

1 **Article type:** Original article

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

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80 **Key words:** alkalinity range, aquatic plants, elevation range, freshwater ecosystem, hydrophytes,  
81 latitude, nestedness, spatial extent, species turnover

82 **Running title:** Beta diversity of aquatic macrophytes

83 **Number of words in the Abstract:** 277

84 **Number of words in main body of the text:** 6555 inclusive of abstract, main text and references

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102 **ABSTRACT**

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

107 **Location:** Global

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

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

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

126 **INTRODUCTION**

127

128 Understanding broad-scale biodiversity patterns has become a fundamental topic in biogeography  
129 and ecology. The importance of explaining these patterns has increased in recent years because they  
130 are intimately related to, for example, ecosystem functioning (Symstad *et al.*, 2003) and resilience  
131 (Folke *et al.*, 2004), biogeographical regionalization (Divisek *et al.*, 2016), niche conservatism  
132 (Alahuhta *et al.*, 2017), species conservation (Brooks *et al.*, 2006) and ecosystem services (Naidoo *et*  
133 *al.*, 2008). Spatial variation in broad-scale diversity patterns is typically driven by natural history  
134 (e.g., past dispersal barriers and evolutionary changes), interactions among species (e.g., competition,  
135 predation and mutualism) and biogeography (e.g., distribution of climate zones, productivity and  
136 habitat heterogeneity) (Willig *et al.*, 2003; Qian & Ricklefs, 2007; Soininen *et al.*, 2007; Field *et al.*,  
137 2009; Baselga *et al.*, 2012). Better knowledge of patterns in biodiversity and their basis is also critical  
138 for managing and adapting to invasive species, land use changes, landscape and habitat degradation,  
139 and increasing temperatures associated with global change (Vörösmarty *et al.*, 2010). Therefore,  
140 studies focussing on broad-scale diversity patterns may directly advance both basic and applied  
141 research.

142

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

150 differences stem from species thinning or from other ecological processes (Baselga, 2010; Legendre,  
151 2014), such as physical barriers or human disturbance, that result in species-poor sites being a subset  
152 of the richest site in the region. Independent of the dissimilarity measure used to represent beta  
153 diversity, it has been reported to decrease with latitude and increase with elevation and area (Jones *et*  
154 *al.*, 2003; Heegaard, 2004; Qian & Ricklefs, 2007; Soininen *et al.*, 2007; Kraft *et al.*, 2011).  
155 Explanations for these patterns in beta diversity stem from effects of energy availability, water-energy  
156 dynamics, climatic variability, habitat heterogeneity and human disturbance (Gaston, 2000; Willig *et*  
157 *al.*, 2003; Socolar *et al.*, 2016). However, the majority of studies on beta diversity have been  
158 conducted at small spatial extents or using coarse resolution data across broad spatial scales (Kraft *et*  
159 *al.*, 2011; Dobrovolski *et al.*, 2012), exposing the lack of beta diversity studies using fine-resolution  
160 data at regional and global scales.

161

162 Increasing evidence indicates, however, that patterns in beta diversity depend on the studied  
163 ecosystem, organisms and geographical location (Soininen *et al.*, 2007; Dobrovolski *et al.*, 2012;  
164 Viana *et al.*, 2016; Wen *et al.*, 2016). Many of the reported patterns in beta diversity concern well-  
165 known, and often charismatic, taxa of terrestrial ecosystems (Qian & Ricklefs, 2007; Melo *et al.*,  
166 2009; Kraft *et al.*, 2011; Wen *et al.*, 2016) but may be unrepresentative of patterns in beta diversity  
167 for organisms in other ecosystems (Soininen *et al.*, 2007). Studies of beta diversity in freshwaters  
168 have often proved to be incongruent with those of terrestrial assemblages (Heino, 2011; Hortal *et al.*,  
169 2015). A few studies have suggested that ecological factors or dataset properties associated with  
170 freshwater communities may override spatial processes in determining beta diversity (Heino *et al.*,  
171 2015; Viana *et al.*, 2016). One possible explanation for these differences is that terrestrial ecosystems  
172 are more directly influenced by climate, whereas water temperatures, which are naturally more  
173 important to aquatic organisms, are more stable. Moreover, the physiological constraints of access to  
174 water and atmospheric gases are fundamentally different for terrestrial and aquatic organisms.



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

177

178 Aquatic macrophytes are among the most under-represented groups in broad-scale studies of  
179 freshwater biodiversity, yet they are an integral structural and functional component of freshwater  
180 ecosystems (Chambers *et al.*, 2008). Few studies on macrophyte diversity have been conducted at  
181 continental or global extents, and these have relied on data scaled to coarse political or biogeographic  
182 regions (Chambers *et al.*, 2008; Chappuis *et al.*, 2012), leading to potentially spurious conclusions  
183 about species distributions at finer scales (Hortal *et al.*, 2015). Although aquatic macrophyte diversity  
184 has been actively studied at local and regional extents, these studies may suffer from ecosystem-  
185 specific characteristics (i.e., varying environmental gradients lead species to respond differently to  
186 abiotic factors among regions), including variation in underlying environmental gradients among  
187 regions (Heino *et al.*, 2015; Viana *et al.*, 2016). For example, aquatic macrophyte diversity studied  
188 using similar methods showed a clear decreasing latitudinal gradient in one region, yet a reversed  
189 latitudinal gradient in another (Alahuhta *et al.*, 2013; Alahuhta, 2015). Thus, explaining and testing  
190 hypotheses related to broad-scale patterns in diversity is difficult with one or a few data sets, and a  
191 more general overview demands comparative analysis of multiple data sets (Crow, 1993; Kraft *et al.*,  
192 2011; Heino *et al.*, 2015).

193

194 In this paper, we examine pairwise- and multiple-site beta diversity of aquatic macrophytes using  
195 data sets for 21 regions from around the world. Specifically, we consider two questions: (1) How is  
196 beta diversity of aquatic macrophytes partitioned between species turnover and nestedness across  
197 study regions on a global scale? (2) Which environmental factors explain variation in these beta  
198 diversity components for aquatic macrophytes across study regions? Based on a continental scale

199 study (Viana *et al.*, 2016), we expected that spatial turnover accounts for most of the overall beta  
200 diversity. We also assumed that latitude does not strongly structure macrophyte beta diversity (Crow,  
201 1993; Chambers *et al.*, 2008). Instead, we hypothesised that macrophyte beta diversity is mostly  
202 explained by variables reflecting variation in local habitat conditions, thus indicating the effect of  
203 environmental heterogeneity on beta diversity (Heegaard, 2004; Viana *et al.*, 2016).

204

## 205 **MATERIALS AND METHODS**

206

### 207 **Macrophyte and explanatory variable data**

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

223 survey methods. The surveys were executed mostly between 1990 and 2012, with the exception of  
224 Canada, China and Britain, where surveys were done during 1970s and 1980s, between 1964 and  
225 2014, and between 1980 and 1998, respectively.

226

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

231

232 The explanatory variables calculated for each regional convex hull included region spatial extent  
233 (km<sup>2</sup>), elevation range (m, Hijmans *et al.*, 2005), modelled alkalinity range in lakes (mequiv. l<sup>-1</sup> at  
234 1/16 degrees resolution, Marcé *et al.*, 2015), predicted range of soil organic carbon mass fraction at  
235 depth of 1 m (1 km resolution, Hengl *et al.*, 2014), areal extent of freshwaters expressed as a  
236 proportion of region spatial extent, herein referred to as proportion of freshwater (% , 1 km resolution,  
237 Latham *et al.*, 2014) and latitude (i.e., coordinate Y originated from each region's centre point) (Table  
238 1). In addition, we examined whether areal extent of artificial surfaces (e.g., surfaces with houses,  
239 roads or industrial sites, Latham *et al.*, 2014) as a proportion of region spatial extent (%), was  
240 correlated with the beta diversity coefficients and other explanatory variables. Regional spatial extent  
241 was a surrogate for sampling effort, as it was strongly positively associated with both numbers of  
242 lakes and number of species present within a region ( $R_{\text{Spearman}} \geq 0.64$ ,  $p < 0.001$ , Appendix S3 in  
243 Supporting Information), but is also an indicator of environmental heterogeneity (see also Gaston,  
244 2000). In addition, elevation range likely illustrates variability in habitats suitable for different  
245 macrophytes (Gaston, 2000; Melo *et al.*, 2009), and it simultaneously served as a proxy for variation  
246 in temperature (correlation with temperature range:  $R_s = 0.92$ ,  $p < 0.001$ ). Elevation range was also

247 positively associated with mean altitude ( $R_S=0.73$ ,  $p<0.001$ ). Following Dormann *et al.* (2013),  
248 multicollinearity was manifested at the level of  $R_S >|0.7|$  and, in these cases, statistically less  
249 significant predictors of beta diversity were excluded from final models (Appendix S2). Carbon  
250 compounds in water directly and indirectly influence macrophytes (Alahuhta & Heino, 2013; Kolada  
251 *et al.*, 2014). We therefore used two different proxies, water alkalinity and soil organic carbon, to  
252 represent these local-scale components. Carbon dioxide and bicarbonate concentration influence  
253 photosynthesis in aquatic macrophytes, while organic carbon (i.e., carbon leached from organic soils)  
254 absorbs light, a common constraint on productivity (Madsen *et al.*, 1996; Vestergaard & Sand-Jensen,  
255 2000). Water alkalinity is also affected by anthropogenic land use (e.g., Vestergaard & Sand-Jensen,  
256 2000; Kolada *et al.*, 2014), enabling us to infer the degree of anthropogenic pressures on macrophyte  
257 beta diversity in lakes located on homogenous geology but lacking lake-level chemistry data. The  
258 relative areal extent of freshwaters within a region was used to indicate availability of potential habitat  
259 for macrophyte growth. Finally, changes in species diversity with latitude are well known, with  
260 species diversity often decreasing towards the Poles (Qian & Ricklefs, 2007). Negative latitude values  
261 were converted to positive in our analysis to compensate for limited data availability on Southern  
262 Hemisphere regions, thereby strengthening the relationship between macrophyte beta diversity and  
263 latitude.

264

### 265 **Beta diversity coefficients for different data sets**

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

271 coefficients: 1) Sørensen coefficient (i.e., a measure of overall beta diversity,  $\beta_{\text{sor/SOR}}$ ), 2) Simpson  
272 coefficient (i.e., a measure of turnover immune to nestedness resulting from species richness  
273 differences,  $\beta_{\text{sim/SIM}}$ ), and 3) a coefficient measuring nestedness–resultant beta diversity ( $\beta_{\text{sne/SNE}}$ ,  
274 Baselga, 2010; Legendre, 2014). The Simpson coefficient defines species turnover without the  
275 influence of richness gradients, whereas the nestedness-resultant component of beta diversity is the  
276 direct difference between  $\beta_{\text{sor/SOR}}$  and  $\beta_{\text{sim/SIM}}$ . For the pairwise-site index, we averaged the pairwise  
277 dissimilarities between all lakes in a region. Because the number of sites affects the multiple-site  
278 index (Baselga, 2010), we resampled the 21 regional datasets to standardize them to a common  
279 number of 21 lakes, the minimum number of lakes found across the regional datasets (in Brazil  
280 Amazon, Table 2), based on 1000 permutations in each region. Both beta diversity indices were  
281 obtained using the R package “betapart” (Baselga *et al.*, 2013). The three beta diversity coefficients  
282 were calculated using the functions `beta.pair` and `beta.sample` for pairwise-site and multiple-site  
283 indices, respectively.

284

## 285 **Statistical analysis**

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

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

302

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

320 with the smallest AICc,  $\Delta$ AICc), because models with AICc differing by  $< 2.0$  are typically  
321 considered to have similar statistical support (Burnham & Anderson, 2002).

322

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

326

## 327 **RESULTS**

328

329 Beta diversity of aquatic macrophytes differed among the 21 study regions, a finding that was mostly  
330 attributable to species turnover (Fig. 2), especially in high beta diversity regions, and applied to both  
331 pair-wise and multiple-site indices. Nestedness accounted only for a small fraction of overall beta  
332 diversity (14% of pairwise site dissimilarity on average) and was most important (although still less  
333 than species turnover) in regions with low overall pairwise–site beta diversity. Macrophyte beta  
334 diversity patterns in the majority of regions were thus explained by variation in species composition  
335 among lakes, rather than differences in species richness. Based on the pairwise-site index, the degree  
336 of macrophyte beta diversity varied clearly among the 21 study regions. The greatest beta diversity  
337 was found in the coastal South American lakes (Salga, 0.90) and Spain (0.92), whereas values were  
338 lowest in both the Brazilian regions (0.43-0.44) and China (0.43). The top models obtained through  
339 beta regression explained similar amounts of variation and included the same important explanatory  
340 variables (Table 2) for both pairwise-site and multiple-site beta diversity indices. The best models  
341 accounted for 28-33% of variation in the Sørensen coefficient, 33-37% in the turnover component  
342 and 27-28% in the nestedness component.

343

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

359

360 In addition to relationships between beta diversity coefficients and environmental variability, certain  
361 environmental variables were correlated with indicators of anthropogenic pressures. Alkalinity range  
362 showed a positive relationship with the relative areal extent of artificial surfaces as proportion of  
363 region spatial extent ( $R_s=0.46$ ,  $p=0.04$ ). Both alkalinity range ( $R_s=0.48$ ,  $p=0.03$ ) and temperature  
364 range ( $R_s=0.56$ ,  $p=0.008$ ) were associated with spatial extent, such that the span in alkalinity and  
365 temperature was greater in regions that covered a greater areal extent. These correlations also impede  
366 the separation of possible independent effects for these factors.



367

368 **DISCUSSION**

369

370 Aquatic macrophytes exhibited considerable regional variation in beta diversity, which was largely  
371 driven by species turnover. Our results thus suggest that turnover in species composition primarily  
372 accounts for macrophyte beta diversity. Aquatic macrophytes have similarly shown high levels of  
373 species turnover at a regional and continental extent (Heegaard, 2004; Boschilia *et al.*, 2016; Viana  
374 *et al.*, 2016). However, our finding conflicts with previous global extent studies on beta diversity in  
375 which nestedness contributed equally or more than species turnover to total diversity of amphibians  
376 (Baselga *et al.*, 2012), fish (Leprieur *et al.*, 2011), macroinvertebrates (Heino *et al.*, 2015) and oribatid  
377 mites (Gergocs & Hufnagel, 2015). In addition, nestedness has been found to outweigh species  
378 turnover in areas affected by glaciations until recent time (Baselga *et al.*, 2012; Dobrovolski *et al.*,  
379 2012). We found no sign of this, as nestedness was typically lowest in regions that were wholly or  
380 partly ice covered during the last glaciation (e.g., Finland, Norway, Canada, China, New Zealand,  
381 Switzerland, US state of Minnesota and UK). Our study thus emphasises that conclusions about  
382 global patterns in beta diversity need verification across a diverse range of organisms, instead of using  
383 only a few well-studied terrestrial taxa, because variable patterns exist in nature and exceptions are  
384 as instructive as conformity.

385

386 Contrary to our *a priori* expectations based on trends found in terrestrial taxa (Willig *et al.*, 2003;  
387 Qian & Ricklefs, 2007; Soininen *et al.*, 2007), beta diversity of aquatic macrophytes increased (albeit  
388 weakly) towards the poles. Based on Rapoport's rule (Stevens, 1989), species ranges and niche width  
389 should increase at higher latitudes, giving rise to a decrease in beta diversity (Soininen *et al.*, 2007).  
390 But, in general, many aquatic assemblages do not exhibit the latitudinal patterns observed for

391 terrestrial taxa, such as mammals, birds and vascular plants (Heino, 2011; Hortal *et al.*, 2015). Even  
392 regarding species richness, one of the most widely-used measures of diversity, aquatic macrophytes  
393 show differing responses to latitude at continental and global scales (Rørslett, 1991; Chambers *et al.*,  
394 2008; Chappuis *et al.*, 2012). In addition, contrasting latitudinal patterns in macrophyte beta diversity  
395 have been found within individual regions (Heegaard, 2004; Viana *et al.*, 2016), likely due to different  
396 study scales and varying sampling techniques used. Our study included only macrophyte data  
397 collected via consistent methods (within each region) and showed that overall beta diversity increases  
398 weakly from the equator towards the poles. However, the relative importance of latitude in explaining  
399 global macrophyte beta diversity was modest, being selected only in two of eleven models. These  
400 two models concerned the overall (Sørensen) beta diversity. In contrast, species turnover and  
401 nestedness did not vary consistently with latitudinal gradient. This is likely because aquatic  
402 macrophytes are more responsive to local environmental conditions than the broad-scale variation in  
403 climate that underlies latitudinal gradients in the beta diversity of other (terrestrial) organism groups.  
404 Aquatic environments moderate extreme climatic conditions, leading to less variation in temperature  
405 in freshwater than terrestrial ecosystems, and this may partly explain the conflict in latitudinal beta  
406 diversity patterns between freshwater and terrestrial assemblages.

407

408 Although the relationship between latitude and macrophyte beta diversity conflicted with that of many  
409 organisms, our results support another reported beta diversity pattern. Habitat heterogeneity has  
410 previously been shown to structure beta diversity for terrestrial plants (Freestone & Inouye, 2006)  
411 and butterflies at a regional extent (Andrew *et al.*, 2012), birds and mammals at a continental extent  
412 (Melo *et al.*, 2009), and oceanic bacteria (Zinger *et al.*, 2011) and fish (Leprieur *et al.*, 2011) at a  
413 global extent. Variation in macrophyte beta diversity in our study regions was predominantly  
414 determined by environmental heterogeneity, primarily the degree of elevation variability (also  
415 correlated with temperature variability) in a region. Thus, beta diversity of aquatic macrophytes

416 (expressed as either multiple–site or pairwise–site diversity) increased with variation in altitude. This  
417 positive association between beta diversity and elevation range likely reflects the greater variety of  
418 habitats or resources available with greater variation in altitude. Wang *et al.* (2012) similarly found  
419 that elevational beta diversity of aquatic micro- and macroorganisms was primarily related to  
420 environmental heterogeneity at a regional extent. Species distributions are typically constrained by  
421 harsh climatic conditions at high altitude (Gaston, 2000), and various aspects of macrophyte  
422 physiology are known to be temperature sensitive (Sculthorpe, 1967; Rooney & Kalff, 2000).  
423 However, the buffering of temperature extremes in aquatic environments allows for continued plant  
424 growth over a wide elevation range. Greater variation in habitats with increasing variation in altitude  
425 is also related to geological and soil properties, as low lying lakes will vary more in water chemistry  
426 due to greater variation in soil and geology, which in turn increase variation in water chemistry (Wang  
427 *et al.*, 2012), as well as from the added influence of human activity. These factors magnify the  
428 elevation gradient which enhances environmental heterogeneity and thus enables the establishment  
429 of a greater variety of macrophyte species, further increasing beta diversity within a region.

430

431 Regional variation in water alkalinity, soil organic carbon availability and spatial extent further  
432 indirectly would have supported the habitat heterogeneity hypothesis in explaining global patterns of  
433 macrophyte beta diversity. However, contrary to our expectations, these individual variables were not  
434 important predictors of macrophyte beta diversity. Alkalinity and soil organic carbon influence  
435 aquatic macrophytes through their differing ability to use bicarbonate or carbon dioxide as a source  
436 of carbon in photosynthesis (Madsen *et al.*, 1996), but also indirectly reflect human effects on  
437 freshwaters. In-lake alkalinity often increases with eutrophication, while nutrient inputs from  
438 agriculture and human effluents tend to be greatest in landscapes dominated by carbonate-rich  
439 minerals (Kolada *et al.*, 2014; Alahuhta, 2015). Similarly, regional spatial extent is often positively  
440 associated with beta diversity, as in our work, because larger areas incorporate higher levels of

441 environmental heterogeneity (Gaston, 2000; Anderson *et al.*, 2011; Heino *et al.*, 2015). Moreover,  
442 spatial extent was also positively related to alkalinity range and temperature range, both expressions  
443 of environmental heterogeneity. These explanations suggest an underlying effect of environmental  
444 heterogeneity on aquatic macrophyte beta diversity that may also be affected by human activities that  
445 impair water quality and physical characteristics of near-shore habitats (Kosten *et al.*, 2009;  
446 Vörösmarty *et al.*, 2010; Alahuhta, 2015).

447

448 Besides discovering novel patterns in macrophyte beta diversity, our main result has practical  
449 implications for environmental management: the conservation of aquatic macrophyte assemblages  
450 that naturally exhibit high species turnover will be most favoured by a regional approach, in which  
451 multiple lakes that span a wide environmental gradient are protected within a region (Socolar *et al.*,  
452 2016). This approach further underlines the need to maximise the total area protected, independent  
453 of the geographical location. Conversely, low biodiversity regions characterized by high nestedness  
454 require conservation actions that prioritise high-diversity sites over those of lower diversity (Socolar  
455 *et al.*, 2016). In these low-biodiversity regions, the possible influence of land-based activities within  
456 a catchment should be carefully evaluated and connectivity among high-diversity habitats should be  
457 maintained.

#### 458 **ACKNOWLEDGEMENTS**

459 We thank Andres Baselga for insightful comments on the calculation of beta diversity. Comments  
460 from Christine Meynard, Solana Boschilia, Chad Larsen and an anonymous reviewer improved the  
461 manuscript considerably. We also thank Lucinda B. Johnson and Sidinei M. Thomaz for providing  
462 Minnesota and part of the Brazilian data, respectively. We appreciate assistance from Konsta  
463 Happonen in producing some of the figures. The gathering of the Finnish data was partly supported  
464 by Biological Monitoring of Finnish Freshwaters under diffuse loading -project (XPR3304) financed

465 by Ministry of Agriculture and Forestry and partly by national surveillance monitoring programs of  
466 lakes. SH and MM were supported by the EU-funded MARS-project (7th EU Framework  
467 Programme, Contract No.: 603378). SALGA-team, especially Gissell Lacerot, Nestor Mazzeo, Vera  
468 Huszar, David da Motta Marques and Erik Jeppesen for organizing and executing the SALGA field  
469 sampling campaign and Bruno Irgang<sup>†</sup> and Eduardo Alonso Paz for help with identification. Swedish  
470 macrophyte data were collected within the Swedish Monitoring Program of macrophytes in lakes  
471 funded by the Swedish Agency for Marine and Water Management. SK was supported by NWO Veni  
472 grant 86312012. Macrophyte data from Brazilian Amazon were collected within a limnological  
473 monitoring program funded by Vale S.A. The vast majority of macrophyte data from Polish lakes  
474 were collected within the State Environmental Monitoring Programme and were provided by the  
475 Inspection for Environmental Protection. Macrophyte data for British lakes were collated by the Joint  
476 Nature Conservation Committee from surveys resourced by the national conservation agencies. Swiss  
477 macrophytes data were collected during a study financially supported by the Swiss Federal Office for  
478 the Environment. Wisconsin data collection was funded by the Wisconsin Department of Natural  
479 Resources and supported by the Wisconsin Cooperative Fishery Research Unit. The Norwegian  
480 macrophyte data were collected within the European Union project ‘LAKES – Long distance  
481 dispersal of Aquatic Key Species’, contract no. env4-ct-97-0585.

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#### 483 **REFERENCES**

- 484 Alahuhta, J. & Heino, J. (2013) Spatial extent, regional specificity and metacommunity structuring  
485 in lake macrophytes. *Journal of Biogeography*, **40**, 1572–1582.
- 486 Alahuhta, J., Kanninen, A., Hellsten, S., Vuori, K.-M., Kuoppala, M. & Hämäläinen, H. (2013)  
487 Environmental and spatial correlates of community composition, richness and status of boreal  
488 lake macrophytes. *Ecological Indicators*, **32**, 172-181.

- 489 Alahuhta, J. (2015) Geographic patterns of lake macrophyte communities and species richness at  
490 regional scale. *Journal of Vegetation Science*, **26**, 564-575.
- 491 Alahuhta, J., Ecke, F., Johnson, L.B., Sass, L. & Heino, J. (2017) A comparative analysis reveals little  
492 evidence for niche conservatism in aquatic macrophytes among four areas on two continents.  
493 *Oikos*, **126**, 136-148.
- 494 Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J.,  
495 Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J., Stegen, J.C. & Swenson,  
496 N.G. (2011) Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing  
497 ecologist. *Ecology Letters*, **14**, 19-28.
- 498 Andrew, M.E., Wulder, M.A., Coops, N.C. & Baillargeon, G. (2012) Beta-diversity gradients of  
499 butterflies along productivity axes. *Global Ecology and Biogeography*, **21**, 352-364.
- 500 Bartoń, K. (2014) MuMIn: multi-model inference. R package version 1.12.1. [https://cran.r-](https://cran.r-project.org/web/packages/MuMIn/index.html)  
501 [project.org/web/packages/MuMIn/index.html](https://cran.r-project.org/web/packages/MuMIn/index.html)
- 502 Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global*  
503 *Ecology and Biogeography*, **19**, 134-143.
- 504 Baselga, A., Orme, D., Vileger, S., Bortoli, D. & Leprieur, F. (2013) betapart: Partitioning beta  
505 diversity into turnover and nestedness components. R package version 1.3.
- 506 Baselga, A., Gomez-Rodrigues, C. & Lobo, J.M. (2012) Historical Legacies in World Amphibian  
507 Diversity Revealed by the Turnover and Nestedness Components of Beta Diversity. *PLoS ONE*,  
508 **7**, e32341.

- 509 Boschilia, S.M., de Oliveira, E.F. & Schwarzbald, A. (2016) Partitioning beta diversity of aquatic  
510 macrophyte assemblages in a large subtropical reservoir: prevalence of turnover or nestedness?  
511 *Aquatic Sciences*, **78**, 615-625.
- 512 Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F.,  
513 Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2008) Global biodiversity conservation  
514 priorities. *Science*, **313**, 58-61.
- 515 Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical*  
516 *information-theoretic approach*, 2<sup>nd</sup> edn. Springer-Verlag, New York, NY.
- 517 Chambers, P.A., Lacoul, P., Murphy, K.J. & Thomaz, S.M. (2008) Global diversity of aquatic  
518 macrophytes in freshwater. *Hydrobiologia*, **595**, 9–26.
- 519 Chappuis, E., Ballesteros, E. & Gacia, E. (2012) Distribution and richness of aquatic plants across  
520 Europe and Mediterranean countries: patterns, environmental driving factors and comparison  
521 with total plant richness. *Journal of Vegetation Science*, **23**, 985-997.
- 522 Cribari-Neto, F. & Zeileis, A. (2010) Beta Regression in R. *Journal of Statistical Software*, **34**, 1-24.
- 523 Crow, G.E. (1993) Species diversity in aquatic angiosperms: latitudinal patterns. *Aquatic Botany*, **44**,  
524 229–258.
- 525 Divisek, J., Storch, D., Zelen, D. & Culek, M. (2016) Towards the spatial coherence of  
526 biogeographical regionalizations at subcontinental and landscape scales. *Journal of*  
527 *Biogeography*, **43**, 2489-2501.
- 528 Dobrovolski, R., Melo, A.S., Cassemiro, F.A.S. & Diniz-Filho, J.A.F. (2012) Climatic history and  
529 dispersal ability explain the relative importance of turnover and nestedness components of beta  
530 diversity. *Global Ecology & Biogeography*, **21**, 191-197.

- 531 Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquéz, J.R.G., Gruber, B.,  
532 Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B.,  
533 Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of  
534 methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 27-  
535 46.
- 536 Ferrari, S. & Cribari-Neto, F. (2004) Beta Regression for modelling rates and proportions. *Journal of*  
537 *Applied Statistics*, **31**, 799-815.
- 538 Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.-F., Kaufman,  
539 D.M., Kerr, J.T., Mittenbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009)  
540 Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**,  
541 132-147.
- 542 Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004)  
543 Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology,*  
544 *Evolution, and Systematics*, **35**, 557-581.
- 545 Freestone, A.L. & Inouye, B.D. (2006) Dispersal limitation and environmental heterogeneity shape  
546 scale-dependent diversity patterns in plant communities. *Ecology*, **87**, 2425-2432.
- 547 Gaston, K. J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- 548 Gergocs, V. & Hufnagel, L. (2015) Global pattern of oribatid mites (Acari: Oribatida) revealed by  
549 fractions of beta diversity and multivariate analysis. *International Journal of Acarology*, **41**, 574-  
550 583.
- 551 Heegaard, E. (2004) Trends in aquatic macrophyte species turnover in Northern Ireland — which  
552 factors determine the spatial distribution of local species turnover? *Global Ecology and*  
553 *Biogeography*, **13**, 397-408.



- 554 Heino, J. (2011) A macroecological perspective of diversity patterns in the freshwater realm.  
555 *Freshwater Biology*, **56**, 1703–1722.
- 556 Heino, J., Melo, A.S., Bini, L.M., Altermatt, F., Al-Shami, S.A, Angeler, D., Bonada, N., Brand, C.,  
557 Callisto, M., Cottenie, K., Dangles, O., Dudgeon, D., Encalada, A., Göthe, E., Grönroos, M.,  
558 Hamada, N., Jacobsen, D., Landeiro, V.L., Ligeiro, R., Martins, R.T., Miserendino, M. L., Md  
559 Rawi, C.S. Rodrigues, M., Roque, F.O., Sandin, L., Schmera, D., Sgarbi, L.F., Simaika, J.,  
560 Siqueira, T., Thompson, R.M. & Townsend, C.R. (2015) A comparative analysis reveals weak  
561 relationships between ecological factors and beta diversity of stream insect metacommunities at  
562 two spatial levels. *Ecology and Evolution*, **5**, 1235-1248.
- 563 Hengl, T., de Jesus, J.M., MacMillan, R.A., Batjes, N.H., Heuvelink, G.B.M., Ribeiro, E., Samuel-  
564 Rosa, A., Kempen, B., Leenaars, J.G.B., Walsh, M.G. & Ruiperez Gonzalez, M. (2014)  
565 SoilGrids1km — Global Soil Information Based on Automated Mapping. *PLoS ONE*, **9**,  
566 e114788.
- 567 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution  
568 interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**,  
569 1965–1978.
- 570 Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015) Seven  
571 shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution,*  
572 *and Systematics*, **46**, 523-549.
- 573 Jones, J.I., Li, W. & Maberly, S.C. (2003) Area, altitude and aquatic plant diversity. *Ecography*, **26**,  
574 411-420.
- 575 Kolada, A., Willby, N., Dudley, B., Nöges, P., Søndergaard, M., Hellsten, S., Mjedge, M., Penning,  
576 E., van Geest, G., Bertrin, V., Ecke, F., Mäemets, H. & Karus, K. (2014) The applicability of

- 577 macrophyte compositional metrics for assessing eutrophication in European lakes. *Ecological*  
578 *Indicators*, **45**, 407-415.
- 579 Kosten, S., Kamarainen, A., Jeppesen, E., van Nes, E.H., Peeters, E.T.H.M., Mazzeo, N., Sass, L.,  
580 Hauxwell, J., Hansel-Welch, N., Lauridsen, T.L., Søndergaard, M., Bachmann, R.W., Lacerot,  
581 G. & Scheffer, M (2009) Climate-related differences in the dominance of submerged  
582 macrophytes in shallow lakes. *Global Change Biology*, **15**, 2503-2517.
- 583 Kraft, N.J.B., Comita, L.S. Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C.,  
584 Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye,  
585 B.D., Harrison, S.P. & Myers, J.A. (2011) Disentangling the Drivers of  $\beta$  Diversity Along  
586 Latitudinal and Elevational Gradients. *Science*, **333**, 1755-1758.
- 587 Latham, J., Cumani, R., Rosati, I. & Bloise, M. (2014) FAO Global Land Cover (GLC-SHARE) Beta-  
588 Release 1.0 Database, Land and Water Division.  
589 [http://www.glcn.org/databases/lc\\_glcshare\\_en.jsp](http://www.glcn.org/databases/lc_glcshare_en.jsp)
- 590 Legendre, P. (2014) Interpreting the replacement and richness difference components of beta  
591 diversity. *Global Ecology and Biogeography*, **23**, 1324-1334.
- 592 Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Durr, H.H., Brosse, S. & Oberdorff, T.  
593 (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures  
594 of past climate changes. *Ecology Letters*, **14**, 325-334.
- 595 Madsen, T.V., Maberly, S.C. & Bowes, G. (1996) Photosynthetic acclimation of submersed  
596 angiosperms to CO<sub>2</sub> and HCO<sub>3</sub><sup>-</sup>. *Aquatic Botany*, **53**, 15-30.
- 597 Marcé, R., Morgui, J.-A., Riera, J.L., Lopez, P. & Armengol, J. (2015) Carbonate weathering as a  
598 driver of CO<sub>2</sub> supersaturation in lakes. *Nature Geoscience*, **8**, 107-111.

- 599 Melo, A.S., Rangerl, T.F.L.V.B. & Diniz-Filho, J.A.F. (2009) Environmental drivers of beta-diversity  
600 patterns in New-World birds and mammals. *Ecography*, **32**, 226-236.
- 601 Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R.E., Lehner, B., Malcolm, T.R. & Ricketts,  
602 T.H. (2008) Global mapping of ecosystem services and conservation priorities. *Proceedings of*  
603 *the National Academy of Sciences USA*, **105**, 9495-9500.
- 604 Qian, H. & Ricklefs, R.E. (2007) A latitudinal gradient in large-scale beta diversity for vascular plants  
605 in North America. *Ecology Letters*, **10**, 737-744.
- 606 R Core Team (2015) R: A language and environment for statistical computing. R Foundation for  
607 Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- 608 Rørslett, B. (1991) Principal determinants of aquatic macrophyte richness in northern European lakes.  
609 *Aquatic Botany*, **39**, 173-193.
- 610 Rooney, N. & Kalff, J. (2000) Inter-annual variation in submerged macrophyte community biomass  
611 and distribution: the influence of temperature and lake morphometry. *Aquatic Botany*, **68**, 321–  
612 335.
- 613 Scheffer, M., van Geest, G.J., Zimmer, K., Jeppesen, E., Søndergaard, M., Butler, M.G., Hanson,  
614 M.A., Declerck, S. & De Meester, L. (2006) Small habitat size and isolation can promote species  
615 richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos*, **112**, 227-231.
- 616 Sculthorpe, C.D. (1967) *The biology of aquatic vascular plants*. Edward and Arnold Publishing,  
617 London.
- 618 Socolar, J.B., Gilroy, J.J., Kunin, W.E. & Edwards, D.P. (2016) How Should Beta-Diversity Inform  
619 Biodiversity Conservation? *Trends in Ecology and Evolution*, **31**, 67-80.

- 620 Soininen, J., Lennon, J.J. & Hillebrand, J. (2007) A Multivariate analysis of beta diversity across  
621 organisms and environment. *Ecology*, **88**, 2830-2838.
- 622 Stevens, G.C. (1989) The latitudinal gradients in geographical range: how so many species co-exist  
623 in the tropics. *American Naturalist*, **133**, 240-256.
- 624 Suren, A.M. & Ormerod, S.J. (1998) Aquatic bryophytes in Himalayan streams: testing a distribution  
625 model in a highly heterogeneous environment. *Freshwater Biology*, **40**, 697–716.
- 626 Symstad, A.J., Chapin III, F.S., Wall, D.H., Gross, K.L., Huenneke, L.F., Mittelbach, G.G., Peters,  
627 D.P. & Tilman, D. (2003) Long-term and large-scale perspectives on the relationship between  
628 biodiversity and ecosystem functioning. *Bioscience*, **53**, 89-98.
- 629 Zinger, L., Amaral-Zettler, L.A., Fuhrman, J.A., Horner-Devine, M.C., Huse, S.M., Welch, D.B.M.,  
630 Martiny, J.B.H., Sogin, M., Boetius, A. & Ramette, A. (2011) Global Patterns of Bacterial Beta-  
631 Diversity in Seafloor and Seawater Ecosystems. *PloS ONE*, **6**, e24570.
- 632 Vestergaard, O. & Sand-Jensen, K. (2000) Alkalinity and trophic state regulate aquatic plant  
633 distribution in Danish lakes. *Aquatic Botany*, **67**, 85-107.
- 634 Viana, D.S., Figuerola, J., Schwenk, K., Manca, M., Hobæk, A., Mjelde, M., Preston, C.D., Gornall,  
635 R.J., Croft, J.M., King, R.A., Green, A.J. & Santamaria, L. (2015) Assembly mechanisms  
636 determining high species turnover in aquatic communities over regional and continental scales.  
637 *Ecography*, **38**, 1-8.
- 638 Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A. Green, P., Glidden, S.,  
639 Bunn, S.E., Sullivan, C.A., Reidy Liermann, C. & Davies, P.M. (2010) Global threats to human  
640 water security and river biodiversity. *Nature*, **467**, 555-561.

- 641 Wang, J.J., Soininen, J., Zhang, Y, Wang, B.X., Yang, X.D. & Shen, J. (2012) Patterns of elevational  
642 beta diversity in micro- and macroorganisms. *Global Ecology and Biogeography*, **21**, 743-750.
- 643 Wen, Z., Yang, Q., Quan, Q., Xia, L., Ge, D. & Lv, X (2016) Multiscale partitioning of small mammal  
644  $\beta$ -diversity provides novel insights into the Quaternary faunal history of Qinghai–Tibetan  
645 Plateau and Hengduan Mountains. *Journal of Biogeography*, **43**, 1412-1424.
- 646 Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal Gradients of Biodiversity: Pattern,  
647 Process, Scale, and Synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273-  
648 309.
- 649
- 650
- 651
- 652
- 653
- 654
- 655 **APPENDIX 1 – DATA SOURCES**
- 656 Crowder, A.A., Bristow, J.M., King, M.R. & Vanderkloet, S. (1977) Distribution, seasonality, and  
657 biomass of aquatic macrophytes in Lake Opinicon (Eastern Ontario). *La Naturaliste Canadien*,  
658 **104**, 441-456.
- 659 Hitchin, G.G., I. Wile, G.E. Miller & N.D. Yan. (1984) *Macrophyte data from 46 southern Ontario*  
660 *soft-water lakes of varying pH*. Ontario Ministry of Environment Data Report DR 84/2.

- 661 Miller, G. E., & Dale, H. M. (1979) Apparent differences in aquatic macrophyte floras of eight  
662 different lakes in Muskoka District, Ontario from 1953 to 1977. *Canadian Field Naturalist*, **93**,  
663 386–390.
- 664 Neil, J., Graham, J. & Warren, J. (1991) Aquatic Plants of Cook Bay, Lake Simcoe, 1987. *Lake*  
665 *Simcoe Environmental Management Strategy*, Technical report B.4.
- 666 Nishihiro, J., Akasaka, M., Ogawa, M. & Takamura, N. (2014) Aquatic vascular plants in Japanese  
667 lakes. *Ecological Research*, **29**, 369-369.
- 668 Ontario Ministry of the Environment and Ministry of Natural Resources (1976) *The Kawartha*  
669 *Lakes Water Management Study - Water Quality Assessment (1972 - 1976)*. Toronto, Ontario.
- 670 Schloesser, D.W., Edsall, T.A. & Manny, B.A. (1985) Growth of submerged macrophyte  
671 communities in the St. Clair - Detroit river system between Lake Huron and Lake Erie.  
672 *Canadian Journal of Botany*, **63**, 1061-1065
- 673 Wile, I. & Hitchin, G. (1977) An assessment of the practical and environmental implications of  
674 mechanical harvesting of aquatic vegetation in Southern Chemung Lake. *Ministry of the*  
675 *Environment and Ministry of Natural Resources*, Toronto, Ontario.

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## 678 **SUPPORTING INFORMATION**

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

680 Appendix S1 Description of lakes and surveys.

681 Appendix S2 An example of convex hull.

682 Appendix S3 Correlation matrix among environmental variables.

683 Appendix S4. Beta diversity and environmental determinants.

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686 **BIOSKETCH**

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689 processes structuring aquatic plants at various spatial scales. He is especially interested to understand  
690 how global change affects aquatic macrophyte distributions across temporal and spatial scales. The  
691 research group is devoted to the study of aquatic plants and other freshwater assemblages from  
692 different perspectives at various spatial scales. Author contributions: J.A. and J.H. conceived the  
693 ideas; all authors participated in the collection of the data; J.A. analysed the data; and J.A. led the  
694 writing to which other authors contributed.

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696 Editor: Christine Meynard

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

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



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

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

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

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

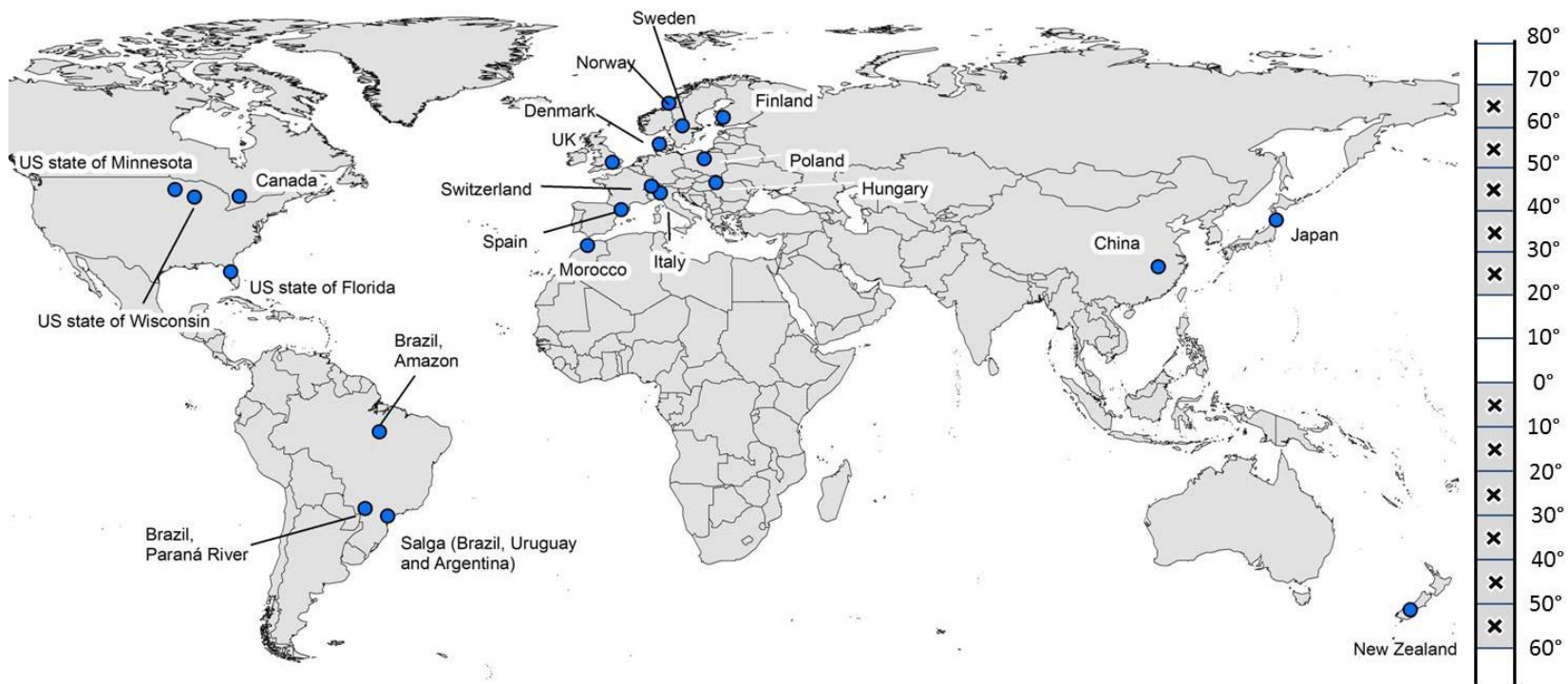
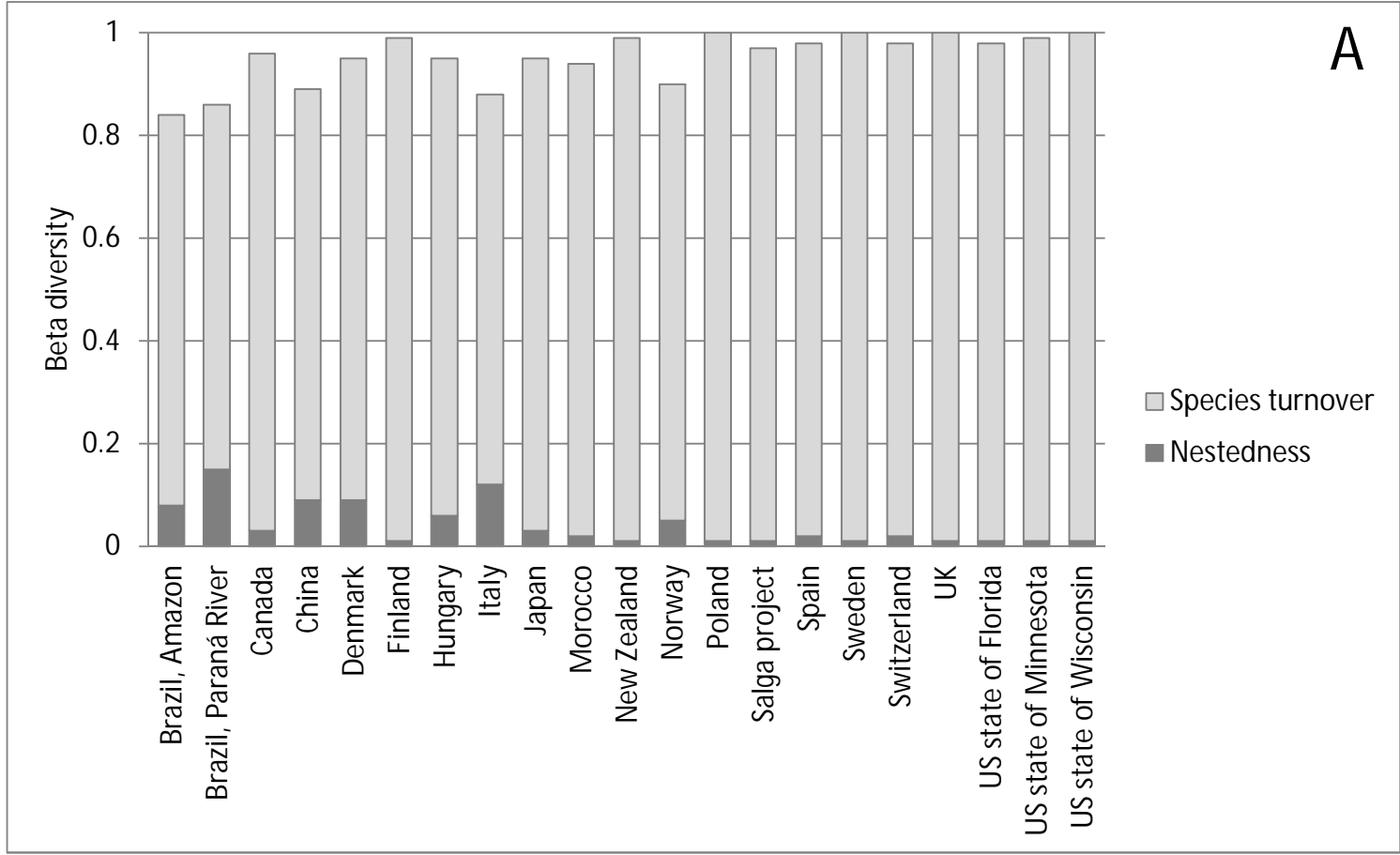


Fig. 1. Study regions are represented in blue circles situated in the middle of convex hulls (n=21). Crosses in the right side panel indicate which latitudinal bands are covered in our work.



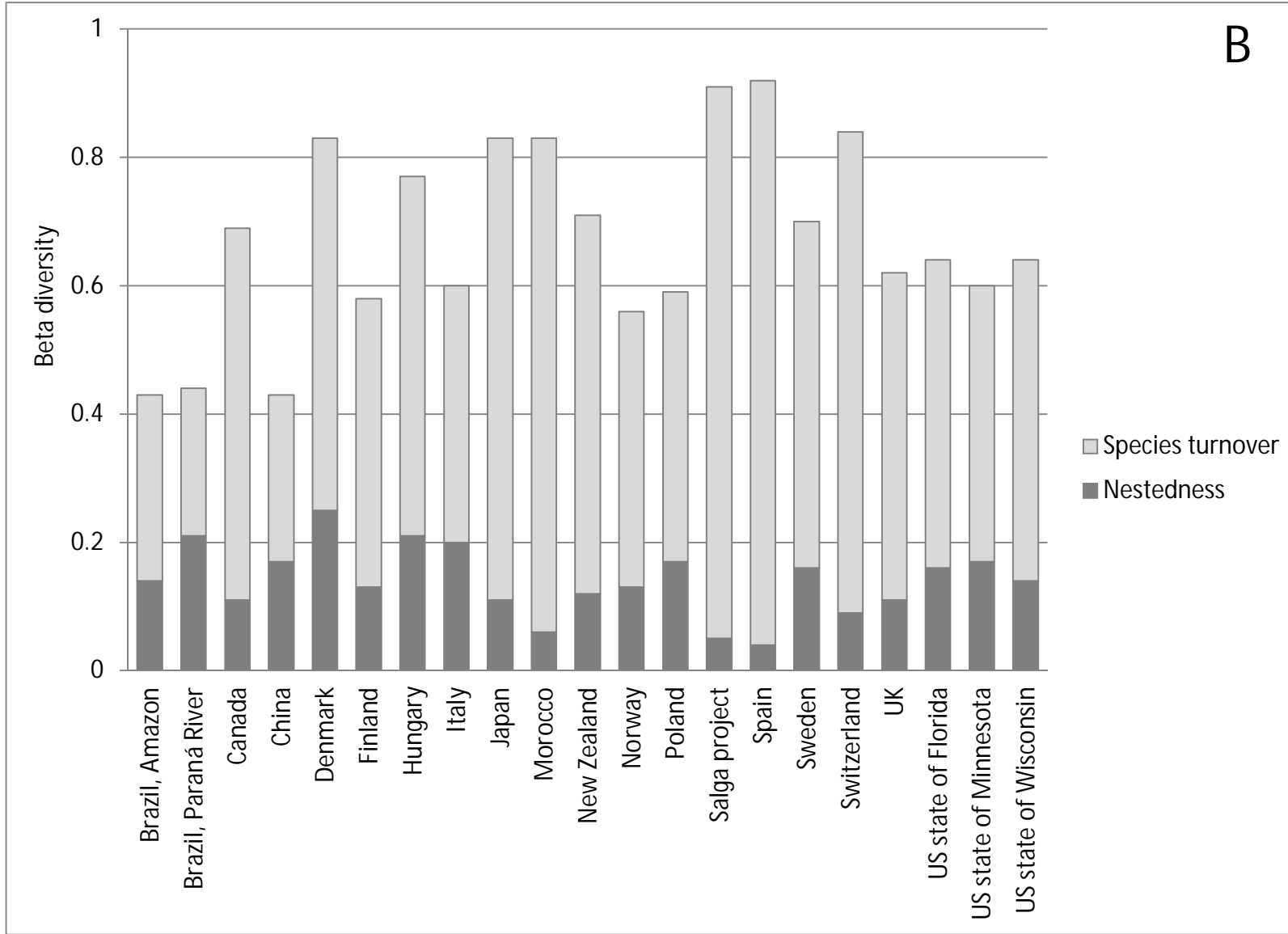


Fig. 2. Simpson dissimilarity (beta diversity due to species turnover) and nestedness dissimilarity (beta diversity due to nestedness-resultant richness differences) that sum to Sørensen dissimilarity (i.e., total beta diversity) based on multiple site (A) and mean of pair-wise (B) beta diversity measures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

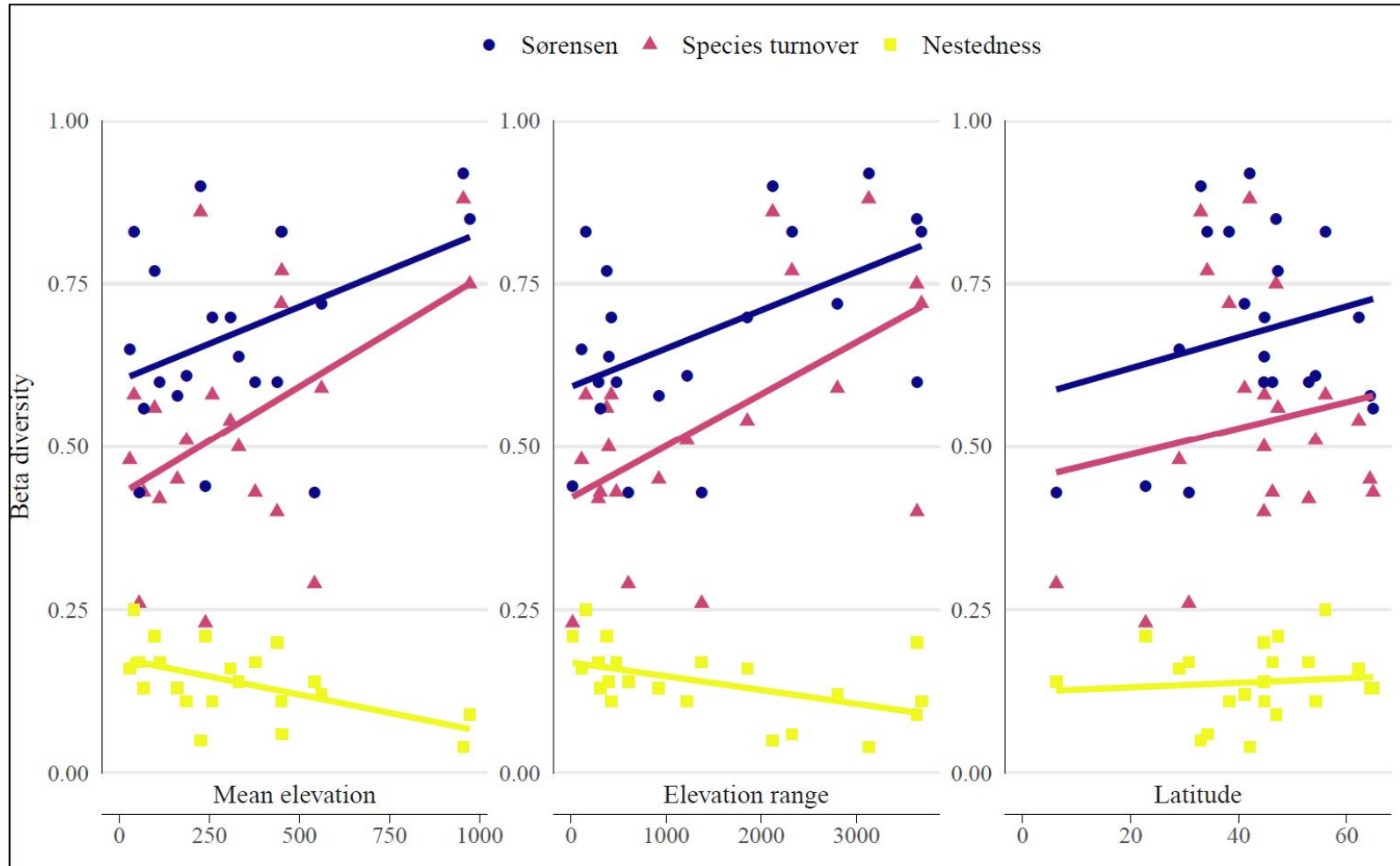


Fig. 3. Relationships between pairwise site beta diversity dissimilarities (i.e., Sørensen, species turnover and nestedness) of freshwater macrophytes and mean altitude, elevation range and latitude. Similar plot for multiple site beta diversity coefficients can be found in Appendix S4.