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

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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 elevation 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 elevation 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.
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., 2017), 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 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 elevation 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 aquatic organisms.
Consequently, there is a need to study diversity patterns of freshwater assemblages at regional and global scales to discover whether they follow the general trends evident in terrestrial organisms.

Aquatic macrophytes are among the most under-represented groups in broad-scale studies of freshwater biodiversity, yet they are an integral structural and functional component of freshwater ecosystems (Chambers et al., 2008). Few studies on macrophyte diversity have been conducted at continental or global extents, and these have relied on data scaled to coarse political or biogeographic regions (Chambers et al., 2008; Chappuis et al., 2012), leading to potentially spurious conclusions about species distributions at finer scales (Hortal et al., 2015). Although aquatic macrophyte diversity has been actively studied at local and regional extents, these studies may suffer from ecosystem-specific characteristics (i.e., varying environmental gradients lead species to respond differently to abiotic factors among regions), including variation in underlying environmental gradients among regions (Heino et al., 2015; Viana et al., 2016). For example, aquatic macrophyte diversity studied using similar methods showed a clear decreasing latitudinal gradient in one region, yet a reversed latitudinal gradient in another (Alahuhta et al., 2013; Alahuhta, 2015). Thus, explaining and testing hypotheses related to broad-scale patterns in diversity is difficult with one or a few data sets, and a more general overview demands comparative analysis of multiple data sets (Crow, 1993; Kraft et al., 2011; Heino et al., 2015).

In this paper, we examine pairwise- and multiple-site beta diversity of aquatic macrophytes using data sets for 21 regions from around the world. Specifically, we consider two questions: (1) How is beta diversity of aquatic macrophytes partitioned between species turnover and nestedness across 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).

MATERIALS 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 (A list of the data sources for two
of these regions is found in Appendix 1, 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 potential negative effects caused by contrasting regional
survey methods. The surveys were executed mostly between 1990 and 2012, with the exception of Canada, China and Britain, where surveys were done during 1970s and 1980s, between 1964 and 2014, and between 1980 and 1998, respectively.

We used convex hulls to delineate the minimal area containing all survey locations within a region (Appendix S2 in Supporting Information, Heino et al., 2015). We then used the convex hulls to extract environmental information for each region and calculated mean and range values, depending on the variable in question, for each of the 21 regions.

The explanatory variables calculated for each regional convex hull included region spatial extent (km²), elevation range (m, Hijmans et al., 2005), modelled alkalinity range in lakes (mequiv. l⁻¹ at 1/16 degrees resolution, Marcé et al., 2015), predicted range of soil organic carbon mass fraction at depth of 1 m (1 km resolution, Hengl et al., 2014), areal extent of freshwaters expressed as a proportion of region spatial extent, herein referred to as proportion of freshwater (%). 1 km resolution, Latham et al., 2014) and latitude (i.e., coordinate Y originated from each region’s centre point) (Table 1). In addition, we examined whether areal extent of artificial surfaces (e.g., surfaces with houses, roads or industrial sites, Latham et al., 2014) as a proportion of region spatial extent (%), was correlated with the beta diversity coefficients and other explanatory variables. Regional spatial extent was a surrogate for sampling effort, as it was strongly positively associated with both numbers of lakes and number of species present within a region (R_{Spearman} ≥ 0.64, p<0.001, Appendix S3 in Supporting Information), but is also an indicator of environmental heterogeneity (see also Gaston, 2000). In addition, elevation range likely illustrates variability in habitats suitable 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). Elevation 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 indices, the calculations were based on the Sørensen dissimilarity, resulting in the following three dissimilarity
coefficients: 1) Sørensen coefficient (i.e., a measure of overall beta diversity, $\beta_{sor/SOR}$), 2) Simpson coefficient (i.e., a measure of turnover immune to nestedness resulting from species richness differences, $\beta_{sim/SIM}$), and 3) a coefficient measuring nestedness–resultant beta diversity ($\beta_{sne/SNE}$, Baselga, 2010; Legendre, 2014). The Simpson coefficient defines species turnover without the influence of richness gradients, whereas the nestedness-resultant component of beta diversity is the direct difference between $\beta_{sor/SOR}$ and $\beta_{sim/SIM}$. For the pairwise-site index, we averaged the pairwise dissimilarities between all lakes in a region. Because the number of sites affects the multiple-site index (Baselga, 2010), we resampled the 21 regional datasets to standardize them to a common number of 21 lakes, the minimum number of lakes found across the regional datasets (in Brazil Amazon, Table 2), based on 1000 permutations in each region. Both beta diversity indices were obtained using the R package “betapart” (Baselga et al., 2013). The three beta diversity coefficients were calculated using the functions beta.pair and beta.sample for pairwise-site and multiple-site indices, respectively.

**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 corrected for small sample size (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 of AICc values among candidate models (i.e., difference between model i and the model
with the smallest AICc, ΔAICc), because models with AICc differing by < 2.0 are typically considered to have similar statistical support (Burnham & Anderson, 2002).

All statistical analyses were conducted in R 3.2.0 (R Core Team 2015). Beta regression was performed using functions in the R package “betareg” (Cribari-Neto & Zeileis, 2010), and candidate models were selected with the R package “MuMIn” (Bartoń, 2014).

RESULTS

Beta diversity of aquatic macrophytes differed among the 21 study regions, a finding that was mostly attributable to species turnover (Fig. 2), especially in high beta diversity regions, and applied to both pair-wise and multiple-site indices. Nestedness accounted only for a small fraction of overall beta diversity (14% of pairwise site dissimilarity on average) and was most important (although still less than species turnover) in regions with low overall pairwise–site beta diversity. Macrophyte beta diversity patterns in the majority of regions were thus explained by variation in species composition among lakes, rather than differences in species richness. Based on the pairwise-site index, the degree of macrophyte beta diversity varied clearly among the 21 study regions. The greatest beta diversity was found in the coastal South American lakes (Salga, 0.90) and Spain (0.92), whereas values were lowest in both the Brazilian regions (0.43-0.44) and China (0.43). The top models obtained through beta regression explained similar amounts of variation and included the same important explanatory variables (Table 2) for both pairwise-site and multiple-site 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 elevation 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 elevation 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 elevation 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 temperature range ($R_S=0.56, p=0.008$) were associated with spatial extent, such that the span in alkalinity and temperature was greater in regions that covered a greater areal extent. These correlations also impede the separation of possible independent effects for these factors.
Aquatic macrophytes exhibited considerable regional variation in beta diversity, which was largely driven by species turnover. Our results thus suggest that turnover in species composition primarily accounts for macrophyte beta diversity. Aquatic macrophytes have similarly shown high levels of species turnover at a regional and continental extent (Heegaard, 2004; Boschilia et al., 2016; Viana et al., 2016). However, our finding conflicts with previous global extent studies on beta diversity in which nestedness contributed equally or more than species turnover to total diversity of amphibians (Baselga et al., 2012), fish (Leprieur et al., 2011), macroinvertebrates (Heino et al., 2015) and oribatid mites (Gergocs & Hufnagel, 2015). In addition, nestedness has been found to outweigh species turnover in areas affected by glaciations until recent time (Baselga et al., 2012; Dobrovolski et al., 2012). We found no sign of this, as nestedness was typically lowest in regions that were wholly or partly ice covered during the last glaciation (e.g., Finland, Norway, Canada, China, New Zealand, Switzerland, US state of Minnesota and UK). Our study thus emphasises that conclusions about global patterns in beta diversity need verification across a diverse range of organisms, instead of using only a few well-studied terrestrial taxa, because variable patterns exist in nature and exceptions are as instructive as conformity.

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 has previously been shown to structure beta diversity for terrestrial plants (Freestone & Inouye, 2006) and butterflies at a regional extent (Andrew et al., 2012), birds and mammals at a continental extent (Melo et al., 2009), and oceanic bacteria (Zinger et al., 2011) and fish (Leprieur et al., 2011) at a global extent. Variation in macrophyte beta diversity in our study regions was predominantly determined by environmental heterogeneity, primarily the degree of elevation variability (also correlated with temperature variability) in a region. Thus, beta diversity of aquatic macrophytes
(expressed as either multiple-site or pairwise-site diversity) increased with variation in altitude. This positive association between beta diversity and elevation range likely reflects the greater variety of habitats or resources available with greater variation in altitude. Wang et al. (2012) similarly found that elevational beta diversity of aquatic micro- and macroorganisms was primarily related to environmental heterogeneity at a regional extent. Species distributions are typically constrained by harsh climatic conditions at high altitude (Gaston, 2000), and various aspects of macrophyte physiology are known to be temperature sensitive (Sculthorpe, 1967; Rooney & Kalff, 2000).

However, the buffering of temperature extremes in aquatic environments allows for continued plant growth over a wide elevation range. Greater variation in habitats with increasing variation in altitude is also related to geological and soil properties, as low lying lakes will vary more in water chemistry due to greater variation in soil and geology, which in turn increase variation in water chemistry (Wang et al., 2012), as well as from the added influence of human activity. These factors magnify the elevation gradient which enhances environmental heterogeneity and thus enables the establishment of a greater variety of macrophyte species, further increasing beta diversity within a region.

Regional variation in water alkalinity, soil organic carbon availability and spatial extent further indirectly would have supported the habitat heterogeneity hypothesis in explaining global patterns 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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REFERENCES

Alahuhta, J. & Heino, J. (2013) Spatial extent, regional specificity and metacommunity structuring in lake macrophytes. Journal of Biogeography, 40, 1572–1582.

Alahuhta, J., Kanninen, A., Hellsten, S., Vuori, K.-M., Kuoppala, M. & Hämäläinen, H. (2013) Environmental and spatial correlates of community composition, richness and status of boreal lake macrophytes. Ecological Indicators, 32, 172-181.
Alahuhta, J. (2015) Geographic patterns of lake macrophyte communities and species richness at regional scale. *Journal of Vegetation Science*, **26**, 564-575.

Alahuhta, J., Ecke, F., Johnson, L.B., Sass, L. & Heino, J. (2017) A comparative analysis reveals little evidence for niche conservatism in aquatic macrophytes among four areas on two continents. *Oikos*, **126**, 136-148.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J., Stegen, J.C. & Swenson, N.G. (2011) Navigating the multiple meanings of $\beta$ diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19-28.

Andrew, M.E., Wulder, M.A., Coops, N.C. & Baillargeon, G. (2012) Beta-diversity gradients of butterflies along productivity axes. *Global Ecology and Biogeography*, **21**, 352-364.

Bartoń, K. (2014) MuMIn: multi-model inference. R package version 1.12.1. https://cran.r-project.org/web/packages/MuMIn/index.html

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. Global *Ecology and Biogeography*, **19**, 134-143.

Baselga, A., Orme, D., Villegier, S., Bortoli, D. & Leprieur, F. (2013) betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.3.

Baselga, A., Gomez-Rodrigues, C. & Lobo, J.M. (2012) Historical Legacies in World Amphibian Diversity Revealed by the Turnover and Nestedness Components of Beta Diversity. *PLoS ONE*, **7**, e32341.
Boschilia, S.M., de Oliveira, E.F. & Schwarzbold, A. (2016) Partitioning beta diversity of aquatic 
macrophyte assemblages in a large subtropical reservoir: prevalence of turnover or nestedness? 
Aquatic Sciences, 78, 615-625.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., 
Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2008) Global biodiversity conservation 
priorities. Science, 313, 58-61.

Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference: a practical 
information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY.

Chambers, P.A., Lacoul, P., Murphy, K.J. & Thomaz, S.M. (2008) Global diversity of aquatic 
macrophytes in freshwater. Hydrobiologia, 595, 9–26.

Chappuis, E., Ballesteros, E. & Gacia, E. (2012) Distribution and richness of aquatic plants across 
Europe and Mediterranean countries: patterns, environmental driving factors and comparison 
with total plant richness. Journal of Vegetation Science, 23, 985-997.

Cribari-Neto, F. & Zeileis, A. (2010) Beta Regression in R. Journal of Statistical Software, 34, 1-24.

Crow, G.E. (1993) Species diversity in aquatic angiosperms: latitudinal patterns. Aquatic Botany, 44, 
229–258.

Divisek, J., Storch, D., Zelen, D. & Culek, M. (2016) Towards the spatial coherence of 
biogeographical regionalizations at subcontinental and landscape scales. Journal of 
Biogeography, 43, 2489-2501.

Dobrovolski, R., Melo, A.S., Cassemiro, F.A.S. & Diniz-Filho, J.A.F. (2012) Climatic history and 
dispersal ability explain the relative importance of turnover and nestedness components of beta 
diversity. Global Ecology & Biogeography, 21, 191-197.
Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquèz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*, 27-46.

Ferrari, S. & Cribari-Neto, F. (2004) Beta Regression for modelling rates and proportions. *Journal of Applied Statistics, 31*, 799-815.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.-F., Kaufman, D.M., Kerr, J.T., Mittenbach, G.G., Oberdorff, T., O’Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography, 36*, 132-147.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics, 35*, 557-581.

Freestone, A.L. & Inouye, B.D. (2006) Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology, 87*, 2425-2432.

Gaston, K. J. (2000) Global patterns in biodiversity. *Nature, 405*, 220–227.

Gergocs, V. & Hufnagel, L. (2015) Global pattern of oribatid mites (Acari: Oribatida) revealed by fractions of beta diversity and multivariate analysis. *International Journal of Acarology, 41*, 574-583.

Heegaard, E. (2004) Trends in aquatic macrophyte species turnover in Northern Ireland — which factors determine the spatial distribution of local species turnover? *Global Ecology and Biogeography, 13*, 397-408.
Heino, J. (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, **56**, 1703–1722.

Heino, J., Melo, A.S., Bini, L.M., Altermatt, F., Al-Shami, S.A, Angeler, D., Bonada, N., Brand, C., Callisto, M., Cottenie, K., Dangles, O., Dudgeon, D., Encalada, A., Göthe, E., Grönlund, M., Hamada, N., Jacobsen, D., Landeiro, V.L., Ligeiro, R., Martins, R.T., Miserendino, M.L., Md Rawi, C.S. Rodrigues, M., Roque, F.O., Sandin, L., Schmera, D., Sgarbi, L.F., Simaika, J., Siqueira, T., Thompson, R.M. & Townsend, C.R. (2015) A comparative analysis reveals weak relationships between ecological factors and beta diversity of stream insect metacommunities at two spatial levels. *Ecology and Evolution*, **5**, 1235-1248.

Hengl, T., de Jesus, J.M., MacMillan, R.A., Batjes, N.H., Heuvelink, G.B.M., Ribeiro, E., Samuel-Rosa, A., Kempen, B., Leenaars, J.G.B., Walsh, M.G. & Ruiperez Gonzalez, M. (2014) SoilGrids1km — Global Soil Information Based on Automated Mapping. *PLoS ONE*, **9**, e114788.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **46**, 523-549.

Jones, J.I., Li, W. & Maberly, S.C. (2003) Area, altitude and aquatic plant diversity. *Ecography*, **26**, 411-420.

Kolada, A., Willby, N., Dudley, B., Nõges, P., Søndergaard, M., Hellsten, S., Mjedge, M., Penning, E., van Geest, G., Bertrin, V., Ecke, F., Mäemets, H. & Karus, K. (2014) The applicability of
macrophyte compositional metrics for assessing eutrophication in European lakes. *Ecological Indicators, 45*, 407-415.

Kosten, S., Kamarainen, A., Jeppesen, E., van Nes, E.H., Peeters, E.T.H.M., Mazzeo, N., Sass, L., Hauxwell, J., Hansel-Welch, N., Lauridsen, T.L., Søndergaard, M., Bachmann, R.W., Lacerot, G. & Scheffer, M (2009) Climate-related differences in the dominance of submerged macrophytes in shallow lakes. *Global Change Biology, 15*, 2503-2517.

Kraft, N.J.B., Comita, L.S. Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B.D., Harrison, S.P. & Myers, J.A. (2011) Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science, 333*, 1755-1758.

Latham, J., Cumani, R., Rosati, I. & Bloise, M. (2014) FAO Global Land Cover (GLC-SHARE) Beta-Release 1.0 Database, Land and Water Division. http://www.glcn.org/databases/lc_glchare_en.jsp

Legendre, P. (2014) Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography, 23*, 1324-1334.

Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Durr, H.H., Brosse, S. & Oberdorff, T. (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters, 14*, 325-334.

Madsen, T.V., Maberly, S.C. & Bowes, G. (1996) Photosynthetic acclimation of submersed angiosperms to CO₂ and HCO₃⁻. *Aquatic Botany, 53*, 15–30.

Marcé, R., Morgui, J.-A., Riera, J.L., Lopez, P. & Armengol, J. (2015) Carbonate weathering as a driver of CO₂ supersaturation in lakes. *Nature Geoscience, 8*, 107-111.
Melo, A.S., Rangerl, T.F.L.V.B. & Diniz-Filho, J.A.F. (2009) Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography, 32*, 226-236.

Naidoo, R., Balmford, A., Costanza, R., Fisher, B, Green, R.E., Lehner, B., Malcolm, T.R. & Ricketts, T.H. (2008) Global mapping of ecosystem services and conservation priorities. *Proceedings of the National Academy of Sciences USA, 105*, 9495-9500.

Qian, H. & Ricklefs, R.E. (2007) A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters, 10*, 737-744.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rørslett, B. (1991) Principal determinants of aquatic macrophyte richness in northern European lakes. *Aquatic Botany, 39*, 173-193.

Rooney, N. & Kalff, J. (2000) Inter-annual variation in submerged macrophyte community biomass and distribution: the influence of temperature and lake morphometry. *Aquatic Botany, 68*, 321–335.

Scheffer, M., van Geest, G.J., Zimmer, K., Jeppesen, E., Søndergaard, M., Butler, M.G., Hanson, M.A., Declerck, S. & De Meester, L. (2006) Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos, 112*, 227-231.

Sculthorpe, C.D. (1967) *The biology of aquatic vascular plants*. Edward and Arnold Publishing, London.

Socolar, J.B., Gilroy, J.J., Kunin, W.E. & Edwards, D.P. (2016) How Should Beta-Diversity Inform Biodiversity Conservation? *Trends in Ecology and Evolution, 31*, 67-80.
Soininen, J., Lennon, J.J. & Hillebrand, J. (2007) A Multivariate analysis of beta diversity across organisms and environment. *Ecology*, **88**, 2830-2838.

Stevens, G.C. (1989) The latitudinal gradients in geographical range: how so many species co-exist in the tropics. *American Naturalist*, **133**, 240-256.

Suren, A.M. & Ormerod, S.J. (1998) Aquatic bryophytes in Himalayan streams: testing a distribution model in a highly heterogeneous environment. *Freshwater Biology*, **40**, 697–716.

Symstad, A.J., Chapin III, F.S., Wall, D.H., Gross, K.L., Huenneke, L.F., Mittelbach, G.G., Peters, D.P. & Tilman, D. (2003) Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *Bioscience*, **53**, 89-98.

Zinger, L., Amaral-Zettler, L.A., Fuhrman, J.A., Horner-Devine, M.C., Huse, S.M., Welch, D.B.M., Martiny, J.B.H., Sogin, M., Boetius, A. & Ramette, A. (2011) Global Patterns of Bacterial Beta-Diversity in Seafloor and Seawater Ecosystems. *PloS ONE*, **6**, e24570.

Vestergaard, O. & Sand-Jensen, K. (2000) Alkalinity and trophic state regulate aquatic plant distribution in Danish lakes. *Aquatic Botany*, **67**, 85-107.

Viana, D.S., Figuerola, J., Schwenk, K., Manca, M., Hobæk, A., Mjelde, M., Preston, C.D., Gornall, R.J., Croft, J.M., King, R.A., Green, A.J. & Santamaria, L. (2015) Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. *Ecography*, **38**, 1-8.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A. Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Reidy Liermann, C. & Davies, P.M. (2010) Global threats to human water security and river biodiversity. *Nature*, **467**, 555-561.
Wang, J.J., Soininen, J., Zhang, Y, Wang, B.X., Yang, X.D. & Shen, J. (2012) Patterns of elevational beta diversity in micro- and macroorganisms. *Global Ecology and Biogeography, 21*, 743-750.

Wen, Z., Yang, Q., Quan, Q., Xia, L., Ge, D. & Lv, X (2016) Multiscale partitioning of small mammal β-diversity provides novel insights into the Quaternary faunal history of Qinghai–Tibetan Plateau and Hengduan Mountains. *Journal of Biogeography, 43*, 1412-1424.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. *Annual Review of Ecology, Evolution, and Systematics, 34*, 273-309.

**APPENDIX 1 – DATA SOURCES**

Crowder, A.A., Bristow, J.M., King, M.R. & Vanderkloet, S. (1977) Distribution, seasonality, and biomass of aquatic macrophytes in Lake Opinicon (Eastern Ontario). *La Naturaliste Canadien, 104*, 441-456.

Hitchin, G.G., I. Wile, G.E. Miller & N.D. Yan. (1984) *Macrophyte data from 46 southern Ontario soft-water lakes of varying pH*. Ontario Ministry of Environment Data Report DR 84/2.
Miller, G. E., & Dale, H. M. (1979) Apparent differences in aquatic macrophyte floras of eight different lakes in Muskoka District, Ontario from 1953 to 1977. *Canadian Field Naturalist, 93*, 386–390.

Neil, J., Graham, J. & Warren, J. (1991) Aquatic Plants of Cook Bay, Lake Simcoe, 1987. *Lake Simcoe Environmental Management Strategy*. Technical report B.4.

Nishihiro, J., Akasaka, M., Ogawa, M. & Takamura, N. (2014) Aquatic vascular plants in Japanese lakes. *Ecological Research, 29*, 369-369.

Ontario Ministry of the Environment and Ministry of Natural Resources (1976) *The Kawartha Lakes Water Management Study - Water Quality Assessment (1972 - 1976)*. Toronto, Ontario.

Schloesser, D.W., Edsall, T.A. & Manny, B.A. (1985) Growth of submerged macrophyte communities in the St. Clair - Detroit river system between Lake Huron and Lake Erie. *Canadian Journal of Botany, 63*, 1061-1065

Wile, I. & Hitchin, G. (1977) An assessment of the practical and environmental implications of mechanical harvesting of aquatic vegetation in Southern Chemung Lake. *Ministry of the Environment and Ministry of Natural Resources*, Toronto, Ontario.

**Supporting Information**

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

Appendix S1 Description of lakes and surveys.

Appendix S2 An example of convex hull.
Appendix S3 Correlation matrix among environmental variables.

Appendix S4. Beta diversity and environmental determinants.

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. $l^{-1}$) | Elevation range (m) | Extent ($km^2$) | Organic 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 |
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 R^2: Maximum likelihood coefficients of determination were obtained through an iterative process.

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

|                  | Multiple site beta diversity |                  | Pair-wise beta diversity |                  |
|------------------|-----------------------------|------------------|--------------------------|------------------|
|                  | Sørensen        | Species turnover | Nestedness | Sørensen | Species turnover | Nestedness |
|                  | I    | D    | I    | D    | I    | D    | I    | D    | I    | D    | I    | D    |
| Elevation        | 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) of freshwater macrophytes and mean altitude, elevation range and latitude. Similar plot for multiple site beta diversity coefficients can be found in Appendix S4.