanic to 6 = circumpolar); d) elevational range (difference between upper and lower elevational limit); e) major biome category (1 = arctic-montane to 9 = mediterranean-atlantic); f) indicator value T (temperature; 1 = cold indicator/alpine-nival to 9 = extreme warmth indicator, x = indifferent); g) hemeroby (influence of man on habitats in which the species is found); h) indicator value L (light; 1 = deep shade to 9 = full light, x = indifferent); and i) sum of substrate types; i.e. on how many different substrates a species is found. More detailed explanations can be found in Appendix S2 of the BET data paper (Van Zuijlen et al., 2023b). For continuous traits, hash marks at the bottom of the plot indicate the deciles of the plotted trait. For categorical traits, the no. of observations (species) is denoted above or below each bar (note that very low numbers may give unreliable predictions).]

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species that occur on only one substrate type are more likely to be threatened with extinction than those that occur on multiple substrate types (Fig. 2i). Responses for other traits that were less informative and/or with low variable importance are shown in Fig. S2.6.

Bioclimatic variables resulted in an RF model with very similar performance metrics as the ecological RF; but with slightly better precision (Table 1). All bioclimatic variables retained in the model are ranked with higher importance than the taxonomic eigenvectors, indicating that the climatic conditions where species occur are better predictors of extinction risk than taxonomic position (Fig. S2.7). The most important predictor of extinction risk is precipitation seasonality, followed by mean annual precipitation, diurnal temperature range, mean annual temperature, amount of precipitation in the warmest quarter, temperature seasonality, temperature of the wettest quarter, and isothermality (Fig. S2.7). The proportion of threatened species regarding bioclimatic variables showed similar patterns: threatened species are more likely at the extremes, while the proportion of threatened species drops to a minimum at median values (Fig. 3). The latter is an effect of the range size (area in km²), as species with widespread distributions automatically end up with the average bioclimate of Europe, and those species are generally not threatened with extinction (Fig. 3e-h, m-p). In addition, high precipitation, precipitation seasonality and temperature of the wettest quarter have higher proportions of threatened species than low values of these variables (Fig. 3a,b,i,k). In contrast, low values of temperature, temperature seasonality and especially isothermality have higher proportions of threatened species than high values (Fig. 3d,j,l).

4. Discussion

We aimed to disentangle which biological and ecological traits and bioclimatic variables best explain extinction risk in European bryophytes. Bioclimatic variables were the best predictors of extinction risk, followed by ecological traits, while the biological traits were of lower importance and resulted in a weaker model. Our first hypothesis, that bryophytes with low dispersal capacities and short life span are more likely to be threatened, was partly confirmed, as we found a higher proportion of threatened species among those with low sporophyte production and large spores, but not with life strategies with a short life span. Our second hypothesis, that threatened species are more likely to be specialists than generalists, was true for all bioclimatic variables and for most ecological traits, especially those that are strongly linked to...
bioclimatic conditions. This is mainly explained by geographic range, as species with widespread distributions automatically represent average bioclimatic conditions of Europe. Using the IUCN criterion B, species with widespread distributions are in most cases not classified as threatened, as they have larger range sizes than the range threshold under criterion B (geographic range in the form of EOO and/or AOO (IUCN, 2022)) for a species to be considered threatened. However, also species with widespread distributions can be classified as threatened when a population size reduction is observed, inferred or predicted (criterion A (IUCN, 2022)). Nevertheless, criterion A was much less often applied in the assessments for European bryophytes than criterion B (38 vs 218 times; https://www.iucnredlist.org), largely due to lack of data on population development, implying that high extinction risk in European bryophytes often – but not always - relates to narrow-ranging species. Furthermore, criterion D (populations very small or restricted, i.e. rare species) was the only applicable criterion for 199 species. These rare species have very restricted ranges in terms of AOO or are occupying <1000 individual equivalents (Bergamini et al., 2019). There are different ways to characterise rarity, for example based on range size, local abundance, and habitat specificity or occupancy (Crisfield et al., 2024; Rabinowitz, 1981), but it is not always straightforward to determine the cause of rarity. A species could be rare because parts of its natural habitat have been destroyed, e.g. wetlands in Central Europe (Tanneberger et al., 2021), and it now occurs under more extreme climatic conditions than before habitat destruction (e.g., only populations left in the Alps or Northern Europe). Alternatively, species may be confined to more extreme climates because of their physiology and are rare because these climates are rare.

The most important bioclimatic variables in relation to extinction risk are precipitation seasonality and mean annual precipitation, which link well with the indicator value K for continentality. This indicator value spans from extreme oceanic to extreme continental and is ranked as the second most important ecological trait. The precipitation-related bioclimatic variables show that the proportion of threatened species is higher at the high values of mean annual precipitation and precipitation seasonality than at low values (when ignoring the drop at medium values for a moment). This is most likely the result of the high number of oceanic species in the British Isles, which are both severely threatened endemic species at the high-precipitation Macaronesian islands, as well as oceanic species in the British Isles, which are both severely threatened by climate change (Hodd et al., 2014; Patiño et al., 2016). In addition, the Macaronesian islands cover wide latitudinal and steep altitudinal gradients with corresponding climate variations, resulting in high habitat diversity. However, large parts of the native vegetation have been altered by human impact over a relatively short time (del Arco Aguilar et al., 2010; Triantis et al., 2010), resulting in severe habitat loss within these high-precipitation areas. On the other end, extreme continental species are also more likely to be threatened according to indicator value K. An explanation for species with high continentality values classified as threatened in the European bryophyte Red List could be that these species have a more eastern distribution and may be on the edge of their range in Europe, thus having a relatively small range within Europe.

We found that macroclimate, represented by bioclimatic variables, strongly relates to extinction risk, even though bryophytes are known to depend very much on microclimate (e.g. Collart et al., 2024; Táboršká et al., 2020). While microclimatic conditions are important on small scales for the distribution of bryophytes (Man et al., 2022), macroclimate becomes more important at larger spatial scales. At the European continental scale, macroclimatic characteristics have been shown to be good predictors of actual bryophyte species distributions (Mateo et al., 2013). However, finer-scale climatic data could be beneficial for predicting changes in species distributions due to climate change, as the resolution of the climatic data has been shown to have a greater impact on the predictions than on the performance of species distribution models (Collart et al., 2024; Patiño et al., 2023).
are not confined to cold areas but are also present at low elevation and in warmer climates (Fig. S2.8). Thus, smaller species are more likely to be threatened, regardless of in which geographic area and climate they occur. One explanation could be that many small-sized species are adapted to disturbances and occur for example in arable fields in which many species are threatened (Bisang et al., 2021). In contrast, large-sized species are often typical for forest floors, where they constitute a significant part of the biomass. Forests are, despite often being heavily managed, less threatened than other habitat types such as mires and bogs, and grasslands in Europe (European Commission et al., 2017). Another explanation could be that many small species are not well-known and more easily overlooked, and due to precautionary principles, those with few locations may be listed as threatened (IUCN, 2022). Size has been pointed out as an important predictor of extinction risk in other taxonomic groups, but the effect is often the opposite, i.e., mammals and birds with a large body size are more often at risk (Davidson et al., 2009; Owens and Bennett, 2000). Large species have longer generation times, which limits their capacity to recover from human threats such as harvesting (Bird et al., 2020; Davidson et al., 2012). Nevertheless, for amphibians it is the smallest species that are most at risk, which are more commonly threatened by habitat modifications and fragmentation (Cardillo, 2021; Ripple et al., 2017).

For bryophytes, generation time does not seem to have a consistent effect on extinction risk, as species with a perennial life strategy as well as short-lived shuttles species are more likely to be threatened, whereas long-lived shuttle species are less likely to be threatened. The difference could lie in vegetative propagation, as long-lived shuttle species often invest early in vegetative diaspores, especially in cases with rare or no sexual reproduction (During, 1992, 1979). In perennials, the ability for clonal growth has partly the same function as the production of vegetative diaspores in the life history of mosses (During, 2007). Further, the long-lived shuttle effect could be driven by Sphagnum species, as most peat mosses are categorized as long-lived shuttle species, and this group has a lower proportion of threatened species compared to the average across all bryophytes. It is noteworthy that the habitats that are formed by Sphagnum, i.e., mires and bogs, are by far the most threatened habitats in Europe (European Commission et al., 2017), but at present many Sphagnum species still have very large populations in northern and north-eastern Europe. In the long run, however, this may change because of ongoing peat extraction and climate change and will most likely have a negative impact on the extinction risk of Sphagnum species (Fluet-Chouinard et al., 2023). This also appears to be true for other wetland species, which are less threatened than species from other habitats across Europe when considered as a whole. In Central and Southern Europe, however, the situation is much more critical for wetlands and their associated species (Hodgetts et al., 2019).

4.3. Importance of taxonomic relatedness

The taxonomic eigenvectors, used as a proxy for phylogenetic relatedness, were among the most important predictors of extinction risk in the models including biological or ecological traits. In the climate model, the importance of taxonomic eigenvectors was lower than the bioclimatic parameters. However, in absolute values, the importance values of the taxonomic eigenvectors were of a similar magnitude in all three models. It indicates that certain groups of related species are more likely to be threatened than other groups of related species. Phylogenetic conservatism, i.e., the tendency for closely related species to share similar attributes, has been documented widely, while the strength of the phylogenetic signal can vary between traits (Bisang et al., 2014; Davies et al., 2013). Also niche conservatism, that is if related groups of species retain their environmental niches and related ecological traits over time, is widespread (Wiens et al., 2010). The taxonomic eigenvectors in our study thus likely reflect variation in ecological and biological traits not or only partly accounted for by the available trait variables selected for this study.

4.4. Model performance and data quality

Although we used a broad set of biological, ecological, and bioclimatic variables, and acquired interpretable results mostly in accordance with theory, the model performance of our RF model using biological traits was rather low, especially in terms of sensitivity. That means that it was harder to predict threatened species correctly compared to non-threatened species. The low accuracy and sensitivity of the biological traits model may have several reasons. For example, the traits we used are not perfect: in some cases, they may be incorrect (e.g., some life strategy classifications due to poor knowledge) or imprecise (e.g., sexual condition is more complex than the dichotomy monoicy and dioicy indicates (Dos Santos et al., 2023; Glimé and Bisang, 2017; Haig, 2016)). Traits may also vary across Europe as a species may perform differently or may have different morphologies in Southern and Northern Europe (e.g., plant size). For some traits many values had to be imputed which may introduce additional uncertainty. Although the ecological, bioclimatic and especially the combined RF model were better in predicting extinction risk, these data are not always accurate either: for instance, the bioclimatic values are based on range maps derived from the European Red List that are not very precise. Finally, the extinction risk categories in the European Red List (Hodgetts et al., 2019) are not flawless as there is currently no database providing reliable data on historic and recent bryophyte occurrences in Europe. Therefore, population trends had to be estimated based on other variables such as declining habitat quality (IUCN, 2022). Further, it may be that some species classified as threatened under IUCN criterion D (populations are very small or restricted) are undersampled and thus more widespread than currently known, and therefore not actually threatened with extinction. Such potential misclassifications could lead to lower model performance as threatened and non-threatened species would become more similar in terms of their traits. Nevertheless, we found some clear and significant relationships even if the data are not free of errors.

4.5. Perspectives and implications

Considering the high importance of extreme values of bioclimatic variables and ecological predictors such as elevational range and indicator values for continentality and temperature, we expect that climate change may become an important driver of bryophytes’ extinction risk in the future (Patiño et al., 2023; Patiño et al., 2016; Zanatta et al., 2020). Notably, climate change will affect the area of suitable climate and thus with the biogeography of Europe. As such, it is not the climate change per se that may be threatening bryophytes, as many bryophytes can be considered “extremophiles”, but the small area where climate change can cause drastic shifts and extinctions. For instance, mountain tops are getting warmer while the area for cold-adapted species is getting smaller in most cases (Eisen and Tingley, 2015). Although our analysis relates to Europe, we would expect a similar pattern, i.e. more threatened species under climatic extremes, on other continents (Urban, 2015), even though some of the extremes in Europe might be a common condition in other regions and vice versa. On the other hand, climate warming may also result in increasing populations and range shift of threatened and non-threatened warm-adapted species that currently have the northern edge of their distribution in southern Europe, although range shifts may happen slower than changes in climate (Zanatta et al., 2020). Yet, despite the apparent importance of future climate change, land use changes have so far been the key driver for recent global biodiversity declines (Jaureguiberry et al., 2022). Finally, even though we found bioclimate and related ecological traits to be the most important predictors for extinction risk in European bryophytes, biological traits related to reproduction and dispersal and traits related to broad ecological tolerances will likely become important for species coping with future climate and land use changes.
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Kristel van Zuijlen: Writing – original draft, Formal analysis, Conceptualization. Irene Bisang: Writing – review & editing, Conceptualization. Michael P. Nobis: Writing – review & editing, Conceptualization. Ariel Bergamini: Writing review & editing, Conceptualization.

Declaration of competing interest
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability
The BET dataset is available at doi.org/10.16904/envi dat.348 (Van Zuijlen et al., 2023b; Van Zuijlen et al., 2023a). The R code for the analyses is available at doi.org/10.5281/zenodo.10971182 (Van Zuijlen, 2024).

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Appendix A. Supplementary data
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