

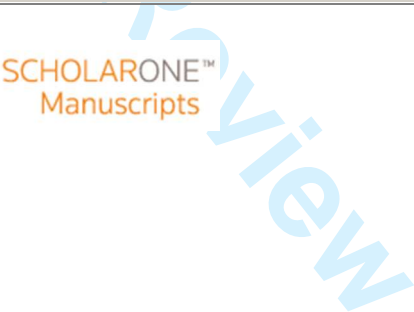


Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude

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Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude

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Key words: Alkalinity range, **Altitudinal range**, Aquatic plants, Freshwater ecosystem, Hydrophytes, Latitude, Nestedness, Spatial extent, Species turnover

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ABSTRACT

Aim: We studied global variation in beta diversity patterns of lake macrophytes using regional data from across the world. Specifically, we examined 1) how beta diversity of aquatic macrophytes is partitioned between species turnover and nestedness within each study region, and 2) which environmental characteristics structure variation in these beta diversity components.

Location: Global

Methods: We used presence-absence data for aquatic macrophytes from 21 regions distributed around the world. We calculated pairwise-site and multiple-site beta diversity among lakes within each region using Sørensen dissimilarity index and partitioned it into turnover and nestedness coefficients. Beta regression was used to correlate the diversity coefficients with regional environmental characteristics.

Results: Aquatic macrophytes showed different levels of beta diversity within each of the 21 study regions, with species turnover typically accounting for the majority of beta diversity, especially in high-diversity regions. **However**, nestedness contributed **30-50% of total** variation in macrophyte beta diversity in low-diversity regions. **The most important environmental factor explaining the three beta diversity coefficients (total, species turnover and nestedness) was altitudinal range, followed by relative areal extent of freshwater, latitude and water alkalinity range.**

Main conclusions: Our findings show that **global patterns in beta diversity of lake macrophytes are caused by species turnover rather than by nestedness.** These patterns in beta diversity were driven by natural environmental heterogeneity, **notably variability in altitudinal range (also related to temperature variation) among regions.** In addition, a greater range in alkalinity within a region, **likely amplified by human activities, was also correlated with increased macrophyte beta diversity.** These findings suggest that efforts to conserve aquatic macrophyte diversity should primarily focus **on regions with large numbers of lakes that exhibit broad environmental gradients.**

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INTRODUCTION

Understanding broad-scale biodiversity patterns has become a fundamental topic in biogeography and ecology. The importance of explaining these patterns has increased in recent years because they are intimately related to, for example, ecosystem functioning (Symstad et al., 2003) and resilience (Folke et al., 2004), biogeographical regionalization (Divisek et al., 2016), niche conservatism (Alahuhta et al., 2016), species conservation (Brooks et al., 2006) and ecosystem services (Naidoo et al., 2008). Spatial variation in broad-scale diversity patterns is typically driven by natural history (e.g., past dispersal barriers and evolutionary changes), interactions among species (e.g., competition, predation, and mutualism) and biogeography (e.g., distribution of climate zones, productivity and habitat heterogeneity) (Willig et al., 2003; Qian & Ricklefs, 2007; Soininen et al., 2007; Field et al., 2009; Baselga et al., 2012). Better knowledge of patterns in biodiversity and their basis is also critical for managing and adapting to invasive species, land use changes, landscape and habitat degradation, and increasing temperatures associated with global change (Vörösmarty et al., 2010). Therefore, studies focussing on broad-scale diversity patterns may directly advance both basic and applied research.

One intrinsic component of biodiversity is beta diversity (i.e., among-site differences in species composition). In general, beta diversity indicates the spatial variation of species composition among communities across space (Anderson et al., 2011), and is essentially related to two different processes (Baselga, 2010): species replacement (i.e., turnover, where one species replaces another with no change in richness) and nestedness (i.e., species richness differences due to species gain or loss). Mechanisms responsible for species replacement originate from environmental filtering, competition and historical events (Melo et al., 2009; Kraft et al., 2011; Wen et al., 2016).

Conversely, nestedness differences stem from species thinning or from other ecological processes (Baselga, 2010; Legendre, 2014), such as physical barriers or human disturbance, that result in species-poor sites being a subset of the richest site in the region. Independent of the dissimilarity measure used to represent beta diversity, it has been reported to decrease with latitude and increase with altitude and area (Jones et al., 2003; Heegaard, 2004; Qian & Ricklefs, 2007; Soininen et al., 2007; Kraft et al., 2011). Explanations for these patterns in beta diversity stem from effects of energy availability, water-energy dynamics, climatic variability, habitat heterogeneity and human disturbance (Gaston, 2000; Willig et al., 2003; Socolar et al., 2016). However, the majority of studies on beta diversity have been conducted at small spatial extents or using coarse resolution data across broad spatial scales (Kraft et al., 2011; Dobrovolski et al., 2012), exposing the lack of beta diversity studies using fine-resolution data at regional and global scales.

Increasing evidence indicates, however, that patterns in beta diversity depend on the studied ecosystem, organisms and geographical location (Soininen et al., 2007; Dobrovolski et al., 2012; Viana et al., 2016; Wen et al., 2016). Many of the reported patterns in beta diversity concern well-known, and often charismatic, taxa of terrestrial ecosystems (Qian & Ricklefs, 2007; Melo et al., 2009; Kraft et al., 2011; Wen et al., 2016) but may be unrepresentative of patterns in beta diversity for organisms in other ecosystems (Soininen et al., 2007). Studies of beta diversity in freshwaters have often proved to be incongruent with those of terrestrial assemblages (Heino, 2011; Hortal et al., 2015). A few studies have suggested that ecological factors or dataset properties associated with freshwater communities may override spatial processes in determining beta diversity (Heino et al., 2015; Viana et al., 2016). One possible explanation for these differences is that terrestrial ecosystems are more directly influenced by climate, whereas water temperatures, which are naturally more important to aquatic organisms, are more stable. Moreover, the physiological constraints of access to water and atmospheric gases are fundamentally different for terrestrial and

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5 177 assemblages at regional and global scales to discover whether they follow the general trends evident
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14 180 Aquatic macrophytes are among the most under-represented groups in broad-scale studies of
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17 181 freshwater biodiversity, yet they are an integral structural and functional component of freshwater
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19 182 ecosystems (Chambers et al., 2008). Few studies on macrophyte diversity have been conducted at
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22 183 continental or global extents, and these have relied on data scaled to coarse political or
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24 184 biogeographic regions (Chambers et al., 2008; Chappuis et al., 2012), leading to potentially
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26 185 spurious conclusions about species distributions at finer scales (Hortal et al., 2015). Although
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29 186 aquatic macrophyte diversity has been actively studied at local and regional extents, these studies
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31 187 may suffer from ecosystem-specific characteristics (i.e., varying environmental gradients lead
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33 188 species to respond differently to abiotic factors among regions), including variation in underlying
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36 189 environmental gradients among regions (Heino et al., 2015; Viana et al., 2016). For example,
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41 191 gradient in one region, yet a reversed latitudinal gradient in another (Alahuhta et al., 2013;
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43 192 Alahuhta, 2015). Thus, explaining and testing hypotheses related to broad-scale patterns in diversity
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45 193 is difficult with one or a few data sets, and a more general overview demands comparative analysis
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48 194 of multiple data sets (Crow, 1993; Kraft et al., 2011; Heino et al., 2015).
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54 196 In this paper, we examine pairwise- and multiple-site beta diversity of aquatic macrophytes using
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59 198 beta diversity of aquatic macrophytes partitioned between species turnover and nestedness across
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199 study regions on a global scale? (2) Which environmental factors explain variation in these beta

diversity components for aquatic macrophytes across study regions? Based on a continental scale study (Viana et al., 2016), we expected that spatial turnover accounts for most of the overall beta diversity. We also assumed that latitude does not strongly structure macrophyte beta diversity (Crow, 1993; Chambers et al., 2008). Instead, we hypothesised that macrophyte beta diversity is mostly explained by variables reflecting variation in local habitat conditions, thus indicating the effect of environmental heterogeneity on beta diversity (Heegaard, 2004; Viana et al., 2016).

MATERIAL AND METHODS

Macrophyte and explanatory variable data

We compiled lake macrophyte data for 21 regions with variable sizes from around the world (Fig. 1). Although only one or a few regions are included from some continents (e.g., only Morocco from Africa), our data set covered all major continents inhabitable by aquatic macrophytes (see Chambers et al., 2008). The regions either closely but not entirely followed a country's political border (e.g., Finland and New Zealand), or were delineated based on natural features (e.g., the Paraná River basin in Brazil and a small area in the Nord-Trøndelag county of Norway). The lakes consisted mostly of natural lentic water bodies (i.e., reservoirs were excluded), but were influenced by anthropogenic pressures to varying degrees (e.g., nutrient enrichment, introduced species, water level fluctuation, isolation and fish farming). The data consisted of presence-absence of vascular macrophyte species that grow exclusively in freshwaters (i.e., hydrophytes). The species data were based on empirical or scientific surveys which were performed all or in part by the authors, with the exception of Canada, China and Japan where data were compiled from existing literature (Appendix S1 in Supporting Information). Macrophytes were surveyed using broadly the same methods within each region, enabling us to compare beta diversity patterns across regions and to minimise the

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8 226 surveys were done during 1970s and 1980s, between 1964 and 2014, and between 1980 and 1998,
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17 229 We used convex hulls to delineate the minimal area containing all survey locations within a region
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19 230 (Appendix S2 in Supporting Information, Heino et al., 2015). We then used the convex hulls to
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24 232 on the variable in question, for each of the 21 regions.
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30 234 The explanatory variables calculated for each regional convex hull included region spatial extent
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33 235 (km²), **altitudinal range** (m, **Hijlmans** et al., 2005), modelled alkalinity range in lakes (mequiv. l⁻¹ at
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35 236 1/16 degrees resolution, Marcé et al., 2015), predicted range of soil organic carbon mass fraction at
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37 237 depth of 1 m (1 km resolution, Hengl et al., 2014), areal extent of freshwaters expressed as a
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40 238 proportion of region spatial extent, **herein referred to as proportion of freshwater** (%), 1 km
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42 239 resolution, Latham et al., 2014) and latitude (i.e., coordinate Y originated from each region's centre
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45 240 point) (Table 1). In addition, we examined whether areal extent of artificial surfaces (e.g., surfaces
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47 241 with houses, roads or industrial sites, Latham et al., 2014) as a proportion of region spatial extent
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49 242 (%), was correlated with the beta diversity coefficients and other explanatory variables. **Regional**
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52 243 spatial extent was a surrogate for sampling effort, as it was strongly positively associated with both
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56 245 Appendix S3 in Supporting Information), but is also an indicator of environmental heterogeneity
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59 246 (see also Gaston, 2000). In addition, **altitudinal range** likely illustrates variability in habitats suitable
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247 for different macrophytes (Gaston, 2000; Melo et al., 2009), and it simultaneously served as a proxy

for variation in temperature (correlation with temperature range: $R_S = 0.92$, $p < 0.001$). **Altitudinal range** was also positively associated with mean altitude ($R_S = 0.73$, $p < 0.001$). Following Dormann et al. (2013), multicollinearity was manifested at the level of $R_S > 0.7$ and, in these cases, statistically less significant predictors of beta diversity were excluded from final models (Appendix S2). Carbon compounds in water directly and indirectly influence macrophytes (Alahuhta & Heino, 2013; Kolada et al., 2014). We therefore used two different proxies, water alkalinity and soil organic carbon, to represent these local-scale components. Carbon dioxide and bicarbonate concentration influence photosynthesis in aquatic macrophytes, while organic carbon (i.e., carbon leached from organic soils) absorbs light, a common constraint on productivity (Madsen et al., 1996; Vestergaard & Sand-Jensen, 2000). Water alkalinity is also affected by anthropogenic land use (e.g., Vestergaard & Sand-Jensen, 2000; Kolada et al., 2014), enabling us to infer the degree of anthropogenic pressures on macrophyte beta diversity in lakes located on homogenous geology but lacking lake-level chemistry data. The relative areal extent of freshwaters within a region was used to indicate availability of potential habitat for macrophyte growth. Finally, changes in species diversity with latitude are well known, with species diversity often decreasing towards the Poles (Qian & Ricklefs, 2007). **Negative latitude values were converted to positive in our analysis to compensate for limited data availability on southern hemisphere regions, thereby strengthening the relationship between macrophyte beta diversity and latitude.**

Beta diversity coefficients for different data sets

We determined beta diversity of aquatic macrophytes using pairwise-site and multiple-site indices based on presence-absence species data within a region. In our study, the pairwise-site index indicated degree of absolute beta diversity within each region, whereas the multiple-site index was used to compare relative differences in beta diversity among regions (Baselga, 2010). For both

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8 274 2) Simpson coefficient (i.e., a measure of turnover immune to nestedness resulting from species
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10 275 richness differences, $\beta_{\text{sim/SIM}}$), and 3) a coefficient measuring nestedness–resultant beta diversity
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12 276 ($\beta_{\text{sne/SNE}}$, Baselga, 2010; Legendre, 2014). The Simpson coefficient defines species turnover without
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15 277 the influence of richness gradients, whereas the nestedness–resultant component of beta diversity is
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17 278 the direct difference between $\beta_{\text{sor/SOR}}$ and $\beta_{\text{sim/SIM}}$. For the pairwise-site index, we averaged the
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22 280 multiple-site index (Baselga, 2010), we resampled the 21 regional datasets to **standardize** them to a
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27 282 Brazil Amazon, Table 2), based on 1000 permutations in each region. Both beta diversity indices
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29 283 were obtained using the R package “betapart” (Baselga et al., 2013). The three beta diversity
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Statistical analysis

We used beta regression to identify which predictor variables explained beta diversity of aquatic macrophytes across the 21 regions. Beta regression, which is an extension of generalized linear models (GLM), was developed for situations where the dependent variable is measured continuously on a standard unit interval between 0 and 1 (Cribari-Neto & Zeileis, 2010). The models are based on beta distribution with parameterization using mean and precision parameters. Similarly to GLMs, the expected mean is linked to the responses through a link function and a linear predictor. The purpose of the link function is to stabilize the error variance and transform the fitted values to the desired application range (Ferrari & Cribari-Neto, 2004). Linear regression using

a logit-transformed response variable is still commonly employed to analyse the type of response data considered in our work. However, this is questionable, because it (a) may yield fitted values for the variable of interest that exceed its theoretical lower and upper bounds, (b) does not allow parameter interpretation in terms of the response on the original scale, and (c) measures proportions typically displaying asymmetry and, hence, inference based on the normality assumption can be misleading (Ferrari & Cribari-Neto, 2004). We therefore used beta regression models with a logistic link function, which is asymptotic in the range 0 to 1 (i.e., the predicted values are automatically in the desired application range).

The models with the most important explanatory variables influencing the beta diversity coefficients were selected based on the second order Akaike Information Criterion (AICc) among all model combinations. AICc takes into account sample size by increasing the relative penalty for model complexity with small data sets, and its use is recommended if, as in our case, the ratio between sample size and model parameters is less than 40 (Burnham & Anderson, 2002). We also examined the possibility of curvilinear relationships between beta diversity coefficients and certain explanatory variables (i.e., region extent, organic carbon and latitude) by entering the quadratic terms of these variables in our models, making the use of AICc even more relevant. In addition, we calculated AIC differences, which can be used to rank different models in order of importance ($AIC_i - AIC_{min}$, with AIC_{min} representing the best model with respect to expected Kullback-Leibler information lost). Akaike weights derived from AIC differences were estimated for each model to extract additional information on model ranking. We also present pseudo R^2 values, which are a squared correlation of linear predictor and link-transformed response and have the same scale as R^2 values (between 0 and 1) (Ferrari & Cribari-Neto, 2004). The relative importance of explanatory variables was evaluated by summing the Akaike weights of the models in which a given variable appears from the exhaustive list of models. A value of <2.0 was used as the threshold for deviation

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3 321 of AICc values among candidate models (i.e., difference between model i and the model with the
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5 322 smallest AICc, $\Delta AICc$), because models with AICc differing by < 2.0 are typically considered to
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8 323 have similar statistical support (Burnham & Anderson, 2002).
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14 325 All statistical analyses were conducted in R version 3.2.0. Beta regression was performed using
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17 326 functions in the R package “betareg” (Cribari-Neto & Zeileis, 2010), and candidate models were
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19 327 selected with the R package “MuMIn” (Bartoń, 2014).
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25 329 **RESULTS**
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32 331 Beta diversity of aquatic macrophytes differed among the 21 study regions, a finding that was
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34 332 mostly attributable to species turnover (Fig. 2), especially in high beta diversity regions, and applied
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37 333 to both pair-wise and multiple-site indices. Nestedness accounted only for a small fraction of
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39 334 overall beta diversity (14% of pairwise site dissimilarity on average) and was most important
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41 335 (although still less than species turnover) in regions with low overall pairwise–site beta diversity.
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43 336 Macrophyte beta diversity patterns in the majority of regions were thus explained by variation in
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46 337 species composition among lakes, rather than differences in species richness. Based on the
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49 338 pairwise-site index, the degree of macrophyte beta diversity varied clearly among the 21 study
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51 339 regions. The greatest beta diversity was found in the coastal South American lakes (Salga, 0.90) and
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53 340 Spain (0.92), whereas values were lowest in both the Brazilian regions (0.43–0.44) and China
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56 341 (0.43). The top models obtained through beta regression explained similar amounts of variation and
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58 342 included the same important explanatory variables (Table 2) for both pairwise-site and multiple-site
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beta diversity indices. The best models accounted for 28-33% of variation in the Sørensen coefficient, 33-37% in the turnover component and 27-28% in the nestedness component.

The most important explanatory variables for all the best models across the two beta diversity indices and different coefficients were altitudinal range (Fig. 3, Appendix S4), proportion of freshwater, latitude range (Fig. 3, Appendix S4) and alkalinity range, yet their relative importance varied somewhat. We found that overall beta diversity (i.e., Sørensen coefficient) and species turnover increased with increasing altitudinal range, latitude and alkalinity range, and decreased with increasing proportion of freshwater. The negative relation between species turnover and proportion of freshwater is probably due to connectivity, which typically increases with proportion of freshwaters, resulting in enhanced exchange of macrophyte species among lakes, thereby lowering turnover. Nestedness was negatively related to the first three variables but was positively associated with proportion of freshwater. Although some explanatory variables (i.e., spatial extent, latitude and organic carbon range) showed a curvilinear relationship with beta diversity coefficients in preliminary analyses, only the linear terms of these variables were selected in the best models. Comparison across all possible models showed that altitudinal range was included in the majority of models, with proportion of freshwater, latitude and alkalinity range all being of secondary importance (Table 3). By contrast, organic carbon and spatial extent were weak predictors of beta diversity across the coefficients.

In addition to relationships between beta diversity coefficients and environmental variability, certain environmental variables were correlated with indicators of anthropogenic pressures. Alkalinity range showed a positive relationship with the relative areal extent of artificial surfaces as proportion of region spatial extent ($R_s=0.46$, $p=0.04$). Both alkalinity range ($R_s=0.48$, $p=0.03$) and

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3 367 temperature range ($R_s=0.56$, $p=0.008$) were associated with spatial extent, such that the span in
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5 368 alkalinity and temperature was greater in regions that covered a greater areal extent. These
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8 369 correlations also impede the separation of possible independent effects for these factors.
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14 371 **DISCUSSION**
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21 373 Aquatic macrophytes exhibited considerable regional variation in beta diversity, which was largely
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23 374 driven by species turnover. Our results thus suggest that turnover in species composition primarily
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25 375 accounts for macrophyte beta diversity. Aquatic macrophytes have similarly shown high levels of
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28 376 species turnover at a regional and continental extent (Heegaard, 2004; Boschilia et al., 2016; Viana
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30 377 et al., 2016). However, our finding conflicts with previous global extent studies on beta diversity in
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33 378 which nestedness contributed equally or more than species turnover to total diversity of amphibians
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35 379 (Baselga et al., 2012), fish (Leprieur et al., 2011), macroinvertebrates (Heino et al., 2015) and
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37 380 oribatid mites (Gergocs & Hufnagel, 2015). In addition, nestedness has been found to outweigh
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40 381 species turnover in areas affected by glaciations until recent time (Baselga et al., 2012; Dobrovolski
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42 382 et al., 2012). We found no sign of this, as nestedness was typically lowest in regions that were
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45 383 wholly or partly ice covered during the last glaciation (e.g., Finland, Norway, Canada, China, New
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47 384 Zealand, Switzerland, US state of Minnesota and UK). Our study thus emphasises that conclusions
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49 385 about global patterns in beta diversity need verification across a diverse range of organisms, instead
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52 386 of using only a few well-studied terrestrial taxa, because variable patterns exist in nature and
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54 387 exceptions are as instructive as conformity.
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Contrary to our *a priori* expectations based on trends found in terrestrial taxa (Willig et al., 2003; Qian & Ricklefs, 2007; Soininen et al., 2007), beta diversity of aquatic macrophytes increased (albeit weakly) towards the poles. Based on Rapoport's rule (Stevens, 1989), species ranges and niche width should increase at higher latitudes, giving rise to a decrease in beta diversity (Soininen et al., 2007). But in general, many aquatic assemblages do not exhibit the latitudinal patterns observed for terrestrial taxa, such as mammals, birds and vascular plants (Heino, 2011; Hortal et al., 2015). Even regarding species richness, one of the most widely-used measures of diversity, aquatic macrophytes show differing responses to latitude at continental and global scales (Rørslett, 1991; Chambers et al., 2008; Chappuis et al., 2012). In addition, contrasting latitudinal patterns in macrophyte beta diversity have been found within individual regions (Heegaard, 2004; Viana et al., 2016), likely due to different study scales and varying sampling techniques used. Our study included only macrophyte data collected via consistent methods (within each region) and showed that overall beta diversity increases weakly from the equator towards the poles. However, the relative importance of latitude in explaining global macrophyte beta diversity was modest, being selected only in two of eleven models. These two models concerned the overall (Sørensen) beta diversity. In contrast, species turnover and nestedness did not vary consistently with latitudinal gradient. This is likely because aquatic macrophytes are more responsive to local environmental conditions than the broad-scale variation in climate that underlies latitudinal gradients in the beta diversity of other (terrestrial) organism groups. Aquatic environments moderate extreme climatic conditions, leading to less variation in temperature in freshwater than terrestrial ecosystems, and this may partly explain the conflict in latitudinal beta diversity patterns between freshwater and terrestrial assemblages.

Although the relationship between latitude and macrophyte beta diversity conflicted with that of many organisms, our results support another reported beta diversity pattern. Habitat heterogeneity

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3 414 has previously been shown to structure beta diversity for terrestrial plants (Freestone & Inouye,
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5 415 2006) and butterflies at a regional extent (Andrew et al., 2012), birds and mammals at a continental
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8 416 extent (Melo et al., 2009), and oceanic bacteria (Zinger et al., 2011) and fish (Leprieur et al., 2011)
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10 417 at a global extent. Variation in macrophyte beta diversity in our study regions was predominantly
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12 418 determined by environmental heterogeneity, primarily the degree of altitudinal variability (also
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15 419 correlated with temperature variability) in a region. Thus, beta diversity of aquatic macrophytes
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17 420 (expressed as either multiple-site or pairwise-site diversity) increased with variation in altitude.
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20 421 This positive association between beta diversity and altitudinal range likely reflects the greater
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22 422 variety of habitats or resources available with greater variation in altitude. Wang et al. (2012)
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24 423 similarly found that elevational beta diversity of aquatic micro- and macroorganisms was primarily
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27 424 related to environmental heterogeneity at a regional extent. Species distributions are typically
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29 425 constrained by harsh climatic conditions at high altitude (Gaston, 2000), and various aspects of
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32 426 macrophyte physiology are known to be temperature sensitive (Sculthorpe, 1967; Rooney & Kalff,
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34 427 2000). However, the buffering of temperature extremes in aquatic environments allows for
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36 428 continued plant growth over a wide altitudinal range. Greater variation in habitats with increasing
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39 429 variation in altitude is also related to geological and soil properties, as low lying lakes will vary
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41 430 more in water chemistry due to greater variation in soil and geology, which in turn increase
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43 431 variation in water chemistry (Wang et al., 2012), as well as from the added influence of human
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48 433 and thus enables the establishment of a greater variety of macrophyte species, further increasing
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51 434 beta diversity within a region.
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57 436 Regional variation in water alkalinity, soil organic carbon availability and spatial extent further
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59 437 indirectly would have supported the habitat heterogeneity hypothesis in explaining global patterns
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438 of macrophyte beta diversity. However, contrary to our expectations, these individual variables

were not important predictors of macrophyte beta diversity. Alkalinity and soil organic carbon influence aquatic macrophytes through their differing ability to use bicarbonate or carbon dioxide as a source of carbon in photosynthesis (Madsen et al., 1996), but also indirectly reflect human effects on freshwaters. In-lake alkalinity often increases with eutrophication, while nutrient inputs from agriculture and human effluents tend to be greatest in landscapes dominated by carbonate-rich minerals (Kolada et al., 2014; Alahuhta, 2015). Similarly, regional spatial extent is often positively associated with beta diversity, as in our work, because larger areas incorporate higher levels of environmental heterogeneity (Gaston, 2000; Anderson et al., 2011; Heino et al., 2015). Moreover, spatial extent was also positively related to alkalinity range and temperature range, both expressions of environmental heterogeneity. These explanations suggest an underlying effect of environmental heterogeneity on aquatic macrophyte beta diversity that may also be affected by human activities that impair water quality and physical characteristics of near-shore habitats (Kosten et al., 2009; Vörösmarty et al., 2010; Alahuhta, 2015).

Besides discovering novel patterns in macrophyte beta diversity, our main result has practical implications for environmental management: the conservation of aquatic macrophyte assemblages that naturally exhibit high species turnover will be most favoured by a regional approach, in which multiple lakes that span a wide environmental gradient are protected within a region (Socolar et al., 2016). This approach further underlines the need to maximise the total area protected, independent of the geographical location. Conversely, low biodiversity regions characterized by high nestedness require conservation actions that prioritise high-diversity sites over those of lower diversity (Socolar et al., 2016). In these low-biodiversity regions, the possible influence of land-based activities within a catchment should be carefully evaluated and connectivity among high-diversity habitats should be maintained.

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For Peer Review

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Description of study lakes and macrophyte survey methods in each region.

Appendix S2 An example of convex hull drawn for UK macrophyte data.

Appendix S3 Correlation matrix among environmental variables used in the study.

Appendix S4. Relationships between multiple site beta diversity dissimilarities (i.e., Sørensen, species turnover and nestedness) and mean altitude, altitudinal range and latitude.

BIOSKETCH

Janne Alahuhta is a postdoctoral researcher in the University of Oulu. His research integrates biogeography, macroecology, community ecology and conservation ecology to study patterns and processes structuring aquatic plants at various spatial scales. He is especially interested to understand how global change affects aquatic macrophyte distributions across temporal and spatial scales. The research group is devoted to the study of aquatic plants and other freshwater assemblages from different perspectives at various spatial scales. Author contributions: J.A. and J.H. conceived the ideas; all authors participated in the collection of the data; J.A. analysed the data; and J.A. led the writing to which other authors contributed.

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Table 1. Explanatory variables used in the study and the number of lakes and species within each region. Negative latitude (Y) values were converted to positive in the analysis to strengthen the relationship between beta diversity coefficients and latitude. Extent: Spatial extent of a region, Organic C: Soil organic carbon range, Waters: areal extent of water within a region as proportion of total spatial extent, Y: latitude.

Region	Number of lakes	Number of species	Alkalinity range (mequiv. l ⁻¹)	Altitudinal range (m)	Extent (km ²)	Org. C (mass fraction)	Waters (%)	Y
Brazil, Amazon	21	27	0.01	603	943	4	0.23	-6.23
Brazil, Paraná River	29	37	0.79	17	368	18	21.08	-22.78
Canada	58	82	3.95	242	82540	33	21.72	44.78
China	36	100	4.75	1374	151400	20	13.36	30.78
Denmark	32	77	4.33	156	17260	30	10.67	56.08
Finland	261	98	3.55	923	315900	110	10.50	64.32
Hungary	50	39	0.59	375	25740	12	1.56	47.28
Italy	22	60	4.04	3637	37980	20	2.20	44.68
Japan	49	93	3.20	3683	216600	28	1.40	38.24
Morocco	33	54	4.33	2322	36520	7	0.51	34.18
New Zealand	205	88	4.58	2800	250800	48	22.16	41.10
Norway	30	30	0.00	309	724	17	23.01	64.90
Poland	475	84	4.34	289	175000	22	1.99	52.99
Salga project (Brazil, Uruguay and Argentina)	67	28	3.63	2119	299300	57	3.88	-32.98
Spain	66	56	4.67	3129	34480	19	2.98	42.04
Sweden	379	101	4.68	1853	403600	68	10.99	62.24
Switzerland	92	60	3.18	3633	26910	35	4.93	46.93
UK	1928	127	4.81	1219	174000	81	2.28	54.24
US state of Florida	205	57	4.45	112	104200	66	5.14	28.99
US state of Minnesota	441	65	4.31	477	152700	58	7.09	46.26
US state of Wisconsin	409	102	3.93	397	141900	22	5.62	44.72

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Table 2. Summary of best models explaining variation in aquatic macrophyte beta diversity for multiple-site and pair-wise dissimilarities within a region. Models were calculated for Sørensen dissimilarity (total beta diversity), Simpson dissimilarity (beta diversity due to turnover) and nestedness dissimilarity (beta diversity due to nestedness-resultant richness differences). Best models with delta <2 are presented, because these models are typically considered to have similar statistical support (Burnham & Anderson, 2002). Waters: Proportion of water within a region, df: degree of freedom, delta: AICc difference between model i and the model with the smallest AICc, Weight: Akaike weight, pseudo R²: Maximum likelihood coefficients of determination were obtained through an iterative process.

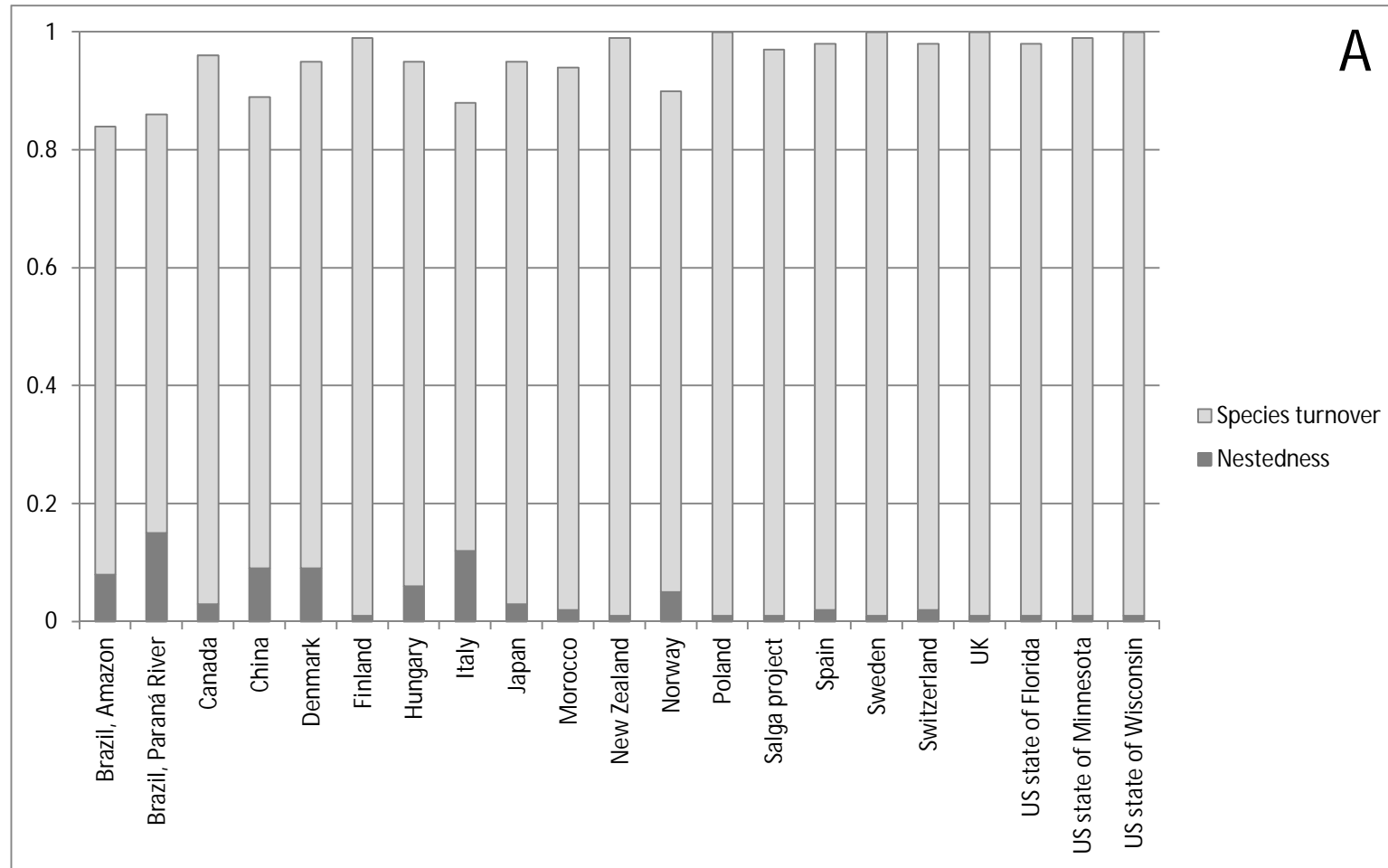
Multiple site beta diversity						Pair-wise beta diversity					
Sørensen	AICc	df	ΔAICc	Weight	Pseudo R ²	Sørensen	AICc	df	ΔAICc	Weight	Pseudo R ²
Altitudinal range	-80.9	3	0	0.435	0.282	Altitudinal range	-21.9	3	0	0.719	0.283
Altitudinal range+Latitude	-79.6	4	1.34	0.223	0.317	Altitudinal range+Latitude	-20.0	4	1.88	0.281	0.301
Altitudinal range+Waters	-79.1	4	1.74	0.182	0.326						
Altitudinal range+Alkalinity	-78.9	4	1.99	0.160	0.309						
range											
Species turnover						Species turnover					
Altitudinal range	-57.2	3	0	0.708	0.325	Altitudinal range	-14.7	3	0	1	0.326
Altitudinal range+Waters	-55.4	4	1.77	0.292	0.366						
Nestedness						Nestedness					
Altitudinal range	-83.9	3	0	1	0.280	Altitudinal range	-62.8	3	0	1	0.269

Table 3. Relative importance (I) of explanatory variables among all model compilations (n=32). 1.00 indicates that the particular variable is selected in all models, whereas 0 represents that the variable is not selected in any of the models. “+” indicates positive and “-“ negative relation between the beta diversity coefficient and that environmental variable. If a given variable was not included among the most important beta diversity models (AICc < 2.0), then the direction of influence was obtained from a full model including all the candidate variables. I: Importance, D: Direction of influence, Altitude: **Altitudinal range**, Alkalinity: Alkalinity range, Extent: Spatial extent of a region, Organic C: Soil organic carbon range, Waters: areal extent of water within a region as proportion of total spatial extent.

	<i>Multiple site beta diversity</i>					<i>Pair-wise beta diversity</i>						
	Sørensen		Species turnover		Nestedness	Sørensen		Species turnover		Nestedness		
	I	D	I	D	I	D	I	D	I	D	I	D
Altitude	0.80	+	0.90	+	0.85	-	0.82	+	0.90	+	0.89	-
Waters	0.33	-	0.30	-	0.23	+	0.26	-	0.25	-	0.17	+
Latitude	0.32	+	0.24	+	0.18	-	0.26	+	0.21	+	0.18	-
Alkalinity	0.25	+	0.22	+	0.20	-	0.24	+	0.22	+	0.17	-
Organic C	0.16	-	0.19	-	0.20	-	0.16	-	0.16	+	0.17	-
Extent	0.16	-	0.17	-	0.20	-	0.16	-	0.16	-	0.17	+



Fig. 1. Study regions are represented in blue circles situated in the middle of convex hulls (n=21). Crosses in the right side panel indicate which latitudinal bands are covered in our work.



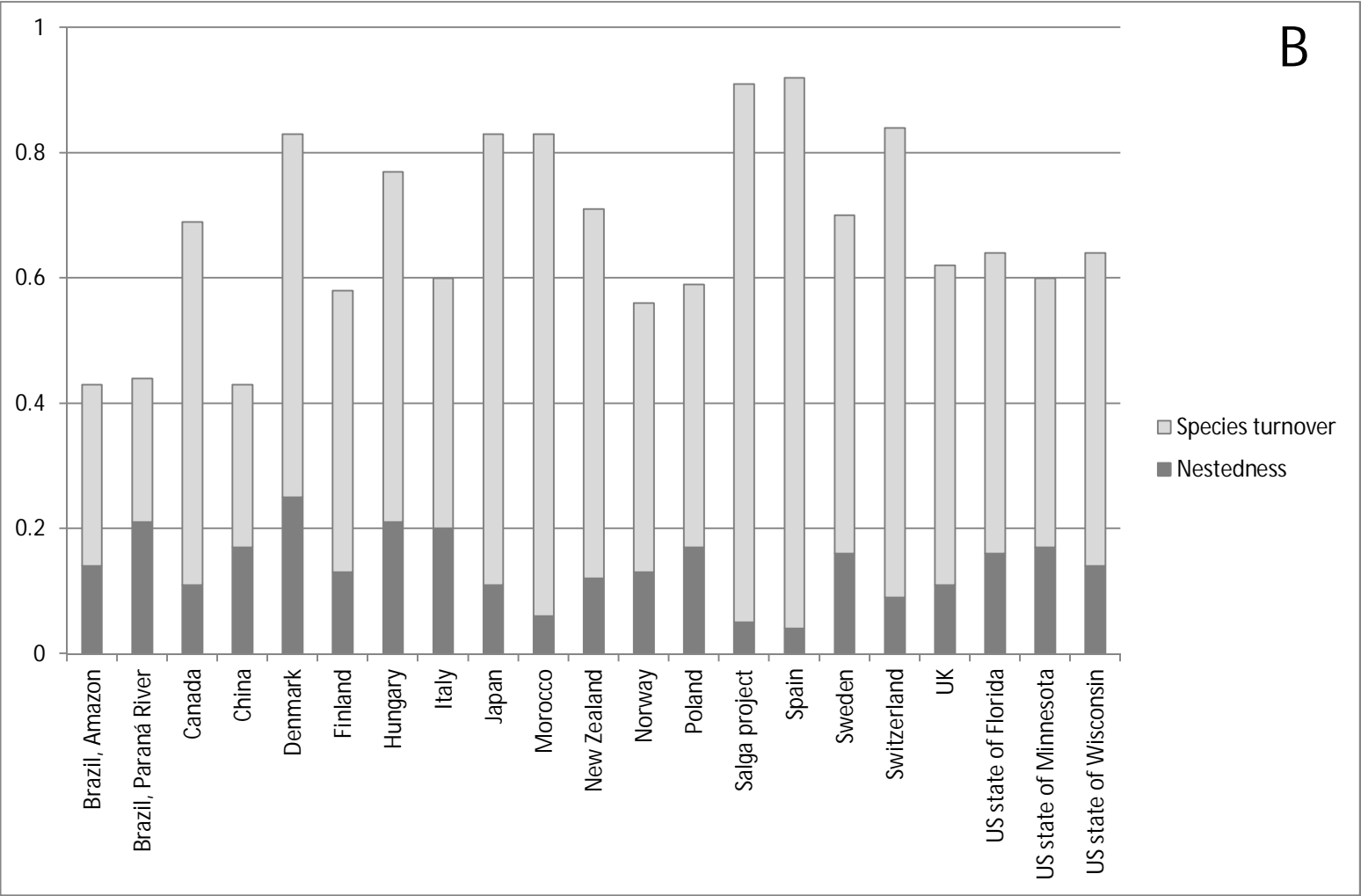


Fig. 2. Simpson dissimilarity (beta diversity due to species turnover) and nestedness dissimilarity (beta diversity due to nestedness-resultant richness differences) that sum to Sørensen dissimilarity (i.e., total beta diversity) based on multiple site (A) and mean of pair-wise (B) beta diversity measures for each study region. Multiple-site beta diversity was based on 21 randomly-selected lakes for each region (except for Brazil, Amazon which had a total n of 21).

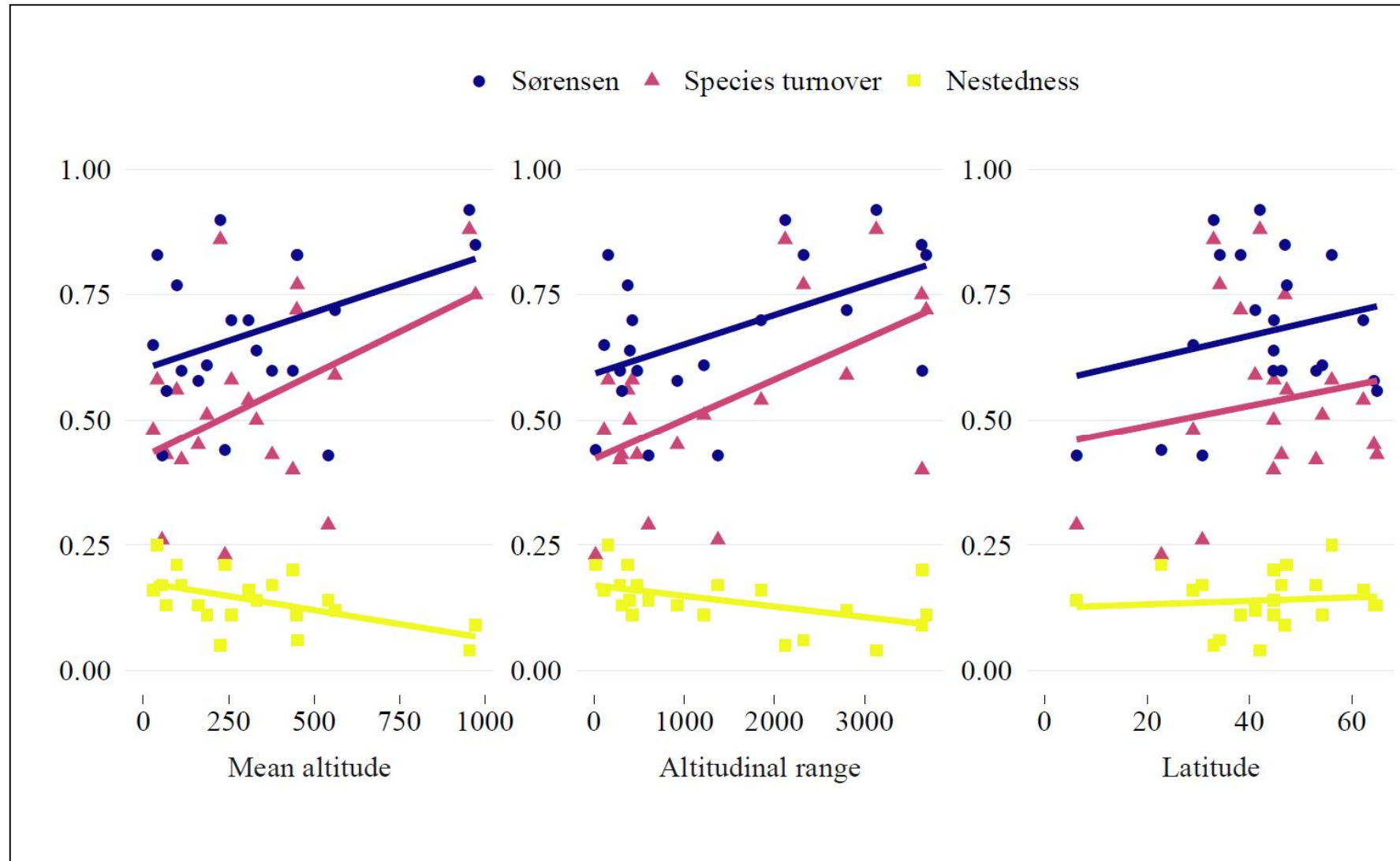


Fig. 3. Relationships between pairwise site beta diversity dissimilarities (i.e., Sørensen, species turnover and nestedness) and mean altitude, altitudinal range and latitude. Similar plot for multiple site beta diversity coefficients can be found in Appendix S4.

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**Global variation in the beta diversity of lake macrophytes is driven by
environmental heterogeneity rather than latitude**

Janne Alahuhta et al.

Journal of Biogeography

Supporting Information

For Peer Review

Appendix S1. Description of study lakes and macrophyte survey methods in each region.

Brazil, Amazon

The sampled lakes are temporary upland lakes located in the National Forest of Carajás-Pará, Brazil. Most sampled lakes are slightly acid and the surrounding area has a soil rich in iron ore. The presence of aquatic macrophyte species was recorded in 21 lakes by observation while walking over the macrophyte stands near the shoreline (parallel to the lake) and in a transect (perpendicularly to the lake) that crosses the lake. Samplings were carried out twice a year during 2004-2005 and 2010-2011, and the pooled data was used in the analyses.

Brazil, Paraná River

Sampled lakes in the Upper Paraná River floodplain are characterized as shallow floodplain lakes, which may be permanently connected with the main river channel or may be isolated with a temporary connection with the main river (during the floods). These lakes vary in pH (from acid to alkaline), water transparency (from clear to turbid water) and nutrient concentration (from oligotrophic to eutrophic). In all lakes we recorded aquatic macrophytes presence by boat at a slow speed along the entire lake shoreline. We also carried out species records on foot in the shoreline using a transect. We used a grapple, treble hooks and a rake to record submersed species. In this area, we sampled 29 lakes quarterly during 2010.

Britain

The lakes used are a subset of the 3500 sites surveyed by the Nature Conservancy Council or its successor national conservation agencies, mainly Scottish Natural Heritage, between 1980 and 1998. Sites are mostly in Scotland and typically small (<50ha) shallow (<3m average depth) and oligotrophic, although the dataset includes base-rich lowland lakes in the southern Britain. Sites varied from near-pristine to moderately degraded. Surveys were carried out from June-mid September by two observers, normally experienced botanists, circumnavigating the shoreline on foot to wading depth, using a rake to collect samples from deeper water and also checking strandline material. In larger water bodies wading surveys were complemented by use of a boat to collect samples from deeper water or inaccessible locations. Aquatic and emergent plants were identified to species and their abundance assessed visually on a 5-point scale. Voucher specimens were retained in a herbarium and sent to national experts for verification. Further details are provided in Duigan et al. (2007).

Canada

The 58 study sites were located in southern Ontario with the majority (n=50) being individual lakes situated north to north-east of Toronto in the Sudbury, Killarney, Muskoka, Haliburton and Kawartha lake districts. The remaining data are from one lake in eastern Ontario and 6 sites in Lake St. Clair (a connecting lake in the Great Lakes system). With the exception of one study, the data are from the 1970s. At the time of the surveys, the more southerly lakes were mesotrophic to eutrophic (as a result of urban or rural settlement and agricultural influences). In contrast, the more northerly lakes were the typical soft-water, unbuffered water bodies characteristic of the Precambrian Shield but with varying exposure to acidifying emissions. For the majority (n=42), macrophytes were sampled along transect lines that extended from shore to the maximum depth of colonization. For the remainder (n=16), macrophytes were sampled at specific locations. Species lists are provided in Ontario Ministries of Environment and Natural Resources (1976), Crowder et al. (1977), Wile and Hitchin (1977), Miller & Dale (1979), Hitchin et al. (1984), Schloesser et al. 1984, and Neil et al. (1991).

China

Most of the studied lakes are located in the mid-lower Yangtze Basin. The lake depths varied between 1 and 12 metres. Many of them are facing intensive human activities, including fishery, eutrophication and river-lake isolation. Macrophytes were surveyed using a belt transect method. The number of transects varied according to a lake size. Field surveys were conducted usually three or four times during a growing season and the recorded species were pooled together per lake for our analysis. The macrophytes were surveyed between 1954 and 2014.

Denmark

Most of the 49 Danish lakes included are located in central Jutland. Most lakes were meso- to eutrophic, alkaline systems with average depth ranging from 0.5 to 16 m. A few humic and low alkaline (i.e., neutral pH or acid) lakes were included too. Macrophytes were surveyed at an area dependent number of observations point, ranging from 75 to 375 points, situated on equidistant transects covering the entire lake area (if shallow) or the potential macrophyte covered area (if deeper) (Johansson and Lauridsen, 2014). Observation points were distributed ensuring similar observation numbers in each depth interval (0.25 to 1 m depth intervals). A relative species distribution, a total species list and percentage coverage were generated for each lake. Surveys were performed between July 1st and August 15th at maximum biomass and before senescence, during the period 2001-2010.

Finland

Majority of the studied 261 lakes were shallow, small humic lakes and many of them were impacted by anthropogenic pressures (i.e., agriculture and urban development). Lake macrophytes were surveyed using a main belt transect method (Kanninen et al., 2013), in which a five-metre-wide transect extends (perpendicularly to the shoreline) from the upper eulittoral to the outer depth limit of vegetation. The transect is divided into zones according to the dominant life-form or species. The number of transects varied depending on lake size. Lake macrophytes are observed by wading or by boat, with the aid of rake and hydroscope. The surveys were done between June and September over the period 2002–2011.

Hungary

All the studied 50 lakes are small, shallow lakes located in an agricultural landscape. Lake macrophytes were surveyed using a transect method. The number of transects parallel to shoreline varied according to lakes size (Schaumburg et al., 2007). All parallel transects contained minimum of four belt transects (two metre wide and perpendicular to the shoreline) extended from the upper eulittoral to the outer depth limit of vegetation. Field surveys were conducted between June and September over the period 2004–2012.

Italy

Majority of the studied 22 lakes were deep, big lakes and impacted by anthropogenic pressures (i.e., agriculture and urban development). Lake macrophytes were surveyed along transects (Azzella et al., 2013; Bolpagni, 2013). Data on aquatic plant diversity and representativeness were collected from each 1-meter depth interval down to the maximum colonization depth. The number of transects varied depending on lake size and sampling effort was tested to evaluate the effectiveness in the evaluation of macrophyte biodiversity. An underwater camera connected to a monitor placed on the boat was used to assess species presence and cover, while a double row rake was used to collect samples to help with macrophyte species identification. The surveys were done between June and September over the period 2009–2010.

Japan

Lakes were selected from the database which describes native vascular aquatic plants in Japan (Nishihiro et al., 2014) and additional data from newly found literatures were added to the database. From the whole database, we used those lakes in this work, in which macrophyte data were surveyed between 1990 and 2014. Selected lakes were distributed between 29.85° and 45.07°N. Lake area ranged from 0.01 to 704.95 km² (median 1.59 km²), and maximum depth ranged from 1 to 326 m (median 6.35 m).

Morocco

Most studied lakes were shallow and were located in the mountains (Middle and High Atlas) or Atlantic plains. These lakes are used by local people for cattle grazing, recreation, water supply and medicinal plants. Lake macrophytes were surveyed on zones (3 x 3 meters) distributed along 2 permanent transects at right angles to one another. The number of zones varied between lakes according to their size. The distance between zones was 3 to 5 meters. All species (amphibious, aquatic) were inventoried, however, only hydrophytes were used in the analyses. Field surveys were executed between February and July over the period 2005-2013.

New Zealand

Macrophyte data was drawn from 205 lakes that were surveyed using the “Quick Survey Method” of Clayton (1983). Surveyed lakes represented mostly of natural water bodies; however, 28 artificial reservoirs were included in the data. As a result, the lakes included those of volcanic origin, glacial formation, dammed rivers, dune, peat and land slip-formed lakes. Lakes were biased towards larger waterbodies located in accessible and populated areas. Consequently lakes included those influenced by anthropogenic nutrient enrichment or by the introduction of alien plants and fish. The timing of surveys was primarily in the austral spring to autumn (November to April), however most submerged species are perennial and present year round. Between 1 and 50 sites were assessed, with generally more sites in larger lakes. At each site scuba divers covered a 2 m wide transect from the shoreline water level to the deepest extent of vegetation, identifying all plant species seen, with the exception of bryophytes.

Norway

The studied 30 high-alkalinity lakes are small in surface area, varying from oligotrophic to eutrophic status and subject to agricultural land use pressure. These lakes situate in Nord-Trøndelag county in the middle of Norway. Lake macrophytes were surveyed along four orthogonal transects perpendicular to the lake shore and situated approximately at its intersection with the four cardinal points (Viana et al., 2014). In addition, the rest of the lake and its edges were visited, and any additional species recorded. The surveys were carried out during the peak of the growing season in 1998, so that all species present in the lake through the season could be detected. Only hydrophytes were used in the analyses.

Poland

All of the 475 lakes are lowland (<200 m a.s.l.), with high-alkalinity non-coloured waters, but differ in morphometry and trophy. Data on macrophytes were collected in the period 2004-2012 within the national lake monitoring programme (425 lakes) and other research projects. Lake macrophytes were surveyed between June and September using the unified field survey procedure based on belt transect method (Ciecierska and Kolada, 2014). The number of transects varied depending on lake size; however, sampling effort has not influenced previous studies on macrophyte community

compositions (Kolada et al, 2014). Within the phytolittoral of each lake, the maximum colonisation depth, the mean vegetation coverage and the relative cover of all the aquatic and emergent plant communities were determined. Only hydrophytes were used in our work.

Salga project (Brazil, Uruguay and Argentina)

The studied lakes situated across the three countries and were small (0.09–2.53 km²) shallow (mean depth <4.5m) and varied greatly in the degree in which they were impacted by anthropogenic pressures (i.e., agriculture and urban development) (Kosten et al., 2009a). Lake macrophytes were surveyed based on observations along 3 – 8 parallel transects perpendicular to the maximum length of the lake and an additional 20 randomly located points. The number of transects varied with the shape and size of the lake. Observations were made from a boat using a rake when necessary (Kosten et al., 2009b; Kosten et al., 2009c). The surveys were done during summer (lakes at latitudes below 30°S) or during dry season (lakes above 30°S) between November 2004 and March 2006 by the same team.

Spain

We enclose data on 66 water bodies holding macrophyte flora and sampled between 2005 and 2009 across Catalonia (NW Spain). The data set includes a diversity of water body typologies from alpine lakes (at high altitude with oligotrophic soft-waters), karstic lakes (high alkaline waters), coastal lagoons (at the shoreline, with brackish waters), permanent ponds and temporary pools (small ponds with annual desiccation period). Water bodies were usually small and shallow and were located along a large altitudinal range (0 - 2573 m a.s.l.). Sampling was conducted by snorkeling, scuba diving or walking with waders around all the water body and collecting macrophyte samples at the different assemblages that were recognized by visual inspection (Chappuis et al., 2014).

Sweden

The studied 379 lakes varied in their environmental conditions and subjectivity to anthropogenic pressures. Macrophyte surveys were conducted between 2008 and 2013 using a transect method, in which the transects were placed perpendicular to the shoreline and distributed around the lake, from the upper eulittoral to the outer limit of vegetation. The number of transects varied according to lake size with larger lakes having more transects and vice versa. Species were identified by diving along the transects with 0.5m in 20-cm depth intervals and in plots of ca. 25 × 50 cm (Naturvårdsverket, 2010).

Switzerland

The water bodies (i.e. ponds and small lakes, with an area less than 1 ha) included in this study are scattered throughout Switzerland along an altitudinal gradient ranging from lowland (305 m.a.s.l.) to alpine areas (2191 m a.s.l.). A fifth of them are of natural origin, whereas the other originated from past or present anthropic activities. The macrophytes of all ponds and lakes were surveyed using a standardized method based on plot sampling (0.5 x 0.5m) along transects (Oertli et al., 2005). The transects were positioned perpendicularly to the longest axis of the water body, at intervals of 5 m for small and 20 m for larger ponds. The number of plots was proportional to the area of the water body and positioned at 5m intervals along transects. The surveys were carried out between June and September over the period 1996 -2004.

US state of Florida

The 205 Florida study lakes ranged from oligotrophic to hypereutrophic with average chlorophylls ranging from < 1.0 µg/L to over 150 µg/L. The lakes were generally shallow and small with 75% of the mean depths less than 4.0 m and 75% of the surface areas less than 200 ha. Plant sampling was conducted during summer months between 1991 and 2013 with a varying number of transects per lake depending on the size of the lake (generally 10 transects per lake). The transects were placed uniformly around the lake and went from open water through the littoral zone of each transect. Plants were collected with divers in deep-water areas and rakes in shallow areas and all identified to species. In addition to species composition, total abundance of all plants in each lake (PAC: percent area covered and PVI: percent volume infested with aquatic plants) was estimated using ecosounding technologies. Both aquatic plant species composition and abundance was measured to examine plant relations to the Limnology of Florida lakes and to assist state agencies with the management of aquatic plants.

US state of Minnesota

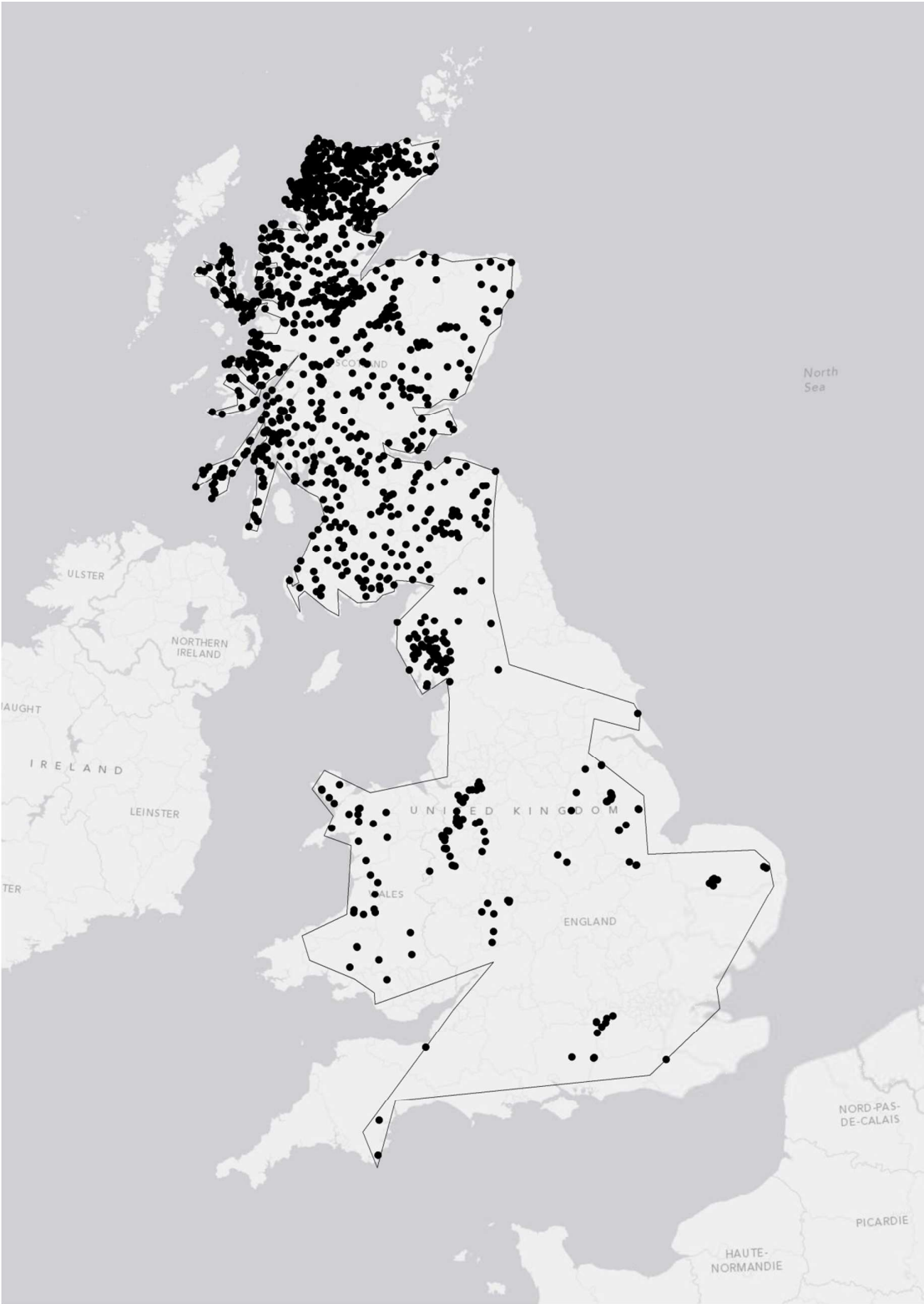
Aquatic macrophyte data from 441 lakes were used, covering the entire US state of Minnesota. Environmental conditions of the study lakes varied from more natural water bodies with lower nutrient and alkalinity values in the northern part of the state to severely anthropogenic-impacted lakes with high trophic status situated in the south (Alahuhta, 2015). The macrophyte data were collected by the Minnesota Department of Natural Resources (Section of Fisheries) between 1992 and 2003. The aquatic plant species were sampled between July and August using a transect method, in which transects were evenly placed around the lake. The 6-m wide transects ran perpendicular to the shore to the maximum depth of vegetation cover, and the number of transects varied depending on lake size. The species were identified from a boat with the help of a grapple.

US state of Wisconsin

Macrophyte data from 409 Wisconsin lakes were surveyed between May and September from 2005-2012 using a point-intercept method as outlined in Hauxwell et al. 2010. Species were

observed from a boat using a double-sided rake sampler at a grid of points projected onto the surface of each lake. Spatial resolution of sample points was calculated as a function of estimated lake littoral area and shoreline complexity as in Mikulyuk et al. 2010. Spatial extent covered the three lake-rich ecoregions of Wisconsin and lakes represent the full gradient of anthropogenic impact, primary productivity, alkalinity, and hydrologic type present in the region (Omernik, 2000; Riera et al., 2000; Mikulyuk 2010).

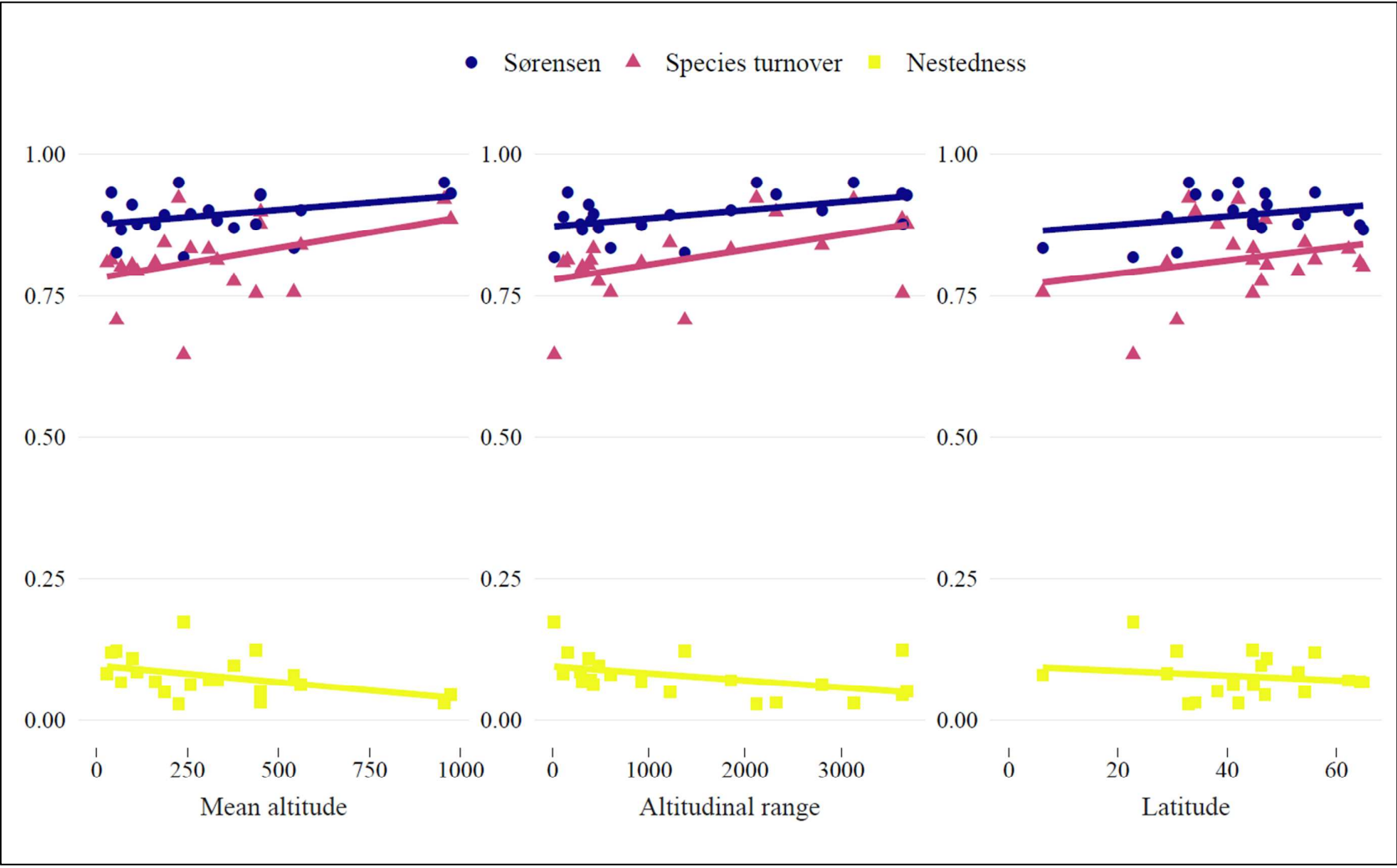
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Appendix S2. An example of convex hull drawn for UK macrophyte data.

Appendix S3. Correlation matrix among environmental variables used in the study. Clay: modelled soil clay, No of spp.: Number of species recorded in lakes within a region, Org. soil C: Organic soil carbon, Annual °C: Annual temperature, Waters: Proportion of freshwaters within a region, p: *** ≤ 0.001 , ** < 0.05 , * < 0.1 .

	Alkalinity range	Altitude, mean	Altitude, range	Clay	Latitude	Org. soil C, range	Spatial extent	Annual °C, mean	Annual °C, range	Waters
Alkalinity range	1	0.01	0.29	-0.03	0.01	-0.10	0.52**	0.01	0.29	0.08
Altitude mean		1	0.73***	0.37*	-0.22	0.03	-0.11	0.01	0.57**	-0.33*
Altitude range			1	0.34*	-0.16	0.02	0.27	0.04	0.92***	-0.35*
Clay				1	-0.76***	-0.56**	-0.31*	0.82***	0.22	-0.44**
Latitude					1	0.35*	0.11	-0.83***	-0.12	0.24
Org. soil C, range						1	-0.54**	-0.51**	0.26	0.39*
Spatial extent							1	-0.43**	-0.48**	0.08
Annual °C, mean								1	-0.03	-0.41*
Annual °C, range									1	-0.24
Waters										1



Appendix S4. Relationships between pairwise-site beta diversity dissimilarities (i.e., Sørensen, species turnover and nestedness) and mean altitude, altitudinal range and latitude.

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