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Little evidence of range size conservatism in freshwater plants across two continents

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Abstract

Aim: Range size conservatism suggests that closely-related species maintain geographic ranges of similar extent. However, consensus regarding this suggestion has not been reached. To shed more light on this phenomenon, we studied freshwater plant range size conservatism, range overlap and environmental niche conservatism using congeneric species comparison in two continents. In addition, we investigated whether a phylogenetic signal is found in the range sizes of aquatic plants.

Location: Europe and North America.

Taxon: Freshwater plants.

Methods: Across spatial resolutions (50 km², 100 km² and 200 km²), we applied Spearman correlations among 347 and 730 pairs of congeneric species in Europe and North America, respectively, and 63 pairs shared between them. In addition, Spearman correlations were used to evaluate how the degree of spatial overlap influences range sizes and which environmental variables explain variation in range sizes. Brownian evolutionary model was used to assess the phylogenetic signal in species range sizes.

Results: We found no evidence of range size conservatism across spatial resolutions for any species and species shared between the continents. In addition, range sizes of more closely related species did not overlap geographically more than those of distantly related ones and no support for environmental niche conservatism was evidenced.

Main conclusions: We found that aquatic plants show no range size conservatism in the Northern Hemisphere. This means that it is challenging to define different range sizes of freshwater plants through species traits. Furthermore, we are unable to predict unknown distributions of extant aquatic plant species based on known distributional attributes of closely related species. However, our findings suggest that the interpretations of previous investigations on the range sizes of aquatic plants remain valid due to lack of range size conservatism. These practical implications encourage studying range size conservatism across realms and regions, especially for understudied organismal groups.

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KEYWORDS

aquatic macrophytes, Brownian motion evolutionary model, EM-Mantel test, hydrophytes, niche conservatism, phylogenetic conservatism, range size, Range size conservatism

1 | INTRODUCTION

Range size conservatism (or range size heritability) has been studied with increasing interest since the late 1980s when the keystone work of Jablonski (1987) was published (see also Gaston, 2003). This concept refers to a tendency of closely related species to maintain geographic ranges of similar extent (Machac et al., 2011; Waldron, 2007; Webb & Gaston, 2003). Range size conservatism has fundamental ecological and evolutionary causes and consequences, emphasizing the importance of this research topic. First, it can increase our understanding of the processes that structure species range sizes by providing support for the importance of differences in species traits. This is because varying geographical range sizes can be determined by species traits through species filtering (Mouillot & Gaston, 2007, 2009). Second, strong phylogenetic conservatism of range sizes means that phylogenetic relationships need to be controlled in a comparative analysis of species range sizes (Morin & Lechowicz, 2013; Morueta-Holme et al., 2013). Hence, interpretations of many previous studies on range sizes would also need to be re-evaluated. Third, in the case of evident phylogenetic conservatism of range sizes, unknown distributions of extant species (e.g. those species in need of conservation) could be predicted based on known distributional characteristics of closely related species (Brown et al., 1996; Mouillot & Gaston, 2007). Although range size conservatism has clear theoretical and practical implications, consensus over this phenomenon across taxa has not been reached (Borregaard et al., 2012; Jablonski, 1987; Li et al., 2018; Machac et al., 2011; Pie & Meyer, 2017; Webb & Gaston, 2003; Zacaï et al., 2017).

Previous investigations on range size conservatism have found evidence to support (Cardillo, 2015; Jablonski & Hunt, 2006; Roy et al., 2009) and refute (Blanchet et al., 2013; Nabout et al., 2010; Webb & Gaston, 2003) the hypothesis, and even highly variable results among clades have been reported (Pie & Meyer, 2017). Despite these contradictory empirical results, range size conservatism is linked to environmental niche conservatism because differences in species' traits and how they respond to environment can be related to differences in geographical range sizes (Mouillot & Gaston, 2009). However, Mouillot and Gaston (2007) demonstrated that a substantial degree of statistically significant range size conservatism may not be related to actual environmental niche conservatism due to lack of biological trait differences among most closely related species (i.e. congeneric species). One conclusion of this disagreement on range size conservatism has been that different methods employed (e.g. congeneric species comparisons vs. phylogenetic autocorrelations) may result in different outcomes when investigating conservatism of species range sizes even for same data set (Waldron, 2007; Machac et al., 2011; see also a review on previous studies in table 1 by Zacaï et al., 2017). Moreover, different findings on range size conservatism

Statement of significance

Range size conservatism refers to a tendency of closely related species to maintain geographic ranges of similar extent. This hypothesis is highly controversial with previous studies supporting and refuting range size conservatism for different organisms. We investigated range size conservatism for freshwater plants in Europe and North America and found no evidence of it. Refuting the range size conservatism hypothesis has several implications for ecological and evolutionary research of freshwater plants.

may partly emerge from different considerations of phylogenetic signal in the previous studies when conservatism in range sizes has been examined (e.g. Münkemüller et al., 2012; Peixoto et al., 2017).

In addition to these methodological issues, there is variation in geographical distribution of species range sizes among different taxa (Blanchet et al., 2013; Cardillo, 2015; Machac et al., 2011; Nabout et al., 2010; Pie & Meyer, 2017; Roy et al., 2009). This further highlights the need to study range size conservatism of less known taxa, such as many freshwater taxa. Aquatic plants have infrequently been studied at broad spatial scales due to lack of suitable data (Alahuhta et al., 2021), and our knowledge on their range sizes is relatively limited. Many aquatic plant species are considered to have wide range sizes, sometimes covering entire Earth (Chambers et al., 2008; Santamaría, 2002). However, a recent study showed that, contrary to previous understanding, only 1% of all aquatic plants have global range sizes and most species occur only in certain continents and ecoregions (Murphy et al., 2019).

Geographic distributions of aquatic plants are generally shaped by climate factors together with local environmental conditions (Gillard et al., 2020; Lacoul & Freedman, 2006; Netten et al., 2011). In addition, aquatic plants have efficient dispersal abilities and can effectively colonize new habitats (Barrat-Segretain, 1996) that may partly explain their broad range sizes. Despite the recent insights into aquatic plant distributions, there is no evidence whether range sizes of this ecologically important biological group are conserved or not. This is because aquatic plants, for example, as primary producers of freshwaters offer feeding, growing and reproduction habitats for other organisms, in addition to influencing water quality (Lacoul & Freedman, 2006). In addition, we are unaware of which factors explain range sizes of aquatic plants. Given the multiple global threats that freshwater environments are facing in our increasingly human-dominated world (e.g. Reid et al., 2019), it is important to study how aquatic plant range sizes and distributions may be affected by anthropogenic impacts.

In this study, we investigated aquatic plant range size conservatism (i.e. do closer relatives have more similar sized ranges), range overlap (i.e. do ranges of closer relatives overlap more) and environmental niche conservatism (i.e. do closer relatives have more similar environmental tolerances) using congeneric species comparison in Europe and North America. In specific, we aimed to answer (Q1) whether there is any difference in range size conservatism between all pairs of congeneric species and pairs of congeneric species shared by both continents, (Q2) does variation in spatial resolution (50, 100 and 200 km²) affect these patterns, (Q3) how the degree of spatial overlap between congeneric species (for all and shared species) influences range sizes, as the degree of spatial overlap can vary depending on the degree of species relatedness (closely vs. distantly related species; Moullot & Gaston, 2009), (Q4) if different environmental variables (i.e. annual mean temperature, annual mean precipitation, alkalinity concentration in water, proportion of freshwaters and area covered by last glaciation maximum) explain range sizes and (Q5) whether a phylogenetic signal is found in the range sizes of aquatic plants. Based on a previous study on spatial species niche conservatism founded on data gathered from local communities (Alahuhta et al., 2017), we expected to find some level of conservatism in species range sizes for aquatic plants. We also expected that there would be no significant differences in range size conservatism

between all congeneric species, as well as congeneric species shared by Europe and North America. In addition, we assumed, according to Moullot and Gaston (2009), that spatial overlap is stronger for more closely related species compared to more distantly related ones. We further expected that the importance of climate factors increases with increasing spatial resolution among congeneric species (see Alahuhta et al., 2020; Willis & Whittaker, 2002). Finally, we hypothesized based on a recent freshwater plant study, where a weak phylogenetic signal of functional traits was detected among mostly convergent lineages (García-Girón et al., 2020) that phylogenetic signal is weak in the range sizes of congeneric species.

2 | MATERIALS AND METHODS

2.1 | Freshwater vascular plant data and species pairs

We used geographic distribution data of freshwater vascular plants across Europe and North America (Figure 1) obtained from Atlas Flora Europaeae (Jalas & 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). For the Atlas Flora

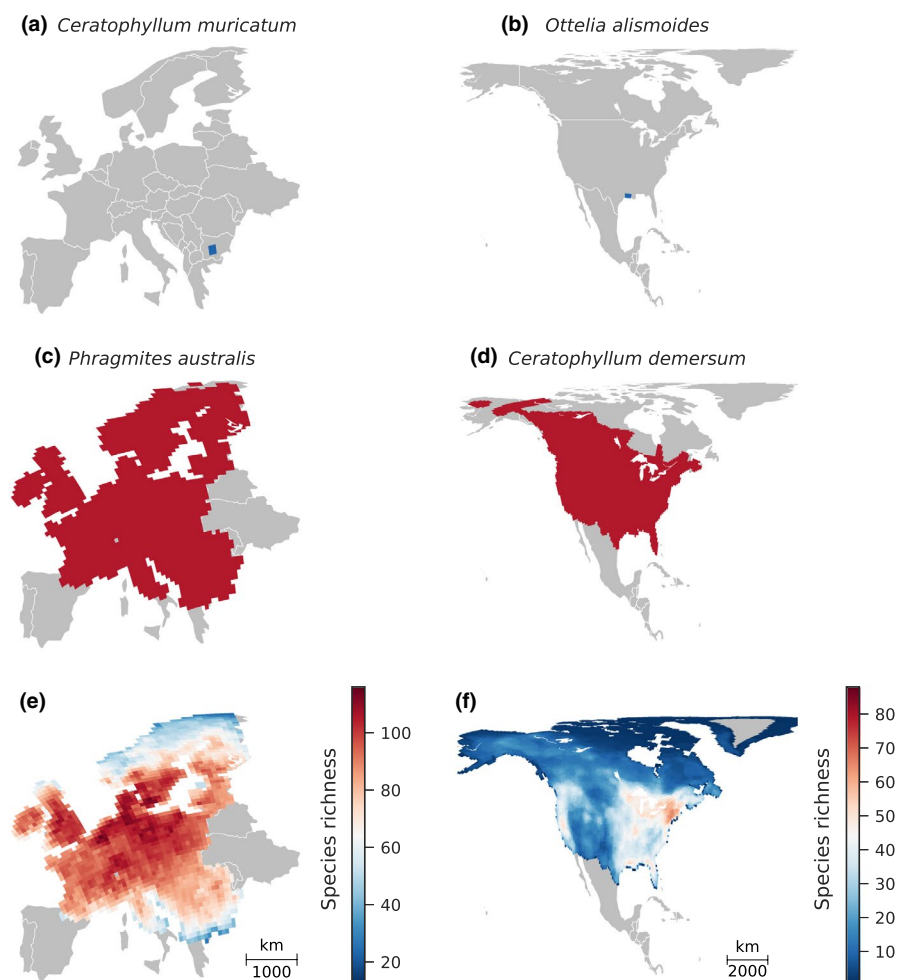


FIGURE 1 Range size distributions of aquatic plants. Maps a (b) and c (d) for Europe (North America) show the species *Ceratophyllum muricatum* (*Ottelia alismoides*) that occupy the smallest range area (within the blue circle) and *Phragmites australis* (*Ceratophyllum demersum*) the largest range area, respectively. Map e (f) displays the species richness for Europe (North America). The species richness of freshwater plants is more homogeneous in Europe, while in North America there are some hotspots located at the east and west of the United States. The maps used the cylindrical equal-area projection [Colour figure can be viewed at wileyonlinelibrary.com]



Europaeae, distributions of 134 freshwater plants were obtained for grid cells of 50 km². The study area was delimited in the east (excluding Russian Federation, Ukraine, Belarus and Moldova) and south (excluding Spain and Portugal). This was done because local and dark (i.e. set of species that are lacking from a study site but inhabiting the surrounding region and potentially able to grow in particular ecological conditions) diversity assessments indicated that biodiversity should be higher in these areas than found in the Atlas, suggesting incompleteness of data for these countries (Nogués-Bravo & Araújo, 2006; Ronk et al., 2016). This suggests that range sizes of some species could have been narrower or broader than in reality if they were found in these cut-off grid cells. In addition, islands were removed from the final data set. For the Flora of North America, distribution maps of 192 freshwater plants were digitized. Grid cell-based maps were found for these 192 species; however, we were forced to exclude information on those species whose distributions were reported at the state level in the USA (see Alahuhta et al., 2020). The study area of North America was restricted to the main continental areas of USA and Canada, excluding Mexico and remote islands due to the data availability. In addition to 50 km² grid cells, 100 and 200 km² were used for further analysis in both continents.

For both species data sets, we strictly focused on vascular plants growing solely in freshwater habitats (i.e. hydrophytes), and marine and peatland species were thus removed from the data following Castroviejo (1986–2012), Crow and Hellquist (2000), Cirujano et al. (2014), Flora of North America Editorial Committee (1993–2007), Schmidt-Kloiber and Hering (2015) and Lichvar (2014). Hence, shoreline vascular plant species and semi-aquatic emergent plants were also excluded from this study. Altogether, 134 and 192 species were recorded in Europe and North America, respectively, with 38 species found in both continents (Table S1). Although we acknowledge that our freshwater species list only consists of a limited number of all aquatic species found in the study continents (Chambers et al., 2008), all important freshwater hydrophyte genera and species (e.g. *Potamogeton* spp.) are present in the data (Alahuhta, Kosten, et al., 2017; Alahuhta, Lindholm, et al., 2018; Baattrup-Pedersen et al., 2015; Capers et al., 2010; Crow, 1993; Murphy, 2002; Willby et al., 2000). Moreover, most of the species used in our study have ranges centred in the Northern Hemisphere (Chambers et al., 2008; Crow, 1993; Willby et al., 2000), and species richness patterns at continental scales follow that of global scale (Alahuhta et al., 2020, 2021; Murphy et al., 2019).

We defined congeneric species (i.e. species belonging to same genus) from aquatic plant data sets described above using taxonomy found in Catalogue of Life (<https://www.catalogueoflife.org/>). The total pairs of congeneric species found in our data were 347 for Europe, 730 for North America and 63 for shared species between these continents. We found that 328 (62) and 545 (60) pairs overlap (i.e. level of over >0%) spatially in Europe (shared) and North America (shared) respectively. The number of pairs increased slightly when we increased the spatial scale from 50 km² to the larger grid cells. At larger spatial scales more species are present in a grid cell and consequently more pairs can be formed (Figure S1). Compared with

the 50 km² grid cells in Europe, the number of pairs at the 100 km² grid cells remained the same and four more pairs were found at the 200 km² grid cells. In North America, there were five more pairs at the 100 km² grid cells and 11 more pairs at the 200 km² grid cells compared with the smallest grid cell size. For shared pairs, the number remained the same in all spatial scales in both continents.

2.2 | Environmental data

Environmental variables used in our study included three bioclimatic variables, water alkalinity, proportion of freshwaters and area covered by the last glaciation maximum. The bioclimatic variables indicate not only energy availability and water level fluctuations for aquatic plants but also potential species dispersal and material leaching from terrestrial land (Alahuhta, Kosten, et al., 2017; Kosten et al., 2009; Netten et al., 2011). These variables derived from WorldClim (Hijmans et al., 2005) included annual mean temperature (°C), variation in annual mean temperature (°C) and annual mean precipitation (mm). Alkalinity is essential for many aquatic plant species as a measure of source of carbon (Iversen et al., 2019). Water alkalinity was defined based on global prediction of concentrations in freshwaters (mequiv. l⁻¹ at 1/16 degrees resolution, Marce et al., 2015). Proportion of freshwater determines the availability of potential habitats for aquatic plants (Jones et al., 2003). It was delineated from FAO's global land cover data and calculated within grid cells (% at 1 km resolution, Latham et al., 2014). Evidence from a recent study suggested that LGM may have some effect on current distributions of aquatic plants (Alahuhta et al., 2018), but no consensus exists on this matter. Area covered by last glaciation maximum (LGM; 1/0 in each grid cell) was assessed based on Ehlers et al. (2011). All the environmental variables, with an exception of LGM, were average values upscaled for studied grid cells.

2.3 | Statistical methods

2.3.1 | Range size conservatism

To quantify the overlapping between pairs of congeneric species, we used the degree of sympatry (s). The overlapped area, quantified by the absolute shared area between pairs of congeneric species in km², is divided by area of more restricted species, that is, one with least geographical area (Chesser & Zink, 1994). Thus, the sympatries can be interpreted as percentage of more restricted species within range of its congeneric species, belonging to interval [0,1]. When $s = 0$ there is no overlap and when $s = 1$, more restricted species is entirely embedded within area of its congeneric species (see Mouillot & Gaston, 2009, and Figure 2 for detailed examples). After calculating this quantity for every pair of congeneric species, we obtained a set of range areas and sympatry values given by $Z = \{[A_1, A_2, s_{12}], \dots, [A_1, A_N, s_{1N}], \dots, [A_N, A_{(N-1)}, s_{(NN-1)}]\}$, where N is the number of species and $s_{ij} = s_{ji}$.

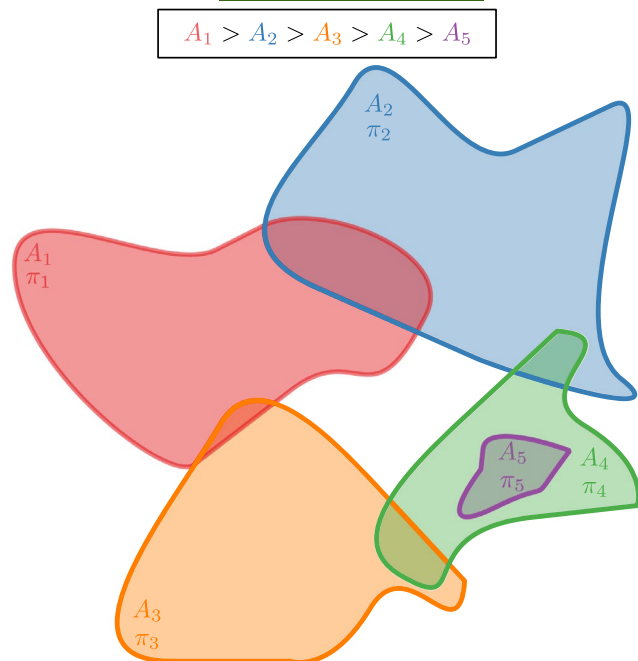


FIGURE 2 Here, we illustrate how sympatry (s) was computed for pairs of species which range size overlapped. Considering five hypothetical species ($\pi_1, \pi_2, \pi_3, \pi_4$ and π_5) in a way that their areas follow the relation: $A_1 > A_2 > A_3 > A_4 > A_5$. The species π_1 overlaps with the species π_2 and π_3 , thus the sympatry coefficients are given by $s_{12} = [A_1 \cap A_2]/A_2$ and $s_{13} = [A_1 \cap A_3]/A_3$ since $A_1 > A_2$ and $A_1 > A_3$. The species π_2 (π_3) also overlaps with the species π_4 , in a way that the sympatry for this pair is $s_{24} = [A_2 \cap A_4]/A_4$ ($s_{34} = [A_3 \cap A_4]/A_4$), since $A_2 > A_4$ ($A_3 > A_4$). There is a scenario where area of one species is totally embedded within area of another species, like with the species π_4 and π_5 . The sympatry, in this case, is $s_{45} = [A_4 \cap A_5]/A_5 = 1$ because A_5 is totally embedded within A_4 . When there is no superposition, $s = 0$, as illustrated for the species π_1 and π_5 [Colour figure can be viewed at wileyonlinelibrary.com]

In order to assess the conservatism as a function of overlapping area between congeneric species, we followed the same procedure as Moullot and Gaston (2009). First, we calculated the sympatry values for each pair of congeneric species to evaluate whether the increase in spatial overlap among congeneric species enhances range size conservatism in freshwater plants. This is because, in the case of range size conservatism, niche conservatism will more probably lead to marked heritability of the range sizes of species when similar niche traits are expressed under more similar environmental conditions (Moullot & Gaston, 2009). Then, correlation of areas considered in the overlap was calculated using the Spearman correlation coefficient (Q1). Since there is no dependent or independent variable, any species can be considered as a variable on x-axis or on y-axis. Therefore, order of each species in the pair may affect the value of the correlation coefficient. To account for this problem, we randomized the order of areas of each pair of congeneric species, calculated the correlation coefficient 1000 times and took its mean value (see Figure S2 for a detailed illustration of the procedure). The same procedure was repeated for each scale (50, 100 and 200 km²)

to evaluate whether the increase in spatial resolution among congeneric species enhances range size conservatism in freshwater plants (Q2). We compared our results with a null model, where the overlapping area was attributed randomly for each pair, considering the same number of species and pairs of congeneric species as Europe (134 species and 328 pairs) and North America (192 species and 545 pairs).

2.3.2 | Range size overlap

To assess whether the range sizes of more closely related species overlap more than those of more distantly related species, we investigated if correlations changed between the sympatry level and increased or decreased in range size overlap (Q3). To do this, subsets of pairs were selected based on their sympatry values (s_{ij}). For instance, if the sympatry degree is $s = 0.3$, we selected pairs with overlapping lower or equal to 0.3 (greater or equal to $1 - 0.3 = 0.7$). For each subset, we calculated the Spearman correlation coefficient between the areas (log-transformed) of all pairs of congeneric freshwater species for Europe, North America and shared species between the continents. This approach enabled us to verify if the range size of congeneric species for freshwater plants had some dependency on their overlap. We considered subsets with at least 30% of pairs when compared with the whole set (e.g. 98 pairs for a total of 328 from Europe). We plotted this trend in correlation coefficients of different levels of sympatry for pairs of congeneric species in two sequences, adopted from Moullot and Gaston (2009). First, we accumulated species pairs beginning with those having the greatest overlap. Second, we began increasing species pairs starting with those with the least overlap. Range size overlap was studied for all spatial resolutions (50, 100 and 200 km²) in both continents, including the set of species shared between them.

To better understand range size overlap of congeneric species, we analysed the Spearman correlations among the range size differences between pairs of congeneric species and their patristic distance, which is related to divergence distances between species (see Phylogenetic signal in species geographic range sizes). To do this, we calculated patristic distances for each pair of congeneric species that overlap and used these distances to select subsets of pairs in the same way we used the sympatry values. For each subset, we calculated Spearman coefficient for pairs that overlap and have patristic distance lower or equal to δ . This analysis was also further used to assess whether speciation events could partly explain overlaps in range sizes of congeneric species.

2.3.3 | Environmental niche conservatism

We further analysed the influence of environmental variables on the overlapping areas between congeneric species (Q4). To do this, for each overlapping area between congeneric species, the distribution of values for each environmental variable was obtained from the grid



cells (Figure S3). These distributions (for the same environmental variable) were then compared for pairs within the same genera of species using the two-sample Kolmogorov-Smirnov test. The influence of environmental variables on overlapping areas was then assessed as the fraction of comparisons that were likely to come from the same distribution ($p \geq 0.01$). Finally, to correlate the environmental variables with the degree of conservatism for congeneric species, distributions were compared considering thresholds based on the degree of sympatry the same way correlations were evaluated. Environmental niche conservatism was investigated across different study resolutions.

2.3.4 | Phylogenetic signal in species geographic range sizes

To evaluate the phylogenetic conservatism of species geographic range sizes (Q5), we applied the evolutionary model-based EM-Mantel test (Debastiani & Duarte, 2017). This approach is based on two steps consisting of a general Mantel test followed by a test based on the Brownian motion evolutionary model. This novel adaptation of the traditional Mantel test has appropriate type I error and strong power to detect phylogenetic signal for continuous variables (see Debastiani & Duarte, 2017). While the conventional Mantel test only examines whether more closely related species have more similar geographic range size, the EM-Mantel test further contrasts the empirical phylogenetic signal to that simulated from a neutral (i.e. null) evolutionary model (for more details, see Debastiani & Duarte, 2017). Here, we used the Brownian motion evolutionary model, which assumes that differences in geographic range sizes are merely accumulated over evolutionary time without strong divergent selection, strong stabilizing selection or changes in the evolutionary rate along the phylogenetic tree (Münkemüller et al., 2012). The null hypothesis of no phylogenetic conservatism was tested for significance using 999 random permutations of range size values across the tips of the phylogenetic tree with the original R code provided by Debastiani and Duarte (2017). We ran the mathematical routine using a square root transformation of the Euclidean distances among species range sizes (see Debastiani & Duarte, 2017). Alpha values less than 0.05 would indicate that species geographic range sizes are more conserved than what would be expected by the Brownian motion evolutionary model. The analyses were conducted for each spatial resolution (i.e. 50, 100 and 200 km²). Similarly, the EM-Mantel procedure was performed considering the set of shared aquatic plant species between the continents and for each of the two continents (i.e. Europe and North America) independently.

Owing to lack of true species-level phylogeny comprising all freshwater plant lineages, we derived the evolutionary relatedness of the study species (Figure S4) from the Open Tree of Life (OTL) project (Hinchliff et al., 2015). We scaled branch lengths to divergence times using the Phylocom's (Webb et al., 2008) *bladj* algorithm

for R, which sets the age of internal nodes based on evolutionary divergence times between ramifications (here, obtained from fossil and molecular data, including Les et al., 2003, Hedges et al., 2015 and Magallón et al., 2015). We accessed phylogenetic data and calculated branch length information with R packages *rotl* (Michonneau et al., 2016) and *branching* (Chamberlain, 2019) respectively.

3 | RESULTS

3.1 | Range size conservatism

The correlation analysis between the range areas of congeneric species presented no significant relationship at every spatial scale considered. Spearman coefficients were close to zero in both continents (−0.075 in Europe and 0.085 for North America considering 50 km² scale, Figure 3a,b). Similar results were observed when shared species between the continents were considered (0.085 in Europe and −0.123 in North America considering 50 km² scale, Figure 3e,f). The results for the other spatial resolutions (100 and 200 km²) followed these same patterns and can be seen in Figure S5. Finally, there was no significant correlation at any degree of sympatry for the null model (Figure 4).

3.2 | Range size overlap

The Spearman correlations between the sympatry level (*s*) and increase or decrease in range size overlap are found from Figure 3c,d,g,h. Red lines represent those correlation coefficients, which were higher for congeneric species that overlap less, with decreasing values when pairs that overlap more were added to the calculation. Oppositely, correlations were lower for congeneric species with more overlap, with increasing values when pairs that overlap less were added to the analysis (in blue lines). Similar pattern was noticed at all scales (Figure S5 and S6). Moreover, the correlation analysis among the range size differences between pairs of congeneric species and their patristic distance present no sign of correlations ($\rho \approx 0$) in both continents (Figure 5). This further means that speciation does not explain range size overlap for congeneric species.

3.3 | Environmental niche conservatism

In our analysis considering the environmental variables, we found that alkalinity was the feature most likely to be equally distributed in overlapping areas of different pairs of congeneric species from the same genera, being the most significant variable in Europe (*) and third most important (***) in North America (Figure 6). Other features with higher fractions of similarity were the percentage of water and the last glaciation maximum. We further observed that all fractions of acceptance increase with increasing spatial scale.

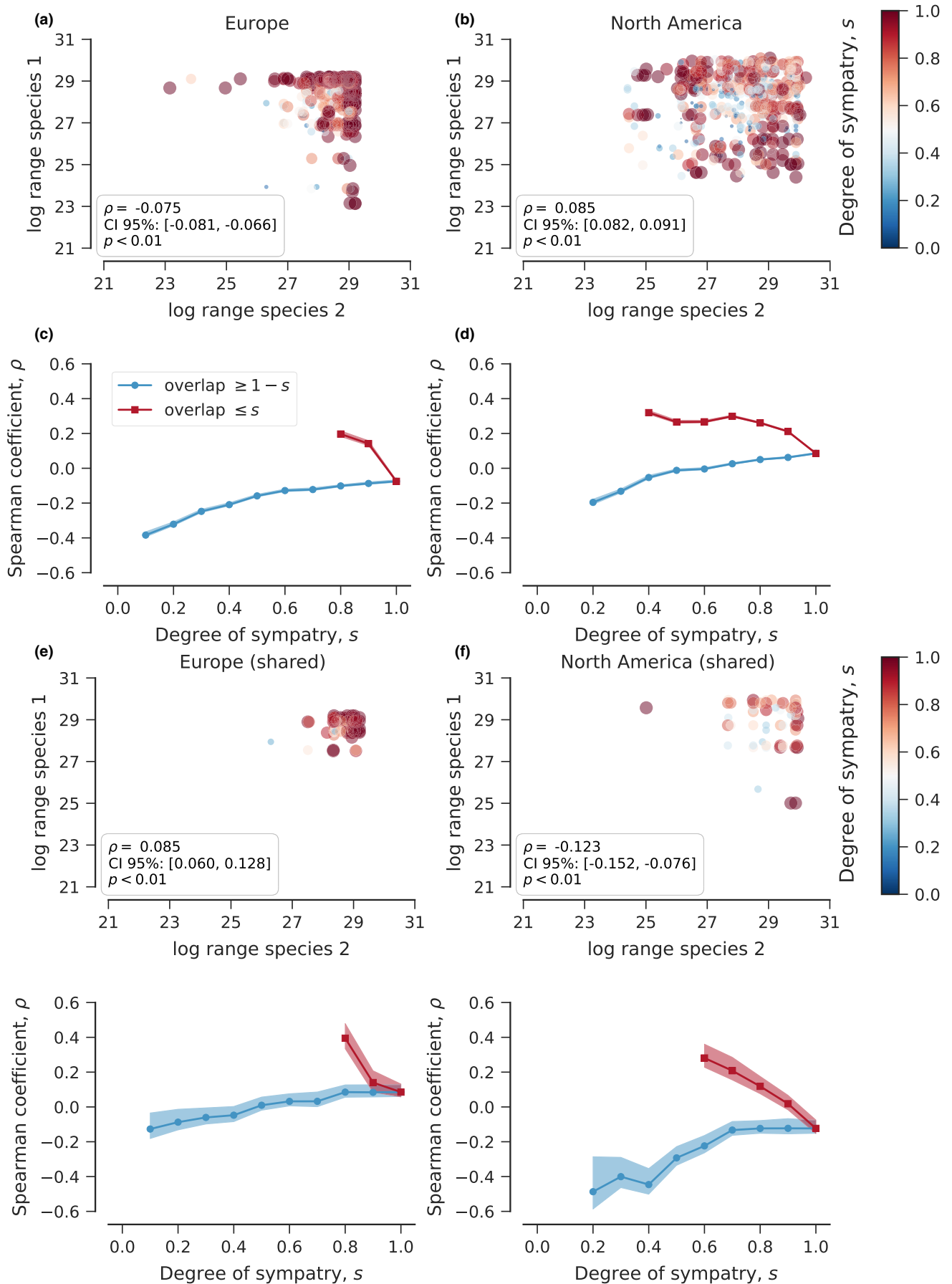




FIGURE 3 Range correlation between congeneric species of aquatic plants for grid cells of 50 km² used to investigate range size conservatism and range size overlap. Panels a and b show the correlation between range sizes of aquatic congeneric species in Europe and North America, respectively, while e and f indicate the same for shared species between continents. The size and colour of the points reflect the values of the degree sympatry. Panels c, d, g and h illustrate the Spearman coefficient for each subset of pairs of congeneric species considering a particular overlap threshold based on the sympatry value. The red (blue) line represents the set considering the pairs of congeneric species with overlapping areas leading to a sympatry value lower than (higher than) or equal to s ($1 - s$). The markers represent the mean value of the Spearman coefficient for 1000 resamples shuffling pairs randomly while the bands are 95% confidence intervals. We considered subsets containing 30% or more pairs in relation to the entire data [Colour figure can be viewed at wileyonlinelibrary.com]

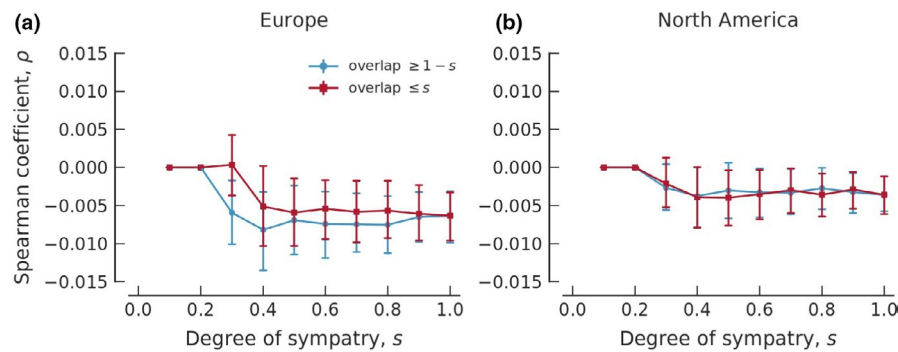


FIGURE 4 Correlation of range size conservatism for the null model. Panels a and b show the Spearman coefficient for the range correlation of the null model considering different intervals of sympatry. We have considered the same number of species and pairs for Europe (134 species and 328 pairs) and North America (194 species and 545 pairs) as the original data for the simulations. We can observe that there is no correlation if a random distribution of overlapping areas is considered. The markers are the mean value of the Spearman coefficient over 1000 randomizations of the null model while the bars are the standard deviation [Colour figure can be viewed at wileyonlinelibrary.com]

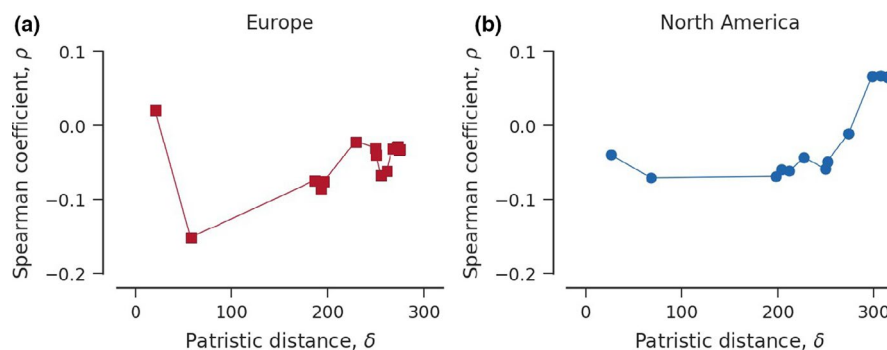


FIGURE 5 Spearman correlations among the range size differences between pairs of congeneric species and their patristic distance, which is related to divergence distances between species (Mya). Pairs that overlap and have patristic distance lower or equal to δ had the Spearman coefficient calculated. We can see that in both continents the relative distance between pairs have little effect on how they overlap [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Phylogenetic signal in species geographic range sizes

Following findings from range correlations, EM-Mantel tests did not show any significant signal of phylogenetic conservatism for species range sizes in both Europe and North America (Table 1). This latter finding was also true for shared species between these continents at different spatial resolutions. Therefore, regardless of the region and the spatial resolution of the analysis, species range sizes were not likely to be phylogenetically conserved in freshwater plants.

4 | DISCUSSION

Contrary to our hypothesis, our results suggested that freshwater plants show no range size conservatism across spatial scales (Q1, Q2) in the Northern Hemisphere. In addition, range sizes of more closely related species did not overlap more than those of more distantly related species, a finding that was opposite to our hypothesis (Q3). Our findings further suggested no evidence for environmental niche conservatism (Q4), as more closely related species did not possess more similar environmental tolerances than more distantly

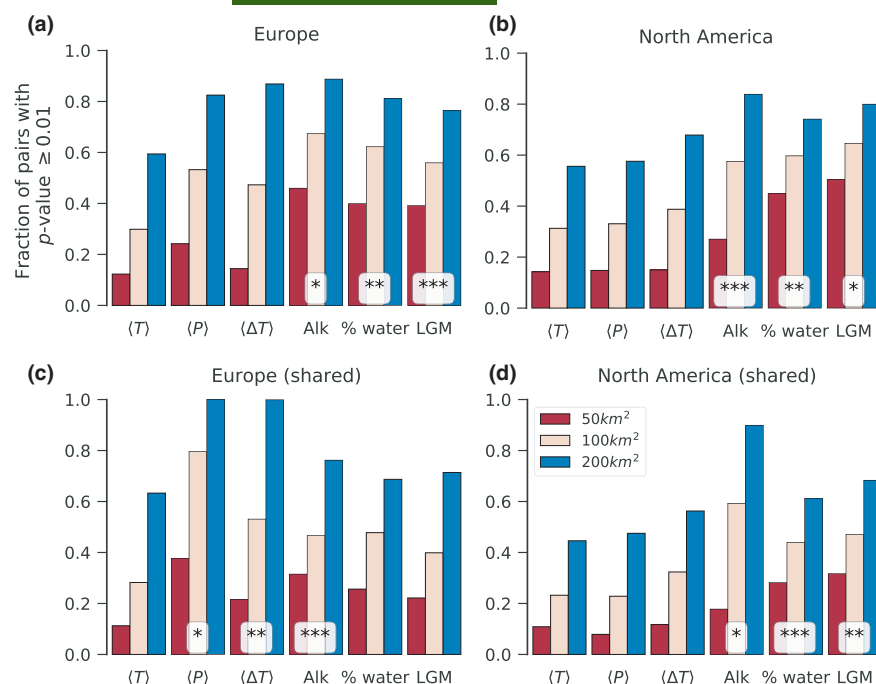


FIGURE 6 Comparison of environmental features among congeneric species. We compared the distributions of the environmental features for all congeneric species within the same spatial scale. The asterisks (*) represent the environmental features that have a bigger fraction of distributions with p -value ≥ 0.01 in the two-sample Kolmogorov-Smirnov test. We observed that alkalinity is always among the top three variables, indicating that this is an important variable for overlapping areas [Colour figure can be viewed at wileyonlinelibrary.com]

Geographic region	Spatial resolution					
	50 km ²		100 km ²		200 km ²	
	Mantel's R	α -value	Mantel's R	α -value	Mantel's R	α -value
Europe	0.03	0.99	0.03	0.99	0.06	0.98
North America	-0.06	0.99	-0.06	0.91	-0.06	0.99
Shared species	0.12	0.93	0.16	0.92	0.11	0.94

TABLE 1 Phylogenetic signal (EM-Mantel; Standard Mantel and Brownian motion simulation – α -value) for species geographic range sizes. Correlations showed no significant differences from neutral model simulations (p - and α -values > 0.05 in all cases). Note that if, and only if, the standard Mantel test is significant ($p < 0.05$), the second step assesses whether such correlation between phylogeny and geographic range size is higher than what would be expected by chance given a Brownian motion evolutionary model ($\alpha < 0.05$)

related freshwater plant species. No support for the hypothesis that climatic effects increase with increasing spatial resolution was found either. Moreover, we did not find any phylogenetic signal in species range sizes for freshwater plants (Q5). The congeneric species comparisons complemented with phylogenetic signal analysis generated new information to this highly debated issue by rejecting the hypothesis of phylogenetic conservatism in species range sizes.

4.1 | Range size conservatism: Do closer relatives have more similar sized ranges and is any phylogenetic signal detected?

The use of different methods has complicated interpretations of patterns in range size conservatism (Machac et al., 2011; Waldron, 2007). When focusing only on Spearman rank correlations of congeneric species pairs, most of the previous studies have found conservatism in species range sizes. For example, Mouillot and Gaston (2009) found relatively strong support for the range size conservatism in a global data set of birds, and a similar finding was reported

on mollusk fossils found on the Gulf and Atlantic Coastal Plain of North America (Jablonski, 1987). Oppositely, Webb et al. (2001) did not find any evidence of range size conservatism for the bird order Anseriformes, whereas a similar lack of support was made for sister species of different avian groups (Webb & Gaston, 2003). Interestingly, Hunt et al. (2005) through re-analysing the bird data of Webb and Gaston (2003), who in turn re-investigated the mollusk data of Jablonski (1987), came to different conclusions about conservatism in species range sizes compared with those made by the original authors. Herrera-Alsina and Villegas-Patraca (2014) also reported that two sister sparrow species had very dissimilar range sizes, but the entire sparrow clade showed phylogenetic signal. These highly controversial inferences seem to stem from variable acknowledgement of phylogeny in the analysis, emphasizing the different viewpoints of macroecology and macroevolution.

Our complementary phylogenetic analysis supported the findings from congeneric species comparisons by revealing the absence of significant phylogenetic signal in aquatic plant range sizes. To do this, we did not consider congeneric species pairs per se, but only branch lengths and nodes of species in the phylogenetic tree (see Debastiani



& Duarte, 2017). More specifically, this analysis evaluated the evolution of range sizes in congeneric species under the hypothesis of phylogenetic conservatism (Revell et al., 2008). We assume that the lack of phylogenetic signal in our study is likely related to a variety of large-scale ecological and evolutionary factors frequently predicted to influence range size variation, including environmental tolerance or niche breadth (Gaston, 2003), colonization and extinction dynamics (Lester et al., 2007) and dispersal ability (Soons et al., 2016; Viana et al., 2013, 2015). This assumption is reasonable given that most freshwater plant lineages are generalists in relation to key ecological gradients at continental scales (Alahuhta, Virtala, et al., 2017) and experience frequent long-distance dispersal events to assure the quick colonization of extensive areas (Santamaría, 2002). However, tests of these hypothetical causes are still limited for aquatic organisms, and no single mechanism has emerged as universal driver of the extent of plant species' geographical distributions. Attaining such a synthesis in the freshwater realm should help us to predict the processes responsible for range size variation (see Lester et al., 2007, for a synthesis in marine ecosystems), but this is beyond the main scope of our present work. Whatever the case, the two different research approaches (i.e. congeneric species comparison and phylogenetic analysis) applied here yielded parallel results and further strengthened our interpretation that range sizes of aquatic plants are not conserved.

4.2 | Range size overlap: Do closer relatives overlap more?

Our results also indicated that more closely related congeneric species do not overlap more than more distantly related ones. Instead, the correlations of least overlapping species ranges decreased as new species pairs with increasing spatial overlap were included to them, and an opposite increasing trend was found for fully overlapped ranges of congeneric species when new species with decreasing overlap were added (Figure 3; Figure S5). These patterns suggested that congeneric species with similar niche traits but not spatially overlapping (i.e. species pairs more likely to undergo different environmental conditions) often have similar geographic range sizes (see also Mouillot & Gaston, 2009).

However, different modes of speciation could influence range sizes differently. For example, if during a speciation event, one of daughter/sister species start off in a small range, then that sister species would have a dissimilar range size compared to older pairs of sister species, which would likely be more similar in range sizes (i.e. the small-ranged sister would have more time to catch up in range size) than recently diverged species. In our study, we assessed this possibility by correlating range size differences between pairs of congeneric species and their patristic distances, which were based on evolutionary divergence distances between species. We found no significant relationship between them. This absence of relationship between range size differences and species patristic distances indicated that recent speciation events are not very likely reasons behind range size overlap for congeneric species.

4.3 | Environmental niche conservatism: Do closer relatives have more similar environmental tolerances?

We further discovered that more closely related congeneric species did not have more similar environmental tolerances compared to more distantly related species, as no correlation between taxonomic relatedness of congeneric species and environmental conditions was found. This indicates that no environmental niche conservatism was evidenced for freshwater plants. Our finding of lack of environmental niche conservatism was further supported by the findings from range size overlap analysis (Figure 3c,d,g,h). The similarity between environmental variables in our study decreases when pairs of congeneric species with higher overlap are considered (see Mouillot & Gaston, 2009). This basically means that the greater overlapping area, the higher is the probability of environmental variables' distributions to be different.

Alkalinity was the most often selected environmental variable explaining range sizes of congeneric species, followed by the proportion of water and the last glaciation maximum. This does not only emphasize the fact that aquatic plant species are adapted to particular local habitat conditions (Iversen et al., 2019; Jones et al., 2003) but also that historical effects have influence on their range sizes. Impact of last glacial maximum on range sizes is surprising because aquatic plants have been suggested to have quickly colonized their current range sizes after the last glaciation maximum in North America (Sawada et al., 2003). A recent study also suggested that historical effects had little effect on mean range sizes of aquatic plants at the assemblage level across Europe and North America (Alahuhta et al., 2020). Although historical effects on congeneric species pairs, which fully overlap in their distributions and show high difference in range size, could be explained by recent speciation events, we found no evidence on this for freshwater plants (see Figure 5). Moreover, Alahuhta et al. (2020) further found that present-day climate affects mean range sizes in aquatic plant assemblages. Alahuhta, Ecke, et al. (2017) also proposed based on local community data that the climate niches of aquatic plants are probably conserved, but that local habitat variable-based niches are not. These contradicting results imply that the range overlap of congeneric species and range sizes of all aquatic plants are controlled by different environmental factors. In addition, studies conducted at different spatial resolutions (i.e. grid cells of varying sizes vs. local communities) can result in indifferent outcomes regarding conservatism in species environmental niches.

In conclusion, our study revealed little evidence for range size conservatism in aquatic plants across Europe and North America. Lack of a phylogenetic signal in determining range sizes was further emphasized by our analysis based on congeneric species comparisons. Likewise, more closely related species did not overlap more than more distantly related ones, and we found no signs of environmental niche conservatism for freshwater plants. Refuting the range size conservatism hypothesis has several implications for ecological and evolutionary research of freshwater plants. As a result, we are unable to define different geographical range sizes of freshwater plants through species traits and predict unknown distributions of

extant aquatic plant species based on known distributional attributes of closely related species (cf. Mouillot & Gaston, 2007). On the other hand, the parallel results of our two different research approaches (i.e. congeneric species comparison and phylogenetic analysis) emphasize that the interpretations of previous investigations on the range sizes of aquatic plants remain valid (Morin & Lechowicz, 2013; Morueta-Holme et al., 2013). Thus, our investigation underscores the importance of studying whether or not range sizes are conserved across regions and ecosystem realms. Moreover, this study is a pioneering signpost for further research on species range sizes of understudied organism groups often inhabiting freshwater systems.

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DATA AVAILABILITY STATEMENT

Data and code used in the study are found from GitHub (<https://github.com/vieirads/JSBI-19-0505>).

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BIOSKETCH

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Janne Alahuhta conceived the original idea. DSV contributed to the study design, processed the data, performed the analysis, and wrote the first manuscript draft together with JA. JGG performed the phylogenetic signal testing. Other authors contributed to the writing, as well as read and approved the final manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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