

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

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41 **SUMMARY**

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

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

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

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

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

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

77 **Running head:** Biodiversity of lake macrophytes among regions

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85 **INTRODUCTION**

86 Freshwater ecosystems harbour much greater levels of biodiversity than terrestrial systems when
87 compared by surface area (Dudgeon et al., 2006) and are the source of numerous ecosystem
88 services vital to human existence (Millennium Ecosystem Assessment, 2005). These ecosystems are
89 also among the most threatened, being exposed to various anthropogenic impacts. The increasing
90 pressures from catchment land use, invasive species, pollution and loss of connectivity have
91 resulted in rapidly declining biodiversity in lakes, rivers and springs (Dudgeon et al., 2006; Vilmi et
92 al., 2017). Climate change will most likely accelerate this negative trend of biodiversity loss in
93 freshwater ecosystems, especially in high-latitude regions (Heino, Virkkala & Toivonen, 2009;
94 Woodward, Perkins & Brown, 2010). This calls for actions, approaches and measures to help
95 conserve threatened freshwater biodiversity across regions (Vilmi et al., 2017). Although the
96 general decline in freshwater biodiversity is well-documented in many studies (Dudgeon et al.,
97 2006; Cardinale et al., 2012), different approaches to measure biodiversity may yield varying
98 information about freshwater biodiversity patterns. Multiple biodiversity indices have been
99 developed to quantify natural characteristics and anthropogenic pressures, but these measure aspects
100 to various degrees (Warwick & Clarke, 1998; Gallardo et al., 2011). Thus, the use of a single index
101 is not typically appropriate in most circumstances. This study provides a complementary approach
102 to better understand patterns and document changes in freshwater biodiversity across different
103 ecosystems and regions.

104

105 Species richness is a classical measure of biodiversity across ecosystems and regions (e.g., Gaston,
106 2000). This index however has many well-known weaknesses related to, for example, sampling
107 effort and habitat type (Warwick & Clarke, 1998; Gotelli & Colwell, 2001). Despite these
108 deficiencies, species richness has proved to be a useful measure to indicate conservation values in

109 freshwaters (Rosset et al., 2013; Hill et al., 2016). An alternative biodiversity measure to
110 complement species richness is taxonomic distinctness, which enables the comparison of variability
111 in the taxonomic relatedness of species in biological communities across different locations,
112 sampling times and sets of samples (Warwick & Clarke, 1995; Vilmi et al., 2016). Thus, taxonomic
113 distinctness can be seen as a proxy for phylogenetic diversity for biological groups, for which
114 information on complete evolutionary phylogenetic relationships is still unavailable (Gallardo et al.,
115 2011; Winter et al., 2013), such as aquatic macrophytes.

116

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

126

127 One measure of taxonomic distinctness is average taxonomic distinctness (AvTD). AvTD is
128 calculated as the sum of all branch lengths connecting two species averaged across all species, thus
129 representing the mean distance between two randomly chosen species (Warwick & Clarke, 1995;
130 Gallardo et al., 2011). AvTD is not typically affected by species richness, but the absence or
131 extinction of closely-related species will increase the index value (Clarke & Warwick, 1998). AvTD
132 is the most suitable approach when the overall phylogenetic distinctiveness within a community is

133 evaluated (Winter et al., 2013). AvTD was originally developed to indicate anthropogenic pressures
134 in marine environments (Warwick & Clarke, 1995), but it is still uncertain how well the index
135 performs in other ecosystem types. For example, AvTD has not always responded strongly to
136 anthropogenic impacts in freshwater ecosystems (Feld et al., 2016; Vilmi et al., 2016) and, in some
137 cases, natural environmental variation may have masked the influence of anthropogenic impacts on
138 AvTD (Heino et al., 2007; Bevilacqua et al., 2011). Moreover, AvTD and species richness explain
139 different facets of biodiversity, and the patterns described by these two indices often differ when
140 multiple environmental gradients and different biological groups are studied (Marzin et al., 2012;
141 Heino et al., 2015a; Vilmi et al., 2016).

142

143 Not only is the indication capability of different biodiversity measures conditional on the
144 investigated environmental gradient and biotic group, but it also often depends on the region
145 studied. Diversity of the same biological group can show completely different patterns in relation to
146 equivalent ecological gradients between any two regions (Heino et al., 2012; Alahuhta & Heino,
147 2013; Tonkin et al., 2016; Alahuhta et al., 2017). For example, macrophyte species richness
148 followed a classical latitudinal gradient in Fennoscandian lakes (Alahuhta et al., 2013), whereas a
149 reversed latitudinal gradient was observed for macrophyte species richness in the Midwestern USA
150 (Alahuhta, 2015). This kind of contrasting diversity patterns can occur because of, for example,
151 different historic legacies, spatial scales, regional species pools, local environmental conditions,
152 biotic relationships and spatial processes (Jackson, Peres-Neto & Olden, 2001; Heino et al., 2015b;
153 Alahuhta & Heino, 2013; Alahuhta et al., 2016). In addition to these deterministic and stochastic
154 factors, the use of various statistical methods to investigate freshwater biodiversity patterns and
155 increasing statistical complexity in ecology makes it challenging to compare results originating
156 from different studies (Liebhold & Gurevitch, 2002). For example, the increasing use of adjusted R^2
157 values have resulted in decreased overall explained variations across different ecosystems (Low-

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

162

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

171

172 **MATERIAL AND METHODS**

173

174 **Study regions and macrophyte surveys**

175

176 We studied lakes situated in four different regions: Fennoscandia including Finland (338 000 km²)
177 and Sweden (450 000 km²), and the Midwestern USA states of Minnesota (225 000 km², hereafter
178 Minnesota) and Wisconsin (170 000 km², hereafter Wisconsin) (Figure S1 in Supporting
179 Information). These regions are generally characterised by similar climatic conditions, with cold
180 snowy winters and relatively warm summers. Finland and Sweden mostly belong to the boreal

181 region, with coniferous forests dominating their landscapes. Minnesota and Wisconsin are situated
182 in the northern edge of the temperate region, characterised mainly by a mixture of different forest
183 types, prairie and agricultural landscapes. Acidic granite bedrock dominates in Fennoscandia,
184 whereas nutrient-rich rocks are at least as common as acidic ones in the Midwestern USA. Water
185 bodies created by the withdrawal of ice-age glaciers form typical sceneries in all four study areas,
186 with inland surface waters covering 10% of Finland, 9% of Sweden, 8% of Minnesota and 17% of
187 Wisconsin. In all of the study regions, many of the lakes are impacted by land use activities (i.e.,
188 agriculture, silviculture and urban development) that are concentrated to the water bodies situated in
189 the southern parts of the study regions. Moreover, Alahuhta et al. (2017b) showed, using almost
190 identical data to our present study, that land use significantly influenced average water quality niche
191 breadths of lake macrophytes in Finland, Sweden and Wisconsin. More detailed information on
192 geographical variation of land use activities within each study region and how human pressures
193 impact the study lakes can be found in Alahuhta et al. (2013), Beck et al. (2010), Naturvårdsverket
194 (2010), Sass et al. (2010) and Stendera & Johnson (2006). The number of studied lakes was 50 in
195 Sweden and Wisconsin and 60 in Finland and Minnesota. The study lakes were randomly selected
196 from a larger database of lakes in Finland and Minnesota (Alahuhta et al., 2013; Alahuhta, 2015) to
197 maintain comparability with the lower numbers of study lakes from Sweden and Wisconsin.

198

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

206 m² squares placed every 2-3 m along a transect, and Swedish aquatic plants were identified along
207 transects in 20-cm depth intervals and in plots of ca. 25 × 50 cm. Transect widths were 6-m in
208 Finland, 0.5-m in Sweden and Wisconsin and 5-m in Minnesota. Number of transects in a lake
209 depended on lake surface area and securing proper view of species composition (Kanninen et al.,
210 2013, Table 1). Macrophytes were surveyed or observed by wading, diving, snorkelling or by boat,
211 using rakes and hydrosopes. Recorded macrophytes included not only hydrophytes but also
212 helophytes (i.e., emergent species and shore plants). Macrophyte survey methods are described in
213 detail for Finland in Alahuhta et al. (2013), for Sweden in Naturvårdsverket (2010), for Minnesota
214 in Alahuhta (2015), and for Wisconsin in Sass et al. (2010). We want to emphasise that the survey
215 methods were identical within each area, enabling us to compare ‘general patterns’ across the
216 regions (see e.g. Heino et al., 2015d; Alahuhta et al., 2017).

217

218 **Macrophyte variables**

219

220 We separated macrophyte species, in addition to all taxa, to hydrophytes and helophytes based on
221 their life form (Akasaka & Takamura, 2011; Alahuhta et al., 2014), and thus used three macrophyte
222 variables in all analyses. Hydrophytes and helophytes differ in their accessibility to carbon and
223 nutrient storages, and indication of water quality and hydro-morphological changes (Toivonen &
224 Huttunen, 1995; Akasaka & Takamura, 2011; Alahuhta et al., 2014; Kolada, 2015). Two different
225 biodiversity indices were calculated for all taxa, hydrophyte and helophyte of macrophytes in this
226 study: species richness and taxonomic distinctness. Species richness is the most common indicator
227 of biodiversity (Gaston, 2000), whereas taxonomic distinctness was used as a proxy for
228 phylogenetic diversity (Clarke & Warwick, 1998). When computing taxonomic distinctness, we
229 first organised the taxonomic data in the following taxonomic levels: species, genus, family, order,

230 class, subdivision and division levels. In the taxonomic levels, distinctness weight is one for
231 different species within the same genera, whereas a two is given to species within the same family
232 but different genera, and so on (see Fig. 1 in Clarke and Warwick, 1998). We then calculated AvTD
233 which is based on presence/absence data. AvTD is the average taxonomic path length between any
234 two randomly chosen species from a community (Clarke & Warwick, 1998): (AvTD=
235 $[\sum \sum_{i<j} \omega_{ij}]/[S(S-1)/2]$), where ω_{ij} is the distinctness weight given to the path length linking
236 species i and j in the taxonomical hierarchical classification and S is the number of species in a lake.
237 We used only the measure of AvTD to indicate phylogenetic diversity patterns, because we were
238 interested in average change instead of variation in phylogenetic diversity. The challenge with
239 AvTD is that the richness of taxa needs to be high enough for the calculation of reliable index
240 values (e.g. more than two species in a community). In our data sets, macrophyte richness was very
241 low (i.e., 0, 1 or 2 species) in some lakes of Sweden, Minnesota and Wisconsin. AvTD values could
242 only be formed if the observed richness was two, resulting in variable numbers of studied lakes
243 among all taxa, hydrophytes and helophytes in the four study regions (Table 2). In these cases,
244 species richness was calculated using identical number of lakes to that of the AvTD. AvTD index
245 values for all macrophyte groupings were calculated in R using the “vegan” package (Oksanen et
246 al., 2016).

247

248 **Explanatory variables**

249 Explanatory variables were alkalinity concentration (mg l^{-1}), elevation (m.a.s.l.), mean annual air
250 temperature ($^{\circ}\text{C}$), water colour (mg Pt l^{-1}), lake area (km^2), maximum lake depth (m), number of
251 studied transects in a lake, and total phosphorus concentration (mg l^{-1}). The explanatory data
252 comprised of well-known environmental characteristics influencing lake macrophytes (Rørslett,
253 1991; Toivonen & Huttunen, 1995; Jeppesen et al, 2000; Jones et al, 2003; Vestergaard & Sand-

254 Jensen, 2006; Sass et al., 2010; Akasaka & Takamura, 2011; Alahuhta, 2015), and the water
255 chemistry variables we used have been evidenced to correlate with those variables absent from our
256 study (e.g., pH, conductivity, Secchi depth, total nitrogen and chemical oxygen demand; Wetzel,
257 2001). Air temperature also has a clear relationship with water temperature in boreal and temperate
258 lakes (Pillgrim et al., 1998; Alahuhta, 2015). Sampling effort can significantly affect species
259 richness (Gotelli & Colwell, 2001), for which the number of studied transects in a lake represented
260 sampling effort. The level of multicollinearity among the explanatory variables was based on
261 bivariate Spearman rank correlation of $|\rho| > 0.7$, following Dormann et al. (2013), and the more
262 significant explanatory variable explaining species richness or AvTD was used in the analysis. For
263 this reason, elevation, which correlated with both mean annual temperature and alkalinity ($R_s = -$
264 0.71 to -0.72 , $p < 0.001$), was removed from the Finnish models. In Sweden, mean annual
265 temperature and elevation were strongly related for hydrophytes and helophytes ($R_s = -0.72$ to -0.73 ,
266 $p < 0.001$), and only the latter explanatory variable was included in the models of these two plant
267 groups. In Wisconsin, mean annual temperature correlated with alkalinity ($R_s = 0.73$, $p < 0.001$), for
268 which mean annual temperature was excluded from the models. In addition, one outlier lake was
269 removed from Wisconsin data sets. We were also interested to examine whether the relationships
270 between macrophytes and the studied environmental gradients (excluding the number of studied
271 transects) were unimodal (e.g., Jeppesen et al., 2000; Murphy, 2002) by adding second order terms
272 of the predictor variables in all the models.

273

274 Water chemistry was based on a single water sample, sampled simultaneously with the macrophytes
275 in Sweden and Wisconsin. In Finland, water chemistry consisted of median values of 1-m surface
276 water samples taken during the growing season (June–September) over the period from 2000 to
277 2008. Water chemistry of Minnesota lakes was based on the average value of multiple samples
278 taken in 2004 that correlated strongly ($r_{\text{Spearman}} > 0.8$) with the long-term water chemistry averages

279 (Alahuhta, 2015). Elevation was obtained from region-specific GIS data bases with the highest
280 resolution (c. 25m). The mean annual temperature was derived from the WorldClim database for
281 lake surface area with the resolution c. 1 km² (Hijmans et al., 2005) and was processed using
282 ArcGIS 10 (ESRI, Redlands, CA, USA).

283

284 **Statistical analysis**

285 First, we correlated species richness and AvTD to evaluate their relationship among macrophyte
286 functional groups and regions. Second, we used linear regression to investigate the relationship
287 between species richness or taxonomic distinctness and environmental gradients in each of the four
288 study regions. If the response variables were not normally distributed, we transformed them using
289 log transformations prior to further analysis. All the predictors were also log-transformed prior
290 analysis to improve their normality and to harmonize their ranges among the regions. The models
291 with the most important explanatory variables influencing species richness and taxonomic
292 distinctness were selected based on the parameter-strict Bayesian Information Criterion (BIC)
293 among all model combinations. BIC takes into account sample size by increasing the relative
294 penalty for model complexity with small data sets (Burnham & Anderson, 2002). In addition, we
295 calculated BIC differences, which can be used to rank different models in order of importance (BIC_i
296 $- BIC_{min}$, with BIC_{min} representing the best model with respect to expected Kullback-Leibler
297 information lost). Weights derived from BIC differences were estimated for each model to extract
298 additional information on model ranking. The relative importance of explanatory variables was
299 evaluated by summing the weights of the models that a given variable appears in the exhaustive list
300 of models. We also produced adjusted R² values, which provide unbiased estimates of the explained
301 variation (Borcard et al., 2011). A value of <2.0 was used as the threshold for deviation of BIC
302 values among candidate models (i.e., difference between model i and the model with the smallest

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

305

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

312

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

325

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

330

331 **RESULTS**

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

345

346 **Species richness in each study region**

347 For all macrophyte species richness, average number of species varied from 12.2 in Sweden to 27.2
348 Finland (Table 2). The lowest number of hydrophyte species was found in Sweden (mean = 6.1),

349 whereas most hydrophyte species per lake were recorded in Wisconsin (mean = 15.4). On average,
350 the helophyte species richness was lowest with 4.9 species in both states of the Midwestern USA
351 and the highest with 15.5 species in Finland.

352

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

358

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

370

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

374

375 **Average taxonomic distinctness in each study region**

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

380

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

386

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

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

396

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

405

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

409

410 **DISCUSSION**

411

412 In the present work, we studied patterns in the species richness and taxonomic distinctness of
413 aquatic macrophytes (i.e., all taxa, hydrophytes and helophytes) along a wide range of
414 environmental gradients in four study regions (i.e., Finland, Sweden, Minnesota and Wisconsin).
415 We found that biodiversity patterns varied among the macrophyte groups and the geographic

416 regions, as species richness and AvTD were explained by different environment gradients among
417 the study regions. Our findings suggest that freshwater biodiversity patterns can clearly differ even
418 in geographically closely-situated areas due to strong local environmental filtering within different
419 regional species pools (Heino et al., 2005; Ruhi et al., 2014). However, we also found some
420 consistent patterns, as increase in species richness was mostly associated with closely-related
421 congeneric macrophyte species across the study regions. In addition, some of the lakes of
422 Fennoscandia were phylogenetically more diverse than expected by chance, whereas some of the
423 lakes of the Midwestern USA were phylogenetically poorer than expected by random draws from
424 the regional species pool. Our results also suggested that taxonomic distinctness does not always
425 respond strongly to lake environmental conditions, which has similarly been evidenced for other
426 freshwater organism groups (Heino et al., 2005; Abellan et al., 2006; Bhat & Magurran, 2006; Feld
427 et al., 2016; Vilmi et al., 2016).

428

429 **Relationship between AvTD and species richness**

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

439 pattern was relatively weak and often non-significant in most of the regions, the trend was
440 consistently negative between species richness and AvTD of macrophytes among the regions.

441

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

457

458 **Variation in AvTD along environmental gradients**

459 AvTD did not describe variation in the studied environmental gradients very well, as these models
460 accounted for a reasonable amount of variation only for Finnish macrophytes and Wisconsin
461 hydrophytes. This relatively low amount of explained variation of AvTD for many of the plant
462 groups across the study regions may result from the fact that the index is based on presence/absence

463 data and assumes a reduction in taxonomic breadth when the degree of anthropogenic impacts
464 increases (Warwick & Clarke, 1998; Heino et al., 2005). However, aquatic macrophytes may
465 respond more strongly to alterations in environmental conditions through changes in relative
466 abundance rather than through changes in assemblage composition (Egertson et al., 2004).
467 Therefore, AvTD may have failed in indicating anthropogenic impacts if they mainly act by
468 influencing the evenness component of assemblage diversity (Bevilacqua et al., 2011). In addition,
469 the reasoning behind the use of AvTD is that species disappearing first from degraded lakes are
470 those that belong to species-poor higher taxa, whereas those that remain belong to more species-rich
471 higher taxa (Clarke & Warwick, 2001; Heino et al., 2007). In our study regions, higher taxonomic
472 levels, from order to subdivision, had more taxa in Fennoscandia than in the Midwestern USA, but
473 these differences were more balanced at the family and genus levels, eventually resulting in highest
474 species numbers in Finland and Wisconsin. This finding suggests, contrary to the original idea of
475 Clarke & Warwick (2001), that higher variability in lower taxonomic levels (e.g., genus) lead to
476 better performance of macrophyte AvTD. Although AvTD implicitly assumes that taxonomically
477 closely-related species involve a general functional homogeneity of species within high taxonomic
478 levels (Warwick & Clarke, 1998; Bevilacqua et al., 2011), functional responses of macrophyte
479 species vary strongly within the same genus, like the species-rich genus *Potamogeton* (Vestergaard
480 & Sand-Jensen, 2006; Beck & Alahuhta, 2016).

481

482 In the best AvTD models in Finland and Wisconsin, the index values increased with decreasing
483 alkalinity for all the three plant groups. The influence of alkalinity on macrophyte species originates
484 from their variable ability to use bicarbonate or carbon dioxide as a source of carbon in
485 photosynthesis (Madsen et al., 1996), the result of which has been found important for macrophytes
486 in different regions (Rørslett, 1991; Murphy, 2002; Vestergaard & Sand-Jensen, 2006; Sass et al.,
487 2010). In addition, AvTD of Finnish macrophytes decreased with increasing total phosphorus (i.e., a

488 proxy for anthropogenic nutrient enrichment), which is in agreement with the finding of Warwick &
489 Clarke (1998). However, a similar pattern was not discovered for the other regions, where AvTD of
490 different macrophyte groups responded to a wide range of environmental gradients. Heino et al.
491 (2007), similarly to our work, used both natural characteristics and anthropogenic pressures in
492 explaining biodiversity indices in streams and suggested that natural characteristics may mask the
493 influence of anthropogenic pressures on taxonomic distinctness. This may also be true in our study
494 based on the poor correlation between macrophyte AvTD and total phosphorus in most regions.
495 However, taxonomic distinctness should be unaffected by natural environmental gradients or
496 sampling effort (Warwick & Clarke, 1998), which brings into question the usability of this index to
497 portray changes in biodiversity along complex environmental gradients.

498

499 Randomization tests evaluating the null hypothesis that the AvTD of a lake is not different from that
500 expected by random draws (Clarke & Warwick, 1998; Warwick & Clarke, 1998) revealed clear
501 differences between the continents. The lakes of Finland and Sweden were sometimes more diverse
502 than expected by chance, whereas lower than expected values were often observed for lakes of
503 Minnesota and Wisconsin. This pattern suggested that some of the lakes in Fennoscandia are
504 phylogenetically more diverse than expected by chance, whereas some of the lakes in the
505 Midwestern USA are phylogenetically poorer than expected by random draws from the regional
506 species pool. As all the study lakes have a similar historical development related to glacial origins
507 (Sawada, Viau & Gajewski, 2003; Alahuhta et al., 2016) and macrophytes are rarely dispersal-
508 limited in these types of permanent lentic systems at regional spatial scales (Mikulyuk et al., 2011;
509 Viana et al., 2014; Alahuhta et al., 2015), we considered that the opposite patterns between
510 continents have emerged from differences in current environmental conditions among the study
511 regions. For example, differences in alkalinity, mean annual temperature and colour were evident
512 among the lakes of two continents. In addition, land use is known to strongly suppress freshwater

513 biodiversity in the southern catchments of Minnesota and Wisconsin (Sass et al., 2010; Mikulyuk et
514 al., 2011; Alahuhta, 2015). Our linear models did not support this reasoning, though. One must bear
515 in mind, however, that the linear models focus on across-lakes diversity patterns, whereas the
516 randomization test is based on AvTD of a single lake at a time. This explains different reasoning
517 resulting from the different statistical methods, and the results of randomization test, in fact, offer
518 complementary information to that of modelling on the diversity patterns of aquatic macrophytes.

519

520 **Macrophyte species richness in relation to environmental gradients**

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

535

536 In general, macrophyte species richness responded to various environmental gradients in most study
537 regions. This was expected, as macrophyte species richness has been known to respond positively to
538 increasing lake area, light availability and depth, and negatively to increased nutrient concentrations
539 (Rørslett, 1991; Lougheed, Crosbie & Chow-Fraser, 2001; Vestergaard & Sand-Jensen, 2006;
540 Akasaka & Takamura, 2011; Alahuhta et al., 2013; Viana et al., 2014; Alahuhta, 2015). Our results
541 largely supported these patterns found in previous studies, as species richness of different
542 macrophyte groups responded positively (showing a linear or unimodal pattern) to alkalinity in
543 Finland and Wisconsin, to climate (either with mean annual temperature or elevation) in all the
544 study regions, to lake area in Finland and Minnesota and to sampling effort in Finland, Minnesota
545 and Wisconsin. For colour and maximum depth, the results varied among the study regions and
546 macrophyte groups. Surprisingly, macrophyte species richness was not uniformly negatively
547 correlated to total phosphorus across the study regions and plant groups, being even positively
548 related to total phosphorus in Minnesota. Contrary to our finding, Sass et al. (2010) and Alahuhta
549 (2015) evidenced that increased total phosphorus related to land use activities decreased
550 macrophyte species richness in the lakes of the Midwestern USA. However, the relationship
551 between macrophyte species richness and total phosphorus was clearly unimodal in Minnesota, with
552 species richness decreasing sharply when the total phosphorus concentrations increased.

553

554 Concluding remarks

555 Our study suggests that variation in different biodiversity indices along multiple environmental
556 gradients can be substantial even for the same biological group in different regions. This finding
557 strongly suggests that a diversity measure detecting environmental changes in one region may not
558 be applicable in another region, but complementary indices are needed to reliably indicate the
559 impacts of anthropogenic pressures on freshwater biodiversity. Based on our findings, analysing

560 variation in species richness is a more powerful tool than taxonomic distinctness to measure
561 biodiversity for aquatic macrophytes as long as sampling effort is accounted for. Instead, using
562 taxonomic distinctness faces many challenges related to lack of consistent detection of
563 anthropogenic pressures on freshwater biodiversity, indication of anthropogenic pressures in
564 species-poor freshwater ecosystems and when variation in natural characteristics is strong.
565 However, randomization tests based on macrophyte AvTD showed consistent patterns between the
566 continents, suggesting that this approach may be more useful when taxonomic distinctness is used
567 as a proxy for phylogenetic diversity in lake macrophytes. Hence, AvTD and species richness can
568 provide valuable and complementary information on biodiversity patterns for freshwater
569 conservation, although more research is needed to corroborate our findings on aquatic macrophytes
570 inhabiting temperate and boreal regions.

571

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573

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585

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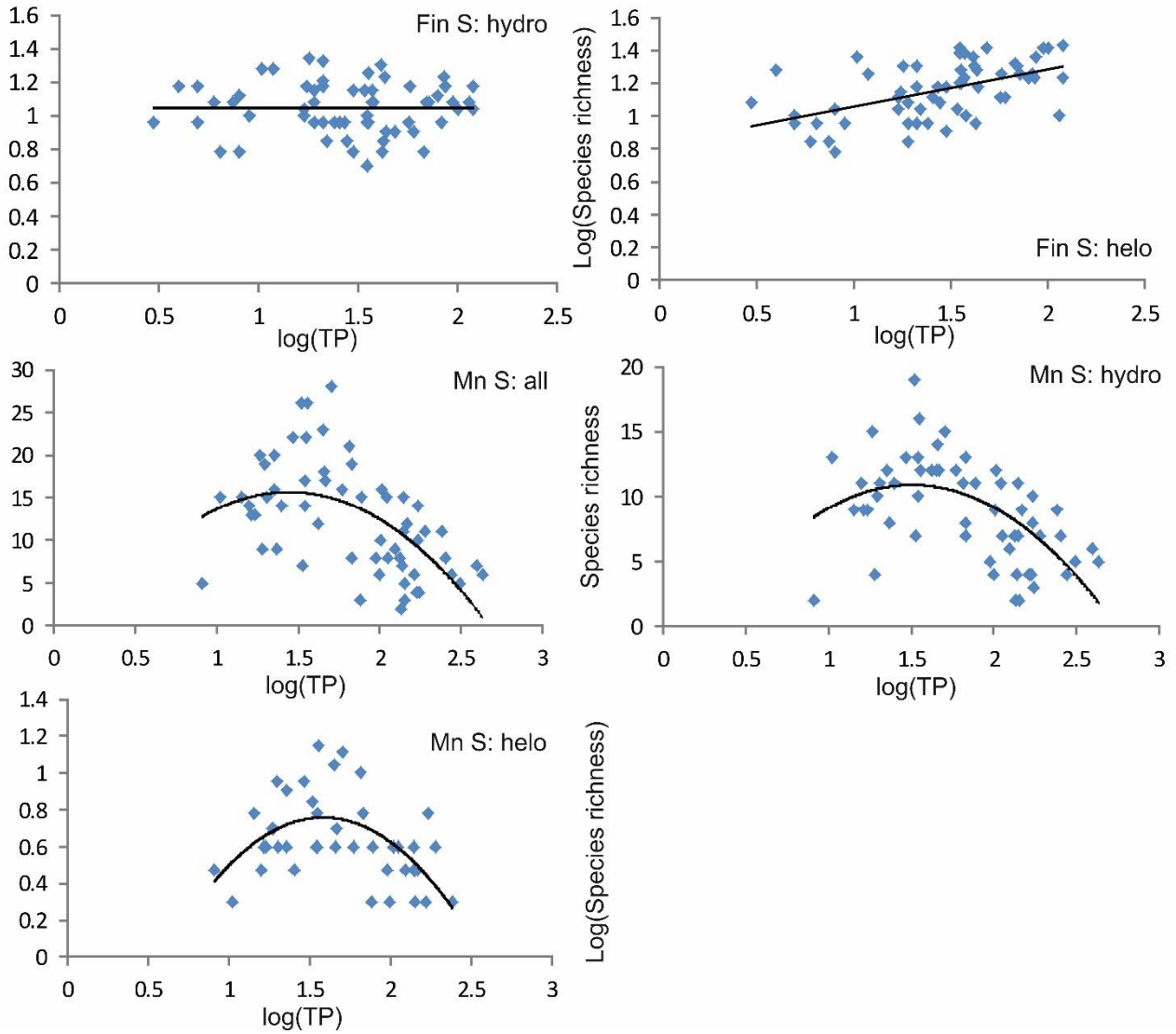
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807 Figure 1. Variation in species richness (S) of macrophyte communities (i.e., all taxa, hydrophytes
 808 and helophytes) in relation to total phosphorus concentrations (TP). Only those correlations are
 809 shown, which were significant based on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

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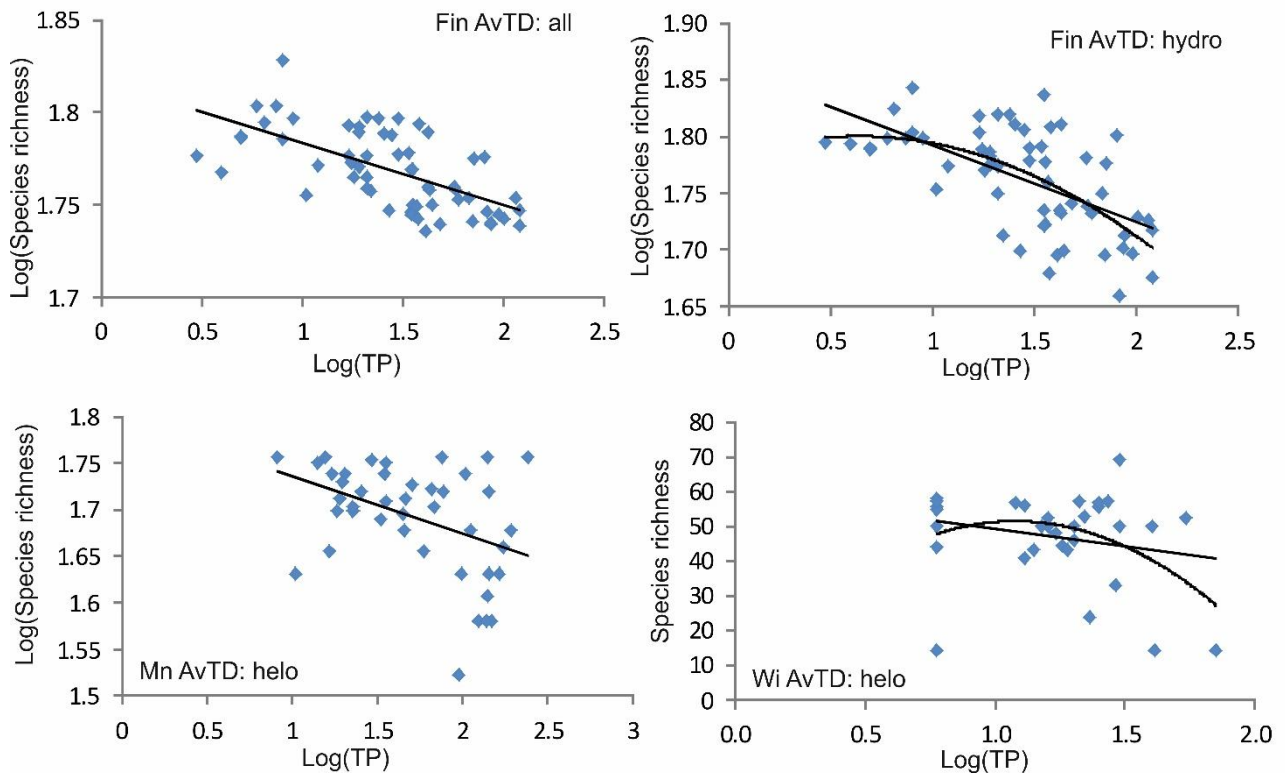
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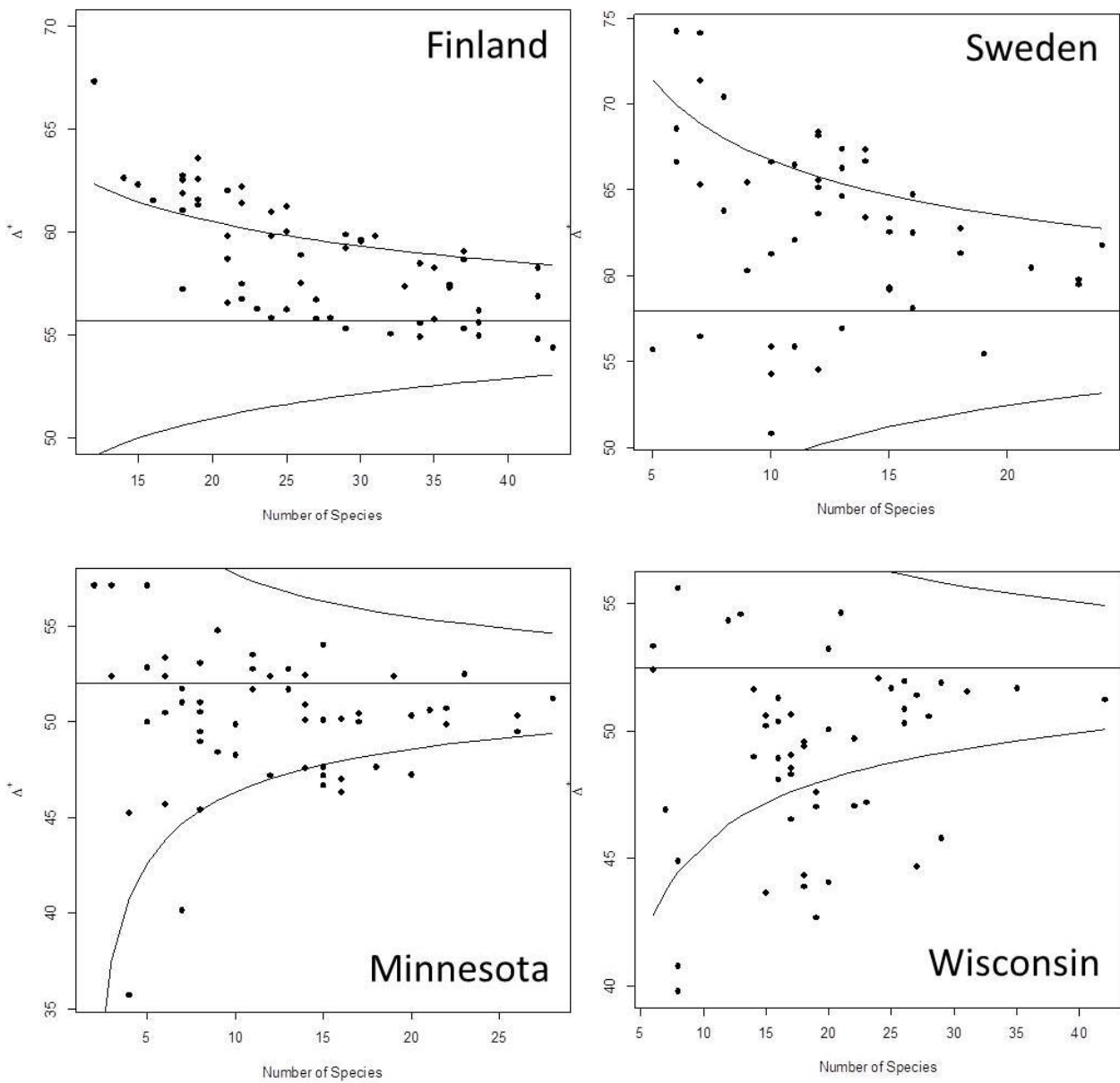
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820 Figure 2. Variation in average taxonomic distinctness (AvTD) of macrophyte communities (i.e., all
 821 taxa, hydrophytes and helophytes) in relation to total phosphorus concentrations (TP). Only those
 822 correlations are shown, which were significant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

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

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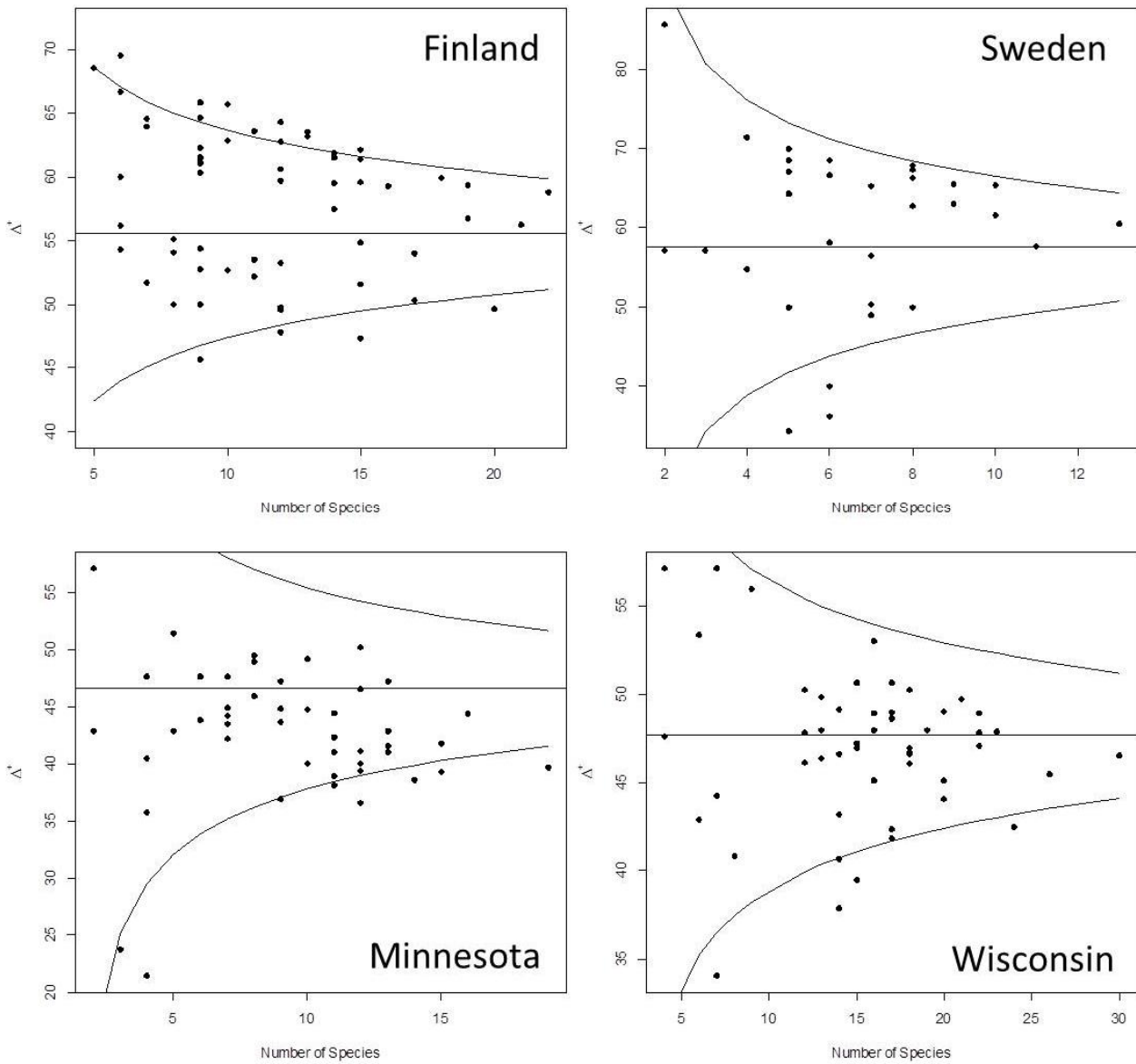
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837 Figure 4. Funnel plots illustrating average taxonomic distinctness (Λ^+) in relation to random
 838 occurrence in hydrophyte species pool. The lines indicate mean and 95% confidence intervals from
 839 random draws of species from the overall hydrophyte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

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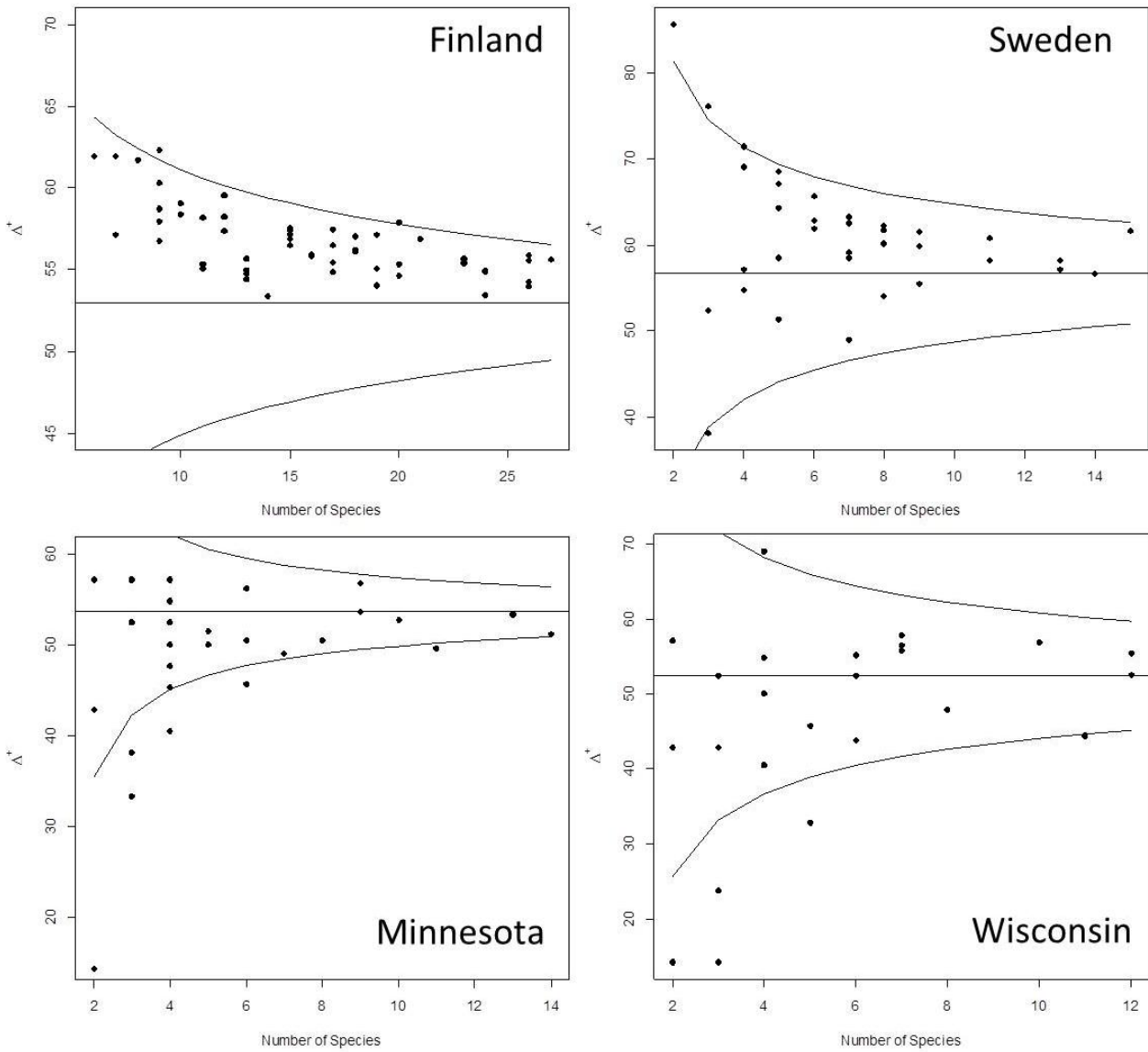
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848 Figure 5. Funnel plots illustrating average taxonomic distinctness (Λ^+) in relation to random
 849 occurrence in helophyte species pool. The lines indicate mean and 95% confidence intervals from
 850 random draws of species from the overall helophyte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

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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
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
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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)
Sweden	Helophytes	+L/-L	+L/-L+Q	na/na	+L/ns	+L/-L	ns/ns	ns/ns	+L/ns
	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
Wisconsin	Helophytes	-L/ns	+L-Q/-L	-L+Q/ns	+L/ns	+L/ns	ns/ns	ns/ns	+L-Q/-L
	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)

