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Rarity in freshwater vascular plants across Europe and North America: Patterns, mechanisms and future scenarios

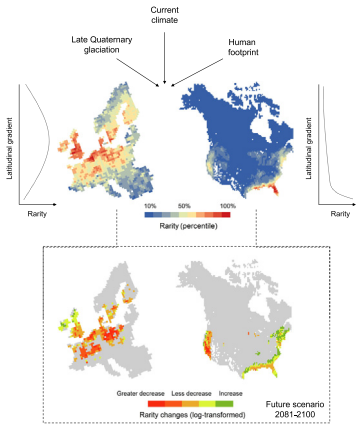
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HIGHLIGHTS

- New empirical studies are repeatedly demonstrating the importance of rare species.
- However, very little is still known about species rarity in the aquatic realm.
- Continental maps suggest variable latitudinal trends in freshwater plants.
- Human footprint, past and present-day climates predict rarity hotspots.
- Current centers of freshwater plant rarity might shrink within a century.

GRAPHICAL ABSTRACT



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ABSTRACT

Patterns of species rarity have long fascinated ecologists, yet most of what we know about the natural world stems from studies of common species. A large proportion of freshwater plant species has small range sizes and are therefore considered rare. However, little is known about the mechanisms and geographical distribution of rarity in the aquatic realm and to what extent diversity of rare species in freshwater plants follows their terrestrial counterparts. Here, we present the first in–depth analysis of geographical patterns, potential deterministic ecogeographical factors and projected scenarios of freshwater vascular plant rarity using 50 × 50 km grid cells across Europe (41°N–71°N) and North America (25°N–78°N). Our results suggest that diversity of rare species shows different patterns in relation to latitude on the two continents, and that hotspots of rarity concentrate in a relatively small proportion of the European and North American land surface, especially in mountainous as well as in climatically rare and stable areas. Interestingly, we found no differences among alternative rarity definitions and measures when delineating areas with notably high diversity of rare species. Our findings also indicate that few variables, namely a combination of current climate, Late Quaternary climate–change velocity and human footprint, are able to accurately predict the location of continental centers of rare species diversity. However, these relationships are not geographically homogeneous, and the underlying factors likely act synergistically. Perhaps more importantly, we provide empirical evidence that current centers of rare species diversity are characterized by higher anthropogenic impacts and might shrink disproportionately within this century as

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the climate changes. Our reported distributional patterns of species rarity align with the known trends in species richness of other freshwater organisms and may help conservation planners make informed decisions mitigating the effects of climate change and other anthropogenic impacts on biodiversity.

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1. Introduction

A key feature of the diversity of life is that the majority of species are rare (Rabinowitz, 1981; Gaston and Blackburn, 2000). Even though spatial patterns of biodiversity have been in focus for well over a century (Wallace, 1878; Gaston, 2000; Blackburn and Gaston, 2003), especially following von Humboldt's seminal work on plant geography (von Humboldt and Bonpland, 1807), much of our knowledge about the natural world stems from the study of common species. Over the last decades, progress has been made towards documenting mechanisms affecting biodiversity variation across taxa and realms (Gaston and Blackburn, 2000; Hillebrand, 2004; Heino, 2011), fostering more thorough tests of the hypotheses put forward to explain the origin and maintenance of biodiversity in general (e.g. Kreft and Jetz, 2007; Swenson et al., 2012; García-Girón et al., 2020a). Beyond range sizes (Gaston, 2003; Gaston and Fuller, 2009), approaches testing for alternative axes of biodiversity, such as rarity, have faced less scrutiny and their properties are not clearly understood (Gaston, 2008; Enquist et al., 2019). This creates a current knowledge gap because both overall species diversity and species rarity must be considered in order to explain the connection between biodiversity, climate, history and geography, with far–reaching implications for ecology and our understanding of species distributional patterns (Kunin and Gaston, 1993; Gaston, 1994, 2000; Albuquerque et al., 2019).

The lack of focus on species rarity challenges our ability to predict biodiversity patterns, not the least because there is a growing body of evidence suggesting that rare species (e.g. geographically restricted species, Rabinowitz, 1981) may have biological and ecological characteristics that differ from those that are less geographically restricted (Gaston, 2008; Siqueira et al., 2012; Alahuhta et al., 2014). Furthermore, not only does rarity inform decisions about biodiversity management and conservation due to its relationships with extinction risk (IUCN Standards and Petitions Subcommittee, 2019), but it also provides insights into theoretical and applied issues in modern ecology (Schwartz et al., 2006), including adaptation, niche evolution, invasiveness, ecosystem function and future dynamics in the face of climate change (Hooper et al., 2005; Knapp, 2011; Mouillot et al., 2013; Musters et al., 2013). For example, researchers have used rarity assessments to rank a list of species or geographical areas with regard to their relative expected sensitivity to range shifts in a changing climate (Enquist et al., 2019).

Rare species make a disproportionate contribution to the potential range of distinctive and vulnerable ecosystem functions that can be provided by high–diversity ecosystems (Mouillot et al., 2013). Despite this, patterns, potential deterministic mechanisms and future scenarios of species rarity have seldom been assessed. Thus far, most research has focused on community–level arrangements of common vs. rare species (Siqueira et al., 2012; Alahuhta et al., 2014) and pairwise comparisons between closely–related species with different range sizes (Kunin and Gaston, 1993). Recently, Enquist et al. (2019) highlighted that areas with a high number of rare species tend to be clustered in well–known hotspots of tropical, subtropical and temperate regions, and concluded that climate change and land use are currently disproportionately impacting the distribution of rarity across land plants at global scales. A general pattern in the terrestrial realm is that the number of rare species is low in northern glaciated regions, increasing towards colonization sources, isolated peninsulas, mountainous areas and the Tropics (Enquist et al., 2019). However, to what extent such findings represent general patterns and can be extrapolated to other realms (e.g. aquatic ecosystems) is still unknown.

Freshwater systems have been examined less rigorously than their terrestrial counterparts (see Heino, 2011 for a review). This is unfortunate given the importance of freshwaters for providing economically important goods and services, and that these environments are highly rich in biodiversity and are increasingly impacted by human activities (Reid et al., 2019). Given that ecogeographical factors (e.g. local environmental features, geography, current climate and historical legacies) structuring species distribution may differ between terrestrial and freshwater environments (Hortal et al., 2015; Kinlock et al., 2018; Iversen et al., 2019; Alahuhta et al., 2021), there is a need for further research on large–scale diversity patterns in the freshwater realm. Among vascular plants, freshwater plants ('aquatic photosynthetic organisms that actively grow permanently or periodically submerged below, floating on, or up through the water surface' of inland freshwater and brackish waterbodies, Chambers et al., 2008, Murphy et al., 2019) are an especially relevant and sensitive group to human impact, with a larger proportion of endangered species than the average (Chappuis et al., 2012). Even if the pool of vascular plants growing in inland waters is usually less taxonomically diverse than that of terrestrial plants (Kahn et al., 1993), these organisms are a conspicuous component of freshwater ecosystems and are responsible for primary production, as well as provide food, habitat, reproduction and foraging possibilities for many aquatic and terrestrial faunas (Lacoul and Freedman, 2006). Importantly, ecogeographical patterns exhibited by terrestrial plants may not be directly applicable to freshwater vascular plants (hereafter referred to as 'freshwater plants') because physiological constraints of access to water and atmospheric gases are fundamentally different in terrestrial and freshwater systems (Iversen et al., 2019). In addition, freshwater plants likely respond differently to temperature compared with terrestrial species due to stabilizing effects of aquatic medium on temperature (García-Girón et al., 2020a).

Several recent studies have examined patterns and underlying mechanisms of species range size and species diversity in freshwater plants at global scales (Alahuhta et al., 2017, 2018; Murphy et al., 2019, 2020; García-Girón et al., 2020a, 2020b), across Europe and North America (Chappuis et al., 2012; Alahuhta et al., 2020; Vieira et al., 2021), and in regions of Africa and the Neotropics (Kennedy et al., 2016; Tapia-Grimaldo et al., 2016). These investigations suggest that freshwater plant diversity across large spatial scales is driven by multiple factors, including gradients in local environmental conditions, differences in catchment land use, orographic barriers and climatic variation, both current and historic. Despite these qualitative statements, we do not know much about the geographical distribution of rarity in these organisms, especially across large geographical areas (see Alahuhta et al., 2014). Since small–ranged species constitute most of Earth's freshwater plant species diversity (Murphy et al., 2019), the challenge remaining is to quantify patterns of rarity and examine competing mechanisms and future scenarios for both the origin and maintenance of rare species distributions.

Here, we take the next step and present an analysis of geographical patterns, potential deterministic ecogeographical factors and future scenarios of freshwater vascular plant rarity across Europe (41°N–71°N) and North America (25°N–78°N). The scale of this analysis is a grid of equal–area quadrats (50 × 50 km) based on the data previously used by Alahuhta et al. (2020) to produce continental maps of species richness in freshwater plants. These data on geographical distributions are not only excellent for comparative purposes, but are also the only relatively fine–grained datasets at continental scales for freshwater plants anywhere. We built our study on the recent ideas of Enquist et al.

(2019), where they studied 'the commonness of rarity' in land plants and found that global change is disproportionally impacting the distributions of rare species in the terrestrial realm. Additionally, we were particularly interested to unravel whether there are similarities or differences in the geographical distribution of rare species diversity and its potential underlying mechanisms between continents due to region–specific features, including contrasting historical legacies, topography and spatial extent (Hawkins and Lawton, 1995). We have chosen to regard rarity as simply being the state of having a small range size, thereby following Reveal's (1981) assertion that rarity '… is merely *the current status of an extant organism* which is *restricted in area* to a level that is *demonstrably less* than the majority of *other organisms* of comparable taxonomic entity' (authors' emphasis). Hence, we seek to limit rarity on the basis of no additional criteria such as abundance, taxonomic distinctness, red lists or similar statements of species endangerment, habitat specificity and persistence through evolutionary time (Kunin and Gaston, 1993; Gaston, 1994).

The objectives of our study are to (i) map the geographical patterns of freshwater plant rarity across Europe and North America; (ii) investigate whether diversity of rare species varies systematically with latitude; (iii) explore how patterns of environmental features, current climate, topography, Ice Age legacies and human footprint affect freshwater plant diversity via impacts on rare species; and (iv) examine the projected impacts of future climate change on the distribution and persistence of rare plant species in inland waters. We hypothesized that (H1) hotspots of rare species would be found in regions with high topographic heterogeneity and in areas with rare and stable climates (Kreft and Jetz, 2007; Alahuhta et al., 2021). We also expected (H2) that diversity of rare species would decline with increasing latitude in both continents (Rosenzweig, 1995; Gaston, 2000; Enquist et al., 2019). Similarly, we hypothesized (H3) that climatic forcing would explain a great deal of variation in rare species diversity (Crow, 1993; Chappuis et al., 2012; Alahuhta et al., 2020; García-Girón et al., 2020a), with topography, Late Quaternary glacial–interglacial climate–change velocity, human footprint, alkalinity and availability of inland waterbodies playing an important supplementary role (Lacoul and Freedman, 2006; Chappuis et al., 2014; Iversen et al., 2019; Murphy et al., 2019, 2020). However, we expected (H4) different ecogeographical constraints to be present in different parts of Europe and North America, i.e. climate velocity after the Last Glacial Maximum (LGM) and current temperature can be assumed to have strong joint effects on diversity of rare species in deglaciated regions (Svenning et al., 2009), whereas human footprint and the availability of potential habitats would be the primary factors in southern areas (Hawkins et al., 2003). Finally, we predicted (H5) that, as climate changes in the coming decades, regions with large concentrations of rare species would also change, with hotspots of rarity experiencing the largest decreases (Anacker et al., 2013; Enquist et al., 2019).

2. Methods

2.1. Freshwater vascular plant data

We used geographical distribution datasets of freshwater plants across Europe and North America at a 50 × 50 km spatial resolution. These data were obtained from the Atlas Flora Europaeae (Jalas and Suominen, 1972–1994; Jalas et al., 1996, 1999; Kurtto et al., 2004), Atlas of North European Vascular Plants (as described in Kalwij et al., 2014), and Flora of North America (Flora of North America Editorial Committee, 1993–2007). In Europe, we limited the study area to 41°N latitude, excluding regions with limited data and uncertain data quality (Nogués-Bravo and Araújo, 2006, Ronk et al., 2015), such as Spain and Portugal, as well as the Russian Federation, Ukraine, Belarus and Moldova. In North America, the study area was restricted to the main continental areas of the United States and Canada, excluding Mexico and remote islands (see Alahuhta et al., 2020 for details). We strictly focused on freshwater plant species that are strongly associated with inland aquatic habitats (i.e. hydrophytes), removing marine and peatland species following Castroviejo (1986–2012), Crow and Hellquist (2000), Cirujano et al. (2014), Lichvar (2014), Schmidt-Kloiber and Hering (2015) and Murphy et al. (2019). Riparian, shoreline and semi–aquatic species were also excluded from our study. Similarly, because of limited geospatial records (often with poor taxonomic resolution), non–vascular plant species were not included in the analyses. Altogether, 134 and 192 freshwater plant species were recorded in Europe and North America using these criteria, respectively. Of these, 38 species were found in both continents. These species represent all the relevant freshwater hydrophyte genera, such as *Ceratophyllum* spp., *Myriophyllum* spp. and *Potamogeton* spp. (Crow, 1993; Willby et al., 2000; Baattrup-Pedersen et al., 2015; Alahuhta et al., 2017, 2018). Most of the species used in our study have ranges centered in the Northern Hemisphere (Crow, 1993; Willby et al., 2000; Chambers et al., 2008), and species richness patterns at continental scales generally follow those seen at global scale (Murphy et al., 2019; Alahuhta et al., 2020).

2.2. Rarity estimates

Rarity is a complex and challenging issue, and finding a useful, objective definition of rarity remains difficult (Rabinowitz, 1981; Gaston, 1994). Traditionally, measures of rarity have been based on a multidimensional concept, including three major axes, i.e. extent of the geographical range, local abundance and habitat specificity (see Rabinowitz, 1981). A species may be rare at large spatial scales either because it has few individuals at many sites or many individuals at few sites (Enquist et al., 2019). However, since these three dimensions are often strongly and positively correlated, each of them represents a general proxy for the multidimensional rarity definition (Magurran, 2004; Siqueira et al., 2012; Alahuhta et al., 2014). To obtain a comprehensive understanding of rarity in freshwater plants, we used two different methods: a 50th quartile criterion (50Q, 50% of the least frequent species were defined as rare, Alahuhta et al., 2014) and an inflection point criterion based on the Barry and Hartigan (1993) product partition model with Bayesian analysis. This algorithm uses the posterior probability of changes over 10,000 Markov chain Monte Carlo (MCMC) iterations, excluding the first 1000 as burn in, to distinguish among common vs. rare species. Given that rarity is defined by a relative range size criterion, differences in samples sizes could offset the rarity classification threshold across continents (Siqueira et al., 2012). In order to avoid this bias, we estimated rarity for Europe and North America independently.

Creating a bivariate classification scheme by comparing species range size to the distribution of range sizes in the species pool introduces a potential context–dependent offset of the classification threshold (e.g. a species with a small Western Palaearctic range but a large Palaearctic range might be classified as being rare even though it is widely distributed overall). Furthermore, biases such as recent taxonomic splits or unclear taxonomic status might drive species rarity (Enquist et al., 2019). To address this, the classifications obtained in this study (see Appendix S1 for details) were compared to classifications derived from an independent global dataset developed by Murphy et al. (2019, 2020). Interestingly, most species (84–93%) identified here as being rare in Europe or North America would indeed be recognized as rare species by other metrics and datasets, with only 1–4% that were clearly erroneous and recognized as common or large–ranged species (Appendix S1).

In order to adjust for the skewed sampling intensity across the study regions, we followed Enquist et al. (2019) and assessed rarefied species diversity using the intuitive Margalef and Menhinick measures for each 50 × 50 km grid cell. Margalef diversity ($\frac{S-1}{\ln N}$) assumes that the total number of observed rare species, S, increases approximately logarithmically with survey effort, N. In a similar vein, the Menhinick index ($\frac{S}{\sqrt{N}}$) assumes that rare species richness increases with N according to a

square root function. Here, we used the number of observations for each grid cell to provide a representation of the sampling intensity for freshwater plants across Europe and North America (Enquist et al., 2019), and considered a 'hotspot of rarity' as any grid cell with a value above the 75th percentile of all sampling–corrected estimates (Sussman et al., 2019). As the Margalef index assumes a logarithmic rarefaction function and the Menhinick assumes a square root function, they represent both a more conservative and a more liberal estimate of rare species diversity, respectively (Legendre and Legendre, 2012).

2.3. Explanatory variables

We considered nine explanatory variables associated with contemporary environmental features, human footprint, areas of high climatic heterogeneity, orographic barriers and instability of past climate (Appendix S2). Environmental features included mean water alkalinity concentration at 50 × 50 km resolution (mequiv l^{-1}, Marcé et al., 2015) and number of freshwaters at 150 m resolution (presence/absence, Lamarche et al., 2017). Alkalinity (a proxy for bicarbonate) is one of the most important water chemistry parameters for freshwater plant species as a measure of carbon source that can be utilized during photosynthesis (Iversen et al., 2019), whereas proportion of freshwaters determines the availability of potential habitats for this group of plants (Jones et al., 2003).

Human footprint was assessed based on the global Human Influence Index (HII) from the NASA Socioeconomic Data and Applications Centre <https://earthdata.nasa.gov>. This measure incorporates nine global data layers corresponding to population density, human land use and infrastructures to estimate the direct human footprint on natural ecosystems (Sanderson et al., 2002) as a proxy of recent anthropogenic pressures on biodiversity.

Current climatic variation does shape freshwater plant distributions at large spatial scales (e.g. Alahuhta et al., 2020; García-Girón et al., 2020a). Therefore, we considered heterogeneity of four climatic variables, i.e. annual mean temperature (°C), annual total precipitation (mm), temperature seasonality (°C) and precipitation seasonality (mm). These variables were averaged for the period 1970–2000 from WorldClim 2.0 (Fick and Hijmans, 2017) and scaled up at 50 × 50 km resolution, representing both average conditions and their variability across the year. To measure climatic heterogeneity, for each grid cell, we calculated the coefficient of variation between the focal cell and its neighboring cells using a queen connection scheme (sensu Ficetola et al., 2017).

To test for 'the orographic barrier hypothesis', we calculated the terrain ruggedness (m) as implemented in the MERIT–Digital Elevation Model (DEM) from the Geomorpho90m global data set (Amatulli et al., 2020), which uses the NASA Shuttle Radar Topographic Mission (SRTM) to provide topographic variables at 3 arc–second resolution (Amatulli et al., 2018). We estimated the magnitude of climate change in each grid cell by calculating the average velocity of climate change from the LGM to present day (expressed as m yr^{-1}, i.e. the speed at which species must migrate over the Earth's surface to maintain constant climatic conditions, Hamann et al., 2015). We obtained these estimates from a set of transient simulations at *c.* 1/5° spatial resolution (Sandel et al., 2011). These models were derived from modern climate data (Hijmans et al., 2005) and the PMIPII data <https://pmip2.lsce.ipsl.fr> for the CCSM3 and MIROC3.2 (Liu et al., 2009) climate outcomes, and included transient forcing changes in greenhouse gases, ice sheets, orbitally–driven insolation variations and meltwater fluxes (see Sandel et al., 2011 for details). The extent of mountainous areas has been shown to be a strong predictor of freshwater plant diversity (Tapia-Grimaldo et al., 2016; Fernández-Aláez et al., 2018), whereas no consensus exists on the influence of Late Quaternary history on aquatic plant diversity, though it appears to be variable across the Earth (Alahuhta et al., 2020; Murphy et al., 2020).

Explanatory variables were resampled using mean values to a grid of 50 × 50 km spatial resolution.

2.4. Statistical analyses

Relationships between diversity of rare species and latitude were evaluated based on linear regressions, accompanied by Akaike Information Criterion (AIC) to assess the importance of linear vs. quadratic relationships.

We used a combination of boosted regression trees (BRT, Elith et al., 2008) and geographically weighted regression models (GWR, Brunsdon et al., 1996) to analyze the relationship between explanatory variables and rarity estimates. In order to obtain model convergence, we trimmed the original number of candidate variables using multivariate linear models for each study region (i.e. separately for Europe and North America). More specifically, we applied forward selection with adjusted R^2 values (adj. R^2) to choose statistically significant explanatory variables to the models (Borcard et al., 2018). The forward selection used two different stopping criteria (significant level α and global adj. R^2) to obtain parsimonious regression models (Blanchet et al., 2008). Prior to forward selection, we evaluated statistical dependence among the explanatory variables using bivariate correlations ($r > |0.7|$, Dormann et al., 2013), transformed these predictors and our response variables to get normally distributed residuals using the bestNormalize package (Peterson and Cavanaugh, 2019), and standardized the explanatory variables to *z*–scores to allow comparison of their slope coefficients. Here, however, we excluded geographical coordinates from these analyses to avoid statistical dependence between latitude and longitude with climate variables (see Alahuhta et al., 2020).

Using the preselected and most parsimonious regression models (Borcard et al., 2018), we implemented BRT analyses (Elith et al., 2008) to describe relationships between freshwater plant rarity and influential explanatory variables. This ensemble method combines the regression tree approach (De'ath and Fabricius, 2000) with a boosting procedure aimed at achieving optimized model accuracy (Schapire, 2003). We applied the gbm.step function implemented in R package dismo (Hijmans, 2017), where regularization methods are utilized to discourage overfitting and balance predictive performance with model fit (see Hastie et al., 2009 for details). After testing, the BRTs were run using Gaussian error distribution, tree complexity of 5, learning rate of 0.01 and bag function of 0.5. Final models were validated using 10–fold cross–validation (CV). This method subsamples the data 10 times according to the previously defined bag function. The final CV correlation is the mean correlation between the testing and training data through 10 runs (Kärnä et al., 2019). We further tested the assumption of spatial independence of model residuals with Moran's I coefficients and correlograms using Bonferroni correction (Cabin and Mitchell, 2000).

Since ecological relationships often vary as a function of location, we further ran GWR analysis to assess the spatial heterogeneity of relationships between explanatory variables and diversity of rare species. The GWR routine is an exploratory technique that pinpoints whether locally–weighted regression coefficients deviate from their mean value, i.e. where non–stationarity occurs within the geographical space (Nakaya et al., 2005). Here, we used a Gaussian model and significant explanatory variables based on forward selection and multiple linear regressions, and adjusted all GWR models for multiple testing following da Silva and Fotheringham (2016). The best bandwidth was identified through a fixed Gaussian kernel and selected the one with the lowest AIC (Ficetola et al., 2017).

Finally, with the previous BRT models, we ran predictions of rare species diversity under future projected climate. To do this, we obtained future climatic variables from WorldClim 2.0 (Fick and Hijmans, 2017) and used the predicted future climate in 2081–2100 constructed by the Model for Interdisciplinary Research on Climate (MIROC6; Tatebe et al., 2019) under Shared Socio–economic Pathway 8.5 (SSP5–8.5) scenario, which has comparatively high greenhouse gas emissions and radiative forcing pathways (O'Neill et al., 2016). Running our models considering this pessimistic scenario allowed us to obtain comparable results with those from Enquist et al. (2019). To match the resolution

of our grid cells, we resampled the climatic variables (i.e. annual mean temperature, annual total precipitation, temperature seasonality and precipitation seasonality) to 50 × 50 km resolution. We compared the differences between estimates of rare species diversity under present and future climates keeping the remaining explanatory variables (see above) the same as present–day (Enquist et al., 2019).

All statistical analyses were performed in R version 3.6.0 (R Development Core Team, 2018). The list of R packages and computational routines that have been used throughout this manuscript is provided in Appendix S3.

3. Results

3.1. Geographical patterns and latitudinal variations in rare species diversity

The geographical distributions of rare species diversity using the 50Q criterion (Fig. 1) and the product partition model with Markov chain Monte Carlo (Appendix S4) were strongly correlated for both Margalef (for Europe, $r_s = 0.99$, $p < 0.001$, for North America, $r_s = 0.40$, $p < 0.001$) and Menhinick (for Europe, $r_s = 0.98$, $p < 0.001$, for North America, $r_s = 0.53$, $p < 0.001$) measures. Similarly, comparing Margalef and Menhinick measures revealed similar geographical distributions and ecogeographical correlations, indicating that both indices result in very similar conclusions (Appendix S5). Hence, we focused on the results based on the 50Q criterion and the Margalef index here.

The distribution of rare species across Europe and North America revealed several geographical areas with high diversity of rare species (i.e. hotspots of rarity, values above the 75th percentile), most of which were associated with areas of high species richness (Fig. 1), i.e. freshwater plant rarity was driven by high numbers of rare species and not low richness of common species (influencing the denominator of the Margalef index). More specifically, rare species cluster in North America in the Atlantic and Gulf Coast of the United States, the western flanks of the Rocky Mountains, the mountainous strip of the California Coast Ranges, extending along the Pacific Temperate Rainforest region, the northeastern flank of the Appalachian Mountains, and across the Neotropical and Californian Floristic Provinces. In Europe, hotspots of rarity comprise the southernmost areas of Scandinavia, the western flank of the Alps, and some Atlantic and Continental regions, including

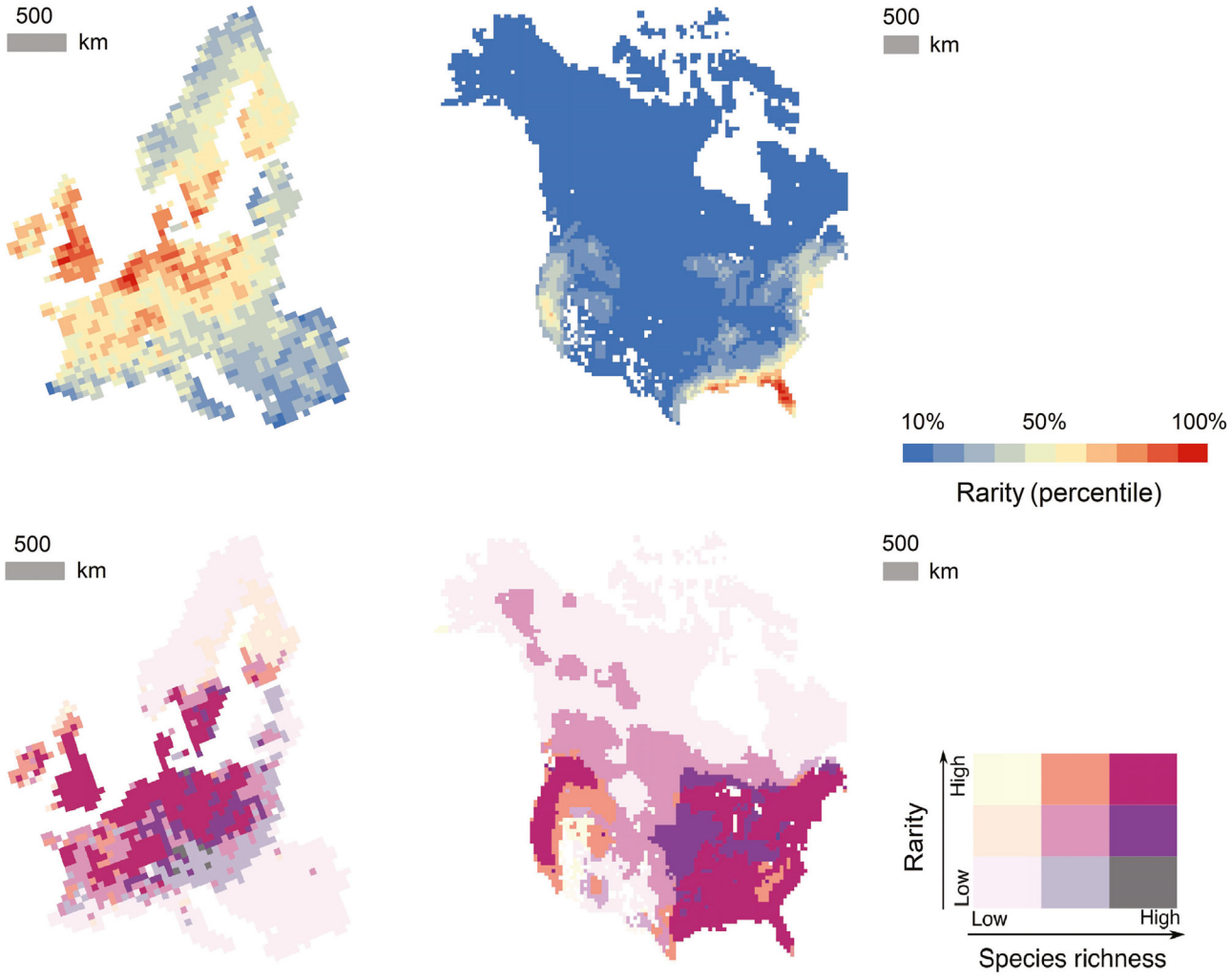


Fig. 1. The geographical distribution of rare species diversity (Margalef index defined by the 50Q criterion) of freshwater plants across Europe and North America at 50 × 50 km resolution (top panels), and bivariate maps comparing diversity of rare species and species richness across the two continents (down panels). Hotspots of rarity seem to be most characteristic of comparatively species–rich land surfaces, with breakpoints based on Jenks natural optimization. In Europe, there are several regions of notably high diversity of rarity in and around the areas of Scandinavia (southern Finland, southern Sweden and the Finnish lake district) and the Atlantic region, including the North European Plain, the Jutland Peninsula, the western flank of the Alps and the British Isles (particularly along the Cambrian Mountains). Areas with high number of rare plant species in North America tend to be clustered in the Atlantic and Gulf Coastal Floristic Province, the southern region of the Pacific Coastal Forest, some mountainous regions (particularly along the western flank of the Rocky Mountains and the California Coast Ranges) and relatively small biogeographical provinces that are strongly distinct from surrounding areas (i.e. the Neotropical Floristic Province of Florida and the Mediterranean chaparral and woodlands of California).

the Jutland Peninsula and the eastern and southern regions of the North European Plain and the British Isles, respectively (see Fig. 1 for a detailed description). Interestingly, areas that currently have high numbers of rare species in Europe and North America experience 1.4–1.9 times greater human footprint (Wilcoxon signed–ranked test, $p < 0.001$) than in each continent on average (Appendix S6). Considering diversity of rare species and latitude (Fig. 2), a decreasing trend was found in North America (*linear*, AIC = 52,733, R^2 (p) = 0.28 (<0.001); *quadratic*, AIC = 52,168, R^2 (p) = 0.34 (<0.001)), whereas the trend was clearly unimodal in Europe (*linear*, AIC = 4,345, R^2 (p) = 0.03 (<0.001); *quadratic*, AIC = 3,847, R^2 (p) = 0.44 (<0.001)). The highest numbers of rare species were recorded in latitudinal band 50–60°N within the area of Europe studied here. By contrast, in North America, diversity of rare species was high up to *c.* 35°N after which it steadily decreased more or less quadratically.

3.2. Potential deterministic mechanisms underlying freshwater plant rarity

After forward selection of explanatory variables (Appendix S7) and multiple linear regressions (Appendix S8), BRTs showed a good performance, explaining from 86.7% to 94.5% of deviance in all the models (Fig. 3). Specifically, internal model fit and CV correlations indicated that our BRT models worked reasonably well (self–statistics = 0.75–0.78 and man cross–validation correlation = 0.50–0.69). Heterogeneity in temperature seasonality (18.4%), with decreasing and then flattening pattern, and the velocity of Late Quaternary climate change (17.3%), with unimodal shape, were the most important variables for rare species diversity in Europe, followed by heterogeneity in annual temperature (17%), annual total precipitation (13.4%) and mean water alkalinity (13%), precipitation seasonality (10.4%), proportion of freshwaters (5.8%) and human footprint (4.7%). For North America, human footprint (23.9%) had the strongest influence on freshwater plant rarity, with diversity of rare species increasing with increasing human footprint until it reached a plateau and the effects of human footprint stabilized. Other important variables were heterogeneity in current climate (including the coefficient of variation in mean annual temperature 20.9%, temperature seasonality 20.5% and precipitation seasonality 12.7%), alkalinity (10.1%), proportion of freshwaters (6.5%) and topography (5.4%). Importantly, we found statistically significant spatial autocorrelation in the first distance classes of our model residuals. However, the relatively low coefficients (Appendix S9) suggest that spatial autocorrelation did not create serious biases in the final BRT models (see Hawkins et al., 2007).

The GWR analysis suggested that relationships between significant explanatory variables and rare species diversity were not homogenous across the two continents (Fig. 4, Appendix S10). Overall, areas of high climatic heterogeneity were particularly important across most of the European landmass (including the British Isles), whereas instability of past climate, human footprint and mean water alkalinity best explained the distribution of rarity in some parts of Western Europe. In North America, heterogeneity of current climate and mean water alkalinity had a consistent effect across the Coastal and Interior Plains, while proportion of freshwaters and topography were strongly linked to diversity of rare species in the Mediterranean chaparral and woodlands of California, the Great Plain grasslands and along the eastern flanks of the Rocky Mountains and the Appalachians. On the other hand, the Great Lakes and Saint Lawrence region, the southern parts of the Canadian Shield and the Mid–Atlantic region of the United States were more strongly related to human footprint.

3.3. Predicted changes in the geographical distribution of rare species diversity

With the previous BRT models, we made predictions of rarity distribution under future projected climate (i.e. 2081–2100, based on the SSP5–8.5 scenario). These showed large and medium reductions in climate suitability for rare species, with the North European Plain, the western flank of the Alps, southern Britain, the California Floristic Province and the Gulf Coast of the United States predicted to experience the largest decreases in both rarity indices. Under future projected climate, however, there might be small increases in climate suitability for rare plant species in several temperate regions of both Europe and North America (Fig. 5).

4. Discussion

We studied geographical patterns, potential ecogeographical mechanisms and future scenarios of freshwater plant rarity across Europe and North America. An important component of our study was to use alternative criteria (i.e. the 50th quartile criterion and the Barry and Hartigan (1993) product partition model with Markov chain Monte Carlo) and measures (i.e. Margalef and Menhinick indices) of rarity and test whether they influenced the outcome of our hypothesis tests. Importantly, we found no clear differences between different rarity criteria and estimates with respect to the geographical areas harboring hotspots of rare species and their underlying factors across Europe and North America (Figs. 1–4, Appendices S4 and S5). In addition, we found evidence both to support and refute our five initial hypotheses.

First, in Europe, diversity of rare species was spatially clumped in the Atlantic region, the North European Plain, the western flank of the Alps

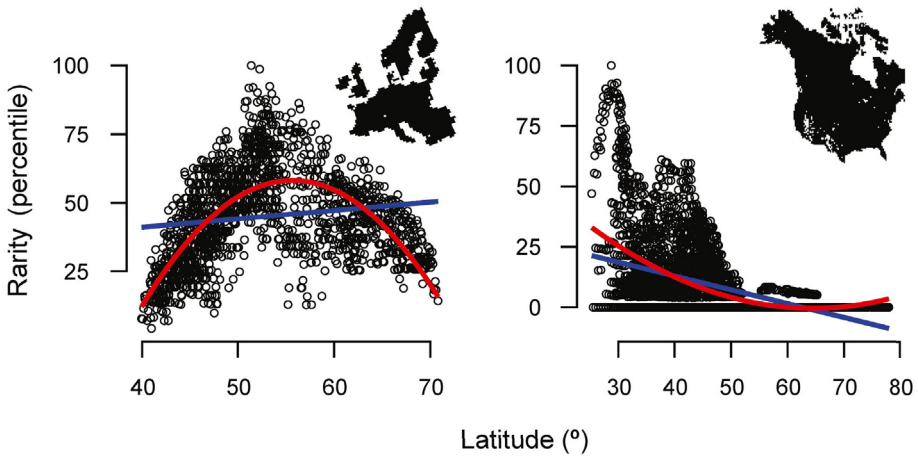


Fig. 2. Rare species diversity (Margalef measure based on the 50Q criterion) of freshwater plants in relation to latitude in Europe and North America. Linear (blue line) and quadratic (red line) relationships were determined by AIC.

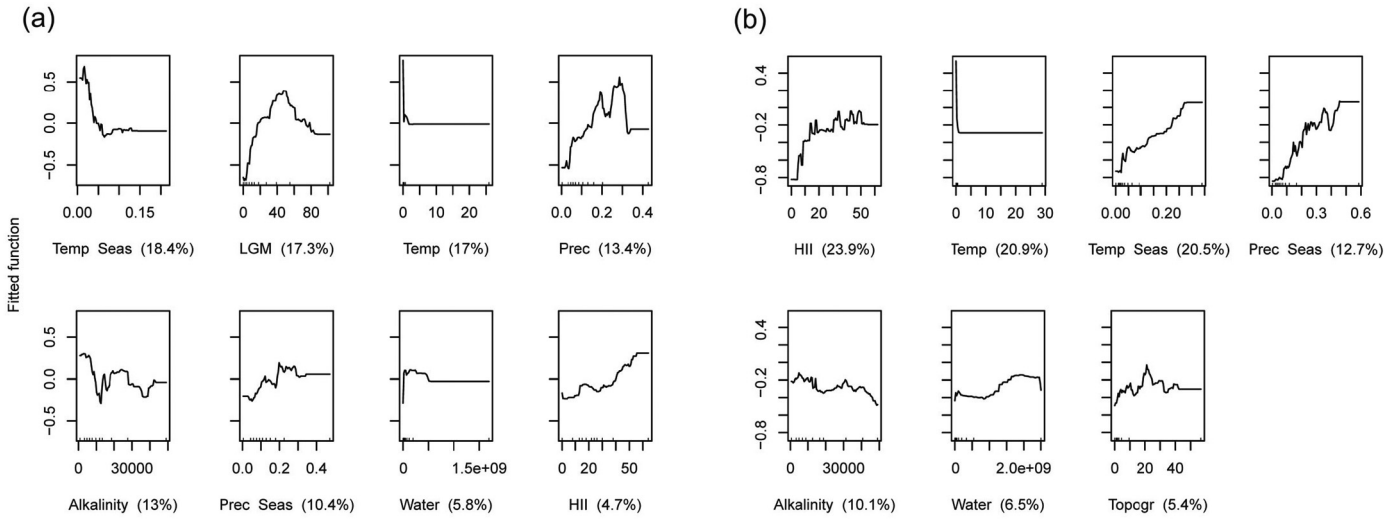


Fig. 3. Partial dependency plots from the BRT models for rare species diversity (Margalef measure based on the 50Q criterion) of freshwater plants across (a) Europe and (b) North America. The graphs show the effect of a predictor variable (x–axis) on the response variable (y–axis). Shown are the significant explanatory variables based on forward selection (Appendix S7) in linear regressions (Appendix S8) following Blanchet et al. (2008). Numerical values (%) below an explanatory variable's name show the relative contribution of the variable to the full model. *Alkalinity*, mean water alkalinity; *HII*, global Human Influence Index (i.e. human footprint); *LGM*, average velocity of climate change since the Last Glacial Maximum; *Prec*, coefficient of variation of annual total precipitation; *Prec seas*, coefficient of variation of precipitation seasonality; *Temp*, coefficient of variation of annual mean absolute temperature; *Temp seas*, coefficient of variation of temperature seasonality; *Topogr*, terrain ruggedness; *Water*, proportion of freshwaters.

and in the Cambrian Mountains of the British Isles. In North America, plant rarity tended to concentrate in southeastern United States, the western flank of the Rocky Mountains and the West Coast (Fig. 1). These findings partly confirmed our first expectation (H1) that hotspots of rare species would be found in and around mountain ranges, as well as in climatically rare (regions with climatic conditions strongly different from neighbouring areas) and stable regions. Unexpectedly (H2), rare species diversity showed different patterns in relation to latitude between Europe and North America. More specifically, freshwater plant rarity varied greatly across North America, being low in the harsher north and higher in the more benign south (i.e. the northernmost latitudinal zone had only *c.* 10% of the number of rare species in the southernmost latitudinal zone; Fig. 2), whereas diversity of rare species did not increase linearly with increasing latitude in Europe, but rather peaked between 50°N and 60°N (Fig. 2). Third, after accounting for geographical location, different combined multi–predictor models explained between 86.7% and 94.5% of the variation in rare species diversity, with current climate, historical constraints and human footprint playing a dominant role (Fig. 3), thereby supporting our third hypothesis (H3) that spatial deterministic effects on rarity are not mutually exclusive. However, these relationships were not homogenous across the two continents (Fig. 4). It thus appears that the rarity pattern of freshwater plants is complex, and that multiple potential deterministic mechanisms are likely to act in concert when accounting for this variation between the continents (H4). Finally, we were able to confirm our fifth hypothesis (H5) that human footprint is now impacting rare species and that current centers of freshwater plant rarity will shrink disproportionately under future climate change (Fig. 5), thereby potentially leading to vulnerability of many of the species they harbor.

The interpretation of comparative and descriptive studies is constrained to some extent by limitations associated with the completeness of the data (see Vinson and Hawkins, 2003). The most significant problem in the data we used was the paucity of information for countries bordering the northern Mediterranean, including the Baetic-Rifan complex, the Pyrenees and some islands (e.g. Balearic Islands and Corsica), as well as for the Balkans and the northernmost regions of North America (>60°N). Since large quantities of primary freshwater plant biodiversity data have still not been published, it is possible that the

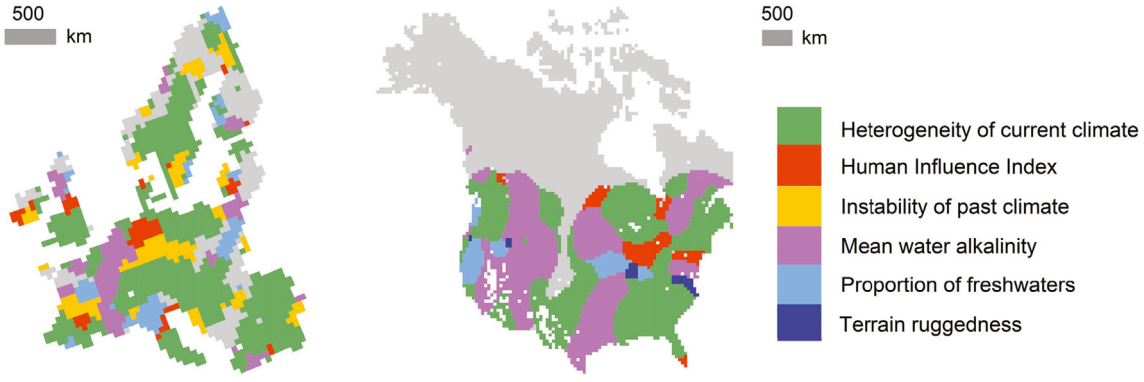


Fig. 4. Explanatory variables most strongly related to the geographical distribution of rare species diversity (Margalef index defined by the 50Q criterion). For each grid cell, the map shows the drivers with the highest local effect size (*t*) according to GWR analysis (Appendix S10). Note that only effect sizes significantly higher than zero (da Silva and Fotheringham, 2016) are mapped. In general, heterogeneity of current climate best explained the geographical distribution of rare species diversity across Europe and North America. However, instability of past climate, human footprint and mean water alkalinity were particularly important for rarity distribution in Atlantic and Continental Europe, while mean water alkalinity and human footprint had also the strongest influence in and around the Great and Coastal Plains, the Intermountain Region, the southern parts of the Canadian Shield and the Mid–Atlantic region of the United States. Interestingly, the proportion of freshwaters and terrain ruggedness best explained patterns of rarity in the California Floristic Province, the oriental part of the Great Plain Grasslands, the eastern flanks of the Rocky Mountains and the Appalachians, the Apennines, and the eastern and western flanks of the Alps and the Carpathians, respectively.

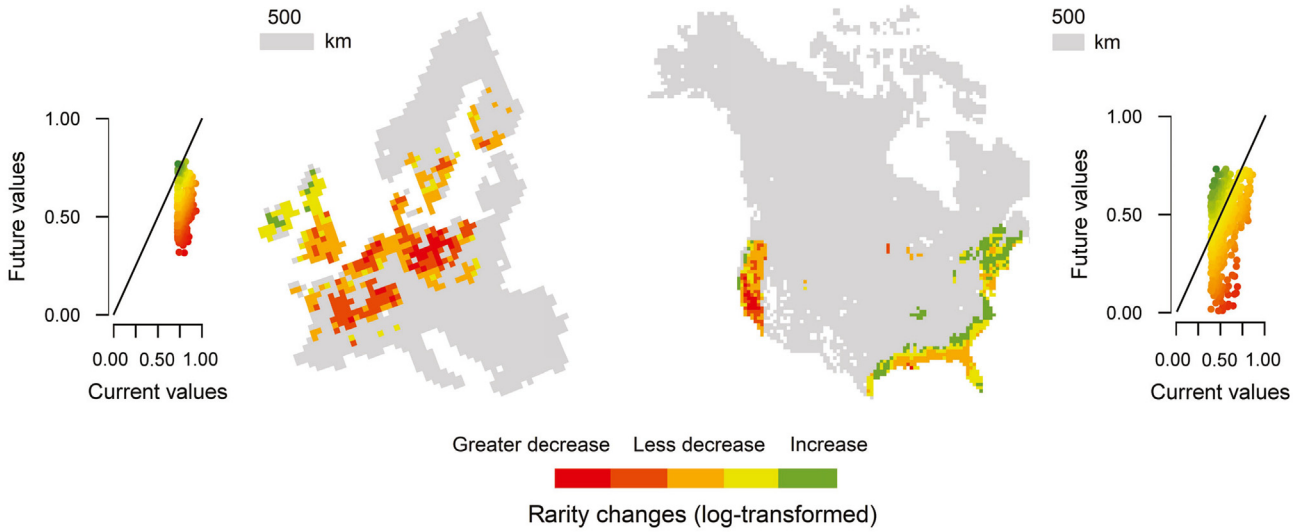


Fig. 5. The predicted change in Margalef rarity measure (log–transformed) under future climate change (2081–2100, based on the SSP5–8.5 scenario from CMIP6, O'Neill et al., 2016) from the BRT analysis. Small increases in climate suitability for rare species are given in green, whereas large and relatively small reductions in climate suitability are in red to red orange and in light orange to yellow, respectively. The diagonal 1:1 line in the scatter plots represents situations of no difference between the predicted current and future diversity of rare species. Note that most points are below the diagonal line, therefore suggesting a reduction of rare species diversity across most of the geographical areas that currently harbor hotspots of rare species of freshwater plants. Our analyses suggest large decreases in climate suitability for rare plant species in the North European Plain, the western flank of the Alps, southern Scandinavia, England and Wales, southwestern North America and the Gulf Coast of the United States. By contrast, several notable temperate areas, including Ireland, Scotland, the northeastern flank of the Appalachian Mountains and the Atlantic Coastal Plain of North America, were predicted to experience small increases in climate suitability for rare species of freshwater plants under future projected climate.

patterns, mechanisms and future scenarios we observed here may change with inclusion of additional data. Hence, interpretation of our results must therefore be tempered with these ideas in mind. However, the geographical distribution data based on Atlas Flora Europaeae (Jalas and Suominen, 1972–1994; Jalas et al., 1996, 1999; Kurtto et al., 2004) and Flora of North America (Flora of North America Editorial Committee, 1993–2007) are comparable to regional plant occurrence datasets and comprise representative subsets of the total freshwater plant diversity across the continents (Murphy et al., 2019, 2020). Below, we outline the patterns that emerged and consider these interpretations as working hypotheses to be further tested as additional botanical data emerges from the understudied areas of Europe, North America and the rest of the world.

4.1. Variable geographical and latitudinal trends in rare species diversity across the continents

The trends in biodiversity along spatial gradients have attracted the attention of naturalists ever since the time of Linnaeus (Gray, 1840, 1846). Among them, the latitudinal diversity gradient is most frequently reported and has been considered as the oldest known ecological pattern (Hawkins, 2001). Relatively few studies have examined the relationships between latitude and freshwater plant diversity at any scale though, and results obtained are inconclusive thus far (Hutchinson, 1975; Crow, 1993; Heino and Toivonen, 2008; Chappuis et al., 2012; Alahuhta, 2015; Alahuhta et al., 2013, 2020, 2021; Murphy et al., 2019; García-Girón et al., 2020b). Here, a linear negative trend was present in North America, which is in accordance with the monotonic decrease at similar latitudinal ranges in terrestrial faunas and floras within the Nearctic realm (e.g. Qian, 1999; Ricketts et al., 1999; Qian and Ricklefs, 2007). Interestingly, this pattern was previously detected for freshwater plant richness in the same study area (Alahuhta et al., 2020). In contrast, diversity of rare species in Europe diverged from the general pattern of decreasing values towards the Poles. The reason for the unimodal latitudinal gradient in the rarity of freshwater plants may be related to the fact that there are several rare plant species not occurring south of Central Europe. Alternatively, this trend might be enhanced by a data bias, given that there is a lack of freshwater plant lists in southern and eastern countries. However, our findings are remarkably similar to the pattern outlined by Alahuhta et al. (2020) for species richness in the Western Palaearctic. Such unimodal latitudinal trends have been found for several other freshwater taxa across Europe (e.g. Hof et al., 2008; Dehling et al., 2010), although different patterns are likely to be found when studies are conducted at different spatial grains and extents (e.g. Heino, 2011; Murphy et al., 2019).

Geographical trends (Fig. 1) pictured more rare species across the central and western part of the area analyzed in Europe – a region that includes southern Scandinavia, the North European Plain, the Jutland Peninsula and the British Isles. This band broadly matches the transition between the boreal and temperate zones and might simply reflect the fact that few rare plant species tolerate boreal and subarctic climates (Svenning et al., 2009). On the other hand, slightly lower diversity of rare species in East–Central Europe may be due to intensive land use in these areas, which has probably caused local extinctions (Ellis et al., 2012). Large numbers of rare species are concentrated in a small proportion of the North American's land surface. Examples include the southeastern part of the continent (particularly along the Neotropical Floristic Province of Florida) and the southwestern edge of the United States, including the Pacific Coastal Forest and the Mediterranean chaparral and woodlands of California. Interestingly, some of these areas coincide with regions that have rare climate conditions (e.g. Florida, southern Louisiana), and are hotter and wetter areas than surrounding grid cells. In this vein, the major disjunction between the tropical and humid subtropical floras in North America is also indicated by the distribution of some freshwater plant families (in this study, for example, Eriocaulaceae, Hydrocharitaceae, Limnocharitaceae, Mayacaceae and Pontederiaceae, Crow, 1993, Santamaría, 2002, Murphy et al., 2019), thereby potentially supporting 'the climatic rarity hypothesis' for freshwater plants (Ohlemüller et al., 2008). In addition, rare plant species are particularly clustered in the coastal areas of the two continents, where human population densities and associated habitat fragmentation are extremely high (Stein et al., 2000). This probably indicates that coastal areas support rare freshwater plant species that have survived or evolved over time in local refugia because of mild, aseasonal climates (Anacker et al., 2013). Alternatively, this relationship might exist because hotspots of freshwater rarity overlap extraordinarily well with

the coastal areas that most benefit population growth and urbanization (Cincotta et al., 2000). In other words, this pattern might be most easily understandable in terms of the most climatically stable areas in and around the coast being also most suitable for widespread human settlements.

4.2. Current climate, historical constraints and human footprint shape freshwater plant rarity

We found that the spatial heterogeneity in annual mean temperature, temperature seasonality, total precipitation and precipitation seasonality were clearly the most important climate predictors of rare species diversity variation at the continental extent, thereby pointing to a water–energy dynamic, where the availability of ambient heat and frost are the limiting factor at high latitudes, and drought constraints the size of the available species pool outside humid regions (Hawkins et al., 2003; Kreft and Jetz, 2007). More specifically, coefficients of variation in mean annual temperature and precipitation seasonality (a variable that encapsulates both amount and temporal occurrence of precipitation) had negative and positive relationships with diversity of rare species (Fig. 3), respectively, suggesting that more rare species are found in less climatically heterogenous regions and in areas where short–term annual variation in precipitation increases. This is not surprising because temperature affects survival, physiology and growth rates of freshwater plants by determining, for example, their flowering period, air–water gas exchanges due to ice and snow cover, seed germination and establishment, nutrient uptake, metabolic events (including photosynthesis, respiration and enzyme–mediated processes), ice erosion and the over–wintering of rhizomes in the substrate (Valley and Heiskary, 2012; Lacoul and Freedman, 2006; Nilsson et al., 2015).

Why diversity of rare species increased consistently throughout the range of variation in precipitation is interesting, and the underlying explanation is not likely straightforward. Interestingly, however, these results partly refute 'the climate variability hypothesis', where seasonal climate variability selects for climate generalists and subsequently leads to the dominance of common, broad–ranging species (Stevens, 1989). Overall, the influence of climate variables on freshwater plant rarity is consistent with their influences on (meta)community arrangements (O'Hare et al., 2012; García-Girón et al., 2020b; Kim and Nishihiro, 2020), species richness and diversity (Crow, 1993; Alahuhta et al., 2017; Murphy et al., 2019; García-Girón et al., 2020a), and geographical range sizes (Alahuhta et al., 2020; Murphy et al., 2020). Perhaps more importantly, however, this study is the first to provide evidence that climate also generates and maintains gradients of rare species diversity in freshwater plants at the continental scale.

During the Pleistocene Ice Ages, large areas of Europe and North America were covered by the ice sheets, making some species in northernmost areas either to shift their distributions southward or go extinct in advance of expanding glaciers (Svenning and Skov, 2007). Several studies suggest that many terrestrial vascular plants (including the majority of trees and other woody plants) have only expanded to fill a relatively small proportion of the area with suitable climate conditions (Svenning et al., 2009; Normard et al., 2011). In Europe, freshwater taxa with limited dispersal ability are geographically restricted to the southern refuges following the onset of the interglacial (Dehling et al., 2010). However, the degree to which patterns in freshwater plant distributions are in accordance with this hypothesis is open to intense debate (Alahuhta et al., 2020; Murphy et al., 2020).

In our work, the average velocity of climate change mirrored the form of the latitudinal gradient in diversity of rare species across Europe (i.e. freshwater plant rarity is higher in areas with relatively high velocities, *c.* 50 m yr^{-1}; Fig. 3) and emerged as one of the most important variables in explaining the overall pattern in this continent. However, observed higher rare species diversity in areas that are climatically unstable was inconsistent with a differential selection for broad–ranged generalists, supporting recent arguments that de–emphasize the role of post–glacial migration lags in the observed range–size patterns of freshwater plants in northern ecoregions (e.g. Alahuhta et al., 2020). In North America, for example, Sawada et al. (2003) found that aquatic plant species closely followed the receding Laurentide Ice Sheet by rapidly moving north into ice–marginal areas across the Great Lakes region. In this regard, our findings are somewhat consistent with 'the stasis post–expansion hypothesis', which proposes that taxa with strong dispersal ability —such as freshwater plants (Santamaría, 2002)— should have rapidly filled their potential ranges after the retreat of ice sheets, after which their ranges remained stable over time (Jablonski, 1987). Indeed, while there is some support for this hump–shaped relationship between species rarity and climate instability both in the fossil record and extant taxa (reviewed in Sheth et al., 2020), we are unaware of any freshwater plant study that has yet empirically supported this model. On the other hand, it is also possible that Late Quaternary climate–change velocity per se is not driving diversity of rare species in freshwater plants, but simply correlates with other mechanistic variables that do have a direct link; for example, relatively high–velocity areas may coincide with those where analogous climate conditions have most expanded since the LGM (Sandel et al., 2011).

We were surprised to find that rare species diversity increased with human footprint across North America. Indeed, this latter relationship seems to be counterintuitive because strongly impacted landscapes should decrease rather than increase the number of rare plant species. As already discussed in previous studies on aquatic and ground beetle faunas (Heino and Alahuhta, 2019; Heino et al., 2019), it might be that rare plant species tend to occur in regions favored by humans or that human impacts causes freshwater plant species to become geographically restricted (Albuquerque et al., 2019). Alternatively, human activities might also provide opportunities for rare species of freshwater plants to colonize newly available habitats, such as quarries and pit lakes.

Other predictors had relatively small contributions to the geographical distribution of rare species diversity across the continents examined (Figs. 3–4). As expected, the observation that mean water alkalinity was slightly negatively correlated with diversity of rare species suggests that some broad–ranged species can use bicarbonate (HCO_3^-) as a source of carbon in photosynthesis and thereby have some competitive advantage over those range–restricted species that cannot (Vestergaard and Sand-Jensen, 2000). Similarly, rare species diversity showed a unimodal increase with greater topographic heterogeneity. This effect appears in North America, where some centers of species rarity appear to contain cool–adapted species near the Rocky Mountains and the California Coast Ranges. The importance of topography may reflect the fact that mountainous areas show greater turnover of habitats (including geological and soil properties), and thus enable the establishment of plant species specialized to rare conditions (Alahuhta et al., 2017, 2018), supporting the importance of mountains as havens of biodiversity (Sandel et al., 2011; Rahbek et al., 2019) and von Humboldt's classic assertions on the issue (von Humboldt and Bonpland, 1807). Similarly, topographically fragmented landscapes might promote speciation due to greater historical possibilities for allopatric and parapatric speciation or may decrease extinction risk due to better possibilities for tracking climate change with small–scale altitudinal range shifts (Sandel et al., 2011; Hortal et al., 2013), thereby maintaining species rarity over time. However, the notable drop in rarity at relatively high terrain ruggedness scores may imply that freshwater ecosystems supporting high rare species diversity do not exist at the highest and steepest areas. Across a variation of nine orders of magnitude in our dataset, the proportion of water in our 50 × 50 km grid cell was a relatively weak, yet significant, predictor of rare species diversity, and explained 5.8–6.5% of the variation of freshwater plant rarity across Europe and North America, respectively (Fig. 3). Interestingly, mountainous regions (the Apennine Mountains and the Carpathians) and some geographical areas affected by landscape aridity (the California Floristic Province

and the oriental part of the Great Plain Grasslands) were particularly prone to the influence of potential habitat availability, supporting a positive species–area relationship (Hawkins et al., 2003).

4.3. Future climate change may affect hotspots of freshwater plant rarity

Climate change has imposed new selection pressures towards the distribution of freshwater plants (Alahuhta et al., 2011; Gillard et al., 2017; Hossain et al., 2017; Sleith et al., 2018). However, converting macroecological patterns into predictions about projected climate change scenarios is often difficult and always challenging. Although we took a conservative approach in deriving meaningful estimates of rare species diversity patterns from our analyses, more attention should be paid to model misspecifications caused by important, but missing, projected environmental variables (e.g. human footprint). Here, we provided evidence that several current centers of species rarity might shrink disproportionately as the climate warms, leading to potentially high vulnerability for many of the freshwater plant species they contain. More specifically, most grid cells containing rare species (including the North European Plain, the western flank of the Alps, southern Scandinavia, England and Wales, southwestern North America and the Gulf Coast of the United States) showed strong reductions in diversity of rare species by 2081–2100 (Fig. 5). These results further emphasize that these areas may result in continentally important centers of conservation concern becoming hotspots of extinction. Not surprisingly, evidence from terrestrial systems also suggests that rare species of vascular plants are also likely to be threatened by climate change across the globe (Enquist et al., 2019).

Projections of the effects of climate change found that diversity of rare species in some areas of the western edge of the Atlantic region in Europe and the Pacific Coast of the United States will decrease by more than 50% within a century (Fig. 5). For example, in California, a biodiversity hotspot with over 2000 endemic plant species (Myers et al., 2000), rare freshwater plants might be unable to adjust their ranges fast enough to spatially track the expected rate of climate change. In addition, future warming is likely to be increased at relatively high elevations (Thuiller et al., 2005) and may further threaten rare montane species there (i.e. the hotspot of the California Coast Ranges) and in the western flank of the Alps. On the other hand, fragmented landscapes in the North European Plain, southern Scandinavia and in the Coastal Plains of southeastern North America will make species extremely sensitive to new climate conditions, not least because the local topography will not be sufficient to buffer a shifting climate by providing niches and upslope refugia (Anacker et al., 2013). That said, the relationships between climate and landscape features are still unresolved and is just beginning to be understood (Roland et al., 2019). Our models suggested that some rare species will colonize new temperate areas (including Ireland, Scotland and the northeastern flank of the Appalachian Mountains), which will probably result in occupation of current climate niches due to a temperature–related increase in the growth rate of some freshwater plant species (Alahuhta et al., 2011).

4.4. A roadmap for conservation planners, environmental managers and policymakers

With limited resources and time, conservation planners and environmental managers are faced with making difficult decisions and setting priorities to conserve what habitat remains. Ultimately, rare species are more prone to strong reductions in population sizes, geographical ranges and extinction threats, and should be high priorities for conservation programs (Pimm and Lawton, 1998). A lesson from our study is that rare species diversity concentrated in a relatively small proportion of the European and North American land surface, thereby making these regions (i.e. southern Sweden, the Finnish lake district, the Atlantic region of Western Europe, the western flank of the Alps, the British Isles, the Atlantic and Gulf Coastal Floristic Province, the western edge of Rocky Mountains, the Pacific coast of the United States and the Neotropical Floristic Province of Florida) of particular conservation importance. Given that areas rich in freshwater plants and hotspots of rarity are likely to overlap (Fig. 1), focusing protection efforts on rare species would also simultaneously protect a large number of other species. Although not all botanical data have been digitalized, it is also remarkable that *c.* 95% and 70% of these areas that harbor a notably high diversity of rare species are threatened by rapid rates of projected climate change in Europe and North America, respectively (Fig. 5). Moreover, these areas are for most part also predicted to inhabit more invasive freshwater plants by the end of this century (Gillard et al., 2017).

Our models further provide early warnings for how conservationists, environmental managers and policymakers should respond to changes in the distribution of rare freshwater plant species. The best answer we have is to preserve the existing hotspots of rarity. Where this is no longer possible, as will probably often be the case, it might be plausible to use ecological restoration and/or to make intervening anthropogenic landscapes more freshwater friendly (Corlett, 2016). Where none of these options are possible, vulnerable rare species may need to be moved artificially to areas that they do not currently inhabit (McLachlan et al., 2007). For example, rare species living in lowlands (e.g. the North European Plain, southern Scandinavia and the Coastal Plains of southeastern North America), some of which may be unable to find refuge from novel, intolerable climates locally (see above), may be prime candidates for assisted migration (Anacker et al., 2013). We acknowledge that such assisted migration is controversial (Corlett, 2016), but alternative options are still limited. Initiatives for the implementation of 'essential biodiversity variables' (Jetz et al., 2019) seem best suited to monitoring freshwater plant rarity and ensuring that these species persist into the future. Similarly, the Global Strategy for Plant Conservation (Secretariat of the Convention on Biological Diversity, 2014) may well need to further emphasize human activities and projected climate change as critical to conserving freshwater plant biodiversity, and recognize the hotspots of rarity outlined in our study for expansion of protected areas in this new decade. The bottom line here is that many factors matter for freshwater plants (e.g. current and future climate, Ice Age legacies and human footprint) and that there is no silver bullet for setting priorities.

5. Concluding remarks

In summary, existing distributions of rare species suggest variable patterns in relation to latitude between Europe and North America, and confirm many regional trends and hotspots anticipated before (Enquist et al., 2019; Murphy et al., 2019; Alahuhta et al., 2020). Specifically, the latitudinal gradient in rare species diversity was strong in the North American landmass, whereas spatial variation in freshwater plant rarity was more complex in the area analyzed in Europe, showing a unimodal response to latitude. These region–specific differences emphasize that macroecological patterns might be confounded when different biogeographical realms are pooled. Moreover, we showed that relatively few variables, namely a combination of current climate, Late Quaternary history and human footprint, are able to accurately predict the location of continental centers of rare species diversity. Interestingly, we further provide evidence that current centers of species rarity are currently characterized by higher human footprint scores and might shrink disproportionately within a century as the climate changes. These results may help conservation planners make more informed decisions mitigating the negative effects of climate change and other anthropogenic stressors.

Ultimately, these findings suggest that the patterns and potential underlying mechanisms of the spatial variation of rarity in freshwater plants may be complex, requiring additional insights from studies conducted at multiple spatial scales and in areas outside of Europe and North America. By incorporating directional effects of the explanatory

variables, future work might extend or validate the deterministic relationships between rarity and the ecogeographical factors proposed in this study. In order to expand our understanding of rarity in freshwater systems, we need more insights from Tropical, Indomalayan, Oceanian and Australasian regions (Murphy et al., 2019; Alahuhta et al., 2021). As these data continue to accumulate for freshwater plants, future studies will undoubtedly provide a more detailed understanding on patterns and future scenarios of rare species diversity; for example, by characterizing species rarity based on niche breadth or population density, which might prove useful for selecting conservation priorities (Sykes et al., 2019). In addition, data on species rarity should be combined with information on existing nature reserves, levels of threat, ecosystem service values and centers of endemism. Achieving all of this would require ecologists to resist the siren song of the local and ecosystem–oriented views that have dominated the study of freshwater systems for a long time. Presumably, this will be highly essential when dealing with the global change effects on these little–known, but highly vulnerable floras.

Data accessibility statement

The original data are available in their primary sources, where they can be obtained from free open data repositories (Alahuhta et al., 2020).

CRediT authorship contribution statement

Jorge García-Girón: Conceptualization, Formal analysis, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Jani Heino:** Writing – original draft, Writing – review & editing, Supervision, Validation, Visualization. **Lars Lønsmann Iversen:** Writing – original draft, Writing – review & editing, Supervision, Validation, Visualization. **Aveliina Helm:** Data curation, Writing – review & editing. **Janne Alahuhta:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Validation, Visualization.

Declaration of competing interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.147491.

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