**A comparative analysis reveals little evidence for niche conservatism in aquatic
macrophytes among four areas on two continents**

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24 SUMMARY

25 One of the most intriguing questions in current ecology is the extent to which the ecological niches
26 of species are conserved in space and time. Niche conservatism has mostly been studied using
27 coarse-scale data of species' distributions, although it is at the local habitat scales where species'
28 responses to ecological variables primarily take place. We investigated the extent to which niches of
29 aquatic macrophytes are conserved among four study regions (i.e., Finland, Sweden and the US
30 states of Minnesota and Wisconsin) on two continents (i.e., Europe and North America) using data
31 for 11 species common to all the four study areas. We studied how ecological variables (i.e., local,
32 climate and spatial variables) explain variation in the distributions of these common species in the
33 four areas using species distribution modelling. In addition, we examined whether species' niche
34 parameters vary among the study regions. Our results revealed large variation in both species'
35 responses to the studied ecological variables and in species' niche parameters among the areas. We
36 found little evidence for niche conservatism in aquatic macrophytes, though local environmental
37 conditions among the studied areas were largely similar. This suggests that niche shifts, rather than
38 different environmental conditions, were responsible for variable responses of aquatic macrophytes
39 to local ecological variables. Local habitat niches of aquatic macrophytes are mainly driven by
40 variations in local environmental conditions, whereas their climate niches are more or less
41 conserved among regions. This highlights the need to study niche conservatism using local-scale
42 data to better understand whether species' niches are conserved, because different niches (e.g., local
43 vs. climate) operating at various scales may show different degrees of conservatism. The extent to
44 which species' niches are truly conserved has wide practical implications, including for instance,
45 predicting changes in species' distributions in response to global change.

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48 INTRODUCTION

49

50 The extent to which ecological niches of species are conserved in space and time has important
51 implications for a wide variety of biogeographical, ecological and evolutionary questions (Wiens
52 and Graham 2005, Pearman et al. 2008, Warren et al. 2008). These questions range from ecological
53 specialization to predicting changes in species' distributions under global change (Wiens et al.
54 2010, Peterson 2011). For example, the reliability of predictions provided by species distribution
55 modelling is questionable if niche shifts have truly taken place in different areas (Bennett et al.
56 2010, Wiens et al. 2005, Wiens et al. 2010). The concept of niche conservatism assumes that a
57 niche of a species remains unchanged or changes only slowly over hundreds to millions of years
58 (Wiens and Graham 2005, Pearman et al. 2008). Furthermore, it assumes environmentally
59 unsuitable conditions can limit a species' geographic range when niche conservatism prevails
60 (Wiens et al. 2010). Although this concept was coined relatively recently (Peterson et al. 1999), the
61 idea of ecological niche dates back to the early 20th century (Grinnell 1917, Elton 1927). Different
62 niche concepts exist (e.g., Hutchinson 1957), including fundamental, realised and existing
63 fundamental niches (see review by Chase and Leibold 2003). A fundamental niche describes the
64 environmental conditions and resources that a species is potentially able to use, whereas the realised
65 niche represents the part of the fundamental niche that the species actually occupies as a result of
66 biotic interactions (e.g., predation, competition and parasitism). The existing fundamental niche is
67 the portion of the fundamental niche that is represented across the area accessible to the species
68 (Peterson et al. 2011).

69

70 Niche conservatism, in relation to the geographical distributions of species, is typically studied
71 using coarse grid-based data of species' ranges at broad spatial extents (Hawkins et al. 2014, Wasof

et al. 2015), while niche shifts in space and time are less frequently investigated using fine-grained data (i.e., samples from local ecosystems) at broad spatial extents (but see Bennett et al. 2010, Valdujo et al. 2013; Wasof et al. 2013). The ready availability of spatial data at medium to coarse scales provides the opportunity to examine niche conservatism with respect to climatic variation (Broennimann et al. 2007, Hawkins et al. 2014, Wasof et al. 2015); however, local habitat niche studies require fine scale data not available across large regions. Fine-grained data enables evaluating effects of the Eltonian noise hypothesis (Soberón and Nakamura 2009). This hypothesis predicts that ecological interactions and species' effects on resources define individual distributions at fine spatial scales, whereas coarse-scaled abiotic factors structure distributions at broader scales.

81

Local-scale habitat variables can strongly affect species' niche shifts even at broad spatial scales, because it is the local habitat to which species respond in the first place (e.g. Wasof et al. 2013). The phenomenon is exemplified by water acidity-related niches of freshwater diatoms which are conserved across continents (Bennett et al. 2010). In many freshwater systems, local water chemistry and habitat structure contribute equally or more strongly than climate to species' distributions and community structure at broad spatial extents (Sharma et al. 2011, Alahuhta 2015). These local habitat variables are also essential in determining species' niche parameters, because ecological gradients across freshwater ecosystems are often strong. For example, wide variation in influential chemical and physical characteristics typically exists within a small geographical area (Elser et al. 2007), and species respond to these major environmental gradients (Bennett et al. 2010, Sharma et al. 2011, Alahuhta and Heino 2013). Typically, researchers are interested in knowing how species' niche positions and niche breadths vary in relation to local habitat variables (Boulangeat et al. 2012, Wasof et al. 2013, Heino and Grönroos 2014), and potential niche shifts can be observed from differences in these habitat niche parameters for the same species across

different areas (Ackerly 2003). Species niches are probably conserved if the distribution-environment relationships are relatively similar for the same species across different study areas.

Recently, dispersal has also been included in the set of important processes affecting the relationship between realised niches and geographical distributions (Soberón 2007, Soberón and Nakamura 2009, Godsoe 2010, Peterson 2011). Dispersal is incorporated in the concept of spatial processes, which depending on their dispersal abilities and possible geographical barriers allows species to track variation in suitable habitats (Heino and de Mendoza, 2016). Species disperse among suitable habitats that are structured as a network of habitat patches, varying in area, degree of isolation and quality, surrounded by unsuitable habitats in the landscape (Hanski 1998, Leibold et al. 2004). Spatial processes can constrain species' responses to environmental variability, thus relating directly to niche conservatism (Wiens et al. 2010). Spatial processes are especially important in lake systems, because adaptation to living in water leads to the formation of well-delimited populations surrounded by an inhospitable terrestrial matrix (Dahlgren and Ehrlén 2005, Hortal et al. 2014). Lake macrophytes are a particularly suitable organismal group for the study of spatial variability because these plants cannot actively move and have strong spatial structure even within lake habitats (Nilsson et al. 2010, Arthaud et al. 2013). To date, it has been assumed that the ecological niches of aquatic macrophytes remain unchanged in space (Chambers et al. 2008), although no actual study has investigated whether or not the niches of aquatic macrophytes are conserved at broad spatial extents.

Our study examines whether or not niches of aquatic macrophytes are conserved between different geographical areas. Our primary aim is to investigate how ecological variables (i.e., local, climate and spatial) explain variation in the distributions of common aquatic macrophyte species in four

120 areas (i.e., Finland, Sweden and the US states of Minnesota and Wisconsin) on two continents
121 (Europe and North America). Our study adds on the work of Bennett et al. (2010) in investigating
122 niche conservatism across different areas and continents, a key aspect of environmental influence
123 on species' distributions and biological communities. That study focused exclusively on a pH
124 gradient across geographic extent and addressed multiple diatom species compositions among
125 several areas. In contrast, we examined a common set of 11 species across the four study areas
126 using multiple lake morphology, water chemistry and climate variables as predictors to assess the
127 extent to which the same species respond to major ecological variables. We also tested whether the
128 strength of ecological variables was consistent among different species and study areas. In addition,
129 we studied whether each species' niche parameters (i.e., niche position and breadth) vary among the
130 study areas. Based on the general assumption of conserved niches for aquatic macrophytes
131 (Chambers et al. 2008), we expected that the majority of individual species would respond similarly
132 to ecological variables in the four study areas. We also hypothesized that each species responds
133 primarily to local and climate variables, because dispersal limitation is not assumed to restrict
134 macrophyte distributions until at very broad spatial extents (Santamaria 2002, Alahuhta and Heino
135 2013). We further assumed that species' niche positions remain relatively similar in different study
136 areas and that niche breadths are fairly wide for all species in all study areas.

137

138 **MATERIALS AND METHODS**

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140 **Study areas and macrophyte species**

141

142 Our study was conducted within four different areas: Finland (338 000 km²), Sweden (450 000
143 km²) and the Midwestern US states of Minnesota (225 000 km², hereafter Minnesota) and
144 Wisconsin (170 000 km², hereafter Wisconsin) (Fig. 1). These four distinct study areas show a clear
145 east-west orientation. Finland and Sweden (east from the Atlantic Ocean) are situated in Northern
146 Europe, and are under the influence of the Gulf Stream, thus having a warmer climate compared to
147 other areas at similar latitudes. Continental climate dominates the inland study areas including
148 Minnesota and Wisconsin (west from the Atlantic Ocean). In addition to these major climatic
149 differences, both Finland and Minnesota have harsher climate conditions than Sweden and
150 Wisconsin. Thus, the study areas show clear variation in ecological conditions beyond their political
151 borders (see Table S1 in supporting information). All four areas are generally characterised by cold
152 snowy winters and relatively warm summers. Boreal coniferous forests dominate in Finland and
153 Sweden. Minnesota and Wisconsin are situated in the northern edge of the temperate region,
154 characterised mainly by a mixture of different forest types, prairie and agricultural landscapes.
155 Water bodies created by the retreat of ice-age glaciers are typical features in all four study areas,
156 with inland surface waters covering 10 % of Finland, 9 % of Sweden, 8 % of Minnesota and 17 %
157 of Wisconsin. The number of studied lakes was 60 in Finland, 59 in Sweden, 60 in Minnesota and
158 50 in Wisconsin. Where the total number of lakes available to us exceeded 60 in a study area
159 (Finland and Minnesota), the study lakes were randomly selected from a larger database of lakes
160 (see also Alahuhta et al. 2013a, Alahuhta 2015).

161

162 Lake surveys were conducted between 2002 and 2008 in Finland, between 2008 and 2010 in
163 Sweden, between 1992 and 2003 in Minnesota, and between 2003 and 2005 in Wisconsin. In all
164 four study areas, lake macrophytes were surveyed during the growing season (June-September)
165 using similar transect methods. Transects were distributed around the lakes and placed
166 perpendicular to the shoreline, from the upper eulittoral to the outer limit of vegetation (or to the

167 deepest point of the basin if vegetation covered the entire lake). Species were identified from the
168 entire transect in Finnish and Minnesota lakes. In Wisconsin, plants were identified within 0.25 m²
169 squares placed every 2-3 m along a transect, and in Sweden, macrophytes were sampled along
170 transects in 20-cm depth intervals and in plots of ca. 25 × 50 cm. Transect widths were 6-m in
171 Finland, 0.5-m in Sweden and 5-m in the US states. Number of transects depended on lake size; the
172 average number per lake was 15 (SD= 4.14) in Finland, nine (SD=1.98) in Sweden, 25 in
173 Minnesota (SD=10) and 14 (SD=1.43) in Wisconsin. Species recorded from each transect were
174 pooled as presence/absence data for each lake. All 11 studied species are relatively common and
175 easy to identify, therefore inadequate sampling effort was not considered to be a problem. In
176 previous investigations from which this study partially used the same macrophyte data, sampling
177 effort did not influence the community composition of aquatic plants (Sass et al. 2010, Alahuhta et
178 al. 2014, Alahuhta 2015). Macrophytes were sampled or observed by wading, diving, snorkelling or
179 by boat, using rakes and hydrosopes. Survey methods are described in detail for Finland in
180 Alahuhta et al. (2013), for Sweden in Naturvårdsverket (2010), for Minnesota in Alahuhta (2015),
181 and for Wisconsin in Sass et al. (2010). It is important to note that the sampling methods were
182 identical within each area. This enabled us to compare patterns among the areas (for a similar
183 broad-scale analysis using macrophytes surveyed with various methods and including partly the
184 same Finnish and Swedish macrophyte data as used here, see Penning et al. 2008, Søndergaard et al.
185 2013).

186

187 We focused on 11 macrophyte species common to all four study areas (Table S2). These species
188 have wide distributions, covering nearly the entire Northern Hemisphere (Chambers et al. 2008).
189 Although our study areas did not span the whole species' ranges, the investigated ecological
190 variables (see below) varied on average widely across the lakes in all study areas, most likely
191 encompassing ecological gradient extremes in each area (i.e., from pristine oligotrophic to eutrophic

192 water quality, from small and shallow to large and deep lakes, and from harsh winters to hot
193 summers). Thus, variation in studied ecological gradients closely mimicked environmental
194 conditions in species' entire ranges. Some species, such as *Ceratophyllum demersum*, *Phragmites*
195 *australis* and *Typha latifolia*, have more or less global distributions, being native in some areas and
196 invasive in others (Santamaria 2002). Four species (*Equisetum fluviatile*, *Phalaris arundinacea*,
197 *Phragmites australis* and *Typha latifolia*) are helophytes (i.e., plants that are rooted in submersed
198 soils or soils that are periodically inundated, with foliage extending into the air) and six species
199 (*Ceratophyllum demersum*, *Eleocharis acicularis*, *E. palustris*, *Lemna minor*, *Potamogeton*
200 *gramineus* and *P. praelongus*) are hydrophytes (i.e. submerged or free-floating macrophytes, see
201 Chambers *et al.* 2008 for detailed definitions). One species, *P. natans*, is generally a floating-leaved
202 species, but can also have submerged forms. Two genera had more than one species (*Eleocharis*
203 *acicularis* and *E. palustris*, and *Potamogeton gramineus*, *P. natans* and *P. praelongus*), enabling
204 comparisons between closely-related species and with representatives of different life forms within
205 the same genus. The studied species are quite flexible with regard to their environmental
206 requirements, growing in various habitats (see below). In addition, many aquatic macrophytes are
207 known to have efficient dispersal abilities, and often aggressively colonize new habitats
208 (Santamaria 2002). Some of the world's most notorious invasive species are indeed aquatic
209 macrophytes (Sheppard *et al.* 2005). Species' prevalence varied among the areas and was often
210 similar between geographically neighbouring study areas (Table S2). We used lake-resolution
211 presence-absence data, because macrophytes were recorded differently among the areas (e.g.,
212 frequency in Sweden and visual abundance estimates in Finland) when investigating the effects of
213 ecological variables that were originated from the same set of explanatory variables on the 11 lake
214 macrophyte species in each of the four study areas.

215

216 **Explanatory variables**

217

218 Explanatory data consisted of lake-specific local, climate and spatial variables (Table S1). Local
219 variables included lake area (km²), maximum lake depth (m), Secchi depth (indicating water
220 transparency based on a Secchi disk, m), water colour (mg Pt l⁻¹), alkalinity concentration (mg l⁻¹),
221 and total phosphorus concentration (mg l⁻¹). Water chemistry, based on a single water sample, was
222 sampled simultaneously with the macrophytes in Sweden and Wisconsin. In Finland, water
223 chemistry comprised of median values of 1-m surface water samples taken during the growing
224 season (June–September) over the period 2000–2008. Water chemistry of Minnesota was based on
225 the average value of multiple samples taken in 2004; however, these values correlated strongly
226 ($r_{\text{Spearman}} > 0.8$) with the long-term water chemistry averages (Alahuhta 2015). Climate variables
227 were lake altitude (with 25 m resolution, m.a.s.l.), mean annual temperature (°C), minimum
228 temperature of the coldest month (°C) and maximum temperature of the warmest month (°C). The
229 climate variables, with the exception of altitude, were derived from the WorldClim database for
230 each lake with the resolution of ca. 1 km² (Hijmans *et al.* 2005), and all the climate variables were
231 processed using ArcGIS 10 (ESRI, Redlands, CA, USA).

232

233 Spatial variables (i.e., those describing spatial structure among the lakes within each study area)
234 were derived from the analysis of distance-based Moran’s eigenvector maps (db-MEM, Borcard et
235 al. 2011). Spatial variables originated from db-MEMs, were orthogonal (linearly independent) and
236 were obtained from spectral decomposition of a truncated distance matrix of the spatial
237 relationships among sampling locations. The first eigenvectors represent broad-scale variation,
238 whereas the ones with small eigenvalues represent finer-scale variation (Diniz-Filho and Bini
239 2005). Eigenfunction-based procedures allow analysis at different spatial scales and are able to
240 address complex patterns of spatial variation. Significant spatial variation manifested in db-MEMs

241 may be a consequence of environmental autocorrelation, dispersal limitation or historical effects on
242 species (Dray et al. 2012). We used geographic coordinates of lake centres to calculate Euclidean
243 distances between lakes, and only positive eigenvectors were employed in additional analyses. We
244 did not use watercourse distances in calculating the geographic distance matrix between the
245 sampling locations, because spatial variables based on Euclidean overland and watercourse distance
246 can represent intricate spatial patterns in the distributions of species in glaciation-originated
247 freshwater systems with relatively stable environmental conditions equally well (Maloney and
248 Munguia 2011, Grönroos et al. 2013, Alahuhta et al. 2015). Separate db-MEM analyses using
249 minimum truncation distances were run separately for each study area (i.e., separately for Finland,
250 Sweden, Minnesota and Wisconsin). These spatial eigenvectors are specific for each study region,
251 thus cannot be directly compared across the different regions. db-MEMs were constructed using the
252 PCNM package in the R environment (Dray et al. 2006).

253

254 **Statistical analyses**

255

256 We used two methods to test for differences in *mean environmental conditions* and *heterogeneity of*
257 *environmental conditions* among the study areas. In contrast to mean conditions, heterogeneity
258 measures variation in environmental conditions within a given study area (e.g., Heino et al. 2013).
259 These analyses were done separately for standardized values of “local”, “climate” and “combined
260 local-climate” variable groups. Mean environmental conditions were investigated using Constrained
261 Analysis of Principal Coordinates (CAP; Anderson and Willis 2003) based on Euclidean distance
262 and using the factor “area” as the constraining variable. We ran an ANOVA-like permutation with
263 199 permutations to test significant separation of areas in multivariate space. Environmental
264 heterogeneity across the lakes within each study area was studied using (1) mean environmental

265 distance each lake to the study area's centroid in multivariate environmental space and (2) tests of
266 homogeneity of multivariate dispersion (PERMDISP; Anderson 2006). PERMDISP utilizes the
267 ANOVA F-statistic to compare among-group (i.e., study areas) differences in the distance from
268 observations to their group centroid. These can be illustrated in Principal Coordinates Analysis
269 (PCoA) multivariate space. Significance of among-study area differences was tested through
270 permutation of least-squares residuals. In each analysis, statistical significance was assessed based
271 on 999 permutations. CAP, PERMDISP and PCoA analysis were performed with VEGAN package in
272 the R environment (Oksanen et al. 2012).

273

274 We approached species' distributions and species' niche conservatism from two complementary
275 viewpoints: species distribution modelling (SDM) and ordinal approach (OA). The aim of the SDM
276 was to compare, among the four study regions, the relative importance of the climatic, local and
277 spatial components of the niche space on each species' distribution within a given region. For SDM,
278 we used generalized linear models (GLM) with binomial error distribution and logit link function to
279 distinguish separately the relationships between each 11 macrophyte species and explanatory
280 variable groups (i.e., local, climate and spatial variables) within the study areas. Total variation in
281 macrophyte species' distribution was partitioned into four pure and joint fractions following the
282 protocol of Anderson and Gribble (1998). The pure fractions were 1) local variables, 2) climate
283 variables, 3) spatial variables, and 4) unexplained variation, followed by the joint fractions of the
284 three explanatory groups. Variation explained by each variable group was evaluated with deviance
285 statistics and based on adjusted D^2 , equivalent to adjusted R^2 , which provides unbiased estimates of
286 the explained variation (Guisan and Zimmermann 2000). The detailed procedures required to
287 estimate these fractions are explained by Borcard et al. (2011) and Legendre et al. (2005). The
288 variable selection for each variable group was done using a built-in forward stepwise selection
289 based on parameter-strict Bayesian Information Criterion (BIC). Although the BIC is recommended

for data sets with a higher number of observations than in our data (Burnham and Anderson 2004), parsimonious models helped us to compare the results across study areas. The analyses were done with RCMDR and MODEVA packages in the R environment (Fox 2005, Barbosa et al. 2014).

In the ordinal approach, we evaluated whether local and climate niches vary among the same 11 species across the study areas using Outlying Mean Index analysis (OMI, Dolédec et al. 2000). The niche parameters from the OMI analysis consist of the OMI index (i.e., niche position) and tolerance (i.e., niche breadth). In the OMI index, species with high values of niche position have marginal niches, and species with low values of niche position have non-marginal niches (Dolédec et al. 2000, Heino and Grönroos 2014). Considering the tolerance index, generalist species have a wide niche breadth, occurring in wide variety of habitats, whereas specialist species are restricted to a narrow range of environmental conditions (Dolédec et al. 2000, Heino and Grönroos 2014). We calculated niche position and niche breadth for each of the 11 species in each study area based on three explanatory variable groups: local, climate and combined local-climate variables. We tested whether a species' niche position and niche breadth varied in relation to the other species across different areas using Spearman correlations. If a species had a marginal niche in one study area and non-marginal in relation to the other species in another area, then species' (realized) niches are probably not fully conserved (Table S1, see also Wasof et al. 2015). Niche parameters were calculated using ADE4 package in the R environment (Dray and Dufour 2007).

RESULTS

Environmental template

313 Variation in local and climate variables was high within each study area (Table S1), and mean
314 environmental conditions varied significantly among the four study areas based on the CAP
315 analysis (local variables: $F = 21.891$, $p = 0.005$; climate variables: $F = 91.334$, $p = 0.005$; combined
316 local-climate: $F = 41.315$, $p = 0.005$). Local heterogeneity based on PERMDISP analysis varied
317 significantly only between Wisconsin and the other study areas ($p = 0.001$; Fig 2). Climatic
318 heterogeneity varied significantly among the study areas ($p = 0.001$), with the exception of Finland
319 and Minnesota ($p = 0.083$). For combined local-climate variables, no statistically significant
320 difference was found between Finland and Minnesota ($p < 0.937$), whereas other areas differed
321 significantly from each other ($p < 0.033$).

322

323 **Response of macrophyte species to ecological variables in different study areas**

324 Contrary to our expectations, the same macrophyte species responded differently to ecological
325 variables in the four study areas (Table 1). Only 3 (*Ceratophyllum demersum*, *Phalaris arundinacea*
326 and *Phragmites australis*) of the 11 species studied were primarily affected by the same major
327 ecological gradient over all the four study areas based on the variation partitioning procedure. The
328 environment had the strongest effect on species' distributions in all study areas, being the most
329 important variable 18 times out of 37 (14 local and 4 climate cases). These results emphasise that
330 local variables dominate over climate constraints in affecting the distributions of aquatic
331 macrophyte species at regional extents. It should be noted that the climatic signal varied in each
332 area likely due to different study extents

333

334 The importance of local and climate variables on the studied species' distributions varied strongly
335 across study areas. Alkalinity was the most important local variable for macrophytes in all study
336 areas, but other local variables inconsistently explained species' distributions (Table 2, Table S3).

337 Of the climate proxy variables, elevation contributed greatest to macrophyte species in Finland and
338 Sweden, whereas minimum temperature of the coldest month had the highest effect on the studied
339 species in Minnesota and Wisconsin. Spatial variables with both large and small eigenvalues (SV1-
340 SV20), indicating broad- and fine-scale variation in spatial structure, were the most influential for
341 the studied species in Finland, Sweden and Minnesota. In Wisconsin, spatial variables representing
342 large scales (SV1-SV8) were most important for the species examined.

343

344 **Niche parameters: differences among species and among areas**

345 Niche positions did not remain relatively similar in different study areas, and niche breadths were not
346 especially wide for all species in all study areas (Table 3). The niche positions were correlated
347 among study areas, but correlations found for niche breadths among the study areas were low
348 (Table 4). In general, niche positions within each continent were positively correlated; however,
349 correlations were negative between the continents. For the niche breadths, species' values for
350 Finland and Sweden were weakly positively correlated based on local, climate or combined local-
351 climate conditions. Other relationships varied incongruently among the study areas.

352

353 **DISCUSSION**

354

355 Species' niches and dispersal-related processes have recently been considered when studying niche
356 conservatism in relation to their geographic distributions (Soberón 2007, Godsoe 2010, Peterson
357 2011). We followed this approach by investigating the influence of local, climate and spatial
358 variables on the distributions of 11 macrophyte species in lakes of four geographically distinct study
359 areas with a wide gradient of environmental conditions. In addition, we examined whether or not

each species had a wide or narrow niche in relation to the other investigated species in different study areas. We believe this is the first instance of a study of niche conservatism using the same set of aquatic macrophyte species with wide geographical ranges.

Contrary to our expectations, the same macrophyte species responded differently to ecological gradients across the four study areas. Only 3 of the 11 species studied were primarily affected by the same pure component across all the study areas based on the variation partitioning procedure. The environment had the strongest effect on species' distributions in all study areas in 18 of 37 occurrences (14 local and 4 climate). These results emphasise that local variables dominate over climate constraints in affecting the distributions of aquatic macrophyte species at regional extents, corroborating previous findings for entire macrophyte communities (see also Kosten et al. 2011, Alahuhta 2015).

Our study is one of the few studies where niche conservatism has been investigated using fine-grained survey data from local ecosystems within different regions and continents (see also Bennett et al. 2010, Valdujo et al. 2013, Wasof et al. 2013). Hence, we were able to associate species with the environmental factors determining their occurrence across lakes. Of the local factors, alkalinity was the most important influencing occurrence of macrophyte species, followed by the physical habitat variables (i.e., maximum depth, Secchi depth and lake area). The influence of alkalinity on macrophytes is related to the use of bicarbonate (HCO_3^-) as a source of carbon for submerged species, directly influencing photosynthesis, growth and long-term survival (Rørslett 1991, Vestergaard and Sand-Jensen 2000). For example, *Ceratophyllum demersum*, an efficient bicarbonate utilizer, was positively associated with the alkalinity across all of the study areas. We also found positive relationships with alkalinity for species that are considered to be less efficient

bicarbonate-users, such as *Lemna minor*, *Potamogeton gramineus* and *P. natans*. However, these relationships were region-specific (see also Alahuhta and Heino 2013, Alahuhta et al. 2014). Whereas alkalinity is a physiological driver that can strongly influence the distribution of some macrophyte species, habitat volume is a physical driver that determines the distribution of aquatic plants within a lake. For example, the depth gradient determines the extent of the littoral zone and strongly affects both submerged and emergent macrophytes, whereas lake area affects more emergent macrophytes (Rørslett 1991, Toivonen and Huttunen 1995, Dahlgren and Ehrlén 2005).

391

Previous niche conservatism studies have mostly examined shifts in climate niches (Hawkins *et al.* 2014, Wasof et al. 2015); however, we found that climate variables contributed less than local variables to the distribution of aquatic macrophytes. Minimum temperature of the coldest month, a proxy for winter shoreline disturbance, had the strongest effect on the distributions of macrophyte species. The relationship between species' distributions and minimum temperature was mostly negative in all the study areas. This is surprising because many helophytes are especially vulnerable to ice-related disturbances (Lind et al. 2014). On the other hand, increase in annual temperature and maximum temperature of the warmest month enhanced occupancy of many macrophyte species. These findings suggest that a longer and warmer growing period contributes to the distributions of macrophyte species, while winter-time shoreline disturbance apparently does not restrict the distributions of studied species. In addition, elevation was negatively related to species distributions, suggesting that the degree of occupancies of many macrophyte species is restricted at high elevations with more extreme climate conditions (Alahuhta et al. 2013b).

405

Although environmental variables strongly influenced macrophyte species' distributions, spatial processes were, quite unexpectedly, also rather important for many macrophyte species. We found

408 that pure spatial fraction contributed most to species' distributions in 16 of 38 cases. Spatial
409 variables can indicate geographically-structured environmental variables missing from the models,
410 historical effects or dispersal limitation on species' distributions (Dray et al. 2012). Our models
411 included many of the most important environmental variables for our target species (Rørslett 1991,
412 Vestergaard & Sand-Jensen 2000, Sass et al. 2010, Mikulyuk et al. 2011). Historical effects are
413 unlikely to influence macrophyte distributions, as many species were known to have rapidly
414 colonized potential habitats after the previous glaciation period (Sawada et al. 2003, Väliiranta
415 2006). Dispersal limitation has sometimes been the key factor structuring aquatic macrophyte
416 communities (e.g., Capers et al. 2010, Padial et al. 2014). Thus, we suggest that spatial processes
417 may also affect the distribution of lake macrophytes, as has been suggested previously (Dahlgren
418 and Ehrlén 2005). However, compared to emergent plants, the distributions of submerged and free-
419 floating species were found to be more strongly influenced by geographical connectivity of lakes
420 (Dahlgren and Ehrlén 2005). In our work, the distributions of the helophytes *Phalaris arundinaceae*
421 and *Phragmites australis* were uniformly affected by spatial variables, whereas no congruent
422 pattern was found for the other species. These incongruent results may be related to different study
423 extents (a single river basin in Dahlgren and Ehrlén 2005 and multiple river basins in our study),
424 and potential dispersal limitation of these species among highly eutrophic lakes in Minnesota and
425 Wisconsin. The latter reasoning is also indirectly supported by previous research on Midwestern
426 macrophytes (Sass et al. 2010, Alahuhta 2015). Finally, the distribution of these helophyte species
427 is geographically restricted in the most northern latitudes of Fennoscandia (Alahuhta et al. 2013b).

428

429 Possible dispersal limitation of these macrophyte species is also related to the Eltonian noise
430 hypothesis, which posits that a species may be absent from a habitat within its environmental niche
431 because of dispersal barriers or biotic interactions (Soberón 2007). Moreover, these ecological
432 interactions and species' effects on environmental resources may define distributions at fine spatial

scales, whereas coarse-scaled abiotic factors (e.g., climate) structure distributions at broader scales, where the effects of species' interactions are lost as statistical noise (Soberón and Nakamura 2009, Peterson et al. 2011). If *P. arundinaceae* and *P. australis* are truly dispersal-limited due to the spatial distribution of eutrophic lakes in the Midwestern and the restrictive climatic conditions of northern latitudes in Fennoscandia that create dispersal barriers for the plants, it further suggests that the Eltonian noise hypothesis may hold for these species studied using fine-resolution lake data. However, this assumption is purely speculative. Hence, a study focussed on evaluating whether or not the Eltonian noise hypothesis is true for aquatic macrophyte species is sorely needed.

441

442 **Niche shifts or conservatism?**

443

We found surprisingly little evidence for niche conservatism in the distributions of the 11 macrophyte species among the four study areas. We assumed that, if species' niches are conserved, the distribution-environment relationships would be relatively similar for the same species between study areas. However, none of our results explicitly supported this expectation. We did find that species were mostly affected by same climate variables (see SDM, Table 3), and climate niche positions were positively related (see OA, Table 4) between study areas within both continents. Wasof et al. (2015) similarly discovered that climate niche parameters indicated niche conservatism for terrestrial vascular plants between Fennoscandia and the Alps. However, we found no similar patterns across all study areas and local variables. Instead, species actually responded incongruently to the local variables, and this outcome persisted whether species were closely-related or not. In addition, the same niche parameters were not correlated, or were even negatively correlated among the study areas. This finding suggests that the same species may have a wide niche breadth and/or

456 non-marginal niche position in one area and a narrow niche breadth or marginal niche position in
457 another area relative to the niches of the other species studied.

458

459 Niche characteristics may be more strongly related to the mean environmental conditions than
460 anticipated; in our study, these differed widely among the study areas. Likely due to different
461 latitudinal gradients, climate heterogeneity and overall environmental heterogeneity were also
462 distinguished between the two continents, but local heterogeneity overlapped among study areas
463 (Fig. 2). Heterogeneity measures based on average environmental distance from lakes to a region's
464 centre represent environmental heterogeneity in a region (Heino et al. 2013, Bini et al. 2014). This
465 suggests that *variation* in local environmental conditions is similar among the study areas. Thus,
466 different responses of the same species to local environmental conditions may not be due to
467 differences in environmental heterogeneity among the study areas, but rather, are more likely due to
468 region-specific niche shifts in aquatic macrophytes in relation to local environmental conditions. A
469 similar finding has been made for understorey plants of temperate forests (Wasof et al. 2013). Non-
470 significant or even negative correlations among study areas in niche positions are in contrast to the
471 idea of conserved niches, which are suggested by our OA comparisons. Local environmental
472 conditions are dependent on natural characteristics (e.g., catchment geology and soil properties) and
473 land use activities, both of which show more fine-scaled variation than the coarser geographical
474 patterns in climate conditions (Elser et al. 2007). Many of the aquatic macrophytes we studied have
475 global or multi-continental ranges (Chambers et al. 2008), indicating lack of strong climatic control
476 on the distributions of these species, even at broad geographical extents. In the case of weak
477 climatic effects, the importance of local habitat conditions should gain more importance. Thus, it is
478 likely that the climate niches of aquatic macrophytes are more or less conserved, whereas the local
479 niches of those species are more likely to be driven by variations in local environmental conditions
480 that interact with spatial processes in each region. Our findings emphasise that different niches may

481 show various degrees of conservatism, and that more effort should be placed on investigating local
482 niches. A similar call to investigate species' distributions by combining broad spatial extent and
483 local resolution has been given, for example, for biotic interactions (Witz et al. 2013), climate
484 change modelling (Ackerly et al. 2010) and phylogenetic diversity (Ulrich et al. 2014).

485

486 Our findings include some degree of uncertainty which needs to be acknowledged. Using simulated
487 data, Soberón and Peterson (2011) demonstrated that the same fundamental niche expressed in
488 different regions with corresponding distinct environmental conditions will produce different
489 existing fundamental niches, and therefore, in all likelihood, different realised niches, even in the
490 absence of competitors and evolutionary processes. This result is essentially related to the definition
491 of existing niche, from which two outcomes can be drawn for our study (Peterson et al. 2011). First,
492 existing niches will be different and will indicate niche shifts, but only as a function of the part of
493 the fundamental niche that is observable. Alternatively, the environmental conditions across the
494 study area are taken into account, and the environments available to the species are used differently
495 between various regions. Irrespective, we are not able to evaluate the possibility of the latter
496 outcome due to different field survey methods (for both macrophyte and environmental variables)
497 among the regions which prevented us from pooling data across data sets. In addition, we employed
498 a random selection of 60 lakes in Finland and Minnesota from a larger population of lakes which
499 narrowed the environmental gradients compared to whole lake data sets. However, the patterns
500 detected would not have been comparable across the study regions if a largely different number of
501 lakes were analysed among the regions. Comparability of patterns across regions would also be
502 jeopardised if randomization were to be based on multiple replication of 60 randomly selected lakes
503 in one area and matched with a single smaller set of lakes in another area.

504

505 There are at least three reasons for the potential lack of niche conservatism in macrophytes: an
506 unsuitable or incomplete set of explanatory variables, genetic variation, or phenotypic plasticity
507 within species. We emphasise, similarly to Wasof et al. (2013), that the explanatory variables used
508 are directly associated with actual ecological mechanisms, which determine the niche for each of
509 the macrophyte species (Rørslett 1991, Toivonen and Huttunen 1995, Vestergaard and Sand-Jensen
510 2000). In addition, the high degrees of unexplained variation using modern statistical methods are
511 commonly reported for various freshwater species and communities (Mikulyuk et al. 2011,
512 Grönroos et al. 2013, Alahuhta 2015, Heino et al. 2015). This leaves us the explanations related to
513 genetic variation and phenotypic plasticity within species. In general, genetic variation may explain
514 niche shift between continents, whereas phenotypic plasticity may be a more important factor in
515 within-continent comparisons (e.g., Ackerly 2003). Macrophytes are typically associated with
516 moderate overall genetic variability, and low within-population, but high among-population genetic
517 variation (Santamaria 2002). However, considerable variability in genetic variation seems to exist
518 among functional groups and species. High genetic variation has been found for many helophytes,
519 whereas hydrophytes have been displayed widespread genetic monomorphism (Barrett et al. 1993).
520 On the other hand, high levels of phenotypic plasticity have been reported for aquatic macrophytes
521 (Santamaria 2002, Eller and Brix 2012). Thus, we assume that phenotypic plasticity is the main
522 explanation behind the lack of niche conservatism across our study areas, although genetic variation
523 may also affect helophytes. More research is needed, however, to confirm assumptions because
524 phenotypically plastic species traits causing incongruent results across our study areas can
525 theoretically still be evolutionarily conserved.

526

527 Our main finding that niches of lake macrophytes may not be conserved over space and time has
528 various ecological implications. Modelling the distributions of invasive species and those of species
529 assumed to respond to climate change is based on the idea that niches are conserved (Wiens et al.

2005, Wiens et al. 2010). If niche shifts have truly taken place in different areas, the reliability of predictions provided by modelling exercises is therefore in question. The accuracy of biological conservation plans and strategies may also need to be updated to account for possible niche shifts in species' distributions. Threatened species may be under severe extinction risk if invasive species' modelled distribution ranges are misleading due to the false assumption that species' niches are conserved. However, the invasive species in our work (*Phragmites australis* and *Phalaris arundinacea* in the North America) showed the strongest tendency towards niche conservatism, because they often tolerate varied environmental conditions and are restricted mostly by spatial processes. Conserved niches of invasive species suggest that distribution ranges modelled in previous studies considering these species are likely correct. In addition, the evaluation of environmental monitoring can become more challenging if the indicator value of the same species in relation environmental variations differs among different areas.

542

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554

555 **DATA ACCESSIBILITY**

556 Data will be published in Dryad data depository if this manuscript is accepted for publication.

557

558 **REFERENCES**

559 Ackerly, D.D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing
560 environments. – *Int. J. Plant Sci.* 164: S165-S184

561 Ackerly, D.D. et al. 2010. The geography of climate change: implications for conservation
562 biogeography. – *Divers. Distrib.* 16: 476-487.

563 Alahuhta, J. 2015. Geographic patterns of lake macrophyte communities and richness at regional
564 extent. – *J. Veg. Sci.* 26: 564-575.

565 Alahuhta, J. and Heino, J. 2013. Spatial extent, regional specificity and metacommunity structuring
566 in lake macrophytes. – *J. Biogeogr.* 40: 1572-1582.

567 Alahuhta, J. et al. 2013a. Environmental and spatial correlates of community composition, richness
568 and status of boreal lake macrophytes. – *Ecol. Indic.* 32: 172-181.

569 Alahuhta, J. et al. 2013b. Climate change and the future distributions of aquatic macrophytes across
570 boreal catchments. – *J. Biogeogr.* 38: 383-393.

571 Alahuhta, J. et al. 2014. Variable response of functional macrophyte groups to lake characteristics,
572 land use, and space: implications for bioassessment. – *Hydrobiologia* 737: 201-214.

573 Alahuhta, J. et al. 2015. Species sorting drives variation of boreal lake and river macrophyte
574 communities. – *Community Ecol.* 16: 76-85.

- 575 Anderson, M.J. 2006. Distance-Based Tests for Homogeneity of Multivariate Dispersions. –
576 Biometrics 62: 245-253.
- 577 Anderson, M.J. and Willis, T.J. 2003. Canonical analysis of principal coordinates: a useful method
578 of constrained ordination for ecology. – Ecology 84: 511-525.
- 579 Anderson, M.J. and Gribble, N.A. 1998. Partitioning the variation among spatial, temporal and
580 environmental components in a multivariate data set. – Aust. J. Ecol. 23: 158–167.
- 581 Arthaud, F. et al. 2013. Short-term succession of aquatic plant species richness along ecosystem
582 productivity and dispersal gradients in shallow lakes. – J. Veg. Sci. 24: 148-156.
- 583 Barbosa A.M. et al. 2014. modEvA – an R package for model evaluation and analysis. R package,
584 version 0.1.
- 585 Barrett, S.C.H. et al. 1993. Evolutionary processes in aquatic plant populations. – Aquat. Bot. 44:
586 104-145.
- 587 Bennett, J.R. et al. 2010. Broad-scale environmental response and niche conservatism in lacustrine
588 diatom communities. – Glob. Ecol. Biogeogr. 19: 724-732.
- 589 Bini, L.M., et al. 2014. Nutrient enrichment is related to two facets of beta diversity for stream
590 invertebrates across the United States. – Ecology 95: 1569-1578.
- 591 Borcard, D. et al. 2011. Numerical ecology with R. Springer, New York.
- 592 Broennimann, O. et al. 2007. Evidence of climatic niche shifts during biological invasion. – Ecol.
593 Lett. 10: 701-709.
- 594 Boulangeat, I. et al. 2012. Niche breadth, rarity and ecological characteristics within a regional flora
595 spanning large environmental gradients. – J. Biogeogr. 39: 204-214.

- 596 Burnham, K.P. and Anderson, D.R. 2004. Multimodel Inference -Understanding AIC and BIC in
597 Model Selection. – Socio. Meth. Res. 33: 261-304.
- 598 Capers, R.S. et al. 2010. The relative importance of local conditions and regional processes in
599 structuring aquatic plant communities. – Freshw. Biol. 55: 952-966.
- 600 Chambers, P.A. et al. 2008. Global diversity of aquatic macrophytes in freshwater. – Hydrobiology
601 595: 9–26
- 602 Chase, J. M. and Leibold, M. A. 2003. Ecological Niches. – Chicago University Press, Chicago.
- 603 Dahlgren, J.P. and Ehrlén, J. 2005. Distribution patterns of vascular plants in lakes –the role of
604 metapopulation dynamics. – Ecography 28: 49-58.
- 605 Diniz-Filho, J.A.F. and Bini, L.M. 2005. Modelling geographical patterns in species richness using
606 eigenvector-based spatial filters. – Glob. Ecol. Biogeogr. 14: 177–185.
- 607 Doledec, S. et al. 2000. Niche separation in community analysis: A new method. – Ecology 81:
608 2914-2927.
- 609 Dray, S. et al. 2012. Community ecology in the age of multivariate multiscale spatial analysis. –
610 Ecol. Monogr. 82: 257-275.
- 611 Dray, S. and Dufour, A.B. 2007. The ade4 package: implementing the duality diagram for
612 ecologists. – J. Stat. Softw. 22: 1-20.
- 613 Dray, S. et al. 2006. Spatial modelling: a comprehensive framework for principal coordinate
614 analysis of neighbour matrices (PCNM). – Ecol. Mod. 196: 483–493.
- 615 Eller, F. and Brix, H. 2012. Different genotypes of *Phragmites australis* show distinct phenotypic
616 plasticity in response to nutrient availability and temperature. – Aquat. Bot. 103: 89-97.

- 617 Elser, J.J. et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in
618 freshwater, marine and terrestrial ecosystems. – *Ecol. Lett.* 10: 1135-1142.
- 619 Elton, J. 1927. *Animal Ecology*. – Sidgwick and Jackson, London.
- 620 Fox, J. 2005. The R Commander: A Basic Statistics Graphical User Interface to R. – *J. Stat. Softw.*
621 14: 1–42.
- 622 Godsoe, W. 2010. Regional variation exaggerates ecological divergence in niche models. – *Syst.*
623 *Biol.* 59: 298-306.
- 624 Grinnell, J. 1917. The niche-relationships of the California Thrasher. – *The Auk* 34: 427–433.
- 625 Grönroos, M. et al. 2013. Metacommunity structuring in stream networks: roles of dispersal mode,
626 distance type, and regional environmental context. – *Ecol. Evol.* 3: 4473-4487.
- 627 Guisan, A. and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. – *Ecol.*
628 *Mod.* 135: 147-186
- 629 Hanski, I. 1998. Metapopulation dynamics. – *Nature* 396: 41-49.
- 630 Hawkins, B. A. et al. 2014. Community phylogenetics at the biogeographical scale: cold tolerance,
631 niche conservatism and the structure of North American forests. – *J. Biogeogr.* 41: 23-38.
- 632 Heino, J. and Grönroos, M. 2014. Untangling the relationships among regional occupancy, species
633 traits, and niche characteristics in stream invertebrates. – *Ecol. Evol.* 4: 1931-1942.
- 634 Heino, J. et al. 2013. Environmental heterogeneity and beta diversity of stream macroinvertebrate
635 communities at intermediate spatial scales. – *Freshw. Sci.* 32: 142-154.

636 Heino, J. et al. 2015. A comparative analysis reveals weak relationships between ecological factors
637 and beta diversity of stream insect metacommunities at two spatial levels. – *Ecol. Evol.* 5:
638 1235-1248.

639 Heino, J. and de Mendoza, G. 2016. Predictability of stream insect distributions is dependent on
640 niche position, but not on biological traits or taxonomic relatedness of species. – *Ecography*,
641 in press

642 Hijmans, R.J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. –
643 *Int. J. Climatol.* 25: 1965-1978.

644 Hortal, J. et al. 2014. Perspectives on the use of lakes and ponds as model systems for
645 macroecological research. – *J. Limnol.* 73: 42-56.

646 Hutchinson, G.E. 1957. Concluding remarks. – *Cold Spring Harb. Symp. Quant. Biol.* 22: 415-427.

647 Kosten, S. et al 2011. Ambiguous climate impacts on competition between submerged macrophytes
648 and phytoplankton in shallow lakes. – *Freshw. Biol.* 56: 1540-1553.

649 Legendre, P. et al. 2005. Analyzing beta diversity: partitioning the spatial variation of community
650 composition data. – *Ecol. Monogr.* 75: 435–450.

651 Leibold, M.A. et al. 2004. The metacommunity concept: a framework for multi-scale community
652 ecology. – *Ecol. Lett.* 7: 601-613.

653 Lind, L. et al. 2014. The role of ice dynamics in shaping vegetation in flowing waters. – *Biol. Rev.*
654 89: 791-804.

655 Maloney, K. O. and Munguia, P. 2011. Distance decay of similarity in temperate aquatic
656 communities: effects of environmental transition zones, distance measure, and life histories.
657 – *Ecography* 34: 287–295.

658 Mikulyuk, A. et al. 2011. The relative role of environmental, spatial, and land-use patterns in
 659 explaining aquatic macrophyte community composition. – *Can. J. Fish. Aquat. Sci.* 68:
 660 1778–1789.

661 Miner, B.G. et al. 2005. Ecological consequences of phenotypic plasticity. – *Trends Ecol. Evol.* 20:
 662 685-692.

663 Naturvårdsverket (2010) Handledning för miljöövervakning - Undersökningstyp: Makrofyter i
 664 sjöar. Available at URL:
 665 <https://www.havochvatten.se/download/18.64f5b3211343cffddb280004851/Makrofyter+i+s>
 666 [j%C3%B6ar.pdf](https://www.havochvatten.se/download/18.64f5b3211343cffddb280004851/Makrofyter+i+s).

667 Nilsson, C. et al. 2010. The role of hydrochory in structuring riparian and wetland vegetation. –
 668 *Biol. Rev.* 85: 837-858.

669 Oksanen, J. et al. 2012. vegan: community ecology package. R package version 2.0-3. Available at:
 670 <http://CRAN.R-project.org/package=vegan>.

671 Padial, A.A. et al. 2014. Dispersal ability determines the role of environmental, spatial and temporal
 672 drivers of metacommunity structure. – *PLoS ONE* 9: e111227.

673 Pearman, P.B. et al. 2008. Niche dynamics in space and time. – *Trends Ecol. Evol.* 23: 149-158.

674 Penning, W.E., et al. 1998. Classifying aquatic macrophytes as indicators of eutrophication in
 675 European lakes. – *Aquat. Ecol.* 42: 237-251.

676 Peterson, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence. – *J.*
 677 *Biogeogr.* 38: 817-827.

678 Peterson, A.T. et al. 2011. Ecological niches and geographic distributions. Princeton University
 679 Press.

680 Peterson, A.T. et al. 1999. Conservatism of ecological niches in evolutionary time. – *Science* 285:
681 1265-1267.

682 Rørslett, B. 1991. Principal determinants of aquatic macrophyte species richness in northern
683 European lakes. – *Aquat. Bot.* 39: 173–193.

684 Santamaria, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and
685 small-scale heterogeneity in a stressful environment. – *Acta Oecol.* 23: 137–154.

686 Sass, L.L. et al. 2010. Response of aquatic macrophytes to human land use perturbations in the
687 watersheds of Wisconsin lakes, U.S.A. – *Aquat. Bot.* 93: 1-8.

688 Sawada, M., et al. 2003. The biogeography of aquatic macrophytes in North America since the Last
689 Glacial Maximum. – *J. Biogeogr.* 30: 999-1017.

690 Sharma, S. et al. 2011. The role of environmental and spatial processes in structuring native and
691 non-native fish communities across thousands of lakes. – *Ecography* 34: 762-771.

692 Sheppard, A.W. et al. 2005. Top 20 environmental weeds for classical biological control in Europe:
693 a review of opportunities, regulations and other barriers to adoption. – *Weed Res.* 46: 93-
694 117.

695 Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – *Ecol.*
696 *Lett.* 10: 1115-1123.

697 Soberón, J. and Nakamura, M. 2009. Niches and distributional areas: concepts, methods, and
698 assumptions. – *Proc. Natl. Acad. Sci. USA*, 106, 19644–19650.

699 Soberón, J. and Peterson, A.T. 2011. Ecological niche shifts and environmental space anisotropy: A
700 cautionary note. – *Rev. Mex. Biodivers.*, 82, 1348-1353.

701 Søndergaard, M. et al. 2013. Maximum growing depth of submerged macrophytes in European
 702 lakes. – *Hydrobiologia* 704: 165-177.

703 Toivonen H. and Huttunen P. 1995. Aquatic macrophytes and ecological gradients in 57 small lakes
 704 in southern Finland. – *Aquat. Bot.* 51: 197–221.

705 Ulrich, W. et al. 2014. Small-scale spatial variability in phylogenetic community structure during
 706 early plant succession depends on soil properties. – *Oecologia* 175: 985-995.

707 Valdujo, P.H. et al. 2013. Environmental correlates of anuran beta diversity in the Brazilian
 708 Cerrado. – *Ecography* 36: 708-717.

709 Vestergaard, O. and Sand-Jensen, K. 2000. Alkalinity and trophic state regulate aquatic plant
 710 distribution in Danish lakes. – *Aquat. Bot.* 67: 85–107.

711 Väliiranta, M., 2006. Long-term changes in aquatic plant species composition in North-eastern
 712 European Russia and Finnish Lapland, as evidenced by plant macrofossil analysis. – *Aquat.*
 713 *Bot.* 85: 224-232.

714 Warren, D.L. et al. 2008. Environmental niche equivalency versus conservatism: Quantitative
 715 approaches to niche evolution. – *Evolution* 62: 2862-2883.

716 Wasof, S. et al. 2015. Disjunct populations of European vascular plant species keep the same
 717 climatic niches. *Global Ecology and Biogeography*, DOI: 10.1111/geb.12375.

718 Wiens, J.J. and Graham, C.H. 2005. Niche conservatism: integrating evolution, ecology, and
 719 conservation biology. – *Annual Rev. Ecol. Evol. Syst.* 36: 519-539.

720 Wiens, J.J. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation
 721 biology. – *Ecol. Lett.* 13: 1310-1324.

722 Witz, M.S. et al. 2013. The role of biotic interactions in shaping distributions and realised
723 assemblages of species: implications for species distribution modelling. – Biol. Rev. 88: 15-
724 30.

725

Table 1. Results of variation partitioning (based on adjusted D²) using Generalized Linear Models (GLM) with binomial error distribution and Bayesian Information Criterion variable selection method. The proportion of explained variation in the distribution of each macrophyte species was divided among pure local, climate and spatial effects, along with their joint fractions (represented by $\cap$). Areas are represented as: FIN: Finland, SWE: Sweden, MN: Minnesota, WI: Wisconsin. NV indicates no variables were selected for species. NA indicates an area not applicable as the number of species observations was too low (prevalence < 5%) or high (prevalence > 95%) to provide a feasible model.

	<i>Equisetum fluviatile</i>				<i>Phalaris arundinacea</i>				<i>Phragmites australis</i>			
	FIN	SWE	MN	WI	FIN	SWE	MN	WI	FIN	SWE	MN	WI
Local	NA	10.88	0.00	NA	-2.05	NA	0.00	0.00	NA	0.00	10.65	NA
Climate	NA	0.00	11.51	NA	4.85	NA	1.48	0.00	NA	1.56	0.00	NA
Spatial	NA	36.85	0.00	NA	8.54	NA	32.65	8.50	NA	7.45	12.54	NA
Local $\cap$ Climate	NA	0.00	0.00	NA	16.19	NA	0.00	0.00	NA	0.00	0.00	NA
Local $\cap$ Spatial	NA	11.04	0.00	NA	3.50	NA	0.00	0.00	NA	0.00	0.58	NA
Climate $\cap$ Spatial	NA	0.00	16.71	NA	-1.87	NA	26.92	12.88	NA	6.36	0.00	NA
All groups	NA	0.00	5.82	NA	7.38	NA	5.25	0.00	NA	0.00	0.00	NA
Unexplained	NA	41.23	65.97	NA	63.45	NA	33.70	78.62	NA	84.63	76.23	NA
	<i>Typha latifolia</i>				<i>Ceraphyllum demersum</i>				<i>Eleocharis acicularis</i>			
	FIN	SWE	MN	WI	FIN	SWE	MN	WI	FIN	SWE	MN	WI
Local	0.00	11.01	0.00	NV	28.69	16.33	21.44	2.47	8.04	18.39	0.00	0.00
Climate	-12.43	0.00	0.00	NV	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.86
Spatial	29.03	0.00	17.62	NV	19.41	0.00	11.76	0.00	15.77	0.00	10.77	0.00
Local $\cap$ Climate	15.75	11.62	0.00	NV	0.00	6.38	0.00	6.35	0.00	0.00	0.00	0.00
Local $\cap$ Spatial	0.00	7.51	0.00	NV	2.96	0.00	8.80	0.00	-1.56	0.00	0.00	0.00
Climate $\cap$ Spatial	19.39	0.00	3.88	NV	0.00	0.00	7.54	0.00	0.00	0.00	0.00	5.16
All groups	3.10	-0.69	0.00	NV	0.00	23.57	7.80	0.00	0.00	0.00	0.00	0.00
Unexplained	45.16	70.54	78.50	NV	48.95	53.72	42.67	91.18	77.75	81.61	89.23	88.97
	<i>Eleocharis palustris</i>				<i>Lemna minor</i>				<i>Potamogeton gramineus</i>			
	FIN	SWE	MN	WI	FIN	SWE	MN	WI	FIN	SWE	MN	WI
Local	14.48	NA	0.00	0.00	14.67	9.52	0.00	4.59	7.74	0.00	6.53	4.49

Climate	0.00	NA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.83	0.00	0.00
Spatial	7.70	NA	22.74	0.08	10.14	4.25	4.35	0.00	0.00	0.00	8.73	0.00
Local $\cap$ Climate	0.00	NA	0.00	0.00	21.36	20.27	0.00	0.00	0.00	6.41	0.00	0.00
Local $\cap$ Spatial	3.29	NA	0.00	-10.65	9.93	22.73	0.00	0.00	0.00	0.00	1.47	0.00
Climate $\cap$ Spatial	0.00	NA	14.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.03	0.00
All groups	0.00	NA	0.00	17.72	3.31	-6.04	0.00	0.00	0.00	0.00	14.82	0.00
Unexplained	74.53	NA	62.68	92.86	40.61	49.27	95.65	95.41	92.26	90.76	58.42	95.51
<hr/>												
<i>Potamogeton praelongus</i>					<i>Potamogeton natans</i>							
	FIN	SWE	MN	WI	FIN	SWE	MN	WI				
Local	8.51	0.00	17.04	0.00	8.51	0.00	17.04	0.00				
Climate	0.00	8.91	0.00	0.00	0.00	8.91	0.00	0.00				
Spatial	0.00	0.00	0.00	45.10	0.00	0.00	0.00	45.10				
Local $\cap$ Climate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
Local $\cap$ Spatial	8.74	0.00	15.50	0.00	8.74	0.00	15.50	0.00				
Climate $\cap$ Spatial	0.00	14.05	0.00	0.00	0.00	14.05	0.00	0.00				
All groups	0.00	0.00	4.84	0.00	0.00	0.00	4.84	0.00				
Unexplained	82.75	77.04	62.63	54.90	82.75	77.04	62.63	54.90				

Table 2. The number of species for which the environmental variable was selected as significant and the direction of the relationship across macrophyte species in each study area. The variable selection was based on the Bayesian Information Criterion (BIC) method in Generalized Linear models (GLM).

	Finland		Sweden		Minnesota		Wisconsin	
	Positive	Negative	Positive	Negative	Positive	Negative	Positive	Negative
<i>Local variables</i>								
Alkalinity	5	0	2	1	3	0	2	0
Colour	0	0	0	2	0	0	0	0
Lake area	1	1	2	1	1	0	0	1
Maximum depth	2	0	0	0	1	0	0	1
Secchi depth	0	1	0	1	2	0	0	0
Total phosphorus	1	0	1	0	0	2	0	1
<i>Climate proxy variables</i>								
Elevation	0	3	0	3	0	1	0	0
Annual temperature	0	0	1	0	0	1	1	0
Minimum temperature	0	2	1	1	0	6	0	3
Maximum temperature	0	0	2	0	1	0	0	0

Table 3. Niche position and breadth of species in three variable groups (local, climate and environmental (i.e., local and climate combined)) across four study areas. A dash (“-”) represents less than three observations in a study area, hence niche parameters were not calculated for that species. A double asterisk (“**”) indicates that species showed a significant deviation of their niche position from the origin.

	Finland			Sweden			Minnesota			Wisconsin		
Niche position	Local	Climate	Environment	Local	Climate	Environment	Local	Climate	Environment	Local	Climate	Environment
<i>Equisetum fluviatile</i>	0.00	0.00	0.00	0.04	0.02	0.06	0.97	4.00**	4.97**	1.10	1.62	2.72
<i>Phalaris arundinacea</i>	1.80**	0.86	2.66**	-	-	-	0.38**	0.83**	1.22**	2.37	2.36	4.73
<i>Phragmites australis</i>	0.01	0.00	0.01	0.03	0.08**	0.11**	0.93	0.84	1.77	-	-	-
<i>Typha latifolia</i>	0.96**	2.44**	3.40**	2.06**	1.62**	3.68**	0.04	0.08	0.13	0.89	0.06	0.95
<i>Ceratophyllum demersum</i>	3.70**	0.39	4.08**	4.43**	3.17**	7.60**	0.09**	0.06**	0.15**	0.20**	0.16	0.36**
<i>Eleocharis acicularis</i>	0.11	0.02	0.12	0.53**	0.07	0.60	0.71	0.26	0.97	0.08	0.15**	0.23**
<i>Eleocharis palustris</i>	0.27**	0.04	0.30	-	-	-	0.63	1.63**	2.26**	0.89	0.48	1.37
<i>Lemna minor</i>	1.41**	0.29**	1.70**	4.74**	2.48**	7.22**	0.32	0.06	0.38	0.34	0.03	0.37
<i>Potamogeton gramineus</i>	0.75**	0.11	0.86	0.58	0.76**	1.35**	1.48**	1.40**	2.89**	0.13	0.01	0.15
<i>Potamogeton praelongus</i>	1.22	0.01	1.24	1.47**	1.05	2.52**	0.76	0.83**	1.59	0.11	0.26	0.37
<i>Potamogeton natans</i>	0.15**	0.02	0.17**	0.07	0.29**	0.36**	2.83**	0.28	3.11**	0.12	0.25	0.37
Niche breadth	Local	Climate	Environment	Local	Climate	Environment	Local	Climate	Environment	Local	Climate	Environment
<i>Equisetum fluviatile</i>	1.70	2.02	1.49	1.30	0.38	0.93	2.98	1.91	3.55	1.57	1.94	3.30
<i>Phalaris arundinacea</i>	0.47	2.27	1.15	-	-	-	2.06	0.64	1.54	0.13	0.12	0.20
<i>Phragmites australis</i>	1.53	0.51	1.57	2.07	2.18	3.02	1.21	2.32	3.11	-	-	-
<i>Typha latifolia</i>	1.80	1.75	2.10	1.62	0.50	1.20	1.96	2.83	3.68	2.19	1.17	1.66
<i>Ceratophyllum demersum</i>	1.06	1.16	1.33	0.21	0.56	0.39	0.88	1.45	0.98	1.30	3.26	3.43
<i>Eleocharis acicularis</i>	1.13	2.26	0.79	0.54	2.64	1.03	2.03	2.94	1.70	1.23	3.17	3.72
<i>Eleocharis palustris</i>	1.40	2.25	1.76	-	-	-	0.66	1.77	1.87	2.03	2.32	3.16
<i>Lemna minor</i>	1.49	1.65	1.69	0.54	0.79	0.46	1.49	0.60	1.77	0.71	2.75	1.09
<i>Potamogeton gramineus</i>	1.88	1.77	2.32	1.05	2.57	1.95	1.32	1.98	2.06	0.72	2.10	0.86
<i>Potamogeton praelongus</i>	1.03	0.07	0.99	2.01	1.62	2.27	1.11	2.34	2.20	0.43	2.78	2.57
<i>Potamogeton natans</i>	2.01	1.75	2.14	1.07	0.92	1.27	1.09	2.89	1.49	0.75	2.30	1.80

Table 4. Spearman correlations for niche position across all species and niche breadth across all species between the study four areas. An Asterisk (“*”) indicates a P-value < 0.05.

		Niche position			Niche breadth		
		Finland	Sweden	Minnesota	Finland	Sweden	Minnesota
Local variables	Finland						
	Sweden	0.93*			0.15		
	Minnesota	-0.65*	-0.70*		-0.01	0.08	
	Wisconsin	0.16	0.14	-0.36	0.24	0.02	0.38
Climate variables	Finland						
	Sweden	0.82*			0.08		
	Minnesota	-0.56	-0.75*		-0.05	0.43	
	Wisconsin	-0.28	-0.40	0.49	-0.31	0.45	-0.07
Combined local-climate variables	Finland						
	Sweden	0.97*			0.22		
	Minnesota	-0.66*	-0.83*		0.18	0.38	
	Wisconsin	0.15	-0.14	0.12	-0.83*	-0.36	-0.33

Figure 1. The location of the lakes studied in each study area, along with the location of Great Lakes in the Midwestern United States. See “Study areas and macrophyte species” for study area details.

Figure 2. Environmental variation (A: local, B: Climate, and C: combined local-climate) within and among study areas (Finland, Sweden, Minnesota and Wisconsin) as illustrated by Principal Coordinates analysis (PCoA) plots. Variation in local gradients differs among the studied

areas, suggesting that local niches may not be conserved. Oppositely, climate conditions overlap within study areas in both continents, for which climate niches are likely conserved.