A comparative analysis of the species richness and taxonomic distinctness of lake macrophytes in four regions: similarities, differences and randomness along environmental gradients

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SUMMARY

1. There has recently been an intensive search for efficient biodiversity measures to quantify conservation value in freshwaters. However, increasing evidence suggests that the performance of different biodiversity measures depends on the studied ecosystem, organisms and geographical location.

2. Our study goal was to compare patterns in species richness and average taxonomic distinctness (AvTD) of aquatic macrophytes along environmental gradients across four study regions (i.e., Finland, Sweden, US state of Minnesota and US state of Wisconsin) situated on two continents. We separately studied all macrophyte species, hydrophytes and helophytes.

3. We used aquatic macrophyte data along with relevant local (i.e., alkalinity, colour, elevation, lake area, maximum lake depth, total phosphorus and number of surveyed transects) and climate (i.e., mean annual temperature) variables surveyed from 50 to 60 lakes using identical methods within each region. Based on linear regression models and Bayesian Information Criterion variable selection method, we correlated species richness and AvTD of lake macrophytes with local environmental and climate variables.

4. Species richness and AvTD of aquatic macrophytes were mostly negatively but not significantly correlated in each region. Both biodiversity measures were correlated with environmental gradients to various degrees among the studied macrophyte groups and regions. Species richness was best explained by alkalinity and lake area in Finland, by elevation, annual mean temperature and total phosphorus in Minnesota, and by alkalinity in Wisconsin. Also, AvTD was best explained by alkalinity, annual mean temperature and total phosphorus in Finland and by alkalinity in Wisconsin. Very weak correlations were found between species richness or AvTD and environmental variables in Sweden.

5. Our study suggested that variation in different biodiversity indices along multiple environmental gradients can be considerable for the same biological group studied in different regions. This finding strongly suggests that a biodiversity measure indicating environmental conditions in one study region may not be applicable in another region, but complementary indices are needed to effectively indicate the impacts of anthropogenic pressures on freshwater biodiversity. Our results further suggested that species richness is a better measure than AvTD to account for conservation value in freshwaters. However, further research is required to evaluate the usefulness of AvTD to indicate conservation value (e.g., randomization tests), because alternative measures are clearly needed for those freshwater taxa lacking complete information on true phylogenetic diversity.

Keywords: Aquatic biodiversity, Aquatic plants, Freshwater biodiversity, Taxonomic diversity

Running head: Biodiversity of lake macrophytes among regions

INTRODUCTION

Freshwater ecosystems harbour much greater levels of biodiversity than terrestrial systems when compared by surface area (Dudgeon et al., 2006) and are the source of numerous ecosystem services vital to human existence (Millennium Ecosystem Assessment, 2005). These ecosystems are also among the most threatened, being exposed to various anthropogenic impacts. The increasing pressures from catchment land use, invasive species, pollution and loss of connectivity have resulted in rapidly declining biodiversity in lakes, rivers and springs (Dudgeon et al., 2006; Vilmi et al., 2017). Climate change will most likely accelerate this negative trend of biodiversity loss in freshwater ecosystems, especially in high-latitude regions (Heino, Virkkala & Toivonen, 2009; Woodward, Perkins & Brown, 2010). This calls for actions, approaches and measures to help conserve threatened freshwater biodiversity across regions (Vilmi et al., 2017). Although the general decline in freshwater biodiversity is well-documented in many studies (Dudgeon et al., 2006; Cardinale et al., 2012), different approaches to measure biodiversity may yield varying information about freshwater biodiversity patterns. Multiple biodiversity indices have been developed to quantify natural characteristics and anthropogenic pressures, but these measure aspects to various degrees (Warwick & Clarke, 1998; Gallardo et al., 2011). Thus, the use of a single index is not typically appropriate in most circumstances. This study provides a complementary approach to better understand patterns and document changes in freshwater biodiversity across different ecosystems and regions.

Species richness is a classical measure of biodiversity across ecosystems and regions (e.g., Gaston, 2000). This index however has many well-known weaknesses related to, for example, sampling effort and habitat type (Warwick & Clarke, 1998; Gotelli & Colwell, 2001). Despite these deficiencies, species richness has proved to be a useful measure to indicate conservation values in freshwaters (Rosset et al., 2013; Hill et al., 2016). An alternative biodiversity measure to complement species richness is taxonomic distinctness, which enables the comparison of variability in the taxonomic relatedness of species in biological communities across different locations, sampling times and sets of samples (Warwick & Clarke, 1995; Vilmi et al., 2016). Thus, taxonomic distinctness can be seen as a proxy for phylogenetic diversity for biological groups, for which information on complete evolutionary phylogenetic relationships is still unavailable (Gallardo et al., 2011; Winter et al., 2013), such as aquatic macrophytes.

Less than two percent of all vascular plants are considered aquatic macrophytes, and only a few groups of angiosperms are fully aquatic, such as Nympheales, Hydrochaharitales, Zosterales, Alismatales and Podostemales (Cook, 1999; Chambers et al., 2008). There are equal numbers of monocots and dicots at the level of superorder for aquatic macrophytes, but relatively more macrophytes are monocots than dicots at the family level (Cook, 1999). However, knowledge on phylogeny is known only for a few aquatic plant lineages, such as Potamogetonaceae (Lindqvist et al., 2006), Hydrocharitaceae (Chen et al., 2013), Alismatales (Ross et al., 2016) and *Sparganium* (Sulman et al., 2013), for which alternative ways to measure macrophyte phylogenetic diversity (e.g., taxonomic distinctness) are currently needed.

One measure of taxonomic distinctness is average taxonomic distinctness (AvTD). AvTD is calculated as the sum of all branch lengths connecting two species averaged across all species, thus representing the mean distance between two randomly chosen species (Warwick & Clarke, 1995; Gallardo et al., 2011). AvTD is not typically affected by species richness, but the absence or extinction of closely-related species will increase the index value (Clarke & Warwick, 1998). AvTD is the most suitable approach when the overall phylogenetic distinctiveness within a community is evaluated (Winter et al., 2013). AvTD was originally developed to indicate anthropogenic pressures in marine environments (Warwick & Clarke, 1995), but it is still uncertain how well the index performs in other ecosystem types. For example, AvTD has not always responded strongly to anthropogenic impacts in freshwater ecosystems (Feld et al., 2016; Vilmi et al., 2016) and, in some cases, natural environmental variation may have masked the influence of anthropogenic impacts on AvTD (Heino et al., 2007; Bevilacqua et al., 2011). Moreover, AvTD and species richness explain different facets of biodiversity, and the patterns described by these two indices often differ when multiple environmental gradients and different biological groups are studied (Marzin et al., 2012; Heino et al., 2015a; Vilmi et al., 2016).

Not only is the indication capability of different biodiversity measures conditional on the investigated environmental gradient and biotic group, but it also often depends on the region studied. Diversity of the same biological group can show completely different patterns in relation to equivalent ecological gradients between any two regions (Heino et al., 2012; Alahuhta & Heino, 2013; Tonkin et al., 2016; Alahuhta et al., 2017). For example, macrophyte species richness followed a classical latitudinal gradient in Fennoscandian lakes (Alahuhta et al., 2013), whereas a reversed latitudinal gradient was observed for macrophyte species richness in the Midwestern USA (Alahuhta, 2015). This kind of contrasting diversity patterns can occur because of, for example, different historic legacies, spatial scales, regional species pools, local environmental conditions, biotic relationships and spatial processes (Jackson, Peres-Neto & Olden, 2001; Heino et al., 2015b; Alahuhta & Heino, 2013; Alahuhta et al., 2016). In addition to these deterministic and stochastic factors, the use of various statistical methods to investigate freshwater biodiversity patterns and increasing statistical complexity in ecology makes it challenging to compare results originating from different studies (Liebhold & Gurevitch, 2002). For example, the increasing use of adjusted R^2 values have resulted in decreased overall explained variations across different ecosystems (Low-

Decarie, Chivers & Granados, 2014). To overcome some of these difficulties in investigating freshwater biodiversity patterns, multiple regions should be investigated simultaneously using the same study approach and identical statistical methods to maintain reliable comparability among the study results (Heino et al., 2015b; Tonkin et al., 2016; Alahuhta et al., 2017a).

Our aim was to compare patterns in species richness and AvTD of aquatic macrophytes along environmental gradients across four study regions (i.e., Finland, Sweden, US state of Minnesota and US state of Wisconsin) situated in two continents. Our specific study questions were: 1) How well do environmental gradients explain patterns in species richness and AvTD of aquatic macrophytes? 2) Do species richness and AvTD of different functional plant groups (i.e., all taxa, hydrophytes and helophytes) respond differently to the underlying environmental gradients? 3) Are differences apparent in these patterns among the four geographical regions? 4) Does variation in the AvTD index values of aquatic macrophytes differ from that of expected by chance?

MATERIAL AND METHODS

Study regions and macrophyte surveys

We studied lakes situated in four different regions: Fennoscandia including Finland (338 000 km^2) and Sweden (450 000 km^2), and the Midwestern USA states of Minnesota (225 000 km^2, hereafter Minnesota) and Wisconsin (170 000 km^2, hereafter Wisconsin) (Figure S1 in Supporting Information). These regions are generally characterised by similar climatic conditions, with cold snowy winters and relatively warm summers. Finland and Sweden mostly belong to the boreal region, with coniferous forests dominating their landscapes. Minnesota and Wisconsin are situated in the northern edge of the temperate region, characterised mainly by a mixture of different forest types, prairie and agricultural landscapes. Acidic granite bedrock dominates in Fennoscandia, whereas nutrient-rich rocks are at least as common as acidic ones in the Midwestern USA. Water bodies created by the withdrawal of ice-age glaciers form typical sceneries in all four study areas, with inland surface waters covering 10% of Finland, 9% of Sweden, 8% of Minnesota and 17% of Wisconsin. In all of the study regions, many of the lakes are impacted by land use activities (i.e., agriculture, silviculture and urban development) that are concentrated to the water bodies situated in the southern parts of the study regions. Moreover, Alahuhta et al. (2017b) showed, using almost identical data to our present study, that land use significantly influenced average water quality niche breadths of lake macrophytes in Finland, Sweden and Wisconsin. More detailed information on geographical variation of land use activities within each study region and how human pressures impact the study lakes can be found in Alahuhta et al. (2013), Beck et al. (2010), Naturvårdsverket (2010), Sass et al. (2010) and Stendera & Johnson (2006). The number of studied lakes was 50 in Sweden and Wisconsin and 60 in Finland and Minnesota. The study lakes were randomly selected from a larger database of lakes in Finland and Minnesota (Alahuhta et al., 2013; Alahuhta, 2015) to maintain comparability with the lower numbers of study lakes from Sweden and Wisconsin.

Lake macrophytes were surveyed between 2002 and 2008 in Finland, between 2008 and 2010 in Sweden, between 1992 and 2003 in Minnesota, and between 2003 and 2005 in Wisconsin. Surveys were executed in all the study areas during the growing season (June-September) using similar transect methods. Transects were distributed around the lakes and placed perpendicular to the shoreline, from the upper eulittoral to the outer limit of vegetation (or to the deepest point of the basin if vegetation covered the entire lake). Macrophyte species were identified from the entire transect in Finnish and Minnesota lakes. Wisconsin macrophyte species were recorded within 0.25

m^2 squares placed every 2-3 m along a transect, and Swedish aquatic plants were identified along transects in 20-cm depth intervals and in plots of ca. 25 × 50 cm. Transect widths were 6-m in Finland, 0.5-m in Sweden and Wisconsin and 5-m in Minnesota. Number of transects in a lake depended on lake surface area and securing proper view of species composition (Kanninen et al., 2013, Table 1). Macrophytes were surveyed or observed by wading, diving, snorkelling or by boat, using rakes and hydroscopes. Recorded macrophytes included not only hydrophytes but also helophytes (i.e., emergent species and shore plants). Macrophyte survey methods are described in detail for Finland in Alahuhta et al. (2013), for Sweden in Naturvårdsverket (2010), for Minnesota in Alahuhta (2015), and for Wisconsin in Sass et al. (2010). We want to emphasise that the survey methods were identical within each area, enabling us to compare 'general patterns' across the regions (see e.g. Heino et al., 2015d; Alahuhta et al., 2017).

Macrophyte variables

We separated macrophyte species, in addition to all taxa, to hydrophytes and helophytes based on their life form (Akasaka & Takamura, 2011; Alahuhta et al., 2014), and thus used three macrophyte variables in all analyses. Hydrophytes and helophytes differ in their accessibility to carbon and nutrient storages, and indication of water quality and hydro-morphological changes (Toivonen & Huttunen, 1995; Akasaka & Takamura, 2011; Alahuhta et al., 2014; Kolada, 2015). Two different biodiversity indices were calculated for all taxa, hydrophyte and helophyte of macrophytes in this study: species richness and taxonomic distinctness. Species richness is the most common indicator of biodiversity (Gaston, 2000), whereas taxonomic distinctness was used as a proxy for phylogenetic diversity (Clarke & Warwick, 1998). When computing taxonomic distinctness, we first organised the taxonomic data in the following taxonomic levels: species, genus, family, order, class, subdivision and division levels. In the taxonomic levels, distinctness weight is one for different species within the same genera, whereas a two is given to species within the same family but different genera, and so on (see Fig. 1 in Clarke and Warwick, 1998). We then calculated AvTD which is based on presence/absence data. AvTD is the average taxonomic path length between any two randomly chosen species from a community (Clarke & Warwick, 1998): (AvTD= $[\sum \sum_{i<j} \omega ij]/[S(S-1)/2]$), where ωij is the distinctness weight given to the path length linking species i and j in the taxonomical hierarchical classification and S is the number of species in a lake. We used only the measure of AvTD to indicate phylogenetic diversity patterns, because we were interested in average change instead of variation in phylogenetic diversity. The challenge with AvTD is that the richness of taxa needs to be high enough for the calculation of reliable index values (e.g. more than two species in a community). In our data sets, macrophyte richness was very low (i.e., 0, 1 or 2 species) in some lakes of Sweden, Minnesota and Wisconsin. AvTD values could only be formed if the observed richness was two, resulting in variable numbers of studied lakes among all taxa, hydrophytes and helophytes in the four study regions (Table 2). In these cases, species richness was calculated using identical number of lakes to that of the AvTD. AvTD index values for all macrophyte groupings were calculated in R using the “vegan” package (Oksanen et al., 2016).

Explanatory variables

Explanatory variables were alkalinity concentration (mg l^{-1}), elevation (m.a.s.l.), mean annual air temperature (°C), water colour (mg Pt l^{-1}), lake area (km^2), maximum lake depth (m), number of studied transects in a lake, and total phosphorus concentration (mg l^{-1}). The explanatory data comprised of well-known environmental characteristics influencing lake macrophytes (Rørslett, 1991; Toivonen & Huttunen, 1995; Jeppesen et al, 2000; Jones et al, 2003; Vestergaard & Sand-

Jensen, 2006; Sass et al., 2010; Akasaka & Takamura, 2011; Alahuhta, 2015), and the water chemistry variables we used have been evidenced to correlate with those variables absent from our study (e.g., pH, conductivity, Secchi depth, total nitrogen and chemical oxygen demand; Wetzel, 2001). Air temperature also has a clear relationship with water temperature in boreal and temperate lakes (Pillgrim et al., 1998; Alahuhta, 2015). Sampling effort can significantly affect species richness (Gotelli & Colwell, 2001), for which the number of studied transects in a lake represented sampling effort. The level of multicollinearity among the explanatory variables was based on bivariate Spearman rank correlation of $|>0.7|$, following Dormann et al. (2013), and the more significant explanatory variable explaining species richness or AvTD was used in the analysis. For this reason, elevation, which correlated with both mean annual temperature and alkalinity ($R_s = -0.71$ to -0.72, $p<0.001$), was removed from the Finnish models. In Sweden, mean annual temperature and elevation were strongly related for hydrophytes and helophytes ($R_s = -0.72$ to -0.73, $p<0.001$), and only the latter explanatory variable was included in the models of these two plant groups. In Wisconsin, mean annual temperature correlated with alkalinity ($R_s=0.73$, $p<0.001$), for which mean annual temperature was excluded from the models. In addition, one outlier lake was removed from Wisconsin data sets. We were also interested to examine whether the relationships between macrophytes and the studied environmental gradients (excluding the number of studied transects) were unimodal (e.g., Jeppesen et al., 2000; Murphy, 2002) by adding second order terms of the predictor variables in all the models.

Water chemistry was based on a single water sample, sampled simultaneously with the macrophytes in Sweden and Wisconsin. In Finland, water chemistry consisted of median values of 1-m surface water samples taken during the growing season (June–September) over the period from 2000 to 2008. Water chemistry of Minnesota lakes was based on the average value of multiple samples taken in 2004 that correlated strongly ($r_{Spearman} > 0.8$) with the long-term water chemistry averages

(Alahuhta, 2015). Elevation was obtained from region-specific GIS data bases with the highest resolution (c. 25m). The mean annual temperature was derived from the WorldClim database for lake surface area with the resolution c. 1 km^2 (Hijmans et al., 2005) and was processed using ArcGIS 10 (ESRI, Redlands, CA, USA).

Statistical analysis

First, we correlated species richness and AvTD to evaluate their relationship among macrophyte functional groups and regions. Second, we used linear regression to investigate the relationship between species richness or taxonomic distinctness and environmental gradients in each of the four study regions. If the response variables were not normally distributed, we transformed them using log transformations prior to further analysis. All the predictors were also log-transformed prior analysis to improve their normality and to harmonize their ranges among the regions. The models with the most important explanatory variables influencing species richness and taxonomic distinctness were selected based on the parameter-strict Bayesian Information Criterion (BIC) among all model combinations. BIC takes into account sample size by increasing the relative penalty for model complexity with small data sets (Burnham & Anderson, 2002). In addition, we calculated BIC differences, which can be used to rank different models in order of importance (BIC_i – BIC_{min}, with BIC_{min} representing the best model with respect to expected Kullback-Leibler information lost). Weights derived from BIC differences were estimated for each model to extract additional information on model ranking. The relative importance of explanatory variables was evaluated by summing the weights of the models that a given variable appears in the exhaustive list of models. We also produced adjusted R^2 values, which provide unbiased estimates of the explained variation (Borcard et al., 2011). A value of <2.0 was used as the threshold for deviation of BIC values among candidate models (i.e., difference between model i and the model with the smallest

BIC, ΔBIC), because models with BIC differing by < 2.0 are typically considered to have similar statistical support (Burnham & Anderson, 2002).

Spatial autocorrelation occurring in statistical models may violate the independence assumption of residuals, for which residuals may bias parameter estimates and can increase type I error rates (Dormann et al., 2007). To evaluate the spatial autocorrelation in our models, we calculated Moran's coefficients based on lake coordinates and using 10 distance classes for response variables (all taxa, hydrophytes and helophytes) and residuals of best linear regression models including most significant explanatory variables in each study region separately.

To complement linear regression models focussing on environmental gradients across all lakes, we tested for the null hypothesis that AvTD of a lake is not different from that expected by chance (Clarke and Warwick, 1998; Heino, Alahuhta & Fattorini, 2015c). This was done by comparing the observed AvTD value with those from 1000 randomizations of the data in the each region. The randomizations selected the same number of species from the overall species list at random as was observed at a lake (for different functional macrophyte groups in a region analysed separately), calculated expected AvTD based on the randomizations, and finally compared the observed AvTD with a distribution of 1000 randomized index values. If AvTD value of a lake is within the 95% confidence limits in a funnel plot, it does not differ from chance and is thus as diverse as could be expected based on lake's environmental gradients (Clarke and Warwick, 1998). On the contrary, a lake is taxonomically less or more diverse than expected by random draws if lake's values locate below or above the confidence limits in a funnel plot, respectively.

All statistical analyses were conducted in R version 3.3.1 (R Core Team, 2016). Candidate models were selected with the R package "MuMIn" (Bartoń, 2016), randomization tests and funnel plots were done using "vegan" package (Oksanen et al., 2016), and spatial autocorrelation was evaluated using "pgirmess" package (Giraudoux, 2016).

RESULTS

All macrophyte functional groups were studied in equal number of lakes in Finland and Sweden (Table 2). However, the numbers of studied lakes were lower for helophytes compared to other macrophyte groups in Minnesota and Wisconsin due to a very low number of species in some lakes, which prevented reliable AvTD calculations in these lakes. Bivariate correlation matrix revealed that the relationships between species richness and AvTD were negative but relatively weak in Finland, Sweden and Minnesota, whereas no such pattern was detected in Wisconsin (Table 3). In our study regions, lakes with a high number of species and low taxonomic distinctness were typically dominated by about 10 genera belonging to the taxonomic orders Poales and Alismatales across the regions. The taxonomic order Lamiales also included many genera across the regions. The taxonomic order Poales is dominated by helophytes, whereas hydrophyte species are mostly present in Alismatales and Lamiales. Lakes in Fennoscandia also included the taxonomic classes Lycopodiopsida and Polypodiopsida, both of which were missing from lakes in Minnesota and the latter class was absent in Wisconsin.

Species richness in each study region

For all macrophyte species richness, average number of species varied from 12.2 in Sweden to 27.2 Finland (Table 2). The lowest number of hydrophyte species was found in Sweden (mean = 6.1), whereas most hydrophyte species per lake were recorded in Wisconsin (mean = 15.4). On average, the helophyte species richness was lowest with 4.9 species in both states of the Midwestern USA and the highest with 15.5 species in Finland.

Linear regression models explained the highest amount of variation of the species richness of all taxa (55% and 53-58%, respectively) and helophytes (69-70% and 69-70%, respectively) in Finland and Minnesota (Table 4). Hydrophyte species richness was also rather well explained in Minnesota and Wisconsin (36-44% and 30-37%, respectively). The models explained variation in the species richness of all macrophyte groups variably in Sweden (8-17%) and Wisconsin (30-45%).

For all macrophyte taxa, species richness was best explained by alkalinity and area in Finland; elevation in Sweden; elevation, mean annual temperature and total phosphorus in Minnesota; and alkalinity and elevation in Wisconsin (Figure 1, Table 4, Table 5). The species richness of hydrophytes was most strongly influenced by alkalinity, area, mean annual temperature, total phosphorus and the number of transects in Finland; elevation, area and the number of transects in Sweden; maximum depth, mean annual temperature and total phosphorus in Minnesota; and alkalinity, elevation and mean annual temperature in Wisconsin. For helophytes, alkalinity, mean annual temperature and area had the highest effect on species richness in Finland; elevation and maximum depth in Sweden; alkalinity, area, elevation, mean annual temperature and total phosphorus in Minnesota; and colour, maximum depth, mean annual temperature and the number of transects in Wisconsin.

Macrophyte species richness showed significant spatial autocorrelation in some of the study regions (n=6) but not in others (n=6). In general, model residuals indicated either a lower degree and/or no significant spatial autocorrelation compared to the original response variables (Table S1-S3).

Average taxonomic distinctness in each study region

AvTD for all taxa varied on average between 49.1 in Wisconsin to 62.9 in Sweden, whereas the values varied on average from 42.8 in Minnesota to 61.0 in Sweden for hydrophytes (Table 2). For helophytes, the lowest AvTD was found in Wisconsin (mean = 47.1) and the highest value in Sweden (mean = 63.0).

Based on the linear regression models (Table 4), variation in AvTD was best explained for all macrophyte taxa in Finland (62-63%) and Wisconsin (17-23%), for Finnish and Wisconsin hydrophytes (47-48% and 36%, respectively), and for helophytes in Finland (26-31%) and Minnesota 26-28%). For other macrophyte groups in Sweden, Minnesota and Wisconsin, the models explained a modest amount of variation in AvTD.

The AvTD of all taxa was best explained by alkalinity, mean annual temperature and total phosphorus in Finland; alkalinity, elevation, maximum depth and the number of transects in Sweden; area, colour, mean annual temperature and the number of transects in Minnesota; and alkalinity in Wisconsin (Figure 2, Table 4, Table 5). For hydrophytes, AvTD was most strongly correlated with alkalinity and total phosphorus in Finland; the number of transects in Sweden, elevation and mean annual temperature in Minnesota; and alkalinity in Wisconsin. AvTD of helophytes was most strongly correlated to alkalinity, area and mean annual temperature in Finland;

alkalinity, colour, elevation, maximum depth and total phosphorus in Sweden; mean annual temperature and total phosphorus in Minnesota; and alkalinity and total phosphorus in Wisconsin.

Funnel plots for all macrophyte taxa indicated that some of the lakes in Finland and Sweden were more diverse than expected by chance, whereas less diverse lakes than expected by chance were found in both Minnesota and Wisconsin (Figure 3). A similar pattern was detected for the hydrophytes of Minnesota and Wisconsin, whereas both more and less diverse lakes were present for the data of Finnish hydrophytes (Figure 4). In Sweden, a few lakes were less diverse than expected by chance for hydrophytes. Considering helophytes, all Finnish and Swedish lakes were as diverse as could be expected by chance, whereas some lakes were less diverse than expected by chance in both Minnesota (nine lakes) and Wisconsin (14 lakes) (Figure 5).

AvTD showed spatial autocorrelation in nine original response variables out of the 12 variables, but coefficients were relatively low for most original variables (Table S1-S3). For model residuals, significant spatial autocorrelation was present in five models out of the 12 models.

DISCUSSION

In the present work, we studied patterns in the species richness and taxonomic distinctness of aquatic macrophytes (i.e., all taxa, hydrophytes and helophytes) along a wide range of environmental gradients in four study regions (i.e., Finland, Sweden, Minnesota and Wisconsin). We found that biodiversity patterns varied among the macrophyte groups and the geographic regions, as species richness and AvTD were explained by different environment gradients among the study regions. Our findings suggest that freshwater biodiversity patterns can clearly differ even in geographically closely-situated areas due to strong local environmental filtering within different regional species pools (Heino et al., 2005; Ruhi et al., 2014). However, we also found some consistent patterns, as increase in species richness was mostly associated with closely-related congeneric macrophyte species across the study regions. In addition, some of the lakes of Fennoscandia were phylogenetically more diverse than expected by chance, whereas some of the lakes of the Midwestern USA were phylogenetically poorer than expected by random draws from the regional species pool. Our results also suggested that taxonomic distinctness does not always respond strongly to lake environmental conditions, which has similarly been evidenced for other freshwater organism groups (Heino et al., 2005; Abellan et al., 2006; Bhat & Magurran, 2006; Feld et al., 2016; Vilmi et al., 2016).

Relationship between AvTD and species richness

Two different conclusions can be drawn from the relationship between species richness and AvTD, depending on the direction the correlation (Warwick & Clarke, 1998; Heino et al., 2005). In the case of a positive relation, an increase in species richness is attributable to species from highly variable taxonomic levels (from taxonomic division to species). When the relationship is negative, increase in species richness is mostly associated with closely-related (e.g., congeneric) species. The correlation between species richness and AvTD of all macrophytes was largely negative across the study regions, suggesting that congeneric macrophyte species, being ecologically quite similar, are either adapted to slightly different niches or avoid direct competition in heterogeneous environmental conditions (Leibold 1998; Chase & Leibold, 2003) within lakes. Although this pattern was relatively weak and often non-significant in most of the regions, the trend was consistently negative between species richness and AvTD of macrophytes among the regions.

We also found some constant patterns between species richness and AvTD for hydrophytes and helophytes between the continents. The relationships between species richness and AvTD were mostly negative for both plant groups in Finland and Sweden, but varied from negative for hydrophytes to positive for helophytes in Minnesota and Wisconsin. Such a clear difference in helophytes between the continents suggested that increase in species richness results mainly from congeneric species in Finland and Sweden, whereas an increase in species richness is associated with species from highly differing taxonomic levels in Minnesota and Wisconsin (see also Warwick & Clarke, 1998; Heino et al., 2005). This difference may result from the variable number of recorded species between the continents, as the number of helophyte species was relatively much lower in Minnesota and Wisconsin compared to that in Finland and Sweden. In addition, the number of taxonomic levels (from subdivision to order) was higher in Fennoscandia than in the Midwestern USA. Thus, a new recorded helophyte species is not likely to be closely-related with already identified species in the lakes of Minnesota and Wisconsin. The situation is opposite in Finland and Sweden, where an added species maybe be a close relative of some of the recorded species.

Variation in AvTD along environmental gradients

AvTD did not describe variation in the studied environmental gradients very well, as these models accounted for a reasonable amount of variation only for Finnish macrophytes and Wisconsin hydrophytes. This relatively low amount of explained variation of AvTD for many of the plant groups across the study regions may result from the fact that the index is based on presence/absence data and assumes a reduction in taxonomic breadth when the degree of anthropogenic impacts increases (Warwick & Clarke, 1998; Heino et al., 2005). However, aquatic macrophytes may respond more strongly to alterations in environmental conditions through changes in relative abundance rather than through changes in assemblage composition (Egertson et al., 2004). Therefore, AvTD may have failed in indicating anthropogenic impacts if they mainly act by influencing the evenness component of assemblage diversity (Bevilacqua et al., 2011). In addition, the reasoning behind the use of AvTD is that species disappearing first from degraded lakes are those that belong to species-poor higher taxa, whereas those that remain belong to more species-rich higher taxa (Clarke & Warwick, 2001; Heino et al., 2007). In our study regions, higher taxonomic levels, from order to subdivision, had more taxa in Fennoscandia than in the Midwestern USA, but these differences were more balanced at the family and genus levels, eventually resulting in highest species numbers in Finland and Wisconsin. This finding suggests, contrary to the original idea of Clarke & Warwick (2001), that higher variability in lower taxonomic levels (e.g., genus) lead to better performance of macrophyte AvTD. Although AvTD implicitly assumes that taxonomically closely-related species involve a general functional homogeneity of species within high taxonomic levels (Warwick & Clarke, 1998; Bevilacqua et al., 2011), functional responses of macrophyte species vary strongly within the same genus, like the species-rich genus *Potamogeton* (Vestergaard & Sand-Jensen, 2006; Beck & Alahuhta, 2016).

In the best AvTD models in Finland and Wisconsin, the index values increased with decreasing alkalinity for all the three plant groups. The influence of alkalinity on macrophyte species originates from their variable ability to use bicarbonate or carbon dioxide as a source of carbon in photosynthesis (Madsen et al., 1996), the result of which has been found important for macrophytes in different regions (Rørslett, 1991; Murphy, 2002; Vestergaard & Sand-Jensen, 2006; Sass et al., 2010). In addition, AvTD of Finnish macrophytes decreased with increasing total phosphorus (i.e., a proxy for anthropogenic nutrient enrichment), which is in agreement with the finding of Warwick & Clarke (1998). However, a similar pattern was not discovered for the other regions, where AvTD of different macrophyte groups responded to a wide range of environmental gradients. Heino et al. (2007), similarly to our work, used both natural characteristics and anthropogenic pressures in explaining biodiversity indices in streams and suggested that natural characteristics may mask the influence of anthropogenic pressures on taxonomic distinctness. This may also be true in our study based on the poor correlation between macrophyte AvTD and total phosphorus in most regions. However, taxonomic distinctness should be unaffected by natural environmental gradients or sampling effort (Warwick & Clarke, 1998), which brings into question the usability of this index to portray changes in biodiversity along complex environmental gradients.

Randomization tests evaluating the null hypothesis that the AvTD of a lake is not different from that expected by random draws (Clarke & Warwick, 1998; Warwick & Clarke, 1998) revealed clear differences between the continents. The lakes of Finland and Sweden were sometimes more diverse than expected by chance, whereas lower than expected values were often observed for lakes of Minnesota and Wisconsin. This pattern suggested that some of the lakes in Fennoscandia are phylogenetically more diverse than expected by chance, whereas some of the lakes in the Midwestern USA are phylogenetically poorer than expected by random draws from the regional species pool. As all the study lakes have a similar historical development related to glacial origins (Sawada, Viau & Gajewski, 2003; Alahuhta et al., 2016) and macrophytes are rarely dispersal-limited in these types of permanent lentic systems at regional spatial scales (Mikulyuk et al., 2011; Viana et al., 2014; Alahuhta et al., 2015), we considered that the opposite patterns between continents have emerged from differences in current environmental conditions among the study regions. For example, differences in alkalinity, mean annual temperature and colour were evident among the lakes of two continents. In addition, land use is known to strongly suppress freshwater biodiversity in the southern catchments of Minnesota and Wisconsin (Sass et al., 2010; Mikulyuk et al., 2011; Alahuhta, 2015). Our linear models did not support this reasoning, though. One must bear in mind, however, that the linear models focus on across-lakes diversity patterns, whereas the randomization test is based on AvTD of a single lake at a time. This explains different reasoning resulting from the different statistical methods, and the results of randomization test, in fact, offer complementary information to that of modelling on the diversity patterns of aquatic macrophytes.

Macrophyte species richness in relation to environmental gradients

Total explained variation of species richness was clearly higher compared to that of AvTD for different macrophyte groups in Finland, Minnesota and Wisconsin. The only exception was Finnish hydrophytes, where the predictor variables accounted for only 8-31% of variation in species richness. More variation was explained in helophyte species richness than in hydrophyte species richness. This was likely due to different growth forms with variable responses to environmental gradients among hydrophytes in our study. Better performing models of hydrophyte species richness would probably be gained if these different growth forms were studied separately (Akasaka & Takamura, 2011; Alahuhta et al., 2014). However, separation of different growth forms would have resulted in much lower species richness across different hydrophyte growth forms, preventing the ability to calculate AvTD for those growth forms having less than two species per lake. In addition, Vilmi et al. (2016) suggested that species richness may be a better indicator than AvTD for aquatic macrophyte biodiversity, because macrophyte communities are not always very rich in species in the northern lakes. Our findings support this reasoning, because the performance of AvTD could be evaluated for all the study lakes only in Finland.

In general, macrophyte species richness responded to various environmental gradients in most study regions. This was expected, as macrophyte species richness has been known to respond positively to increasing lake area, light availability and depth, and negatively to increased nutrient concentrations (Rørslett, 1991; Lougheed, Crosbie & Chow-Fraser, 2001; Vestergaard & Sand-Jensen, 2006; Akasaka & Takamura, 2011; Alahuhta et al., 2013; Viana et al., 2014; Alahuhta, 2015). Our results largely supported these patterns found in previous studies, as species richness of different macrophyte groups responded positively (showing a linear or unimodal pattern) to alkalinity in Finland and Wisconsin, to climate (either with mean annual temperature or elevation) in all the study regions, to lake area in Finland and Minnesota and to sampling effort in Finland, Minnesota and Wisconsin. For colour and maximum depth, the results varied among the study regions and macrophyte groups. Surprisingly, macrophyte species richness was not uniformly negatively correlated to total phosphorus across the study regions and plant groups, being even positively related to total phosphorus in Minnesota. Contrary to our finding, Sass et al. (2010) and Alahuhta (2015) evidenced that increased total phosphorus related to land use activities decreased macrophyte species richness in the lakes of the Midwestern USA. However, the relationship between macrophyte species richness and total phosphorus was clearly unimodal in Minnesota, with species richness decreasing sharply when the total phosphorus concentrations increased.

Concluding remarks

Our study suggests that variation in different biodiversity indices along multiple environmental gradients can be substantial even for the same biological group in different regions. This finding strongly suggests that a diversity measure detecting environmental changes in one region may not be applicable in another region, but complementary indices are needed to reliably indicate the impacts of anthropogenic pressures on freshwater biodiversity. Based on our findings, analysing variation in species richness is a more powerful tool than taxonomic distinctness to measure biodiversity for aquatic macrophytes as long as sampling effort is accounted for. Instead, using taxonomic distinctness faces many challenges related to lack of consistent detection of anthropogenic pressures on freshwater biodiversity, indication of anthropogenic pressures in species-poor freshwater ecosystems and when variation in natural characteristics is strong. However, randomization tests based on macrophyte AvTD showed consistent patterns between the continents, suggesting that this approach may be more useful when taxonomic distinctness is used as a proxy for phylogenetic diversity in lake macrophytes. Hence, AvTD and species richness can provide valuable and complementary information on biodiversity patterns for freshwater conservation, although more research is needed to corroborate our findings on aquatic macrophytes inhabiting temperate and boreal regions.

ACKNOWLEDGEMENTS

Sampling of Finnish macrophyte data was a joint contribution of Biological Monitoring of Finnish Freshwaters under diffuse loading -project (XPR3304) financed by Ministry of Agriculture and Forestry and national surveillance monitoring programs of lakes. Swedish macrophyte data were surveyed within the Swedish Monitoring Program of macrophytes in lakes funded by the Swedish Agency for Marine and Water Management. We are grateful for Minnesota and Wisconsin Departments of Natural Resources for collecting the macrophyte data. We especially thank Carol Reschke from the University of Minnesota Duluth for her work in combining and performing quality control for the Minnesota macrophyte data used in the analysis, and the Minnesota DNR staff for collecting the macrophyte data. This study was supported by grants from the Academy of

Finland (267995 and 285040). This is contribution no. 607 of the Natural Resources Research Institute of the University of Minnesota Duluth.

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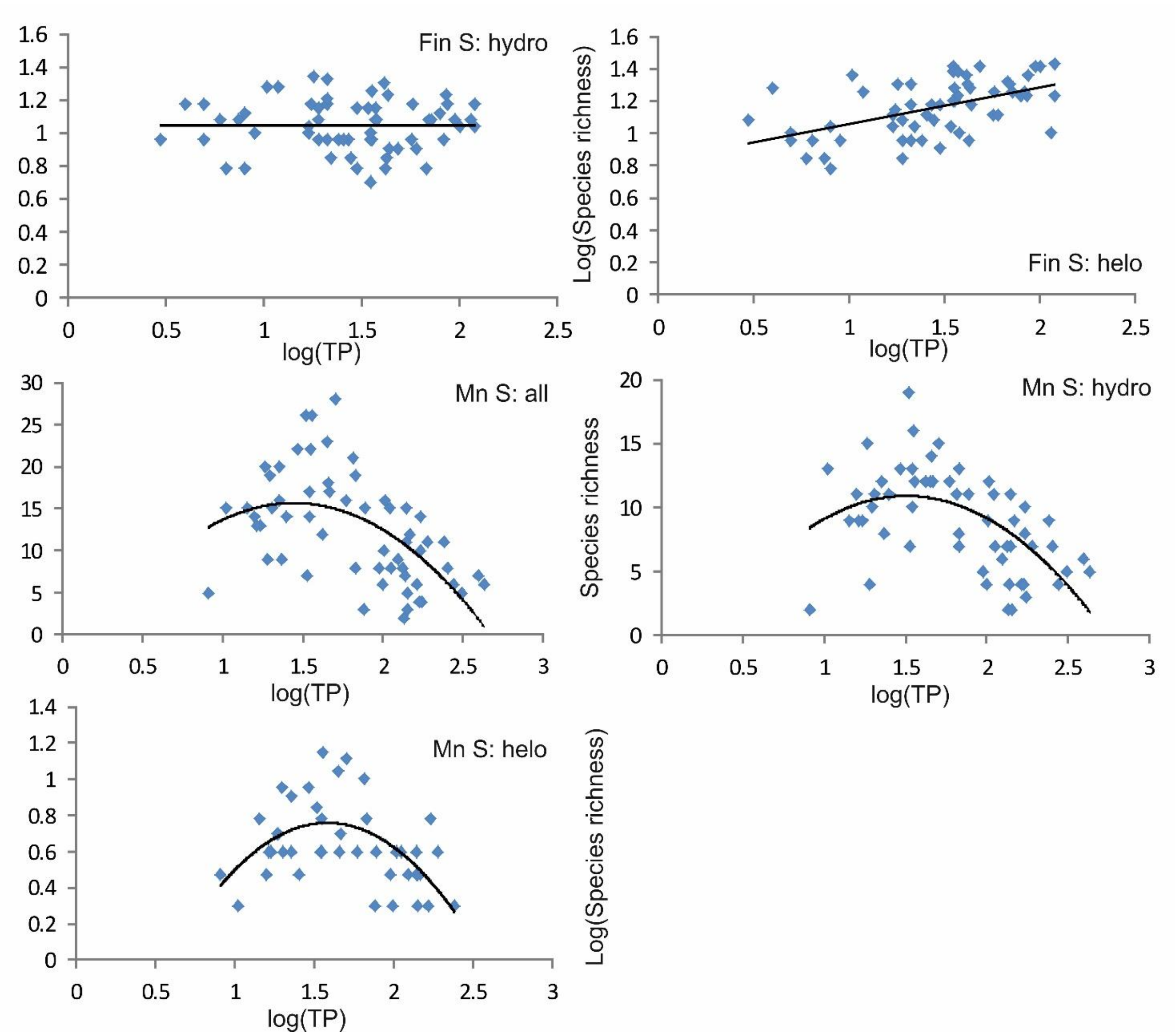

Figure 1. Variation in species richness (S) of macrophyte communities (i.e., all taxa, hydrophytes and helophytes) in relation to total phosphorus concentrations (TP). Only those correlations are shown, which were significant based on linear regression models with Bayesian Information Criteria variable selection method. Fin: Finland, Mn: Minnesota, all: All taxa, hydro: Hydrophytes, helo: Helophytes.

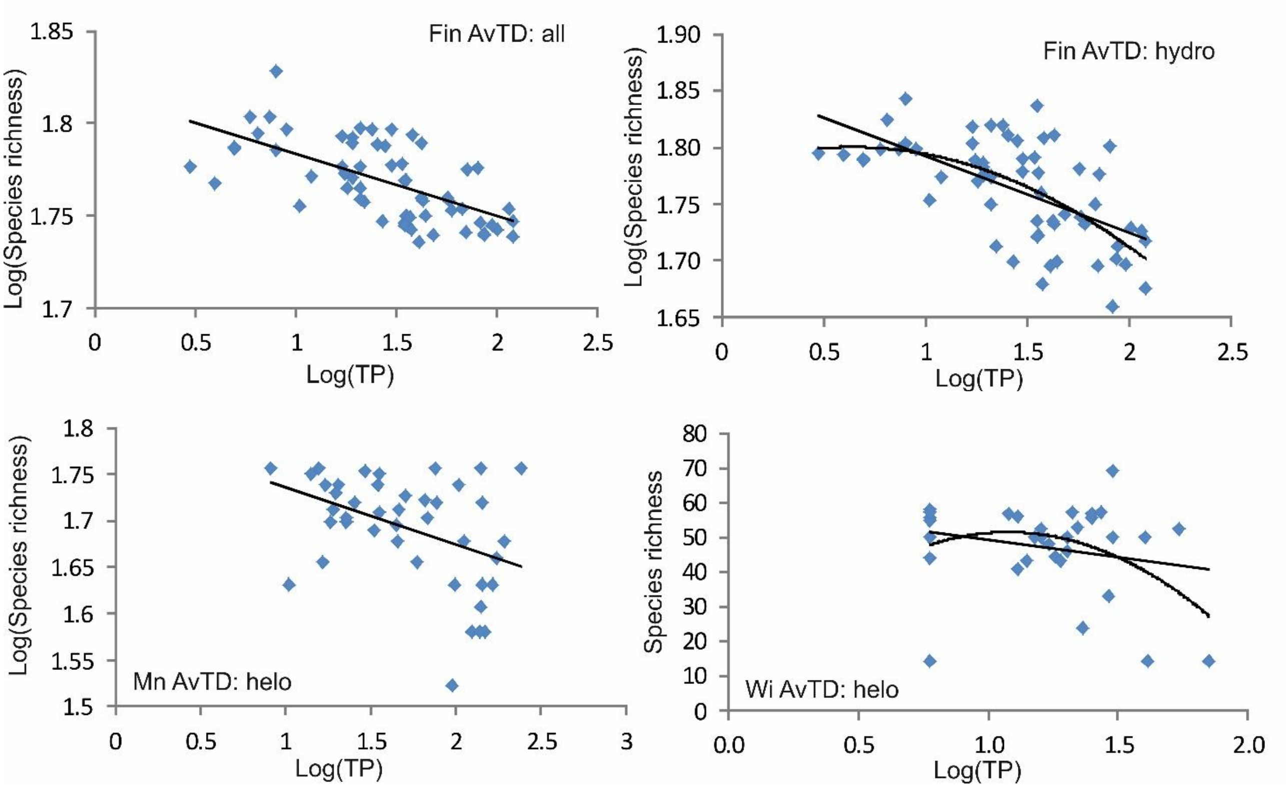

Figure 2. Variation in average taxonomic distinctness (AvTD) of macrophyte communities (i.e., all taxa, hydrophytes and helophytes) in relation to total phosphorus concentrations (TP). Only those correlations are shown, which were significant based on linear regression models with Bayesian Information Criteria variable selection method. Fin: Finland, Mn: Minnesota, Wi: Wisconsin, all: All taxa, hydro: Hydrophytes, helo: Helophytes.

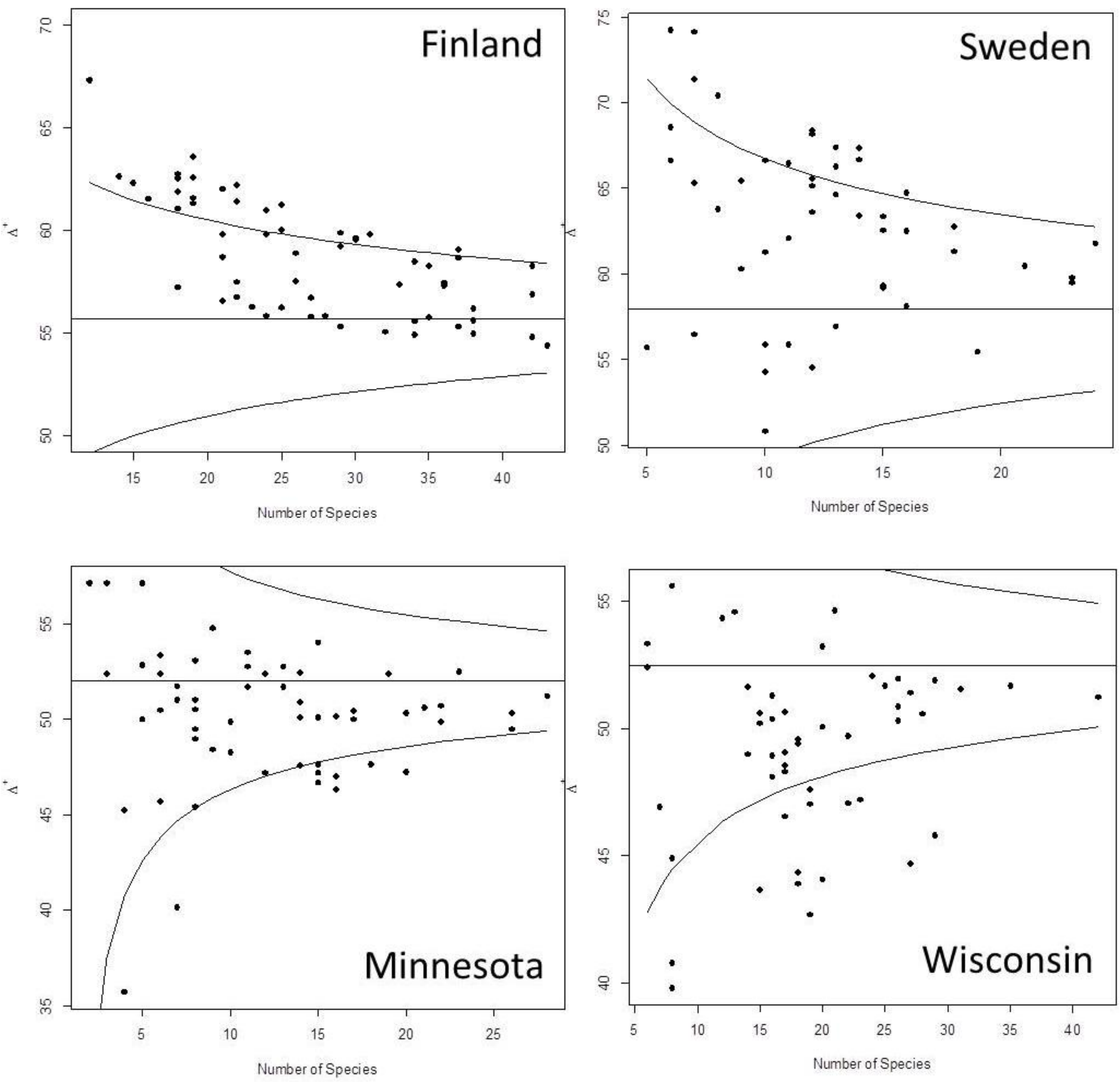

Figure 3. Funnel plots illustrating average taxonomic distinctness ($\wedge^{+}$) in relation to random occurrence in all species pool. The lines indicate mean and 95% confidence intervals from random draws of species from the overall all species list for Finland, Sweden, Minnesota or Wisconsin.

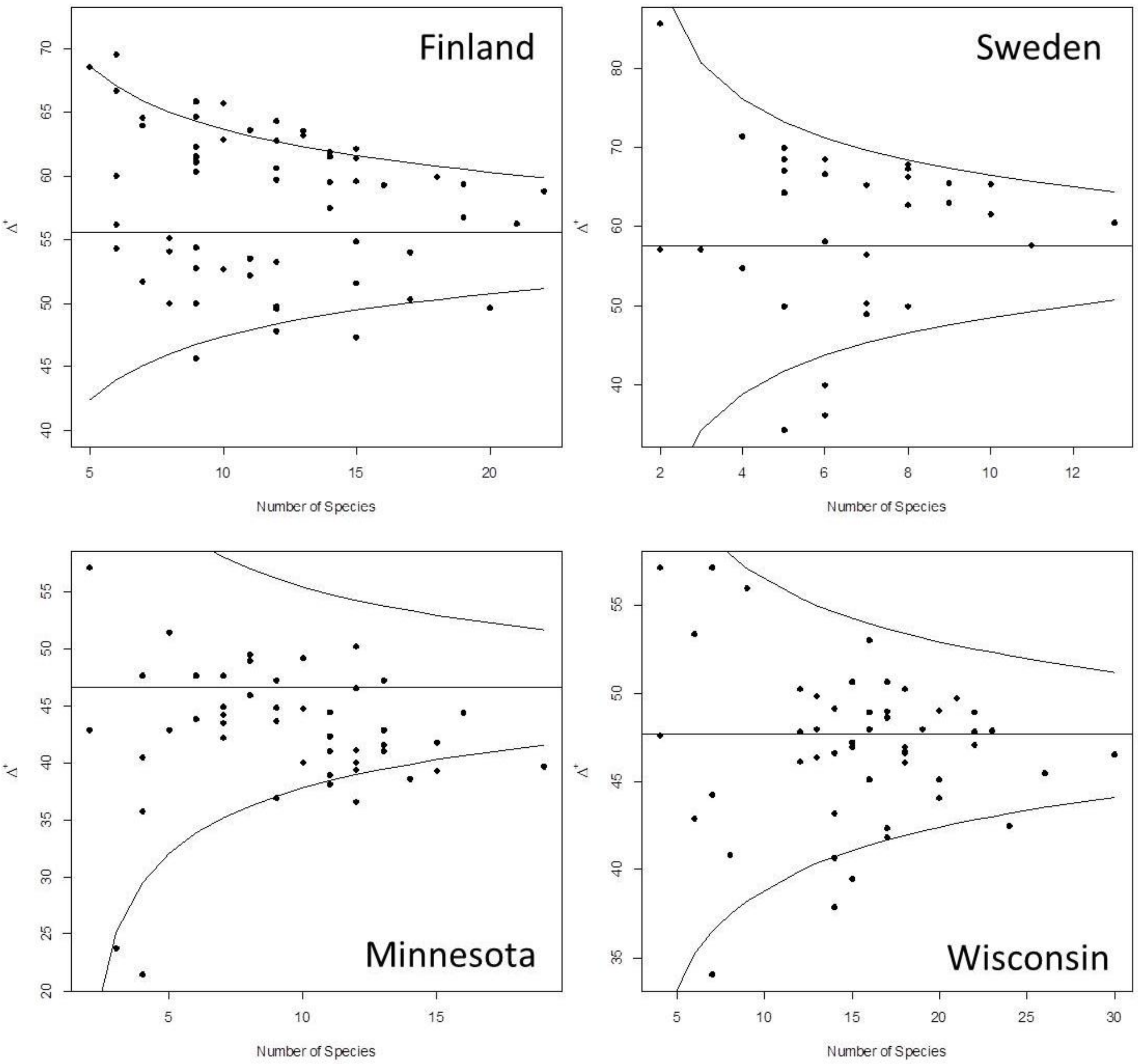

Figure 4. Funnel plots illustrating average taxonomic distinctness ($\wedge^+$) in relation to random occurrence in hydrophyte species pool. The lines indicate mean and 95% confidence intervals from random draws of species from the overall hydrophyte species list for Finland, Sweden, Minnesota or Wisconsin.

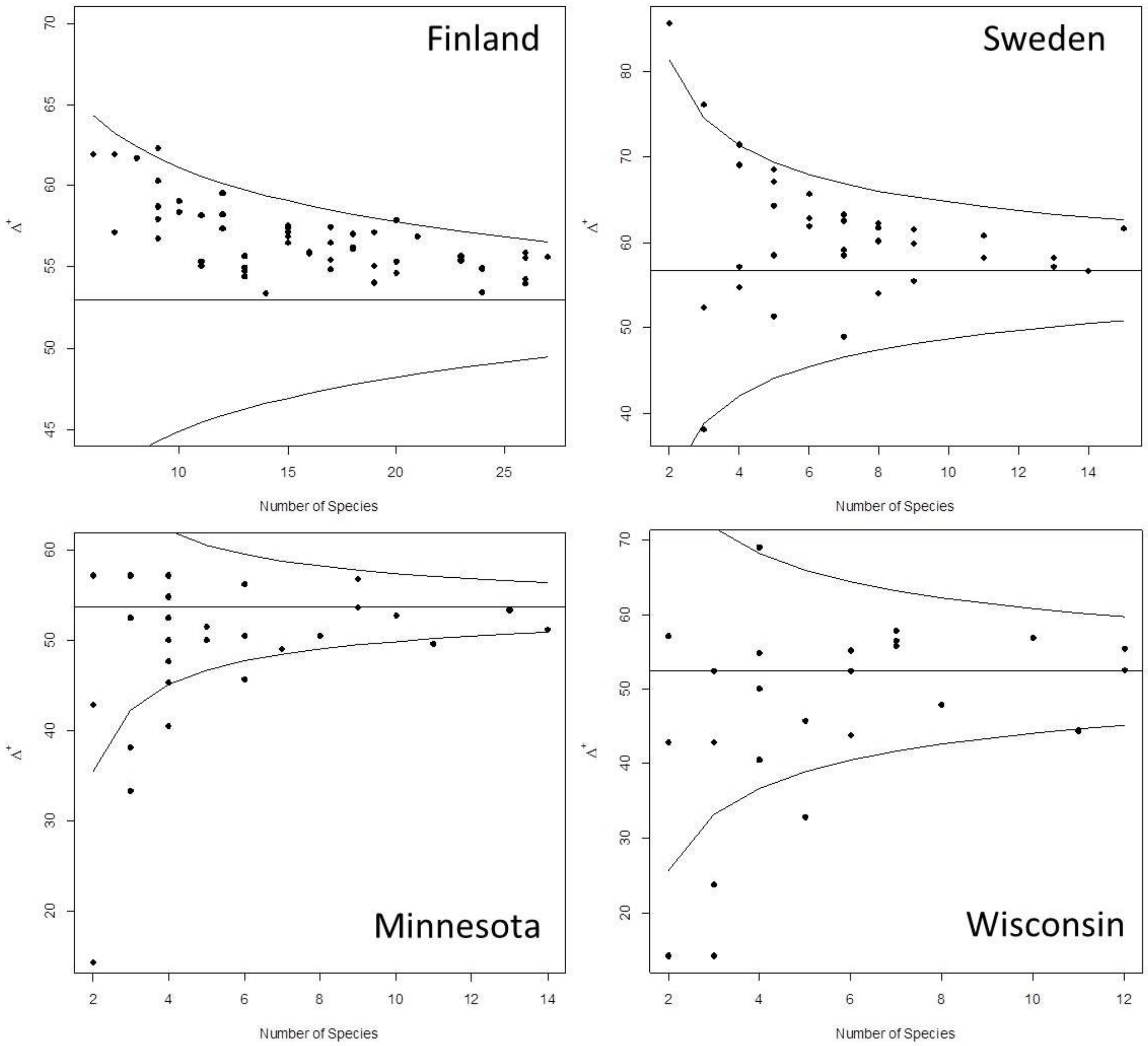

Figure 5. Funnel plots illustrating average taxonomic distinctness (Λ^+) in relation to random occurrence in helophyte species pool. The lines indicate mean and 95% confidence intervals from random draws of species from the overall helophyte species list for Finland, Sweden, Minnesota or Wisconsin.

Table 1. Descriptive statistics of explanatory variables and the number of studied transects in each study area.

	Finland				Sweden				Minnesota				Wisconsin			
	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Alkalinity (mmol l^{-1})	0.22	0.02	0.89	0.18	0.49	0.01	2.83	0.75	1.30	0.05	2.36	0.53	0.85	0.04	2.03	0.63
Annual temperature (°C)	2.77	-0.24	4.83	1.15	3.83	-1.44	7.88	2.84	5.64	2.50	7.27	1.28	5.89	3.85	8.23	1.72
Color (mg Pt l^{-1})	97.40	10.00	325.00	63.70	52.70	2.50	151.50	43.00	20.50	3.50	93.80	16.00	10.41	2.50	30.00	6.60
Elevation (m.a.s.l.)	105.57	31.90	228.90	42.93	204.34	3.00	746.00	178.31	342.85	251.83	529.27	59.98	365.59	239.00	503.00	109.24
Lake area (km^2)	5.80	0.30	38.80	8.20	3.2	0.04	51.70	7.60	3.00	0.20	21.90	3.70	0.55	0.20	1.36	0.29
Max. depth (m)	14.10	2.00	69.70	12.20	13.70	1.10	47.00	10.00	14.10	2.60	44.90	10.20	10.59	3.05	21.64	4.40
Number of transects	14.6	7	26	4.2	9	5	14	1.9	24.6	10	50	10.2	14.4	14	20	1.4
Total phosphorus (µg l^{-1})	38.90	3.00	120.00	30.80	13.80	1.00	64.00	13.80	100.10	8.10	429.80	92.60	21.92	6.00	71.00	21.60

Table 2. Number of studied lakes (n), and mean, minimum, maximum and SD of species richness (S) or average taxonomic distinctness (AvTD) for all taxa, hydrophytes and helophytes in each study region. The number of lakes can vary between different functional macrophyte groups within a region, because average taxonomic distinctness can only be calculated when there are two or more species found in a lake.

		n	S mean	S min.	S max.	S SD	AvTD mean	AvTD min.	AvTD max.	AvTD SD
Finland	All taxa	60	27.2	12	43	8.1	58.8	54.4	67.3	2.9
	Hydrophytes	60	11.8	5	22	4.1	58.2	54.6	69.5	5.9
	Helophytes	59	15.5	6	27	5.8	56.8	53.4	62.3	2.2
Sweden	All taxa	50	12.2	5	24	4.8	62.9	50.8	74.3	5.2
	Hydrophytes	47	6.1	2	13	2.5	61.0	34.3	58.7	9.7
	Helophytes	48	6.7	2	15	3.3	63.0	38.1	85.7	8.9
Minnesota	All taxa	60	12.4	2	28	6.3	50.1	35.7	57.1	3.6
	Hydrophytes	58	9.0	2	19	3.9	42.8	21.4	57.1	5.5
	Helophytes	44	4.9	2	14	2.9	48.9	14.3	57.1	8.1
Wisconsin	All taxa	49	19.3	6	42	7.3	49.1	39.8	55.6	3.6
	Hydrophytes	49	15.7	4	30	5.4	47.0	34.0	57.1	4.5
	Helophytes	33	5.0	2	12	2.8	47.1	14.3	69.1	13.1

Table 3. Bivariate Spearman correlation matrix between species richness and average taxonomic distinctness for different functional plant groups and different regions. ***: $p \leq 0.001$; **: $p \leq 0.01$; *: $p \leq 0.05$.

	All taxa	Hydrophytes	Helophytes
Finland	-0.716***	-0.233	-0.640***
Sweden	-0.253	0.006	-0.521***
Minnesota	-0.143	-0.238	0.232
Wisconsin	0.156	-0.072	0.251

Table 4. Summary of analyses explaining the relationship between species richness (S) or average taxonomic distinctness (AvTD) and explanatory variables based on linear regression using Bayesian Information Criterion (BIC) variable selection method. Models with delta <2 are shown. Separate analyses were done for all taxa of aquatic macrophytes, hydrophytes and helophytes. ^2: Quadratic term of explanatory variable. Abbreviations; Alkal: Alkalinity, Area: Lake surface area, Elev: Elevation, TempA: Average annual temperature, TP: total phosphorus, Depth: Maximum depth, Transects: The number of studied transects in a lake.

All Taxa	**Region**	**Selected variables**	**df**	**BIC**	**Delta**	**Weight**	**adjR2**	**p**
S	Finland	Alkal+Area	4	-4.40	0.00	1.00	0.55	*<0.001*
	Sweden	Elev	3	56.00	0.00	0.24	0.08	*0.026*
		Elev+Depth	4	56.10	0.10	0.23	0.13	*0.015*
		Elev+Area	4	56.50	0.53	0.18	0.12	*0.018*
		Elev+Transects	4	57.40	1.43	0.12	0.11	*0.027*
		Alkal+Elev+Area	5	57.60	1.57	0.11	0.15	*0.014*
	Minnesota	Elev+TempA+TempA^2+TP+TP^2	7	368.10	0.00	0.28	0.53	*<0.001*
		Elev+TempA+TempA^2+TP+TP^2+Transects	9	368.20	0.07	0.27	0.58	*<0.001*
		Elev+Elev^2+TempA+TempA^2+TP+TP^2	8	368.50	0.44	0.22	0.55	*<0.001*
		Elev+Area+TempA+TempA^2+TP+TP^2	9	369.60	1.57	0.13	0.57	*<0.001*
		Elev+TempA+TempA^2+TP+TP^2+Transects	8	369.80	1.76	0.11	0.54	*<0.001*
	Wisconsin	Alkal+Alkal^2	4	328.20	0.00	0.35	0.33	*<0.001*
		Alkal+Alkal^2+Elev	5	328.20	0.07	0.34	0.36	*<0.001*
		Alkal+Alkal^2+TempA	5	329.50	1.34	0.18	0.35	*<0.001*
		Alkal+Alkal^2+Elev+Elev^2	6	330.00	1.81	0.14	0.38	*<0.001*
AvTD	Finland	Alkal+TempA+TP	5	233.00	0.00	0.62	0.62	*<0.001*
		Alkal+TempA+TP+Depth	6	232.10	0.96	0.38	0.63	*<0.001*
	Sweden	Elev	3	315.30	0.00	0.33	0.05	0.070
		Elev+Depth	4	315.80	0.50	0.28	0.09	*0.039*
		Transects	3	316.70	1.40	0.20	0.02	0.158
		Alkal	3	316.90	1.60	0.19	0.02	0.177

	Minnesota	Transects	3	328.20	0.00	0.20	0.09	*0.011*
		Area+Color+TempA	5	329.30	1.07	0.12	0.16	*0.005*
		TempA+Transects	4	329.40	1.11	0.11	0.12	*0.010*
		Color+TempA+Transects	5	329.50	1.27	0.11	0.16	*0.005*
		Depth+TempA+Transects	5	329.60	1.39	0.10	0.16	*0.005*
		Area+Depth+TempA	5	329.70	1.43	0.10	0.16	*0.005*
		Area	3	329.70	1.45	0.10	0.07	*0.025*
		Color+Transects	4	329.70	1.50	0.09	0.11	*0.012*
		Depth+Transects	4	330.20	1.95	0.08	0.11	*0.015*
	Wisconsin	Alkal+Alkal^2	4	264.20	0.00	0.46	0.23	*<0.001*
		Alkal	3	265.20	1.01	0.28	0.17	*0.002*
		Alkal+Elev	4	265.40	1.14	0.26	0.21	*0.002*
Hydrophytes								
S	Finland	Alkal+Area+Area^2+TempA+TempA^2+TP	8	50.80	0.00	0.24	0.29	*<0.001*
		Alkal	3	52.00	1.20	0.13	0.08	*0.019*
		Alkal+Transects	4	52.10	1.32	0.12	0.12	*0.010*
		Alkal+Area+Area^2+TempA+TP	7	52.20	1.44	0.12	0.24	*0.001*
		Alkal+TempA+TP+Transects	6	52.50	1.67	0.10	0.20	*0.003*
		Alkal+Area+Area^2+Transects	6	52.60	1.80	0.10	0.20	*0.003*
		Alkal+TempA+TempA^2+TP+Transects	7	52.60	1.86	0.09	0.24	*0.001*
		Alkal+Area+Area^2+TempA+TempA^2+TP+Transects	9	52.70	1.87	0.09	0.31	*0.000*
	Sweden	Elev+Area	4	225.90	0.00	0.27	0.14	*0.012*
		Elev	3	226.20	0.32	0.23	0.08	*0.027*
		Elev+Transects	4	226.30	0.49	0.22	0.13	*0.016*
		Elev+Area+Area^2	5	227.00	1.17	0.16	0.17	*0.011*
		Elev+Area+Transects	5	227.70	1.82	0.12	0.16	*0.014*
	Minnesota	Depth+TempA+TempA^2+TP+TP^2	7	309.80	0.00	0.48	0.44	*<0.001*
		TempA+TempA^2+TP+TP^2	4	311.00	1.23	0.26	0.39	*<0.001*
		Depth+TempA+TempA^2	5	311.00	1.27	0.26	0.36	*<0.001*
	Wisconsin	Alkal+Alkal^2+Elev	5	298.40	0.00	0.43	0.36	*<0.001*
		Alkal+Alkal^2+TempA	5	299.90	1.53	0.20	0.34	*<0.001*

		Alkal+Alkal^2	4	300.00	1.61	0.19	0.30	*<0.001*
		Alkal+Alkal^2+Elev+TempA	6	300.20	1.86	0.17	0.37	*<0.001*
AvTD	Finland	Alkal+TP	4	358.20	0.00	0.52	0.47	*<0.001*
		Alkal+TP+TP^2	5	359.50	1.35	0.27	0.48	*<0.001*
		Alkal+TempA+TP	5	360.00	1.82	0.21	0.48	*<0.001*
	Sweden	Transects	3	354.30	0.00	1.00	0.04	*0.100*
	Minnesota	Elev+TempA	4	368.20	0.00	0.48	0.12	*0.010*
		TempA+TempA^2	4	369.50	1.28	0.29	0.15	*0.009*
		Elev+Elev^2+TempA	5	370.10	1.85	0.23	0.14	*0.011*
	Wisconsin	Alkal+Alkal^2	4	278.80	0.00	0.72	0.36	*<0.001*
Helophytes								
S	Finland	Alkal+Area+TempA+TP	6	6.30	0.00	0.55	0.70	*<0.001*
		Alkal+Area+Color+TempA	6	6.70	0.38	0.45	0.69	*<0.001*
	Sweden	Elev+Depth	4	77.00	0.00	1.00	0.12	*0.021*
	Minnesota	Alkal+Elev+Elev^2+TempA+TempA^2+TP+TP^2	9	39.80	0.00	0.44	0.69	*<0.001*
		Alkal+Elev+Elev^2+Area+TempA+TempA^2+TP+TP^2	10	40.60	0.84	0.29	0.70	*<0.001*
		Alkal+Elev+Elev^2+Color+TempA+TempA^2+TP+TP^2	10	40.70	0.91	0.28	0.70	*<0.001*
	Wisconsin	Color+Depth+Depth^2+TempA+TempA^2	7	54.70	0.00	0.37	0.38	*0.002*
		Elev+Color+Depth+Depth^2+TempA+TempA^2	8	55.50	0.84	0.24	0.41	*0.002*
		Elev+Color+Depth+Depth^2+TempA+TempA^2+Transects	9	55.60	0.91	0.24	0.45	*0.002*
		Color+Depth+Depth^2+TempA+TempA^2+Transects	8	56.50	1.79	0.15	0.39	*0.003*
AvTD	Finland	Alkal+Area	4	-225.80	0.00	0.70	0.26	*<0.001*
		Alkainity+Area+TempA+TempA^2	6	-224.20	1.69	0.30	0.31	*<0.001*
	Sweden	Alkal	3	-46.70	0.00	0.24	0.09	*0.022*
		Elev+Depth	4	-45.70	1.03	0.15	0.12	*0.019*
		Elev	3	-45.60	1.13	0.14	0.07	*0.040*
		Alkal+Elev+Depth	5	-45.50	1.22	0.14	0.17	*0.011*
		Color+Color^2+TP	5	-45.30	1.38	0.13	0.17	*0.011*
		Color+TP	4	-45.00	1.70	0.11	0.11	*0.027*

	Alkal+Depth	4	-44.70	1.99	0.10	0.11	*0.030*
Minnesota	TempA	3	275.60	0.00	0.68	0.26	*<0.001*
	TempA+TP	4	277.10	1.51	0.32	0.28	*<0.001*
Wisconsin	Alkal	3	271.50	0.00	0.35	0.03	0.159
	TP+TP^2	4	271.80	0.30	0.32	0.09	0.088
	TP	3	271.90	0.40	0.32	0.02	0.194

Table 5. Direction of relationships between species richness (S) or average taxonomic distinctness (AvTD) and explanatory variables in each region. The left side sign refers to S and the right side sign to AvTD (S/AvTD). Note that a predictor can have a linear or unimodal effect on macrophyte variables depending on individual models. L: linear term, Q: quadratic term, ns: variable not selected for a particular biodiversity index, na = parameter was not included among the explanatory variables due to multicollinearity. p values are not given, because they varied among the models.

		Alkalinity	**Mean annual temperature**	**Elevation**	**Colour**	**Lake area**	**Max. depth**	**Number of transects**	**Total phosphorus**
Finland	All taxa	+L/-L	ns/-L	na/na	ns/	+L/	ns/-L	ns/ns	ns/-L
	Hydrophytes	+L/-L	+L-Q (or -L)/-L	na/na	-L/ns	+L-Q/ns	ns/ns	+L/ns	-L/-L (or +L-Q)
	Helophytes	+L/-L	+L/-L+Q	na/na	+L/ns	+L/-L	ns/ns	ns/ns	+L/ns
Sweden	All taxa	+L/+L	ns/ns	+L/-L	ns/ns	-L/ns	-L/+L	-L/+L	ns/ns
	Hydrophytes	ns/ns	na/na	+L/ns	ns/ns	-L (or +L-Q)/ns	ns/ns	-L/+L	ns/ns
	Helophytes	ns/+L	na/na	+L/-L	ns/-L (or –L+Q)	ns/ns	-L/+L	ns/+L	ns/ns
Minnesota	All taxa	ns/ns	+L-Q/-L	-L+Q (or –L/ns	ns/+L	+L/-L	ns/-L	+L/-L	+L-Q/ns
	Hydrophytes	ns/ns	+L-Q/-L (or +L-Q)	ns/-L (or +L-Q)	ns/ns	ns/ns	+L/ns	ns/ns	+L-Q/ns
	Helophytes	-L/ns	+L-Q/-L	-L+Q/ns	+L/ns	+L/ns	ns/ns	ns/ns	+L-Q/-L
Wisconsin	All taxa	+L-Q/-L (or –L+Q)	-L/ns	+L (or +L-Q)/-L	ns/ns	ns/ns	ns/ns	ns/ns	ns/ns
	Hydrophytes	+L-Q/-L+Q	-L/ns	+L/ns	ns/ns	ns/ns	ns/ns	ns/ns	ns/ns
	Helophytes	ns/-L	+L-Q/ns	+L/ns	-L/ns	ns/ns	+L-Q/ns	+L/ns	ns/+L-Q (or-L)