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CURRENT CLIMATE OVERRIDES HISTORICAL EFFECTS ON SPECIES RICHNESS AND RANGE SIZE OF FRESHWATER PLANTS IN EUROPE AND NORTH AMERICA

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Abstract

1. The latitudinal diversity gradient (LDG) hypothesis suggests that species richness should be highest at low latitudes, whereas Rapoport's rule states that largest ranges ought to be found for species at high latitudes. However, there is no consensus over these patterns and their underlying drivers in the freshwater realm.
2. We investigated species richness and mean range size of freshwater plants in 50 km × 50 km grid cells across Europe (40°N to 71°N) and North America (25°N to 78°N), supplemented with data based on 1° latitudinal bands for mean range size. We were especially interested to find out whether there are similarities and differences in these ecogeographical patterns and their underlying drivers between the continents due to their contrasting historical characteristics, spatial extent and topography.
3. First, we used partial regression to reveal whether species richness and mean range size of freshwater plants have a linear or quadratic relationship with latitude. Second, we employed variation partitioning based on partial regression to model relationships between plant species richness and mean range size and four explanatory variable groups (i.e., environmental features, current climate, historical climate and geographical location). Third, we utilized boosted

regression tree analysis to further investigate species richness and mean range size of freshwater plants in relation to a set of explanatory variables.

4. Our results revealed that species richness showed relatively similar patterns in relation to latitude between the continents. Similarly, mean range size trends were alike in North America whether we used 50 km x 50 km grid cell data or 1° latitudinal bands. Instead, different patterns in mean range size emerged between the used data sets in Europe. For both of species richness and mean range size, current climate (with different individual predictor variables) was the main driver in both the continents, but historical effects had a small influence on the response variables.

5. *Synthesis.* Our findings indicated that major ecogeographical rules can strongly vary for the same taxonomic group across broad scales between continents. It is also premature to rely solely on well-known terrestrial taxonomic groups when drawing generalizations about ecogeographical rules.

INTRODUCTION

An increasing number of investigations has led to a few ecogeographical rules which generally occur across many taxa and realms (Gaston, Chown, & Evans, 2008). However, these ecogeographical patterns have often been based on research of well-known taxa which typically inhabit terrestrial ecosystems (Field et al., 2009; Gaston & Blackburn, 2000), whereas exceptions to these rules have been found from many highly diverse and less-studied organism groups that occur in freshwater ecosystems (Iversen et al., 2019; Kinlock et al., 2018). Because understanding ecogeographical patterns is important for both fundamental and applied research (Díaz et al., 2019; Vilmi et al., 2017), more information is needed from understudied taxa and undervalued ecosystems to gain more profound understanding of the degree of generality of these major patterns across the world. Two ecogeographical patterns that have been intensively studied are latitudinal diversity gradient related to species richness and Rapoport's rule originating from variation in species range sizes.

The latitudinal diversity gradient (LDG) hypothesis indicates that species richness decreases from the Equator toward the poles (Gaston, 2000; Hillebrand, 2004). For many taxa, ranging from terrestrial plants and butterflies to birds and mammals, the LDG has been evidenced at broad spatial scales (Field et al., 2009; Hillebrand, 2004; Kinlock et al., 2018). However, there have also been clear exceptions to this rule in some hyperdiverse organism groups, such as among insects, many microbes and fungi (Kouki et al., 1994; Tedersoo & Nara, 2010; Soininen, 2012; Tedersoo et al., 2014). The key drivers underlying the LDG originate from explanations broadly related to current climate, historical effects and biome area (Gaston & Blackburn, 2000; Lomolino, 2000; Currie et al., 2004; Svenning & Skov, 2007; Hortal et al., 2011). First, the effect of current climate on species richness stems from the idea that warmer and less variable climate around the Equator offers more energy and less harsh environmental conditions to sustain more species compared to high-latitude areas with colder and harsher climate (Currie et al., 2004). Second, ice ages have created variable evolutionary legacies among areas, as evolutionary history should be longer at low-latitude areas compared with high latitudes, which have undergone recurring ice ages (Lomolino, Riddle, & Whittaker, 2017). Most species were eliminated during ice ages in the high-latitude areas (Hewitt, 1999; Hortal et al., 2011), which they re-colonized after the retreat of ice sheets (Sawada, Viau, & Gajewski, 2003; Svenning & Skov, 2007). However, ice age effects have not been uniform across the highest latitudes. Third, the species richness-biome area relationship yields from the assumption that reduced extinction risk and increased speciation probability exist in the larger areas of tropical biomes compared to those at higher latitudes (Lomolino, 2000). These key drivers of the LDG are associated with hypothesis categories of ecological limits, diversification rates and time for species accumulation with variable degree, which in turn are dictated by four fundamental ecological processes (i.e., selection, ecological drift, dispersal and speciation) (Pontarp et al., 2018). At broad scales, selection, ecological drift and dispersal determine species geographical occurrence and evolution of species traits. Species, which poorly adapt to the environment or are poor competitors for resources, likely have low fitness and ultimately become extinct (Pontarp et al., 2018). These processes inevitably interact with each other but can help us to better understand how key drivers underlie the LDG.

The main idea behind the Rapoport's rule is that species occurring at high latitudes have, on average, larger ranges than species occurring in low latitudes (Stevens, 1989; Brown et al., 1996).

This rule also embraces the assumption that species richness is higher at low latitudes, because smaller ranges allow more species to coexist in a given area (Stevens, 1989). At high latitudes, species should have large ranges, leading to lower number of species present there. This association between range size and species richness was further considered by Sizling et al. (2009), who suggested that Rapoport's rule holds true only when larger range sizes co-vary with decreased range overlap. Thus, inverse Rapoport's rule is possible under a normal LDG if species with more broad ranges in the tropics also have a strong range overlap due to non-linear temperature gradient (Tomašových, Jablonski, Berke, Krug, & Valentine, 2015). Findings from previous empirical studies have been conflicting (Gaston, Blackburn, & Spicer, 1998), revealing evidence to support (Sanders, 2002) but especially to refute (Murphy et al., 2019; Outomuro & Johansson, 2019; Pintor, Schwarzkoff, & Krockenberger, 2015) Rapoport's rule. When support for Rapoport's rule has been found, it has been typically prevailing above latitudes north of 40° and 50° (Rohde, 1996; Gaston et al., 1998). The drivers of range size variation have been hypothesized to result from climatic and historical factors but also biome area (Stevens, 1989; Brown, 1995; Stevens, 1996). First, species inhabiting high latitudes with high climatic seasonality are thermal generalists, thus having broader ranges along latitude. Second, recurring ice ages have eliminated species that have narrow ranges at high latitudes. Third, biome area may not only influence range sizes through variation in species richness and habitat availability but also via the effects of longitudinal area depending on used data (Tomašových et al., 2016). These drivers generating range size variation are not only directly linked with the corresponding drivers of the LDG but also to the four fundamental ecological processes structuring species occurrences geographically (Pontarp et al., 2018). However, the existence of Rapoport's rule and its underlying drivers have rarely been studied in the freshwater realm, hindering our possibilities to tackle global change effects in these valuable ecosystems (Heino & Alahuhta, 2019).

Many freshwater taxa have been inadequately studied in a macroecological context (Heino, 2011). For example, our understanding of the LDG and Rapoport's rule in aquatic plants is highly insufficient. Moreover, patterns found for terrestrial plants may not be applicable to aquatic plants, because access to water and atmospheric gases is essentially variable for terrestrial and aquatic species, and aquatic plants likely respond differently to temperatures than their terrestrial counterparts due to mitigating effects of freshwater environments (Alahuhta et al., 2017). Previous

studies on the LDG based on aquatic plants have rarely covered a continental or a global extent (e.g., Carvalho, Bini, Diniz-Filho, & Murphy, 2009; Grimaldo et al., 2016; but see Murphy et al. 2019), and in the few exercises conducted up to now, data have been scaled to coarse political or biogeographical regions (Chambers, Lacoul, Murphy, & Thomaz, 2008; Chappuis, Ballesteros, & Gacia, 2012). Regarding Rapoport's rule, we are not aware of any previous study on aquatic plants, where variation in species range sizes has been correlated with latitude at continental and larger scales. This severe deficiency of research hinders our possibilities to make generalizations that major ecogeographical patterns prevail in understudied taxa and ecosystems, such as plants in freshwater ecosystems.

The overall purpose of our work was to compare ecogeographical patterns and their underlying drivers in freshwater plants in Europe and North America to reveal possible similarities and differences between the continents reflecting differences in historical characteristics, spatial extent and variable topography. More specifically, our study aims were to investigate (1) whether there is a latitudinal gradient in species richness and mean range size of aquatic plants, and (2) what are the drivers (i.e., contemporary environmental features, current climate and historical effects) behind variation in species richness and mean range size of freshwater plant taxa across Europe and North America. We hypothesized that (1) species richness decreases with increasing latitude (Gaston, 2000), and (2) mean range size in a regional assemblage increases with increasing latitude (Stevens, 1989). In addition, we expected that current climate drivers LDG and mean range size patterns in aquatic plants at the spatial resolution and extent (Chappuis et al., 2012), but it is difficult to estimate relative roles of different explanatory variables on these ecogeographical rules due to lack of previous investigations.

MATERIAL AND METHODS

Species data and used response variables

In Europe, to obtain estimations of species range sizes, we merged the two largest plant atlases available in Europe: Atlas Florae Europaeae (Jalas & Suominen, 1972; Jalas, Suominen, & Lampinen, 1996; Jalas, Suominen, Lampinen, & Kurtto, 1999; Kurtto, Lampinen, & Junikka,

2004) and Atlas of North European Vascular Plants (Hultén & Fries, 1986) as described in (Kalwij, Robertson, Ronk, Zobel, & Pärtel, 2014). The combined set of data represent the most comprehensive broad-scale plant distribution data to date in Europe, with distribution information for 5221 European plant taxa (species and subspecies). Data covered most of Europe, divided into 50 km × 50 km grid-cells. As the data quality is poorer in the south, we limited the study area to north of 41°N latitude, and North of Spain (Pyrenees), Russia, Moldova, Belarus and Ukraine were also excluded. In North America, we used species range maps from Flora of North America (Flora of North America Editorial Committee, 1993+) that were digitized to grid cells of 50 km x 50 km. The study area was restricted to the main continental USA and Canada, excluding Mexico and remote islands. We sorted the data using global water mask at 150 m resolution (Lamarche et al., 2017) to include only those grid cells, which had freshwater (>0%). We further sorted the grid cells by including the grid cells, which contained $\geq 50\%$ of continental land, as we were interested in freshwater environments, but not in marine environments. These criteria resulted in 1561 equal-sized grid cells in Europe and 7011 equal-sized grid cells in North America (Figure 1). In addition, we combined 50 km x 50 km grid cells to 1°N latitudinal bands (from 40°N to 71°N in Europe and from 25°N to 78°N in North America) for additional analysis regarding mean range size. This enabled us to better compare our findings with previous studies, where only latitudinal extent was considered when investigating Rapoport's rule (e.g., Stevens, 1989; Brown et al. 1993; Tomašových et al., 2016).

Figure 1. Species richness and mean range size of aquatic plants in Europe and North America in 1561 and 7011 grid cells of 50 km x 50 km, respectively.

We studied vascular aquatic plants growing permanently in lakes, ponds, streams and rivers (i.e., hydrophytes), but were unable to distinguish species based on habitat where they grow (lentic vs. lotic habitats). Vascular plants inhabiting peatlands and marine environments were excluded from

the data sets. In addition, shore vascular plant species and semi-aquatic emergent plants were removed from the data. For the European data set, we selected freshwater plant species using the categorization of European hydrophytes (Willby, Abernethy, & Demars, 2000) and Ellenberg Moisture index (Ellenberg et al., 1991), with moisture values ranging between 10 (“aquatic”) and 12 (“underwater”). All species belonging to hydrophytes and/or having moisture value at least 10 recorded in the Atlases were used in our study in Europe. For the North American data set, we selected aquatic plant species based on Wetland Indicator Status (“Almost always occur in wetlands”, <https://plants.usda.gov/wetinfo.html>), Cook (1990) and the Flora of North America. For some families (e.g., Asteraceae, Brassicaceae, Crassulaceae, Cyperaceae, Poaceae, Polygonaceae and Primulaceae), distributions maps were on US state-level only so these families were excluded from the data. However, all important freshwater plant genera, such as *Potamogeton*, were included in the data. Our study was based on presence-absence information of 157 and 216 vascular aquatic plant species in Europe and North America, respectively (Table S1 in the Supporting Information).

We used two response variables: species richness and mean range size at the assemblage level (sensu Gaston et al., 2008). Species richness in each grid cell was calculated using the presence-absence data of freshwater plants. Mean range size was defined as the average number of grid cells occupied by all species detected in a given grid cell. First, we calculated occupancy for each species (i.e., in how many grid cells it was detected). Then, we added up all species occupancies in a given grid cell and divided it by the number of species found in that grid cell (see Heino and Alahuhta, 2019). Mean range size was separately calculated for both 50 km x 50 km grid cells and 1° latitudinal bands.

Explanatory variables

Thirteen explanatory variables explaining contemporary environmental features, current and historical climate, and spatial location were used in our study (Table S2). Environmental features included proportion of freshwaters at 150 m resolution (presence/absence, Lamarche et al., 2017), mean water alkalinity concentration at 50 km resolution (mequiv. l⁻¹, Marcé et al., 2015), proportion of cropland at 1 km resolution (%), Latham et al. 2014) and proportion of urban areas at

1 km resolution (%), Latham et al., 2014). Alkalinity is one of the most important water chemistry variables for aquatic plants at the level of freshwater ecosystems (Iversen et al., 2019). Current climate variables consisted of annual mean temperature (°C), range in annual mean temperature (°C) and annual precipitation (mm). These climate variables were averaged for period 1960-1990 from WorldClim at ca. 1 km resolution (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), and they showed relatively similar patterns along latitude in the both continents (Figure S1 & S2). Historical climate variables represented conditions that occurred during the Last Glacial Maximum (ca. 22 000 years ago) and comprised climate anomaly (i.e., historical climate minus current climate) and climate velocity calculated for mean annual temperature and mean annual precipitation derived from WorldClim at 10-minute resolution. The climate velocity refers to the speed at which species must migrate over the earth's surface to maintain constant climatic conditions (Carroll, Lawler, Roberts, & Hamann, 2015; Hamann, Roberts, Barber, Carroll, & Nielsen, 2015). The velocities between historical climate and current climate were calculated by measuring for each cell in a historical climate grid the geodetic distance between the cell and its closest climatic match in a grid representing current climate. This approach is an implementation of the distance-based velocity algorithm proposed by Hamann et al. (2015). The algorithm relies on a user-defined climatic threshold, which determines what constitutes a matching climate between a grid cell and another cell that has a similar value in a different period of time. We used ± 0.5 °C and ± 25 mm as thresholds of similarity for mean annual temperature and mean annual precipitation, respectively. Latitude and longitude of centre points of each grid cell were used as spatial variables to describe spatial patterns in response and explanatory variables. All the variables were scaled to grid cell resolution and to latitudinal bands in additional mean range size exercises before further analysis using ArcGIS and the calculation of climatic velocity was done with Python programming language within ArcGIS.

Statistical methods

First, we evaluated multicollinearity among explanatory variables based on bivariate correlation (>0.7), Dormann et al., 2013). To maintain comparability in study results between the continents, we removed collinear explanatory variables from both data sets, although the problem was evident only in either Europe or North America (Table S3 & S4). Due to high correlation with one or more other explanatory variables, proportions of cropland (correlated with annual mean temperature in

Europe and North America, $R_{\text{Spearman}} = 0.74$ and 0.78 , respectively) and urban development (with annual mean temperature in North America, $R_{\text{Spearman}} = 0.71$) as well as temperature anomaly (with annual mean temperature in Europe, $R_{\text{Spearman}} = 0.80$) and precipitation anomaly (with mean annual precipitation velocity in North America, $R_{\text{Spearman}} = -0.79$) were removed from further analysis.

Second, we calculated correlation between species richness and mean range size of aquatic plants per grid-cell in both continents. Before further analysis, we transformed our response variables to improve normality using `bestNormalize` package in R (Peterson & Cavanaugh, 2019). The relationship between species richness or mean range size and latitude was evaluated based on linear regression, accompanied by Akaike Information Criteria (AIC) to assess the importance of linear vs. non-linear relationship. Further, we used variation partitioning based on linear regression to model the relationships between transformed species richness and mean range size and four explanatory variable groups (i.e., environmental features, current climate, historical climate and geographical location). In the variation partitioning, we followed the protocol by Borcard et al. (2018) to distinguish total variation in species richness and mean range size into four pure and 11 joint effects, in addition to unexplained fraction (Anderson & Cribble, 1998). We applied forward selection with adjusted R^2 values to choose statistically significant explanatory variables to the models. Adjusted R^2 values give unbiased estimates of the explained variation by taking into account different number of explanatory variables in models (Borcard et al., 2018). The forward selection using two stopping rules (global test with all variables and individual variables separately, $p < 0.05$) was applied (Blanchet, Legendre, & Borcard, 2008). Both linear and quadratic terms of the explanatory variables were used to capture the potential non-linear responses. Variation partitioning and forward selection were done separately for Europe and North America.

To get a better understanding of non-linear relationships between species richness or mean range size and influential explanatory variables, we further analyzed both data sets using boosted regression trees (BRT) (Elith, Leathwick, & Hastie, 2008) implemented in R package “`gbm`” (Ridgeway, 2017). In the BRT analysis, we only used significant explanatory variables based on forward selection in linear regression following Blanchet et al. (2008). However, we excluded

geographical location (coordinates) from the analysis to avoid collinearity between latitude and longitude and climate variables. We applied function “gmb.step”, where regularization methods are utilized to discourage overfitting and balance predictive performance with model fit (Hastie et al., 2001). For the both response variables, raw values were used and the BRTs were performed using Poisson error distribution, tree of complexity of 5, learning rate of 0.01 and bag function 0.5, following Elith et al. (2008).

To evaluate for spatial autocorrelation in the BRTs, we calculated Moran’s I coefficients and correlograms with 10 distance classes based on geographical coordinates and model residuals using Bonferroni correction (Cabin & Mitchell, 2000). Spatial autocorrelation measures were done using “correlog” in R package “pgirmess” (Giraudoux, 2017).

RESULTS

Species richness and mean range size were negatively correlated in both continents (Europe: $R_{\text{Spearman}} = -0.59$, $p < 0.001$; North America: $R_{\text{Spearman}} = -0.61$, $p < 0.001$; Figure 2). We found differences in relationship between species richness or mean range size and latitude between the continents. Considering species richness and latitude (Figure 3), a clear unimodal pattern was found in Europe (linear: $\text{AIC} = 4265$, $R^2 = 0.10$; quadratic: $\text{AIC} = 2724$, $R^2 = 0.67$), whereas the trend was almost linear in North America (linear: $\text{AIC} = 14539$, $R^2 = 0.50$; quadratic: $\text{AIC} = 13557$, $R^2 = 0.52$). Species richness was highest in 55°N latitude in Europe. In North America, species richness was high until 45°N latitude after which it decreased more or less linearly. When studying the relationship between mean range size and latitude (Figure 3), the trend was slightly U-shaped in Europe (linear: $\text{AIC} = 4279$, $R^2 = 0.10$; quadratic: $\text{AIC} = 3710$, $R^2 = 0.37$) and increasing linear relationship, which levelled off in the high-latitudes, was evidenced in the North America (linear: $\text{AIC} = 15361$, $R^2 = 0.43$; quadratic: $\text{AIC} = 14209$, $R^2 = 0.55$). The highest mean range sizes were recorded in southern parts of Europe (45°N), whereas mean range sizes peaked in 60°N latitude in North America. When considering mean range size only in relation to latitudinal bands, the pattern was increasing and strongly linear in Europe and North America, respectively (Figure S3). Species range sizes suggested nestedness pattern in Europe (Figure S4), whereas both turnover and nestedness were detected in North America (Figure S5).

Bivariate correlation among predictor and climate variables were stronger in North America than in Europe, when considering 50 km x 50 km grid cells (Table S3 & S4). Similarly, mean range size along 1°N latitude bands correlated more with climate variables in North America than in Europe (Table S5 & S6).

Figure 2. The relationship between mean range size and species richness (S) of aquatic plants in Europe and North America.

Figure 3. Species richness and mean range size of aquatic plants in relation to latitude in Europe and North America. Both linear and quadratic relationships are shown. Values of species richness and mean range size are transformed.

In variation partitioning (Table 1), the overall explained variation for species richness was 81.0% in Europe and 77.0% in North America, whereas 57.3% and 81.8% of total variation for mean range size was accounted for in Europe and North America, respectively. However, the importance of different pure and joint effects varied between the continents. For species richness, the highest pure fraction was found for geographical location (21.2%) in Europe, and for current

climate (9.6%, Table S7) and historical effects (9.6%) in North America. Of the joint effects, current climate and geographical location had the highest contribution in both Europe (29.6%) and North America (34.9%). Current climate, historical effects and geographical location together were also important in Europe (12.6%) and to some extent in North America (8.4%). For mean range size, geographical location of pure fractions (18.1%) had the highest influence in Europe, whereas the importance of pure effects remained modest in North America. Of the joint contributions, current climate (Table S7) and geographical location had the strongest effect in Europe (22.3%) and North America (51.8%). Together, current climate, historical effects and geographical location also had some importance for mean range size in Europe (7.9%) and North America (12.2%). The significant individual explanatory variables for species richness were similar between the continents (Table S8) and varied slightly for mean range size (Table S9).

Table 1. Variation partitioning based on linear regression for species richness and mean range size divided among contemporary environmental variables, climate variables, historical variables and geographical location (coordinates), along with their joint fractions. Statistically significant (<0.05) pure fraction based on the anova function are in italic. Abbreviations: NA = North America

	Species richness		Range Size	
	Europe	NA	Europe	NA
Environment	<0.01	<0.01	<0.01	<0.01
Climate	<i>0.04</i>	0.10	0.04	0.03
History	<i>0.01</i>	0.10	0.01	0.01
Geographical location	<i>0.19</i>	0.01	0.15	0.04
Environment+Climate	<0.01	<0.01	0.00	0.01
Climate+History	<0.01	0.05	0.01	0.02
Environment+History	<0.01	0.01	0.00	0.00
Environment+Geographical location	0.00	<0.01	0.01	<0.01
Climate+Coordinate	0.29	0.35	0.25	0.52
History+Geographical location	0.00	0.00	0.00	0.00
Environment+Climate+Geographical location	<0.01	<0.01	0.02	0.02
Environment+Climate+History	<0.01	0.00	0.00	0.00

Climate+History+Geographical location	0.15	0.08	0.09	0.12
Environment+History+Geographical location	<0.01	<0.01	<0.01	<0.01
Environment+Climate+History+Geographical location	0.05	0.07	0.00	0.05
Unexplained	0.25	0.23	0.44	0.17

BRTs using significant explanatory variables from previous linear regressions were very strong, explaining from 86.1 to 96.6% of deviance in all the models (Figure 4). For species richness, annual mean temperature with unimodal shape (i.e., highest species richness at median temperatures) and annual mean precipitation with increasing and then flattening pattern (i.e., species richness increased with increasing precipitations until it has no effect anymore) showed highest relative influences in Europe (57.4% and 9.8%, respectively) and North America (51.6% and 31.4%). These best predictors were followed by alkalinity (9.3%), precipitation velocity (9.1%), temperature velocity (8.5%) and proportion of freshwaters (5.9%) in Europe, and temperature velocity (5.3%), annual temperature range (4.2%), proportion of fresh water (3.9%), alkalinity (1.9%) and precipitation velocity (1.6%) in North America. For mean range size, annual temperature range (28.8%) was the most important variable in Europe, with mean range size increasing along increasing variation in temperature, followed by annual mean temperature (22.4%) (first mean range size decrease and then increase along temperature gradient), proportion of fresh water (13.1%), precipitation velocity (12.8%), annual mean precipitation (11.7%) and temperature velocity (11.3%). In North America, annual mean temperature had the strongest influence on mean range size (60.1%), with mean range size decreasing from median annual temperature onwards. Other influential variables were annual mean precipitation (20.9%) (mean range size decreasing with decreasing precipitation until ca. 1000 mm values after which the pattern levelled off), annual temperature range (7.8%), precipitation velocity (5.4%), temperature velocity (2.3%), alkalinity (2.2%) and proportion of freshwaters (1.4%).

Figure 4. Partial dependency plots from the boosted regression tree models for species richness and mean range size of aquatic plants in Europe and North America. Shown are the significant predictor variables based on forward selection in linear regression following Blanchet et al. (2008) and their relative influences. Abbreviations: Annual temp. = current annual mean temperature, Temp. range = range in annual mean temperature, Annual prec. = current annual precipitation, LGM temp. = velocity in temperature since the Last Glacial Maximum (LGM), LGM prec. = velocity in precipitation since the LGM, Water = proportion of freshwaters.

We found statistically significant ($p < 0.005$) spatial autocorrelation in all the model residuals of BRTs. However, the highest coefficients were found in the first distance classes, varying from 0.125 and 0.044 for species richness (Table S10), and 0.059 and 0.011 for mean range size (Table S11) in Europe and North America, respectively. These low coefficients suggest that spatial autocorrelation does not create serious bias in our BRT models (see Hawkins et al. 2007). In other distance classes, the coefficients were even lower. Due to broad study extents, spatial patterns

seem to mimic inherent latitudinal climate gradients in our work found for original species richness and mean range size variables (Figure S1 & S2).

DISCUSSION

Ecogeographical rules have typically resulted from findings for well-known terrestrial taxa (Brown et al., 1996; Gaston et al., 2008; Hillebrand, 2004). However, much less is known about whether or not these rules also apply in freshwater ecosystems and in poorly-studied taxa. Therefore, we studied species richness and mean range size of aquatic plants in relation to latitude, environmental features, current climate gradients and historical effects across Europe and North America. First, we found that species richness and mean range size were negatively correlated in both continents. Second, species richness showed relatively similar and mean range size indicated very different patterns in relation to latitude between Europe and North America. However, patterns were more congruent between the continents for mean range size when considering only latitudinal bands. Third, when excluding geographical location, current climate was the main driver of species richness and mean range size in both continents, but historical effects had a small influence on these response variables. Annual mean temperature had the strongest contribution to species richness in both continents. Mean temperature range, followed by mean annual temperature, shaped variation in mean range size in Europe, whereas both mean annual temperature and mean annual precipitation influenced mean range size of aquatic plants in North America. These findings suggest that complex patterns and their underlying drivers in species richness and range size can be found between continents even for the same taxonomic group.

Different patterns but similar drivers of species richness in Europe and North America

We found evidence both to support and refute our first hypothesis that the species richness of aquatic plants decreases with increasing latitude. A unimodal pattern between species richness and latitude was found in Europe (i.e., refuting the hypothesis), whereas a linear negative trend was evidenced in North America (i.e., supporting the hypothesis). A previous study on aquatic plants suggested that an unimodal pattern between species richness and latitude exists in Europe (Chappuis et al., 2012), but this study was executed at a country resolution. Similar unimodal

latitudinal pattern for species richness was evidenced for freshwater fauna across Europe (Dehling, Hof, Brändle, & Brandl, 2010). However, evidence on the LDG from Europe may not be representative of the global pattern (Murphy et al., 2019).

Our findings indicate that hypothesis basis behind our LDGs originate from ecological limits rather than diversification rates or time for species accumulation (see Pontarp et al., 2018). Strong climatic influence, and lack of historical effect, found in our work implies that selection through (mean) temperature filtering is likely the main driver of the LDG for aquatic plants at broad scales. A recent simulation study suggested that in most scenarios the LDG emerges from ecological limits instead of diversification rate (Etienne et al., 2019). They also modelled that diversification rates underlie the LDG compared with ecological limits only when speciation and dispersal rates are low. In this case, however, the LDG would be quite weak, opposite to the found trend for aquatic plants in Europe and North America. In addition, spatial processes rarely structure aquatic plant metacommunities (Alahuhta et al., 2018) and different pathways of long distance dispersal are well-documented for aquatic plant species (Viana, Santamaría, & Figuerola, 2016).

Current climate (i.e., mean annual temperature) was the main environmental driver of aquatic plant species richness at the continental extent. Mean annual temperature mirrored the form of latitude in explaining species richness. Temperature influences physiological responses (e.g., seed germination in addition to onset and rate of seasonal growth) of aquatic plants (Lacoul & Freedman, 2006), which are also sensitive to cold temperatures through freezing of sediment, ice erosion, limiting of light penetration and air-water gas exchanges due to thick ice and snow cover (Nilsson, Polvi, & Lind, 2015; Valley & Heiskary, 2012). Thus, aquatic plant species richness first increased with enhancing nutrient concentrations and temperature until ~55°N latitude, but then it declined with too harsh climate conditions in our study continents. Mean annual temperatures also positively correlated with proportions of cropland and urban development in both the study continents. It seems that the LDGs of aquatic plants originated from the interplay between climate and land use, also reflecting productivity in freshwater ecosystems. Species richness of aquatic plants typically increases with increasing availability of nutrients in oligotrophic waters after which it begins to decrease when the nutrient concentrations become too high (Phillips, Willby, &

Moss, 2016; Salgado et al., 2018). Moreover, nutrient concentrations often positively correlate with cropland and urban development (Johnson, Richards, Host, & Arthur, 1997), further affecting aquatic plant species richness (Akasaka, Takamura, Mitsuhashi, & Kadono, 2010; Alahuhta, Kanninen, & Vuori, 2012). This complex interaction between climate and land use was also possibly manifested through geographical location, which was the most important variable explaining species richness of aquatic plants in Europe.

Current climate also overrode the influence of climate history in explaining variation in species richness of aquatic plants. In several studies on terrestrial vascular plants, historical effects have been important for current species distributions (Liu et al., 2018; Svenning & Skov, 2007). European freshwater fauna does neither seem to have reached equilibrium and may still be influenced by history (Dehling et al., 2010). In our work, historical climate effects together with current climate were influential in Europe and North America based on variation partitioning, and climate velocity variables' relative contributions were from few percentages to nearly 10 in the BRT models. This weak importance of historical effects is not surprising as many aquatic plants have extensive reproduction abilities (e.g., both sexual and asexual) together with efficient dispersal strategies (e.g., water-, wind- and bird-mediated dispersal) (Brochet, Guillemain, Gauthier-Clerc, & Green, 2009; Santamaría, 2002; Soomers et al., 2013). Sawada et al. (2003) also found that many aquatic plant species rapidly colonized their current distribution ranges in North America after the Last Glacial Maximum. These findings suggest that aquatic plants can track their climate optima over relatively short time periods. Despite our findings were quite evident, we acknowledge that other measures of historical effects, such as time since colonization of a region by a clade (e.g., Stephens & Wiens, 2003), could have yielded to different results on the importance of historical effects on freshwater plants.

We found that proportion of water and degree of alkalinity in a 50 km × 50 km grid cell had marginal effects on species richness of aquatic plants, challenging the idea that contemporary environmental features drive aquatic plant species richness at broad scales. This finding seems odd at first sight (e.g., Iversen et al., 2019); however, it makes perfect sense in the light of our spatial resolution and relatively high overall wetness of our study area. Dehling et al. (2010) similarly

argued that availability of freshwater habitat does not influence aquatic animals across Europe due to the coarse resolution of their study. In general, aquatic plants inhabit the shallow fringes of lakes and rivers, because lack of light prevents photosynthesis and further plant growth in deep parts of water bodies (Søndergaard et al., 2013). Similarly, high water velocity in large temperate rivers inhibits species to root in the sediment (Madsen, Chambers, James, Koch, & Westlake, 2001). Thus, the most suitable habitats for aquatic plants are shallow and small lakes, ponds and streams, which are challenging to observe at our spatial resolution of our study. In addition, completely arid environments are mostly lacking in our study continents for which our conclusion regarding habitat availability should be treated with caution. Habitat area is likely to be a better predictor of species richness of aquatic plants at finer resolutions and in continents with higher variability in moisture conditions (e.g., Murphy et al., 2019). Different patterns may also have emerged if lentic and lotic plant species were analyzed separately but this was not possible with the current data sets (e.g., Hof, Brändle, & Brandl, 2006).

Complex patterns and drivers of mean range size between the continents

Our results mostly supported the second hypothesis that mean range size should increase with increasing latitude (Stevens, 1989; Brown, 1995). Support for Rapoport's rule was found from North America, where mean range size increased along increasing latitude in a linear fashion, up to the highest latitudes. Mean range size also mostly increased with increasing latitude in both the continents, when considering it along 1°N latitudinal bands, giving further endorsement for the Rapoport's rule. Range sizes in Europe showed nestedness, meaning that narrow-ranging species were nested within the distributions of broad-ranging species, with a decreasing number of broad-ranging species towards low latitudes (Hausdorf & Hennig, 2003). This suggests that high-latitude aquatic plant species either expand towards low latitudes or low-latitude plant taxa emerged at lower latitudes and differ in their abilities to disperse to higher latitudes (Tomašových et al., 2016). In North America, no clear distinction between nestedness and turnover was seen but both of them seem to be taking place simultaneously. Thus, in addition the nested patterns of narrow-ranging aquatic plant species, some narrow-ranging species are also replaced by broad-ranging species towards high latitudes (Tomašových et al., 2016).

Mean annual temperature had the strongest influence on mean range size, showing a negative curvilinear relationship. These evidences suggest that low latitude species have small ranges and species in high latitudes possess large ranges in North America. The reason for the decrease in mean range size of aquatic plants in the northernmost latitudes may originate from the fact that there are some northern species not inhabiting southern parts of North America. Thus, although most aquatic plant species have large ranges in the northern parts of the study area, the restricted-range species occurring in the north result in the decrease of mean range size approximately north of 60°N. This is not surprising because climatic conditions in the Arctic are both too cold and dry for vascular aquatic plant species (Lacoul & Freedman, 2006). However, we also acknowledge that our species data is quite limited in the most northern parts of North America (>60°N), making it challenging to draw final conclusions about the found pattern and its underlying mechanisms there.

Interestingly, findings from Europe were very different depending on the data used. For the 50 km x 50 km grid cell data, mean range size was in U-shaped relation with the latitude, whereas positively curvilinear pattern was evidenced using the latitudinal extent data. Both evidence suggest that largest ranges not only occur in high latitudes but they are also relatively broad in low latitudes. Hump-shaped patterns were found for several host organism groups (from fish to bird) of freshwater trematode fauna across Europe (Thieltges et al., 2011). They further argued that these findings originate from dispersal barriers for the studied parasite faunas. We doubt whether such dispersal barriers exist for aquatic plants, because geographical variables were strongly related to climate and land use (Table S2, S3). Moreover, annual temperature range and annual mean temperature, being the most significant explanatory variables based on BRTs, showed contrasting influences on mean range size in Europe. Annual temperature range had curvilinear but positive relation with the mean range size, suggesting that wider species ranges are found when variation in temperature increases. This suggestion refers to northern latitudes. Mean annual temperature showed a U-shaped trend with mean range size, indicating that largest species ranges were located in low and high latitudes. It seems that patterns of mean range size of aquatic plants are complex in Europe due to intricate latitudinal gradients in climate (see also Figure S1). Investigation of Rapoport's rule is thus challenging in this continent, especially in lower latitudes, because a strong latitudinal variation in climate conditions is a precondition for the Rapoport's

rule (Gaston et al., 2008). This was further highlighted that fact that geographical location clearly explained most variation for mean range size in Europe based on variation partitioning.

We found that current climate is the main determinant of mean range size in Europe and North America, with historical effects showing modest contribution to mean range size pattern. Our results contradict with many other studies in which different factors primarily contributed to range size. For example, climate velocity was one of the chief environmental drivers of range sizes for plant species across the New World (Morueta-Holme et al., 2013). Their study was based on BIEN database (<http://bien.nceas.ucsb.edu/bien/>), where both terrestrial and aquatic plants are combined, and they did not distinguish ecologically different assemblages from each other. The variable findings between our and their investigations emphasize the need to examine ecologically different species assemblages separately, because dominating organism groups may mask the opposite effects of smaller organism groups on species ranges when studied together (Henriques-Silva, Pinel-Alloul, & Peres-Neto, 2016; Liu et al., 2018).

CONCLUSIONS

To our knowledge, this is one of the first studies that has examined species richness and mean range size of aquatic plants across continents using large grid cell-based data. Our findings revealed that major ecogeographical rules can strongly vary for the same taxonomic group between continents. We discovered support for the LDG and Rapoport's rule in North America, but variable evidence was found for these ecogeographical rules in Europe. An increasing number of investigations have evidenced context dependency (e.g., due to variation in underlying environmental gradients among study regions) in the local community studies (Alahuhta et al., 2018; Heino et al., 2015; Tonkin, Heino, Sundermann, Haase, & Jähnig, 2016), but our results suggest that such strong lack of uniformity in the driving environmental variables can exist in broad-scale studies. Moreover, our results suggest that it is risky to rely solely on well-known terrestrial taxonomic groups when drawing generalizations about ecogeographical rules. Understudied taxonomic groups can provide different insights into these rules. Thus, we urge researchers to focus directly on understudied taxonomic or ecological groups across broad spatial scales to improve our knowledge of ecogeographical patterns, which creates the fundamental basis

for ecology and biogeography. This is highly essential when dealing with the global change effects on vulnerable ecosystems, such as freshwaters.

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AUTHOR CONTRIBUTIONS

Alahuhta conceived the original idea, with contribution from Heino. Alahuhta, Heino and Antikainen designed methodology. Alahuhta and Antikainen analyzed the data. Alahuhta led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mgqnk98w8>

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