

1 **Average niche breadths of species in lake macrophyte communities respond to**
2 **ecological gradients variably in four regions on two continents**

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42 **ABSTRACT**

43 Different species' niche breadths in relation to ecological gradients are infrequently examined
44 within the same study and, moreover, species niche breadths have rarely been averaged to account
45 for variation in entire ecological communities. We investigated how average environmental niche
46 breadths (climate, water quality and climate-water quality niches) in aquatic macrophyte
47 communities are related to ecological gradients (latitude, longitude, altitude, species richness and
48 lake area) among four distinct regions (Finland, Sweden and US states of Minnesota and
49 Wisconsin) on two continents. We found that correlations between the three different measures of
50 average niche breadths and ecological gradients varied considerably among the study regions, with
51 average climate and average water quality niche breadth models often showing opposite trends.
52 However, consistent patterns were also found, such as widening of average climate niche breadths
53 and narrowing of average water quality niche breadths of aquatic macrophytes along increasing
54 latitudinal and altitudinal gradients. This result suggests that macrophyte species are generalists in
55 relation to temperature variations at higher latitudes and altitudes, whereas species in southern,
56 lowland lakes are more specialised. In contrast, aquatic macrophytes growing in more southern
57 nutrient-rich lakes were generalists in relation to water quality, while specialist species are adapted
58 to low-productivity conditions and are found in highland lakes. Our results emphasize that species
59 niche breadths should not be studied using only coarse-scale data of species distributions and
60 corresponding environmental conditions, but that investigations on different kinds of niche breadths
61 (e.g., climate vs. local niches) also require finer resolution data at broad spatial extents.

62

63 **Keywords:** Aquatic plants, Climate, Lakes, Latitude, Niche width, Water quality

64

65 **INTRODUCTION**

66

67 Understanding ecological phenomena in complex systems has posed a significant challenge to
68 researchers (Low-Decarie et al. 2014), despite the availability of massive amounts of high quality
69 data. Coarse-scale (e.g., grid cell-based resolution at a regional, continental or global scale) data on
70 species distributions has revealed many interesting patterns in biodiversity, such as the latitudinal
71 gradient in species diversity (Willig et al. 2003). Such coarse-scale data have many restrictions
72 related to, for example, false species presences and limited availability of local environmental
73 variables that narrow the possibilities of studying variation in biodiversity at finer scales (Guisan
74 and Thuiller 2005; Franklin 2010). Therefore, many scientists have emphasised the increasing need
75 to examine biodiversity patterns by combining broad spatial extent (i.e., from regional to global
76 extents) with local resolution data (i.e., empirical survey-based data) on species distributions and
77 environmental conditions (Ackerly et al. 2010; Beck et al. 2012). However, our current assumptions
78 about ecological patterns have been challenged (e.g., species diversity-latitude relationship),
79 because accepted biodiversity gradients may not hold when examined through the lens of fine-
80 resolution data spanning broad spatial extents (Heino et al. 2011). Comparative studies using fine-
81 resolution data from multiple regions have further shown that species can respond differently to the
82 same ecological gradients among the regions (Kraft et al. 2011; Alahuhta and Heino 2013;
83 Henriques-Silva et al. 2013; Bini et al. 2014; Heino et al. 2015a; Alahuhta et al. 2016a). These
84 conflicting results have especially been found in freshwater ecosystems, where, at broad spatial
85 extents, habitat-level factors (i.e., water quality and habitat structure) contribute equally or more
86 strongly than climate to species distributions and community structure (Heino 2011; Beck et al.
87 2013; Alahuhta 2015; Beck and Alahuhta 2016).

88

89 One of the fundamental species characteristics is its niche breadth, which generally describes the
90 suite of environments or resources that species can inhabit or use (Brown 1984; Dolodec et al.
91 2000). The niche breadth hypothesis states that species that have broad tolerances of environmental
92 gradients and are able to use a wide range of resources are also widely distributed (Morin and
93 Lechowicz 2013; Slatyer et al. 2013). On the other hand, species occupying a small range of
94 environmental conditions are specialists with narrower distributions (Botts et al. 2012; Heino and
95 Grönroos 2014). The hypothesis further predicts that both regional distribution and local abundance
96 mirror the degree to which local environmental conditions meet a species' requirements (Brown
97 1984). In addition, these patterns in the distribution of generalist and rare species are expected to
98 persist across temporal scales, as abundant species are more consistently present through time than
99 rare ones, and widely-distributed species are more consistently distributed through time, and vice
100 versa (Brown 1984; Heino 2005). For ecological gradients other than range size, the relationship of
101 species niche breadth with environmental gradients has often been variable depending on the
102 methods and the ecosystem studied (Vazques and Stevens 2004; Cirtwill et al. 2015).

103

104 Some studies have reported a positive relationship between niche breadth and latitude (Sunday et al.
105 2011; Rasmann et al. 2014), and the latitudinal gradient in species diversity is one of the most
106 commonly recognised ecological phenomena (Willig et al. 2003). This positive relationship
107 postulates that species in the tropics are more specialised than temperate species due to lower
108 variability in environmental conditions in the low-latitude ecosystems (MacArthur 1972). However,
109 Vasquez and Stevens (2004) found no such correlation in their meta-analysis, and Cirtwill et al.
110 (2015) found support for the latitude-niche breadth hypothesis only for freshwater species but not
111 for terrestrial, marine or estuarine species. For brachyuran crabs, only temperate species
112 demonstrated a positive relationship between niche breadth and latitude (Papacostas and Freestone

113 2016). Furthermore, Lappalainen and Soininen (2006) discovered a negative correlation between
114 niche breadths of fishes and latitude.

115

116 The latitude-niche breadth hypothesis has gained variable degrees of support over the years.
117 However, the relationship between niche breadth and biodiversity is even more complex. Increase
118 in biodiversity often enhances the number of mutualistic relationships (Bascompte et al. 2003), for
119 which the correlation between diversity and niche breadth can be positive if mutualism enables co-
120 occurrence of species. However, increased species richness also generally increases competition
121 (MacArthur 1972), which can have either positive or negative effects on niche breadth. If increased
122 competition drives a species to specialise its resource use, biodiversity has a negative correlation
123 with niche breadth (MacArthur 1968). Chejanovski and Wiens (2014) found that species richness
124 was negatively associated with mean climatic niche breadth for temperate tree frogs, as climatic
125 zones with high species richness contained more species with narrower climatic niche breadths. In
126 contrast, the relationship is positive when species begin to utilize wider environmental gradients,
127 mimicking behaviour of a generalist species (MacArthur 1968). Biodiversity is also related to
128 habitat size, as species diversity typically increases with habitat size (MacArthur 1972; Rørslett
129 1991). However, little is known about how biodiversity, habitat size and their combination *per se*
130 affect niche breadth of species.

131

132 Species niche breadths can also be viewed from a community ecology perspective by averaging
133 single species niche breadths to account for the whole community composition (Doledec et al.
134 2000). In this community-based approach (Figure 1), species with varying niche breadths (from
135 narrow to wide tolerances of environmental conditions) simultaneously co-occur in a community,
136 emphasising the importance of competition among species (Ricklefs 2008). For example, a negative

137 relationship between average niche breadth and species richness results from increased competition
138 among species that have a broader niche which in turn decreases species diversity (Doledec et al.
139 2000). By taking competition into account, species niche breadth hypotheses can be applied to
140 community-based average niche breadths. Although species niche breadths have been studied
141 intensively across ecosystems (e.g., Morin and Lechowicz 2013; Slatyer et al. 2013; Heino &
142 Grönroos 2014; Cirtwill et al. 2015), community-based average niche breadths have received less
143 attention.

144

145 Studies on species niche breadth in freshwater ecosystems have focused on a few well-known
146 organism groups, such as fish and macroinvertebrates (Heino 2005; Lappalainen and Soininen
147 2006; Heino and Grönroos 2014; McCauley et al. 2014; Faulks et al. 2015; Cirtwill et al. 2015;
148 Tonkin et al. 2016). Much less is known about aquatic macrophytes, which are key primary
149 producers in freshwaters in addition to providing habitat, shelter and breeding area for various other
150 aquatic and terrestrial species (Garcia-Llorente et al. 2011). Considering ecological gradients, many
151 aquatic macrophytes have wide distribution range sizes, suggesting that they have broad tolerance
152 of environmental gradients (Chambers et al. 2008). Macrophyte species richness is shown to follow
153 the classical latitudinal trend (Chappuis et al. 2012); however, species diversity has sometimes
154 peaked at intermediate latitudes or shown no relationship with latitude (Crow 1993), depending on
155 the study scale. Studies on the species richness–area relationship of aquatic macrophytes have often
156 shown a positive correlation (Rørslett 1991; Alahuhta 2015), although disparate results have been
157 reported (Hinden et al. 2005; Vestergaard and Sand-Jensen 2006). To our knowledge, however, no
158 previous investigations have studied the relationship between average environmental niche breadths
159 and ecological gradients for aquatic macrophyte communities across different study regions situated
160 on different continents.

161

162 We examined how average environmental niche breadths (i.e., climate, water quality and combined
163 climate-water quality) of aquatic macrophytes are related to ecological and spatial gradients (i.e.,
164 latitude, longitude, altitude, species richness and lake area; hereafter ecological gradients) among
165 four distinct regions (i.e., Finland, Sweden and Midwestern USA states of Minnesota and
166 Wisconsin) on two continents (Europe and North America). Previous works have primarily
167 investigated niche breadth of individual species in relation to ecological gradients. In contrast, only
168 a handful of studies have examined average niche breadth pooled across species to comprise the
169 whole community composition (e.g., Figure 5 in Doleddec et al. 2000). Following the niche breadth
170 model, we predicted (H1) that increasing latitude results in widening of average climate and water
171 quality niche breadths across each study region. This is because climate conditions become harsher
172 and lakes become more unproductive towards the northern latitudes (Heino and Toivonen 2008;
173 Beck et al. 2013; Alahuhta 2015). We also assumed (H2) that longitude is positively correlated with
174 average niche breadths in our study regions due to increasing influence of continental climate
175 towards east in Fennoscandia (Sweden<Finland) and towards west in the midwestern USA
176 (Minnesota>Wisconsin) (see Online Resource 1). In addition, a latitudinal gradient in average niche
177 breadth may stem from the climatic variation from the Equator towards the Poles that is also
178 mirrored in altitudinal gradient (Körner 2007). On the other hand, nutrient-rich geology is typically
179 more common at low altitudes, for which highland lakes are often less productive (Elser et al. 2007;
180 Matthews 2014). Thus, we hypothesised (H3) that increasing altitude also widens average climate
181 and water quality niche breadths of aquatic macrophytes. Species richness is expected to have a
182 negative effect on average niche breadth (H4), because competition forces species to specialise on
183 different resources or environment when the number of species increases in a region (MacArthur
184 1968; Cardinale 2011). Finally, increasing lake area is hypothesized (H5) to be related to narrow

185 average niche breadths due to more diverse habitats with more environmental specialist species
186 being found in larger lakes than in smaller ones (Rørslett 1991; Lappalainen and Soinen 2006).

187

188 **MATERIAL AND METHODS**

189

190 **Study areas and macrophyte surveys**

191

192 Our study spanned over four different areas: Finland (338 000 km²), Sweden (450 000 km²) and the
193 Midwestern USA states of Minnesota (225 000 km², hereafter Minnesota) and Wisconsin (170 000
194 km², hereafter Wisconsin) (Figure 2). All of these study areas are generally characterised by similar
195 climatic conditions with cold snowy winters and relatively warm summers. The influence of
196 continental climate increases towards east in the Fennoscandia and towards west in the Midwestern
197 USA. The majority of Finland and Sweden belong to the boreal region with coniferous forests
198 dominating their landscapes. Minnesota and Wisconsin are situated in the northern edge of the
199 temperate region, characterised mainly by a mixture of different forest types, prairie and
200 agricultural landscapes. Water bodies created by the withdrawal of ice-age glaciers form a typical
201 scenery in all four study areas, with inland surface waters covering 10 % of Finland, 9 % of
202 Sweden, 8 % of Minnesota and 17 % of Wisconsin. The number of studied lakes was 50 in all the
203 study areas. The study lakes were randomly selected from a larger database of lakes in Finland and
204 Minnesota to maintain comparability with the numbers of study lakes of Sweden and Wisconsin.

205

206 Lake macrophyte surveys were conducted between 2002 and 2008 in Finland, between 2008 and
207 2010 in Sweden, between 1992 and 2003 in Minnesota, and between 2003 and 2005 in Wisconsin.

208 The surveyed aquatic plants included both hydrophytes (i.e., isoetids, floating-leaved, elodeids,
209 ceratophyllids and lemnids) and helophytes (i.e., emergent) species. Lake macrophytes in all the
210 study areas were surveyed during the growing season (June-September) using similar transect
211 methods. Transects were distributed around the lakes and placed perpendicular to the shoreline,
212 from the upper eulittoral to the outer limit of vegetation (or to the deepest point of the basin if
213 vegetation covered the entire lake). Species were recorded from the entire transect in Finnish and
214 Minnesota lakes. Wisconsin plants were recorded within 0.25 m² squares placed every 2-3 m along
215 a transect. In Sweden, macrophytes were identified along transects in 20-cm depth intervals and in
216 plots of ca. 25 × 50 cm running in parallel with the transect along the plots' long side. The inter-
217 distance between plots varied depending on lake morphology in Sweden. In Swedish lakes with
218 steep shorelines, plots were placed consecutively to meet the requirement of 20-cm depth intervals,
219 while in shallow lakes, inter-distance between consecutive plots was tens of meters. Transect widths
220 were 6-m in Finland, 0.5-m in Sweden and Wisconsin and 5-m in Minnesota. Number of transects
221 depended on lake size and the average number of transects per lake was 15 (Min. = 10, Max. = 26,
222 SD = 4.14) in Finland, nine (Min. = 5, Max. = 14, SD = 1.98) in Sweden, 25 in Minnesota (Min. =
223 10, Max. = 42, SD = 10) and 14 (Min. = 14, Max. = 20, SD = 1.43) in Wisconsin. Sampling effort
224 did not influence the community composition of aquatic plants in the previous studies using a
225 subset of the same data (Sass et al. 2010; Alahuhta et al. 2014; Alahuhta 2015). Macrophytes were
226 surveyed or observed by wading, diving, snorkelling or by boat, using rakes and hydrosopes.
227 Macrophyte survey methods are described in detail for Finland in Alahuhta et al. (2013), for
228 Sweden in Naturvårdsverket (2010), for Minnesota in Alahuhta (2015), and for Wisconsin in Sass et
229 al. (2010). We want to emphasise that the survey methods were identical within each study area
230 (and similar among the regions), enabling us to compare general patterns across the areas (see e.g.
231 Heino et al. 2015b). With these survey methods, mean number of species per region ranged from 82
232 in Finland and 48 in Sweden to 45 in Minnesota and 66 in Wisconsin.

233

234 **Niche breaths of macrophytes and descriptions of explanatory variables**

235

236 We investigated whether average niche breadths (i.e., climate, water quality and climate-water
237 quality) varied among the macrophyte communities across each study area (Figure 1). We first used
238 Outlying Mean Index analysis (OMI, Dolédec et al. 2000) to obtain a measure of niche breadth for
239 each species in each study area (see Figure 1). This method quantifies ecological niches with regard
240 to niche breadth of species along multiple environmental gradients. The niche breadth is the extent
241 of the distribution of species along measured environmental gradients. Generalist species have a
242 wide niche breadth, occurring in wide variety of habitats, whereas specialist species are confined to
243 a narrow range of environmental conditions (Dolédec et al. 2000; Heino and Grönroos 2014). The
244 OMI analysis measures the niche breadth (i.e., tolerance) for each individual species. In our study,
245 we averaged species-level niche breadths over a lake to account for the variation in niche breadth in
246 macrophyte community composition within each lake (Figure 1). Niche breadth was calculated
247 using ADE4 package in the R environment (Dray and Dufour 2007).

248

249 We calculated average niche breadths of macrophyte communities in each study region based on
250 three explanatory variable groups: climate, water quality and combined climate-water quality
251 variables (i.e., all the variables in climate and water quality together). Climate variables were
252 comprised of mean annual temperature (°C), minimum temperature of the coldest month (°C) and
253 maximum temperature of the warmest month (°C) (Online Resource 1). The minimum temperature
254 of the coldest month was used as a proxy for harsh winter conditions, such as ice erosion, depth of
255 snow and ice cover and freezing of sediments, which strongly affect aquatic macrophytes (Lind et
256 al. 2014; Alahuhta et al. 2016b). These climate variables with a single value per variable were

257 derived from the WorldClim database (Current Conditions 1960-1990) for each lake by delineating
258 temperatures for lake surface area with the resolution of ca. 1 km² (30 arc seconds, Hijmans et al.
259 2005), and all the climate variables were processed using ArcGIS 10 (ESRI, Redlands, CA, USA).
260 Water quality variables consisted of water colour (mg Pt l⁻¹), alkalinity concentration (mg l⁻¹), and
261 total phosphorus concentration (mg l⁻¹) that have well-known effects on aquatic macrophytes.
262 Alkalinity is related to use of carbon by aquatic vegetation, whereas total phosphorus concentration
263 reflects directly trophic status of lakes (Rørslett 1991; Vestergaard and Sand-Jensen 2000; Alahuhta
264 2015). Water colour mainly mirrors water transparency, which is important determinant of
265 macrophyte growth in catchments dominated by peatlands, such as in our study regions (Sass et al.
266 2010; Alahuhta et al. 2013; Beck et al. 2013). The used variables also correlate strongly with other
267 water quality variables missing from our data, such as total nitrogen, Secchi depth, chlorophyll-a,
268 turbidity and conductivity (Heegaard et al. 2001; Elser et al. 2007; Alahuhta et al. 2012; Beck et al.
269 2013). Thus, the variables used provided a good overall representation of water quality in our study
270 lakes. These water quality variables were based on a single water sample per lake and were sampled
271 simultaneously with the macrophytes in Sweden and Wisconsin. Water quality variables obtained
272 for each lake in Finland comprised of median values of 1-m surface water samples taken during the
273 growing season (June–September) over the period 2000–2008. In Minnesota, water quality was
274 based on the average value of multiple samples (mean number of taken samples was 10 for
275 alkalinity, seven for colour and 13 for TP per lake) taken in 2004 that correlated strongly ($r_{\text{Spearman}} >$
276 0.8) with the long-term water quality averages (Alahuhta 2015). In the final variable group, we
277 combined climate and water quality variables together by using all explanatory variables in average
278 niche breadth models (i.e., average climate-water quality niche breadth).

279

280 Three different average niche breadths of species for each lake (climate, water quality and climate-
281 water quality) were studied in relation to ecological gradients representing latitude and longitude

282 (based on lake centroids), lake altitude (m a.s.l.), observed macrophyte species richness per lake and
283 lake surface area (m) within each study region (Figure 1). In addition to these ecological
284 explanatory variables, we used proportion of urban and arable land within 250m buffer zone
285 surrounding a lake to control for human impact on average niche breadths in our study (hereafter
286 ‘human impact’). Land use in the vicinity of the lake shoreline has been evidenced to have a
287 stronger effect on water quality and aquatic biota than land use within whole topographic catchment
288 area (Akasaka et al. 2010; Alahuhta et al. 2012).

289

290 **Statistical analysis**

291

292 We used linear regression models to examine the relationship between average niche breadths and
293 explanatory variables within each study area. If the response variables were not normally
294 distributed, we transformed them using log, square or square root transformations prior to further
295 analysis. We then removed explanatory variables showing bivariate correlation of $r > |0.7|$,
296 following (Dormann et al. 2013), to other explanatory variables with higher importance to average
297 niche breadths. As a result, longitude and altitude were excluded from further analysis in Wisconsin
298 (Online Resource 2). In addition, an outlier lake was deleted from Finnish average climate niche
299 breadths models. The models with the most important explanatory variables influencing the average
300 niche breadths were selected based on the second order Akaike Information Criterion (AICc)
301 among all model combinations. AICc takes into account sample size by increasing the relative
302 penalty for model complexity with small data sets, and its use is recommended if, as in our case, the
303 ratio between sample size and model parameters is less than 40 (Burnham and Anderson 2004). In
304 addition, we calculated AIC differences (Δ), which can be used to rank different models in order of
305 importance ($AIC_i - AIC_{min}$, with AIC_{min} representing the best model with respect to expected

306 Kullback-Leibler information lost). Akaike weights derived from AIC differences were estimated
307 for each model to extract additional information on model ranking. A value of $\Delta < 2.0$ was used as
308 the threshold for deviation of AICc values among candidate models (i.e., difference between model
309 *i* and the model with the smallest AICc), because models with AICc differing by < 2.0 are typically
310 considered to have similar statistical support (Burnham & Anderson, 2002). We also produced
311 adjusted R^2 values, which provide unbiased estimates of the explained variation (Borcard et al.
312 2011). The variable selection was done using the MuMin package (Bartoń 2016) in the R.

313

314 To further analyse collinearity among explanatory variables in regression models, we used
315 commonality analysis to decompose (linear) regression effects to unique and common components
316 (Nathans et al. 2012). The unique effects indicate how much variance is exclusively explained by a
317 single explanatory variable, whereas common effects represent how much variance is shared by an
318 explanatory variable set (i.e., attributed to two or more explanatory variables, Ray-Mukherjee et al.
319 2014). Thus, a higher value of common effect (i.e., the sum of all commonalities associated with a
320 predictor) compared to unique effect indicates a greater collinearity among explanatory variables
321 (Nathans et al. 2012; Ray-Mukherjee et al. 2014). Negative commonalities can occur if some of the
322 correlations among predictor variables have opposite trends (Ray-Mukherjee et al. 2014).

323 Compared to other similar statistical methods, commonality analysis is independent of variable
324 order that can bias stepwise regression and can efficiently address multicollinearity unlike
325 hierarchical regression (Petrocelli 2003; Nathans et al. 2012; Ray-Mukherjee et al. 2014). We used
326 commonality analysis on full models including all explanatory variables to gain complementary
327 information in addition to best linear models using AICc variable selection method. Beside of
328 commonality effects, we calculated beta and structure coefficients. Beta coefficients measure an
329 explanatory variable's total contribution to the regression equation (Ray-Mukherjee et al. 2014).
330 Structure coefficients are bivariate correlations between an explanatory variable and the predicted

331 dependent variable's score resulting from the regression model (Nathans et al. 2012). Unlike beta
332 coefficients, structure coefficients are independent of collinearity among explanatory variables
333 (Ray-Mukherjee et al. 2014). Commonality analysis was executed using the yhat package (Nimon
334 et al. 2013) in the R program.

335

336 Finally, we used Moran's I coefficients on 10 distance classes to account for spatial autocorrelation
337 in the response variable and residuals of the best models based on AICc. Spatial autocorrelation was
338 assessed using pgirmess package (Giraudoux 2016) in the R program.

339

340 **RESULTS**

341 **Average climate niche breadths**

342

343 Mean values of average niche breadths varied from 1.92 (SD: 0.29) in Finland and 1.34 (0.38) in
344 Sweden to 1.75 (0.42) in Minnesota and 1.69 (0.35) in Wisconsin. The best average niche breadth
345 models explained 31-38 % of variation in Finland and Minnesota, 45-47 % of variation in
346 Wisconsin and 67 % of variation in Sweden (Table 1). Among the best average niche breadth
347 models, latitude was selected in all the models in all the study regions (Figure 3, Online Resource
348 3). Climate niche breadths of Finland, Sweden and Minnesota widened with increasing latitude,
349 whereas the relationship was negative in Wisconsin (Table 1, Figure 4). However, latitude showed
350 collinearity to other explanatory variables in Sweden and Minnesota, as common effect explained
351 almost all variation in the regression models (Table 2, Online Resource 4). Human impact was also
352 included in almost all the best models in each region. The correlation between average niche
353 breadths and human impact was positive in Wisconsin and negative in all other study regions.

354 Similarly to latitude, however, the contribution of common effect was high for human impact in
355 Sweden, Minnesota and Wisconsin. Lake altitude, together with lake area, was among the most
356 important explanatory variables only in Sweden, showing a positive relationship with average niche
357 breadths. Although both of these explanatory variables showed some degree of unique effect, large
358 amounts of common effects indicated collinearity. Species richness was selected in the topmost
359 average niche breadth models solely in Wisconsin, as average niche breadths widened with
360 increasing species richness. Unique effects contributed the majority of variation for species richness
361 in Wisconsin.

362

363 Spatial autocorrelation was detected in the average climate niche breadths, as two distance classes
364 in Finland and Minnesota, and three distance classes in Sweden and Wisconsin were statistically
365 significant ($p < 0.05$, Online Resource 5). However, no spatial structure was found from the residuals
366 of best models in Sweden and Wisconsin. In Finland, the first distance class of residuals of the best
367 model showed significant spatial autocorrelation. A spatial autocorrelation was found from the
368 residuals of other best model in Minnesota; however, the amount of spatial structure was markedly
369 lower (coefficient value 0.17) compared with the original response variable (0.26 and 0.10).

370

371 **Average water quality niche breadths**

372

373 Among the lakes, average water quality niche breadths were 1.15 (0.22) in Finland, 0.91 (0.34) in
374 Sweden, 0.86 (0.20) in Minnesota and 0.78 (0.22) in Wisconsin. The amount of explained variation
375 among the best water quality niche breadth varied from 75 % in Finland and 46-51 % in Sweden to
376 18-20 % in Minnesota and 40-42 % in Wisconsin (Table 2). Latitude was among the best average

377 water quality niche breadth models in our study regions, with the exception of Minnesota (Figure 3,
378 Online Resource 3). The relationship between average niche breadths and latitude was negative in
379 study regions where it was selected as an important explanatory variable (Table 2, Figure 5).
380 However, unique effect of latitude was considerable only in Wisconsin (Table 4, Online Resource
381 4). Human impact was also included in the best models in Finland, Sweden and Wisconsin,
382 showing a positive association with average niche breadths. Unique effect of human impact was
383 large in Finland and Sweden. Longitude explained average niche breadths in Sweden and
384 Minnesota, where it was independent of collinearity. Average water quality niches widened with
385 increasing longitude in both the study regions. Altitude was selected among the best average niche
386 breadth models in Finland, Sweden and Minnesota. The correlation between average niche breadths
387 and altitude was negative in Fennoscandia and positive in Minnesota. Lake area was an important
388 variable in Finland, Sweden and Wisconsin and this explanatory variable showed both unique and
389 common effects on average niche breadths. An increase in lake area resulted in decreased average
390 niche breadths in Sweden and Wisconsin, whereas the opposite trend was found in Finland. Species
391 richness influenced average water quality niche breadths in Finland, Minnesota and Wisconsin. This
392 relationship was positive in Finland and Wisconsin as well as in Minnesota, and the common effect
393 explained the majority of variation for species richness in these study regions.

394

395 Evaluation of spatial autocorrelation revealed that average water quality niche breadth variables
396 were spatially structured, as two distance classes in Finland and Sweden, one distance class in
397 Minnesota and three distance classes in Wisconsin showed significant spatial autocorrelation
398 (Online Resource 5). However, residuals of the best regression models displayed less spatial
399 autocorrelation in all four study regions.

400

401 **Average climate-water quality niche breadths**

402

403 Average climate-water quality niche breadths across the lakes were 1.75 (0.17) in Finland, 1.20
404 (0.21) in Sweden, 1.58 (0.32) in Minnesota and 1.93 (0.40) in Wisconsin. The best models
405 explained 22-23 % of variation in Finland, 7-14 % of variation in Sweden, 35-40 % of variation in
406 Minnesota and 44-47 % of variation in Wisconsin (Table 3). The controlling factor, human impact,
407 was among the most important explanatory variables in all four study regions (Figure 3, Online
408 Resource 3). The correlation between average niche breadth and human impact was positive across
409 the regions, with the exception of Minnesota, where the relationship was negative. Human impact
410 showed collinearity to other variables in three of the four regions (Table 4, Online Resource 4).
411 Latitude was included in one or more of the best models in Finland, Minnesota and Wisconsin, but
412 the pattern varied from positive in Finland and Minnesota to negative in Wisconsin (Figure 6). The
413 unique effect of latitude was large in Finland and Wisconsin, indicating that the role of collinearity
414 was minor. Longitude explained average climate-water quality niche breadths in Finland and
415 Minnesota with opposite signs (negative in Finland and positive in Minnesota). Both unique and
416 common effects were present for longitude in both the study regions. Altitude was included in the
417 best models in Fennoscandia and Minnesota. Average niche breadths narrowed with increasing
418 altitude in Finland and widened with increasing altitude in Sweden and Minnesota. In Finland,
419 altitude showed strong collinearity but unique effects were large in Sweden and Minnesota. Lake
420 area contributed to average niche breadths in Sweden and Minnesota, with the relationship between
421 average niche breadth and lake area being positive in the former region and negative in the latter
422 region. Collinearity to other explanatory variables was indicated for lake area in Minnesota.

423

424 Detection of spatial autocorrelation varied among the study regions (Online Resource 5). However,
425 spatial structuring was found in model residuals of the best models only in Finland and Sweden,
426 where absolute coefficients were lower or equal (but only in the first-ranked model) in model
427 residuals (0.08-0.48 and 0.16) compared to original response variable (0.56 and 0.17), respectively.
428 In the Midwestern USA, no or only a modest amount of spatial autocorrelation was found in the
429 residuals of the best regression models.

430 .

431

432 **DISCUSSION**

433

434 The patterns between three different average niche breadths and ecological gradients were generally
435 variable across our four study regions. The importance of the ecological gradients varied between
436 average climate and water quality niche breadth models, often showing opposing patterns. For
437 example, altitude had a considerable influence on the water niche breadth models, while the
438 opposite was discovered for the climate models. On the other hand, different study regions
439 displayed similar patterns for some ecological gradients. For example, latitude had a significant
440 effect on the climate and water quality niche breadth models across the study regions, and a similar
441 universal pattern was discovered for human impact. Below, we consider the patterns in average
442 niche breadths and ecological gradients in relation to our *a priori* hypotheses.

443

444 Our first two hypotheses (H1 and H2) stated that increasing latitude should result in increasing
445 average climate and water quality niche breadths of aquatic macrophytes across each study region
446 (Sunday et al. 2011; Alahuhta 2015). In addition, we also expected that increasing longitude

447 increases average climate niche breadths. We found support for latitude-originated hypotheses, but
448 not for longitude. Average climate niche breadths were mostly positively associated with latitude.
449 Agreeing with MacArthur (1972), this finding indicates that aquatic macrophytes growing in lower
450 latitudes are more specialized to warmer temperatures, whereas northern generalist species are more
451 tolerant of a wider variation in climatic conditions. At high latitudes, macrophytes endure shorter
452 growing seasons and ice-related impediments, such as ice cover restricting light and carbon
453 availability in water, ice erosion and freezing of the sediments (Lind et al. 2014; Alahuhta et al.
454 2016b). Because the environmental conditions are harsh and competition in this narrower gradient
455 is greater, widening of a species niches enables the species to remain viable in such conditions.

456

457 In contrast to temperature, water quality niche breadths showed, quite unexpectedly, opposite
458 relationships with latitude. This finding suggests that aquatic macrophytes growing in lower
459 latitudes maybe specialised species adapted to nutrient-rich waters, whereas northern generalist
460 species may tolerate wider variation in water quality. This reasoning received further support from
461 the positive relationship between average water quality niche breadths and human impact across
462 study regions. In all the study regions, anthropogenic influences are strongest in the southern lakes
463 resulting in increased nutrient and alkalinity concentrations and decreasing water transparency (Sass
464 et al. 2010; Alahuhta et al. 2013; Beck et al. 2013; Alahuhta et al. 2015). In addition, a longitudinal
465 pattern in soil type is found in Minnesota, where glacial-originated nutrient-poor soils of eastern
466 ecoregions change to fine-grained nutrient-rich soils in the western parts of the state (Omernik
467 1987). These natural and anthropogenic influences lead to a widening of the water quality gradient
468 towards southern lakes and also towards the west in Minnesota. Thus, species need to have wide
469 niche breadths to tolerate extreme nutrient enrichment, which is common in the fine-grained soils
470 used for agricultural activities in the southern parts of these study areas.

471

472 Our third hypothesis (H3) stated that increasing altitude should lead to wider average climate and
473 water quality niches of aquatic macrophytes. We found no evidence to support this assumption. In
474 contrast, water quality niche breadths of aquatic macrophytes narrowed with increasing altitudes in
475 Fennoscandia, suggesting that species are specialists to nutrient enrichment in water at lower
476 altitudes, while highland species are generalists capable of growing in wider water quality
477 gradients. This pattern may reflect the fact that more productive soil types are found at lower
478 altitudes within each of our study regions (Sass et al. 2010; Alahuhta et al. 2011; Alahuhta 2015). In
479 addition, anthropogenic pressures dominate landscapes at lower altitudes, and together with
480 nutrient-rich soils, may further increase the length of the water quality gradient for lowland lakes in
481 Finland and Sweden. Altitude might be related to lake order, with species in headwater lakes
482 exhibiting different niche breadths than those in downstream lakes. However, an opposite pattern
483 was discovered for Minnesota (but not for Wisconsin), as water quality niche breadths widened
484 with increasing altitude. For climate niche breadths, altitude contributed to models only in Sweden,
485 whereas it was not selected among important variables explaining climate niche breadths in other
486 study regions. This finding suggests that variation in temperature along with the altitudinal gradient
487 was probably too modest to influence average climate niche breadths of aquatic macrophytes in
488 most of the study regions, and a larger variation in altitude may have resulted in clearer
489 relationships between average climate niche breadths and altitude.

490

491 Our fourth hypothesis (H4) predicted that species richness would have a negative effect on average
492 niche breadth, because competition forces a species to specialise in their resource utilization when
493 the number of species increases in a lake (MacArthur 1968; Cardinale 2011). However, we found
494 only a marginal support for this hypothesis. Species richness had little effect on average climate

495 niche breadths of aquatic macrophytes, and the relationship was positive for a few average niche
496 breadths in some study regions. At regional scales, species richness shows opposite patterns
497 between the continents, as regional and local species richness follows a latitudinal gradient in
498 Fennoscandian lakes (Heino and Toivonen 2008; Alahuhta et al. 2011), whereas a reversed
499 latitudinal gradient is observed in the lakes of Midwestern USA (Sass et al. 2010; Beck et al. 2013).
500 However, species richness responded differently to average niche breadths even between study
501 regions within each of the two continents. For example, species richness was positively associated
502 with average climate breadths in Wisconsin and negatively in Minnesota. These results suggest that
503 it is difficult to find universal trends between average niche breadths and species richness for
504 aquatic macrophytes. Following the reasoning behind assessing variation in average niche breadths
505 (Doledec et al. 2000), this may be due to variable degrees of competition among species in lakes
506 found in the different study regions.

507

508 Our last hypothesis (H5) assumed that increasing lake area leads to narrower average niche breadths
509 due to more diverse habitats with more environmentally specialised species being found in larger
510 lakes compared to smaller ones (Rørslett 1991; Lappalainen and Soinen 2006). We found little
511 evidence for this hypothesis, as lake area was included in the topmost climate model in Sweden and
512 in the best water quality models in Finland, Sweden and Wisconsin. Lake area is typically
513 positively correlated with aquatic macrophytes in northern latitudes (Rørslett 1991; Alahuhta et al.
514 2013; Alahuhta 2015); however, the direction of the effect in water quality models varied among
515 the study regions within the continents in our study (i.e., Finland vs. Sweden). Because lake area
516 varied strongly among the study lakes, we considered that it is not linked coherently to either
517 climate or water quality niche breadths of aquatic macrophytes. Competition among species with
518 different abilities to colonise available habitats in a lake may also have resulted in the absence of
519 congruent patterns between average niche breadths and lake area.

520

521 Evaluation of the hypotheses related to average niche breadths and ecological gradients proved to
522 be highly challenging due to variable patterns found in the different four study regions. We were
523 able to find consistent support only for the average niche breadth –latitude relationships. This may
524 be due to the fact that many of the ecological gradients examined showed collinearity, posing
525 difficulty in explaining the role of a particular gradient in the average niche breadth of aquatic
526 macrophytes. However, the processes behind these ecological gradients are often similar. For
527 example, the climatic effect typically governs latitudinal, longitudinal and altitudinal gradients.
528 Therefore, we did not consider collinearity among the ecological gradients to be a severe issue in
529 our study. Instead, competition among species with variable niche breadths in a community and
530 different degrees of competitive effects for the same species among regions probably resulted in the
531 absence of clear patterns between average niche breadths and the ecological gradients examined.
532 Interestingly, climate and water quality showed reverse patterns in the majority of study regions that
533 was further reflected in lower overall explained variations in climate-water quality models
534 compared to individual climate or water quality niche breadth models. Kockemann et al. (2009)
535 discovered that niche breadth was positively related to range size in the case of temperature, but not
536 in the case of soil-related variables. Their finding supports our conclusion that researchers cannot
537 rely on studying only one type of niche breadth when making strong conclusions about the
538 relationship of species niche breadths to ecological gradients. This also highlights the importance of
539 the availability of high-quality data, as different measures of niche breadths cannot be examined
540 using only coarse-scale data. Rather, information on species distributions and related environmental
541 conditions are needed at finer resolutions combined with broad spatial extents to better understand
542 how different species niche breadths respond to ecological gradients.

543

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Table 1. Best models on the relationship between average climate niche breadth and explanatory variables (lake coordinates, lake area, lake altitude, species richness and human impact) based on linear regression with second order Akaike's Information Criterion (AICc) variable selection algorithm and delta (Δ) < 2 for each study area. AICc difference between model i and the model with the smallest AICc, Weight: Akaike weight, adj.R²: adjusted R². \uparrow indicates positive and \downarrow negative correlation between niche breadth and the selected explanatory variable.

Variables	AICc	Δ	Weight	adj. R²	Variables	AICc	Δ	Weight	adj. R²
<i>Finland</i>					<i>Sweden</i>				
Human(\downarrow)+Y(\uparrow)	-29.6	0.00	1	0.31	Altitude(\uparrow)+Area(\uparrow)+Human(\downarrow)+Y(\uparrow)	0.6	0.00	1	0.67
<i>Minnesota</i>					<i>Wisconsin</i>				
Human(\downarrow)+Y(\uparrow)	37.5	0.00	0.68	0.38	Richness(\uparrow)+Y(\downarrow)	12.6	0.00	0.29	0.47
Human(\downarrow)	39	1.55	0.32	0.34	Human(\uparrow)+Richness(\uparrow)+Y(\downarrow)	12.6	0.06	0.28	0.48
					Y(\downarrow)	12.8	0.25	0.25	0.45
					Human(\uparrow)+Y(\downarrow)	13.5	0.92	0.18	0.46

Table 2. Best models on the relationship between average water quality niche breadth and explanatory variables (lake coordinates, lake area, lake altitude, species richness and human impact) based on linear regression with second order Akaike's Information Criterion (AICc) variable selection algorithm and delta (Δ) < 2 for each study area. AICc difference between model i and the model with the smallest AICc, Weight: Akaike weight, adj.R²: adjusted R². \uparrow indicates positive and \downarrow negative correlation between niche breadth and the selected explanatory variable.

Variables	AICc	Δ	Weight	adj. R ²	Variables	AICc	Δ	Weight	adj. R ²
<i>Finland</i>					<i>Sweden</i>				
Altitude(\downarrow)+Area(\uparrow)+Human(\uparrow)+Richness(\uparrow)	-68.7	0	0.61	0.75	Altitude(\downarrow)+Area(\downarrow)+Human(\uparrow)+Y(\downarrow)	8.5	0.00	0.26	0.51
Area(\uparrow)+Human(\uparrow)+Richness(\uparrow)+Y(\downarrow)	-67.8	0.92	0.39	0.75	Altitude(\downarrow)+Human(\uparrow)+Y(\downarrow)	9.1	0.59	0.20	0.49
					Area(\downarrow)+Human(\uparrow)+Y(\downarrow)	10.0	1.52	0.12	0.48
					Area(\downarrow)+Human(\uparrow)+X(\uparrow)+Y(\downarrow)	10.3	1.76	0.11	0.50
					Altitude(\downarrow)+Area(\downarrow)+Human(\uparrow)	10.3	1.80	0.11	0.48
					Altitude(\downarrow)+Area(\downarrow)+Human(\uparrow)+X(\downarrow)	10.4	1.90	0.10	0.50
					Human(\uparrow)+Y(\downarrow)	10.4	1.93	0.10	0.46
<i>Minnesota</i>					<i>Wisconsin</i>				
X(\uparrow)	-24.5	0.00	0.36	0.18	Area(\downarrow)+Richness(\uparrow)+Y(\downarrow)	-60.2	0	0.35	0.42

Richness(↓)+X(↑)	-24.0	0.50	0.28	0.19	Richness(↑)+Y(↓)	-60.1	0.15	0.30	0.40
Altitude(↑)+X(↑)	-23.3	1.21	0.20	0.18	Area(↓)+Human(↑)+Richness(↑)+Y(↓)	-59.2	1.02	0.20	0.42
Altitude(↑)+Richness(↓)+X(↑)	-23.0	1.49	0.17	0.20	Human(↑)+Richness(↑)+Y(↓)	-59.0	1.21	0.18	0.40

Table 3. Best models on the relationship between average climate-water quality niche breadth and explanatory variables (lake coordinates, lake area, lake altitude, species richness and human impact) based on linear regression with second order Akaike's Information Criterion (AICc) variable selection algorithm and delta (Δ) < 2 for each study area. AICc difference between model i and the model with the smallest AICc, Weight: Akaike weight, adj.R²: adjusted R². \uparrow indicates positive and \downarrow negative correlation between niche breadth and the selected explanatory variable.

Variables	AICc	Δ	Weight	adj. R ²	Variables	AICc	Δ	Weight	adj. R ²
<i>Finland</i>					<i>Sweden</i>				
X(\downarrow)+Y(\uparrow)	-41.3	0.00	0.43	0.22	Altitude(\uparrow)+Human(\uparrow)	-15.8	0.00	0.45	0.12
Human(\uparrow)+X(\downarrow)+Y(\uparrow)	-40.3	0.50	0.34	0.23	Altitude(\uparrow)+Area(\uparrow)+Human(\uparrow)	-15.3	0.49	0.35	0.14
Altitude(\downarrow)+X(\downarrow)+Y(\uparrow)	-40.1	1.22	0.23	0.22	Altitude(\uparrow)	-14.3	1.53	0.21	0.07
<i>Minnesota</i>					<i>Wisconsin</i>				
Altitude(\uparrow)+Human(\downarrow)+X(\uparrow)	11.0	0.00	0.27	0.39	Human(\uparrow)+Y(\downarrow)	19.9	0.00	0.43	0.47
Human(\downarrow)	12.0	1.99	0.16	0.35	Human(\uparrow)+Richness(\uparrow)+Y(\downarrow)	20.7	0.75	0.30	0.47
Altitude(\uparrow)+Area(\downarrow)+Human()	12.0	1.01	0.16	0.38	Y(\downarrow)	20.9	0.96	0.27	0.44
Altitude(\uparrow)+Human(\downarrow)	12.1	1.12	0.15	0.36					

Altitude(↑)+Area(↓)+Human(↓)+X(↑)	12.3	1.34	0.14	0.40
Human(↓)+Y(↑)	12.7	1.70	0.12	0.36

Table 4. Results of commonality analysis for each predictor variable based on regression models for average climate niche breadths (A), average water quality niche breadths (B) and average climate-water quality niche breadths (C) for each region. β = beta coefficients, SE = standard estimations, SC = structure coefficients, Unique = unique effect of variation for each predictor in the regression models, Common = shared effect of variation for each predictor in the regression models, and Total = combined effect (i.e., sum of unique and common effects) of variation for each predictor in the regression models. See Material and Methods for details.

A) Finland							Sweden					
Predictors	β	SE	SC	Unique	Common	Total	β	SE	SC	Unique	Common	Total
X	-0.29	4.44E-07	0.32	0.04	0.01	0.05	-0.04	4.07E-07	0.13	0.00	0.01	0.01
Y	0.63	3.53E-07	0.84	0.15	0.18	0.33	0.29	1.70E-07	0.72	0.02	0.35	0.36
Altitude	-0.02	1.53E-03	0.76	0.00	0.27	0.27	0.48	3.35E-04	0.88	0.07	0.47	0.54
Area	-0.20	4.93E-03	-0.26	0.02	0.01	0.03	0.21	4.43E-03	0.43	0.04	0.09	0.13
Richness	0.01	5.18E-03	-0.37	0.00	0.06	0.07	0.05	7.68E-03	-0.30	0.00	0.06	0.06
Human	-0.40	2.74E-03	-0.54	0.09	0.05	0.14	-0.25	2.06E-03	-0.55	0.05	0.16	0.21
Minnesota							Wisconsin					
Predictors	β	SE	SC	Unique	Common	Total	β	SE	SC	Unique	Common	Total
X	0.06	0.056	0.32	0.00	0.04	0.04	0.00	0.000	0.00	0.00	0.00	0.00
Y	0.22	0.067	0.87	0.02	0.29	0.32	-0.62	0.038	-0.94	0.20	0.26	0.46
Altitude	0.15	0.001	0.44	0.01	0.07	0.08	0.00	0.000	0.00	0.00	0.00	0.00
Area	-0.08	0.023	0.36	0.00	0.05	0.06	-0.06	0.130	-0.31	0.00	0.05	0.05
Richness	0.09	0.010	0.63	0.00	0.16	0.17	0.21	0.006	-0.21	0.04	-0.01	0.02
Human	-0.37	0.005	-0.92	0.05	0.31	0.36	0.21	0.004	0.75	0.03	0.27	0.29
B) Finland							Sweden					
Predictors	β	SE	SC	Unique	Common	Total	β	SE	SC	Unique	Common	Total
X	-0.36	3.02E-07	-0.35	0.00	0.29	0.29	0.03	4.40E-07	-0.15	0.00	0.01	0.01

Y	0.61	2.40E-07	0.62	0.00	0.12	0.13	-0.27	1.83E-07	-0.65	0.02	0.22	0.23
Altitude	-0.18	1.04E-03	0.05	0.01	0.49	0.50	-0.27	3.62E-04	-0.75	0.02	0.29	0.31
Area	-0.06	3.35E-03	0.10	0.04	0.12	0.16	-0.18	4.79E-03	-0.41	0.03	0.07	0.10
Richness	-0.05	3.52E-03	0.15	0.04	0.40	0.44	-0.07	8.31E-03	0.22	0.00	0.02	0.03
Human	0.13	1.86E-03	0.44	0.14	0.38	0.51	0.43	2.23E-03	0.75	0.16	0.15	0.31

Minnesota							Wisconsin					
Predictors	β	SE	SC	Unique	Common	Total	β	SE	SC	Unique	Common	Total
X	0.57	0.030	0.88	0.20	0.00	0.20	0.00	0.000	0.00	0.00	0.00	0.00
Y	-0.02	0.036	0.17	0.00	0.01	0.01	-0.58	0.018	-0.82	0.17	0.15	0.32
Altitude	0.18	0.001	-0.05	0.02	-0.02	0.00	0.00	0.000	0.00	0.00	0.00	0.00
Area	0.05	0.012	-0.16	0.00	0.01	0.01	-0.18	0.061	-0.43	0.03	0.06	0.09
Richness	-0.16	0.005	-0.19	0.01	0.00	0.01	0.39	0.003	0.06	0.12	-0.12	0.00
Human	0.08	0.003	-0.11	0.00	0.00	0.00	0.17	0.002	0.63	0.02	0.17	0.19

C)	Finland						Sweden					
Predictors	β	SE	SC	Unique	Common	Total	β	SE	SC	Unique	Common	Total
X	-0.04	2.23E-07	-0.62	0.07	-0.03	0.03	0.12	3.55E-07	0.01	0.00	0.00	0.00
Y	-0.05	1.77E-07	-0.40	0.14	-0.03	0.11	-0.18	1.48E-07	0.37	0.01	0.02	0.03
Altitude	-0.15	7.68E-04	-0.80	0.01	-0.01	0.00	0.45	2.92E-04	0.66	0.06	0.03	0.09
Area	0.25	2.47E-03	0.45	0.00	0.00	0.00	0.20	3.87E-03	0.47	0.04	0.01	0.04
Richness	0.26	2.60E-03	0.75	0.00	0.01	0.01	-0.07	6.70E-03	-0.43	0.00	0.03	0.04
Human	0.50	1.38E-03	0.81	0.01	0.05	0.06	0.30	1.80E-03	0.32	0.08	-0.06	0.02

Minnesota							Wisconsin					
Predictors	β	SE	SC	Unique	Common	Total	β	SE	SC	Unique	Common	Total
X	0.19	0.041	0.38	0.02	0.04	0.06	0.00	0.000	0.00	0.00	0.00	0.00
Y	0.07	0.050	0.76	0.00	0.26	0.26	-0.55	0.041	-0.94	0.16	0.30	0.45
Altitude	0.33	0.001	0.53	0.06	0.07	0.13	0.00	0.000	0.00	0.00	0.00	0.00
Area	-0.15	0.017	0.32	0.01	0.03	0.05	-0.06	0.141	-0.32	0.00	0.05	0.05
Richness	0.03	0.008	0.48	0.00	0.10	0.10	0.16	0.007	-0.28	0.02	0.02	0.04

Human	-0.45	0.004	-0.90	0.07	0.29	0.36	0.27	0.004	0.81	0.04	0.29	0.34
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Fig. 1. Conceptual model of our study using climate niche breadth as an example. Individual niche breadths are calculated for each species found in a lake (only three species as an example given in the figure) and then averaged across the whole community. For other niche breadths (i.e., water quality and climate-water quality), the concept is identical using different variables in the OMI analysis (water colour, alkalinity concentration and total phosphorus concentration for water quality models, and all seven climate and water quality variables for climate-water quality models)

Fig. 2. Maps of the study regions with investigated lakes marked with different symbols (n=50 lakes per region)

Fig. 3. Number of times a particular explanatory variable was selected in the topmost models ($\Delta < 2$) of average climate niche breadth (A), average water quality niche breadth (B) and average climate-water quality niche breadth (C) in each study region. For climate niches, the number of best models varied from one in Finland and Sweden to two in Minnesota and four in Wisconsin, whereas the number of best water quality niche models was two in Finland, seven in Sweden and four in Minnesota and Wisconsin. For climate-water quality niches, the number of best models was three in Finland, three in Sweden, six in Minnesota and three in Wisconsin

Fig. 4. The relationship between average climate niche breadths and latitude in Finland (A), Sweden (B), Minnesota (C) and Wisconsin (D)

Fig. 5. The relationship between average water quality niche breadths and latitude in Finland (A), Sweden (B), Minnesota (C) and Wisconsin (D)

Fig. 6. The relationship between average climate-water quality niche breadths and latitude in Finland (A), Sweden (B), Minnesota (C) and Wisconsin (D). Note that the latitude values differ among the regions

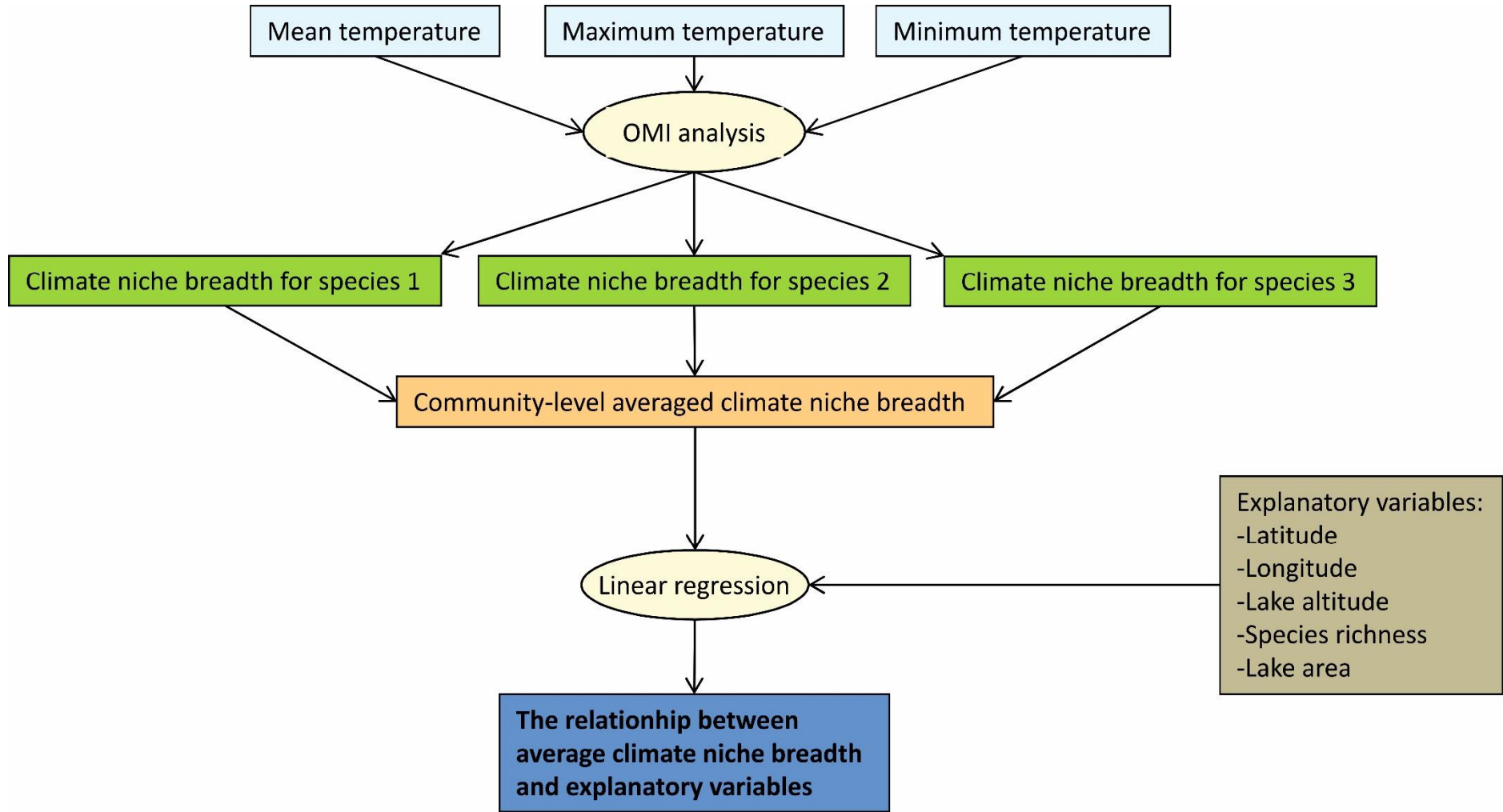


Fig. 1.

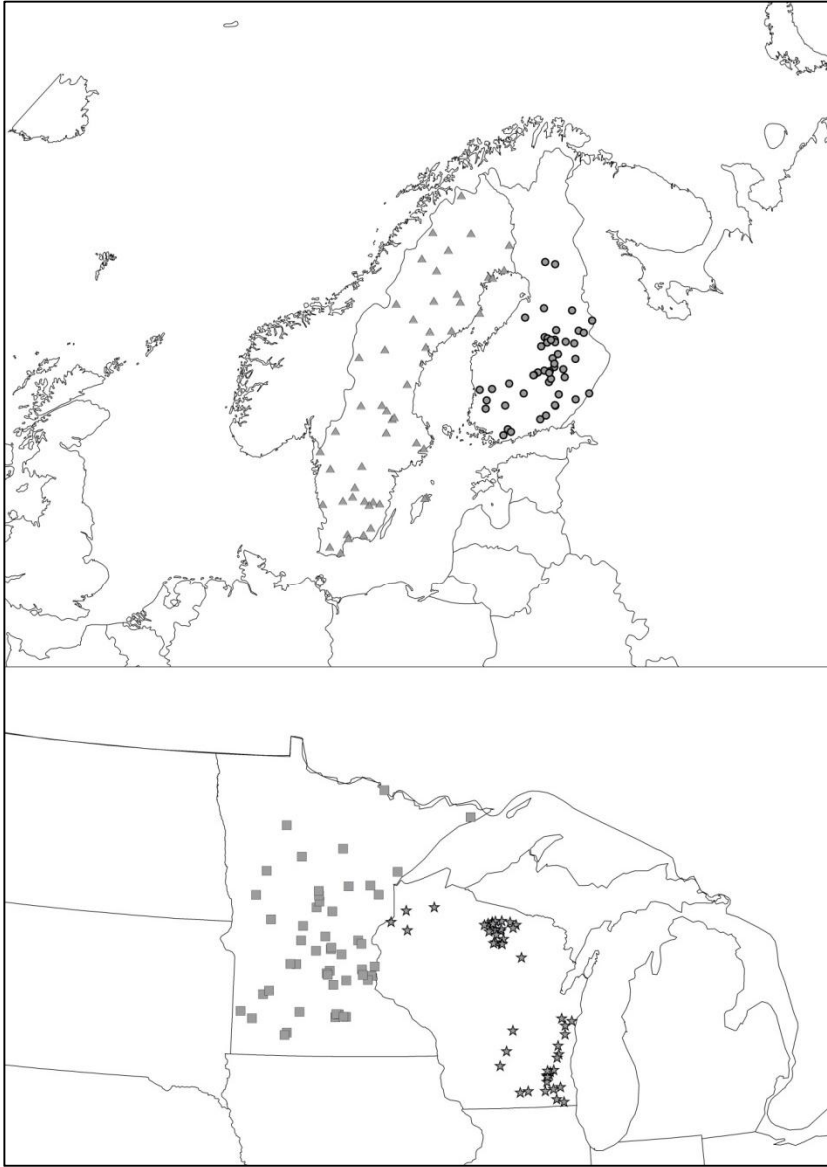
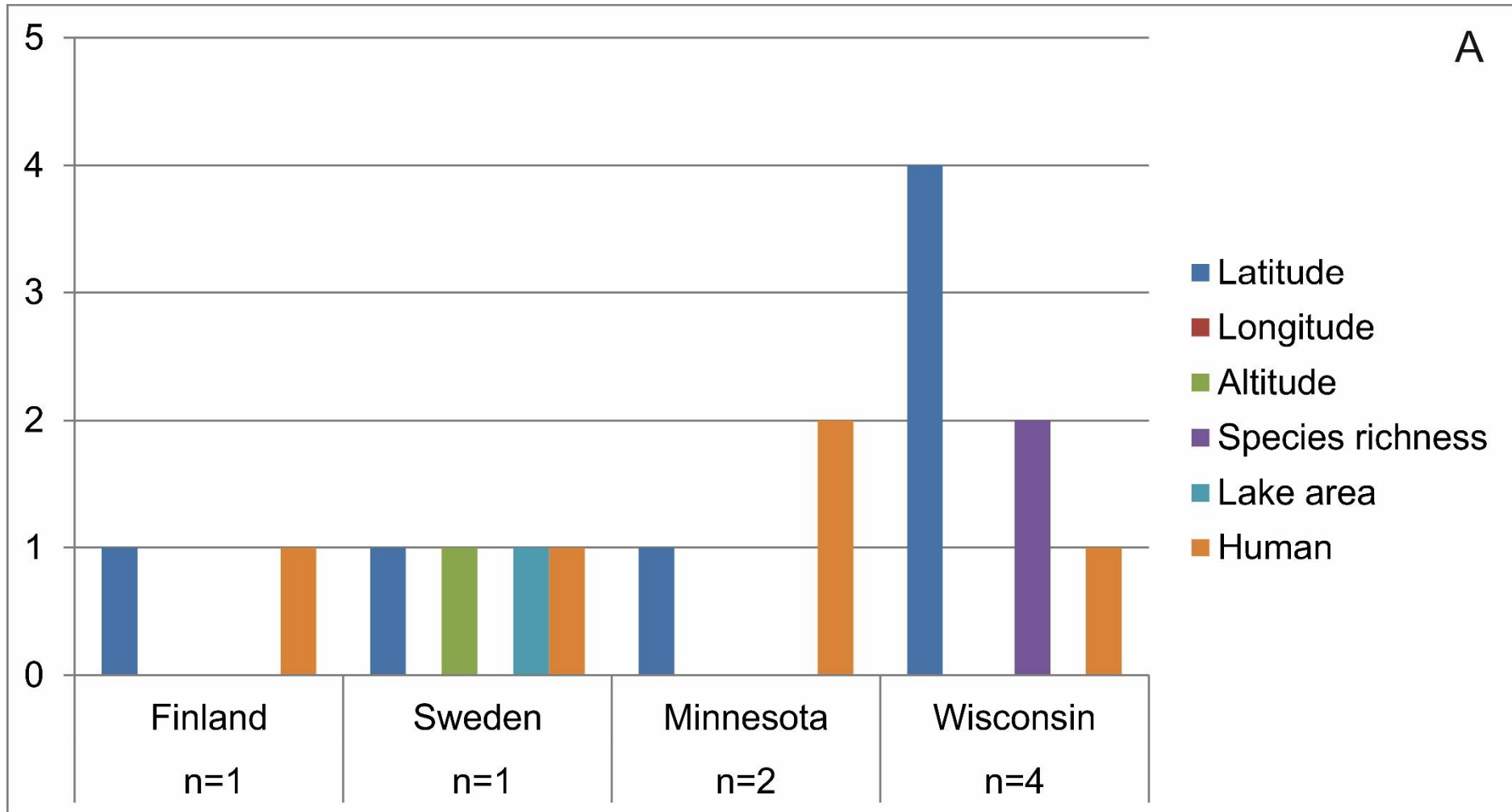
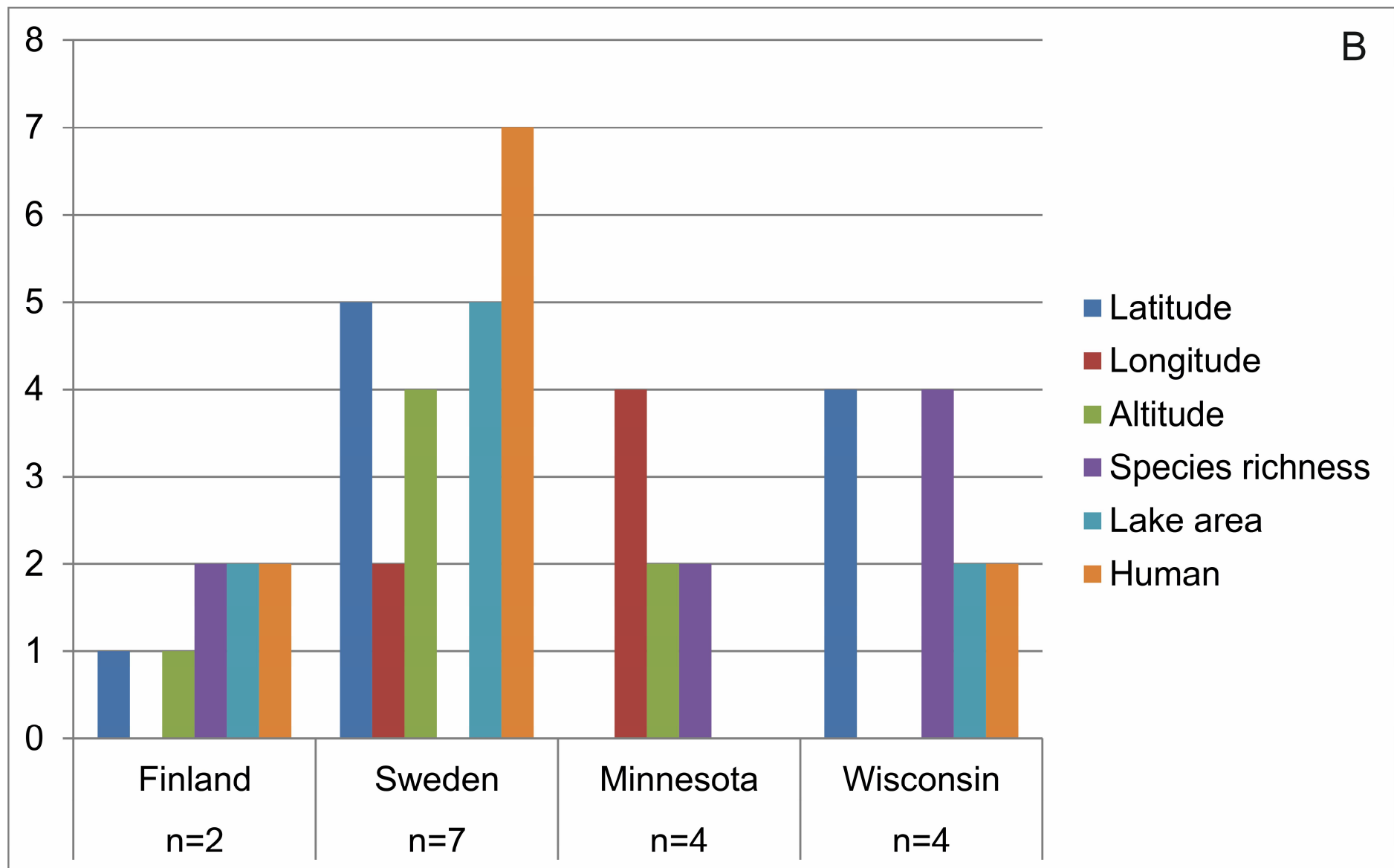


Fig. 2.

A



B



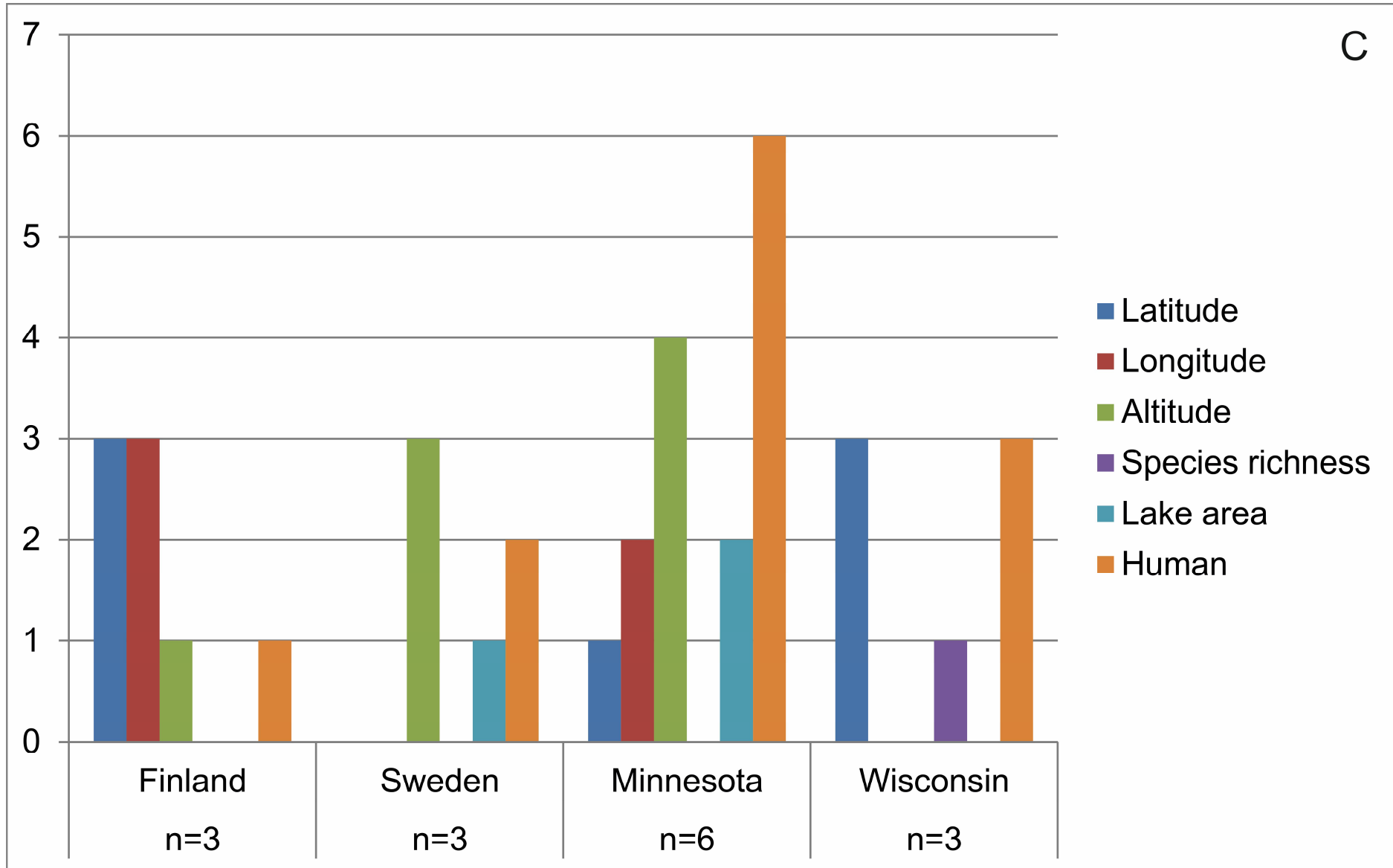


Fig. 3.

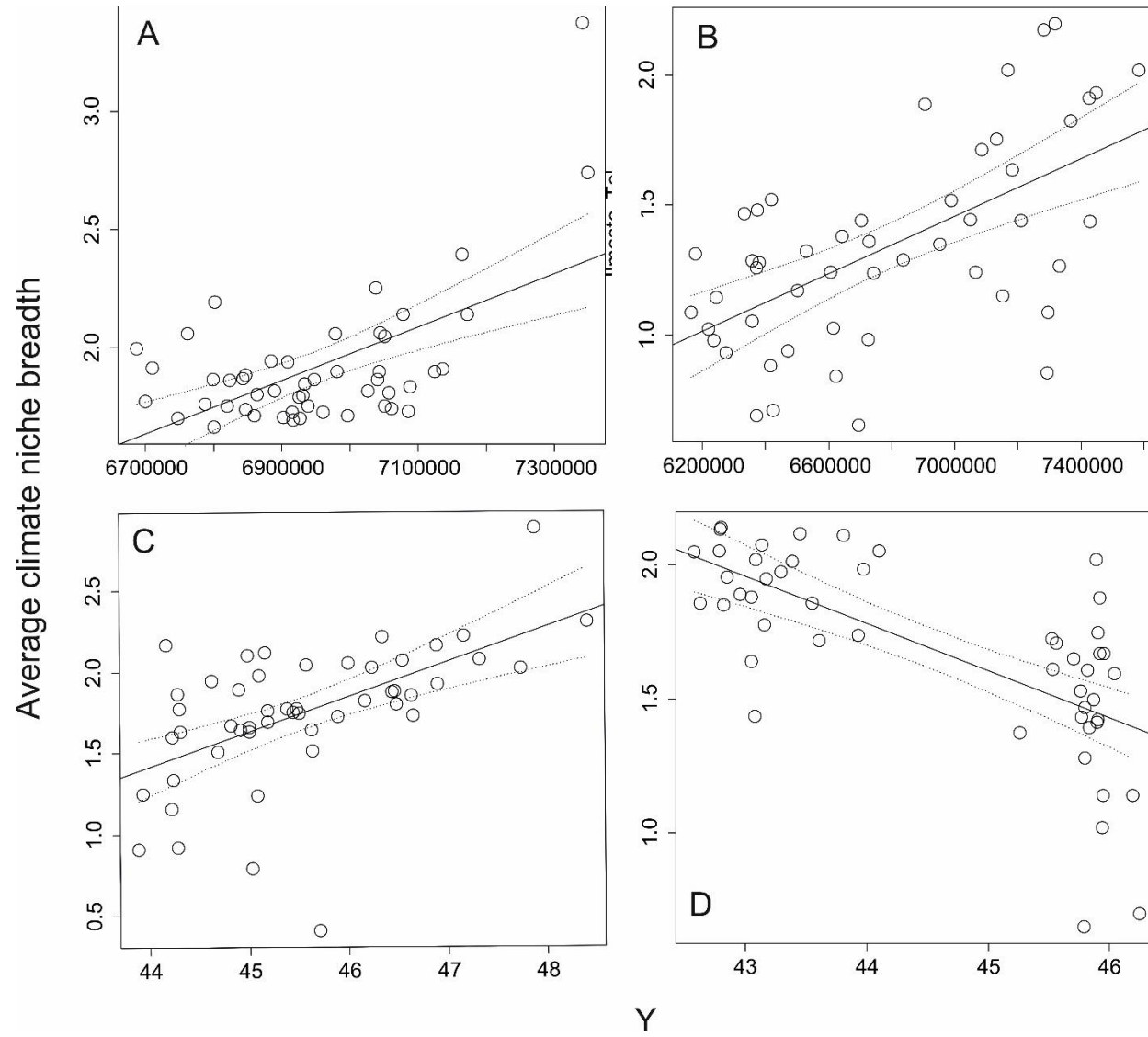
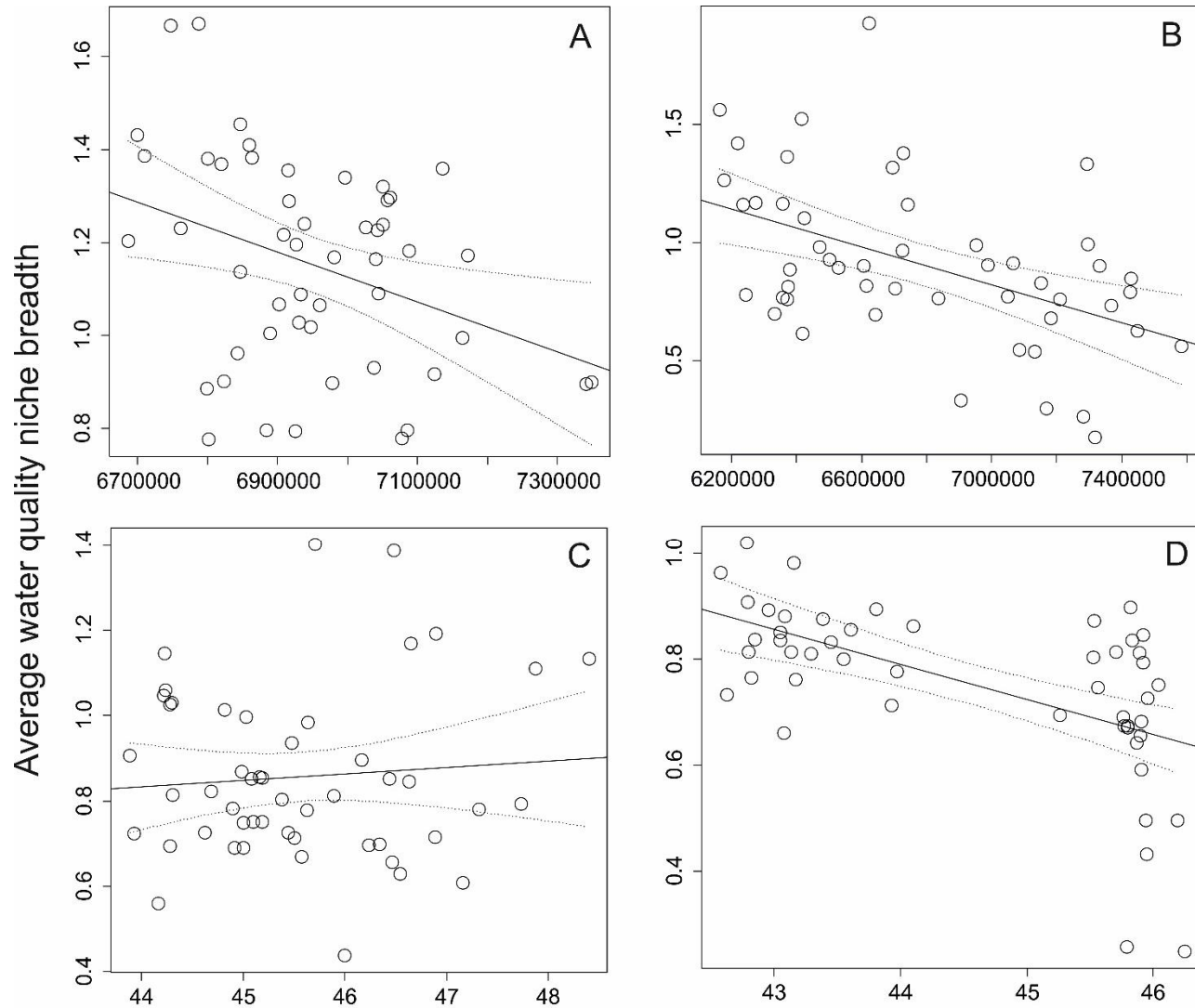


Fig. 4.



Y

Fig. 5.

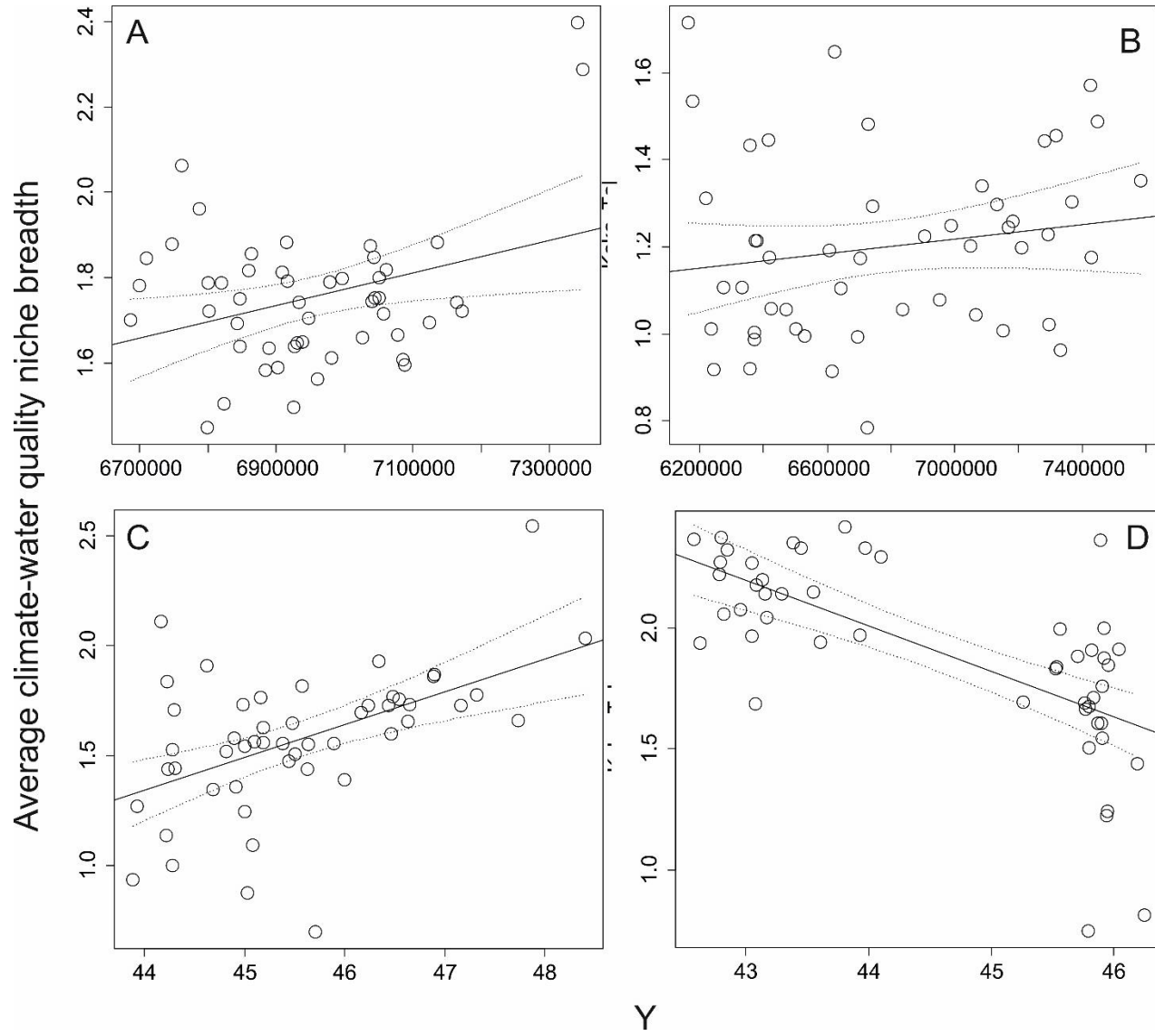


Fig. 6.

