

Regional and local determinants of macrophyte community compositions in high-latitude lakes of Finland

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15 **KEYWORDS:** Ancylus Lake, Aquatic plants, Finland, Glaciation, Grime's plant strategy,

16 Macrophytes, Species traits, Supra-aquatic lakes

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19 **ABSTRACT**

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21 Species distributions are structured by regional and local determinants, which operate at multiple
22 spatial and temporal scales. The purpose of our work was to distinguish the relative roles of local
23 variables, climate, geographical location and post glaciation condition (i.e. delineation between
24 supra- and subaquatic lakes during the post-glacial Anculys Lake) in explaining variation in
25 macrophyte community composition of all taxa, helophytes and hydrophytes. In addition, we
26 investigated how these four explanatory variable groups affected macrophyte strategy groups based
27 on Grime's classification. Using partial linear regression and variation partitioning, we found that
28 macrophyte communities are primarily filtered by local determinants together with regional
29 characteristics at the studied spatial scale. We further evidenced that post glaciation condition
30 indirectly influenced on local water quality variables, which in turn directly contributed to the
31 macrophyte communities. We thus suggest that regional determinants interact with local-scale
32 abiotic factors in explaining macrophyte community patterns and examining only regional or local
33 factors is not sufficient for understanding how aquatic macrophyte communities are structured
34 locally and regionally.

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41 **INTRODUCTION**

42

43 Species distributions are explained by regional and local determinants, operating at multiple spatial
44 and temporal scales. Regional factors are related to broad-scale historical and biogeographical
45 effects, originating, for example, from previous glaciations, current climate patterns, major dispersal
46 barriers and evolutionary changes (Whittaker et al., 2001; Ricklefs, 2004). These regional
47 determinants of species distributions are influential at continental (e.g., glaciations) and inter-
48 regional (e.g., climate) scales over long temporal periods (Willis & Whittaker, 2002). Local abiotic
49 and biotic ecological factors structure local species distributions within short contemporary time
50 periods, ranging from disturbances and environmental conditions to species interactions (Willis &
51 Whittaker, 2002; Ricklefs, 2004). These regional and local determinants are hierarchically
52 structured so that regional processes and constrains interact with local-scale biotic and abiotic
53 factors in explaining species community patterns (Whittaker et al., 2001; McGill, 2010). Thus,
54 studying only regional or local determinants may not be sufficient for understanding how species
55 communities are structured locally and regionally (Ricklefs, 2004, Svenning et al., 2010).

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57 Many studies have investigated the roles of regional vs. local factors and their impact on species
58 distributions; however, disagreement exists concerning their relative importance in structuring local
59 communities (Ricklefs, 2004; Soininen, 2014). Disparity over the dominance of regional and local
60 factors in explaining local communities also stems from the differences between study systems in
61 relation to geographic location and habitat. For example, high-latitude regions can exhibit strong
62 regional effects on local communities due to geographic variability in the influence of the past
63 glaciations (Svenning & Skov, 2003; Svenning et al., 2010; Alahuhta et al., 2013). In freshwater
64 ecosystems, variable patterns in the relative importance of regional and local determinants on local

65 communities have strongly depended on the studied biological assemblage (De Bie et al., 2012;
66 Alahuhta & Heino, 2013; Viana et al., 2014; Heino et al., 2015; McCann, 2015). These freshwater
67 examinations have focussed on distinguishing local environmental conditions from regional spatial
68 processes in explaining local communities. However, much less attention is given to actual
69 historical effects, such as the Pleistocene glaciation period, in explaining freshwater communities.

70

71 The latest major glaciation period in Europe took place during the Pleistocene, causing massive
72 regional losses of fauna and flora (Svenning, 2003; Koch & Barnosky, 2006). A several-kilometre-
73 thick ice sheet covered most of northern Europe (incl. the whole landmass of present-day Finland)
74 until deglaciation began over 13 000 BP (Eronen, 2005), creating a major barrier for species
75 dispersal and leading to isolated populations (Svenning & Skov, 2003). When the ice sheet slowly
76 melted in present-day Northern Europe, a large post-glacial water body, called Ancylus Lake,
77 emerged (9 500 – 8 300 BP, Tikkanen & Oksanen, 2002). Species dispersal possibilities were
78 equally poor during the glaciation period, but melting of ice during the Ancylus Lake phase resulted
79 in the rise of water level over 200 metres above the current sea level and enabled free dispersion of
80 aquatic species (i.e., subaquatic area). However, high-altitude areas were above the maximum water
81 level of Ancylus Lake and thus not enclosed by the lake (i.e., supra-aquatic area, Tikkanen &
82 Oksanen, 2002). As a result, dispersion potential of aquatic species was likely different between
83 subaquatic and supra-aquatic areas, as supra-aquatic lakes were spatially and more effectively
84 isolated from each other by surrounding land and were limited by dispersal process. No previous
85 studies have yet examined whether freshwater communities established in subaquatic and supra-
86 aquatic lakes show different patterns of regional and local factors.

87

88 Aquatic macrophyte communities are ecologically and scenically important components of high-
89 latitude freshwater lakes by providing nutrition, shelter and breeding areas for other aquatic and
90 terrestrial species (Toivonen & Huttunen, 1995; Vestergaard & Sand-Jensen, 2000; Alahuhta et al.,
91 2016). Aquatic flora also store nutrients, decreases erosion and affect the quality and quantity of
92 sediments (Lacoul & Freedman, 2006; Alahuhta et al., 2012). Macrophytes can be classified into
93 functional groups, of which helophytes (i.e., emergent species) and hydrophytes (i.e., aquatic plants
94 growing on or below the water surface) form the most-recognized life forms (Toivonen &
95 Huttunen, 1995; Alahuhta et al., 2014). Helophyte and hydrophyte species respond differently to
96 environmental conditions. Helophytes obtain carbon dioxide from the atmosphere, uptake nutrients
97 from sediments and are more sensitive to cold winters, whereas hydrophytes mainly acquire carbon
98 oxide and nutrients directly from water and are sheltered beneath the ice cover during winters
99 (Toivonen & Huttunen, 1995; Hellsten, 2001; Lind et al., 2014). Dispersal modes also vary to some
100 extent between these functional macrophyte groups, as helophytes combine intensive vegetative
101 growth with wind dispersed seed production resulting in high colonization capability (Barrat-
102 Segretain, 1996; Saarnel et al., 2014). Oppositely, hydrophytes are more dependent on water and
103 waterfowl for dispersing propagules to new habitats (Claussen et al., 2002; Soons et al., 2015).
104 Although much is known about the relationships between aquatic flora and environmental
105 conditions, fewer studies have examined the relative importance of local and regional factors in
106 structuring local assemblages of different macrophyte functional groups.

107

108 Besides belonging to different functional plant groups, aquatic macrophytes can also be categorised
109 based on life history strategy (Grime, 1977), in which species are classified as competitive (C),
110 stress-tolerant (S) and ruderal (R). Competitors (C) are plant species growing in areas of low stress
111 and disturbance, thus having good competition capabilities. Stress can be defined as conditions such
112 as lack of light or nutrients, whereas disturbance can be caused by wind or drought. Competitors

113 can outcompete other plants by reserving available resources such as growth area or nutrients.
114 Favourable characteristics of competitors include rapid growth rate, high productivity and wide
115 phenotypic plasticity. The latter property describes highly flexible morphology and reallocation of
116 resources depending on conditions experience by the plant. For example, the large-sized helophyte,
117 *Phragmites australis*, is a typical C-strategist representing aquatic plants. Stress-tolerant plant
118 species (S) occupy areas of high intensity stress and low intensity disturbance, such as in deep-
119 water environments. Species have adapted to this strategy with slow growth rates, long-lived leaves,
120 high rates of nutrient retention, and low phenotypic plasticity. They are adapted to environmental
121 stresses through physiological variability. Typical examples include large isoetids such as *Isoetes*
122 *lacustris* or *Lobelia dortmanna* with evergreen leaves adapted to lack of nutrients and light. Ruderal
123 plant species (R) are adapted to high-intensity disturbance and low-intensity stress. These species
124 are fast-growing, have short life cycles and vigorous seeds production. Plants that have adapted this
125 strategy are often found colonizing recently disturbed land, and are often annuals. Typical examples
126 are small-sized isoetids like *Ranunculus reptans* and *Elatine hydropiper* occupying the eroded
127 littoral zone.

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129 The overall purpose of our study was to investigate the importance of regional and local factors on
130 aquatic macrophyte communities in 80 Finnish lakes. Firstly (I), we researched the relative roles of
131 post glaciation condition, geographical location, climate characteristics and local water quality in
132 explaining variation in aquatic macrophyte composition of all taxa, helophytes and hydrophytes.
133 Secondly (II), we investigated if aquatic macrophytes categorized as dominant competitive, stress-
134 tolerant and ruderal plant groups, based on the life history strategy classification (Grime, 1977),
135 respond similarly to these four explanatory variable sets. Based on previous findings (Toivonen &
136 Huttunen, 1995; Vestergaard & Sand-Jensen, 2000; Alahuhta et al., 2014), we expected to find that
137 all macrophyte communities respond primarily to local determinants. We also hypothesised that

138 macrophyte communities are affected by regional variables, as latitudinal gradient derived from
139 climatic variation is known to structure macrophytes at regional scales (Heino & Toivonen, 2008;
140 Alahuhta, 2015). In addition, we supposed that glaciation period does not influence macrophyte
141 communities anymore, because many plant species disperse efficiently, have wide range sizes and
142 spatial processes have rarely been important factors controlling macrophytes even at regional scales
143 (Barrat-Segretain, 1996; Claussen et al., 2002; Viana et al., 2014; Alahuhta et al., 2015).

144

145 **MATERIAL AND METHODS**

146

147 **Study area and supra delineation**

148 We used aquatic macrophyte data from 80 boreal lakes (<100 km²) distributed across Finland (Fig.
149 1). Half of the lakes (40) were situated in high-altitude supra-aquatic areas, which were above the
150 maximum water level during the existence of Ancylus Lake in ca. 9 000 BP (Table 1). The Ancylus
151 Lake was the largest post-glacial sea lake in Fennoscandia, covering over 60% of Finland's surface
152 area (Tikkanen & Oksanen, 2002). As the supra-aquatic areas were not enclosed by the Ancylus
153 Lake and terrestrial land surrounded supra-aquatic lakes in a way similar to modern times, aquatic
154 plants established in these 40 lakes have been efficiently spatially isolated from each other by a
155 non-habitable terrestrial matrix and thus limited by dispersal processes. Another 40 lakes were
156 situated in subaquatic areas, which were below sea level during the existence of Ancylus Lake. A
157 sudden rise in water level, when the Ancylus Lake was established, has likely led to the loss of
158 many macrophyte species from their original sites. However, new colonies have probably formed in
159 shallower areas, as species were able to disperse freely throughout the lake. These subaquatic lakes
160 were randomly chosen from a larger set of lakes (see Alahuhta et al., 2012). The separation between
161 supra- and subaquatic areas (Fig. 1) was based on the map found in Tikkanen & Oksanen (2002).

162

163 **Macrophyte and explanatory variables**

164 Aquatic macrophytes were surveyed using a main belt transect method, in which a five-metre-wide
165 transect was sampled from the upper eulittoral to the outer limit of vegetation, or to the deepest
166 point of the basin if vegetation covered the entire lake (see method in Kanninen et al., 2013a).
167 Macrophytes were observed by fording or by boat, with the assistance of rakes and hydrosopes.
168 The number of transects varied between six and 36 (mean = 13, SD = 5.5), depending on lake size.
169 These surveys were carried out during the growing season between 2006 and 2011. During the
170 surveys, species consisted of all aquatic vascular plants and macroalgae from the family *Characeae*
171 were recorded and these documented species were studied in this work (Alahuhta et al., 2012). The
172 total number of recorded species was 108 of which 46 were helophytes and 62 were hydrophytes.

173

174 Macrophyte community composition variables were calculated separately for all taxa, helophytes
175 and hydrophytes. In addition, we separated plant species into dominant plant strategy groups (C, S
176 or R) based on Grime (1977) and Grime et al. (1988). Information on 36 species traits was based on
177 Jalas (1958, 1965, 1980). Aquatic plant strategy properties based on Rørslett (1989) and Murphy et
178 al. (1990) were used to define the dominant strategies for all the studied plants. The list of dominant
179 plant strategy groups for each species is given in Online Resource S1. If species possessed a certain
180 species trait, this was recorded and the cumulative number of species traits over all 36 traits
181 representing each plant strategy group was calculated. Then, a species was classified to that
182 dominant plant strategy group (C, S or R) for which the number of species traits was the highest
183 (e.g. if 4 traits represented C, 2 traits represented S and 6 traits represented R, then the species was
184 grouped as a ruderal (R) species). In some rare cases with same amount of traits for R and C, the
185 final strategy was selected by using the most common strategy of the overall genus. The species

186 were divided into dominant plant strategy groups as follows: 71 competitors, 22 stress-tolerant and
187 16 ruderal species (Online Resource S1).

188

189 Although with Grime's strategy plants often possess characteristics from two or three classes, we
190 were forced to categorize species as a single dominant class (i.e. exclusively to C, S or R) due to
191 statistical methods used in this work (see below). Thus, all species were included in both
192 macrophyte community composition and plant strategy variables, maintaining their comparability.
193 Dispersal and reproduction are also acknowledged in Grime's classification, as competitive species
194 disperse efficiently, whereas ruderal species produce vast amounts of propagules for reproduction
195 (Grime et al., 1988). Dispersal and reproduction abilities of stress-tolerant species are low compared
196 to C- and R-species.

197

198 The explanatory variables consisted of local variables, climate variables, one historical variable
199 indicating post glaciation condition (supra- and subaquatic areas) and spatial structure (geographical
200 coordinates). Local variables were alkalinity in water (mmol/l), total phosphorus in water ($\mu\text{g/l}$),
201 water colour (mg Pt/l) and lake area (km^2), whereas climate variables were comprised of growing
202 degree days ($> 5^\circ\text{C}$, Pirinen et al., 2012) and January temperature ($^\circ\text{C}$). Alkalinity is related to the
203 ability of some macrophyte species to utilize bicarbonate as a source of carbon, giving these species
204 a competitive advantage over others (Vestergaard & Sand-Jensen, 2000). Total phosphorus reflects
205 lakes trophic conditions (Alahuhta, 2015). Water colour is used to mirror at what water depth
206 species can exist, as availability of light for photosynthesis decreases strongly towards deeper water
207 columns in lakes with high humic content (Toivonen & Huttunen, 1995). Lake area indicates
208 horizontal habitat availability with larger lakes having more different habitats available for
209 macrophyte establishment (Lacoul & Freedman, 2006). Of the climate variables, growing degree

210 days is directly related to the length and intensity of the growing season, whereas the January
211 temperature was used as a proxy for harsh winter conditions, which affect macrophytes through
212 thick ice cover, ice erosion and freezing of sediments (Hellsten, 2001; Lind et al., 2014).
213 Information on local variables was obtained from the Hertta database for the period of 2006–2011
214 (growing season only), based on mean values of 1 metre surface samples for water quality variables
215 (http://www.syke.fi/en-US/Open_information). Climate variables for lake area were derived from
216 the Finnish Meteorological Institute for the period 1981–2010 with the resolution of 1km (Pirinen et
217 al., 2012). ArcGIS 10 (ESRI, Redlands, CA, US) was used to process both climate variables. Lake
218 coordinates (Y = latitude, X = longitude) were based on centre points from each lake, gathered
219 using ArcGIS.

220

221 **Statistical analyses**

222 We used partial redundancy analyses (pRDA) to distinguish the relationships between variation in
223 macrophyte and explanatory variable groups. pRDAs were employed with Hellinger transformed
224 presence-absence matrices of aquatic macrophytes, because the transformation makes the data
225 analysable using linear methods (Legendre & Gallagher, 2001). The protocol of Borcard et al.
226 (1992) was followed for pRDAs, as total variation in macrophyte variables was partitioned into 16
227 fractions: (a) pure effect of local variables, (b) pure effect of climate variables, (c) pure effect of
228 post glaciation condition, d) pure effect of geographical position (i.e. lake coordinates); and their
229 joint effects (altogether 11 joint fractions), followed by unexplained variation. The detailed
230 procedures to estimate these fractions are explained in Borcard et al. (2011).

231

232 Variation explained by each variable group was evaluated with adjusted R^2 , which provides
233 unbiased estimates of the explained variation (Peres-Neto et al., 2006). In forward selection, type I

234 errors can be avoided by using adjusted R^2 values, which are also comparable between different
235 models as the number of explanatory variable is taken into account (Blanchet et al., 2008). In
236 addition, utilization of adjusted R^2 values can lead to negative pure fractions in a variation
237 partitioning procedure (Borcard et al., 2011). For joint fractions, negative adjusted R^2 values can
238 also indicate multicollinearity among studied explanatory variables. Following the procedure of
239 Blanchet et al. (2008), forward selection to obtain significant variables for further analysis was
240 based on the Monte Carlo permutation test (999 permutations, $\alpha = 0.05$) and two stopping rules: $p >$
241 0.05 or the adjusted R^2 value of the reduced model exceeded that of the global model. Explanatory
242 variables showed a variable degree of multicollinearity (total phosphorus and colour: $R_{\text{Spearman}} =$
243 0.74 , $p < 0.001$; latitude and climate variables: $R_s = |0.96-0.98|$, $p < 0.001$), although this does not
244 impair the variation partitioning procedure used in our study (Oksanen et al., 2012). All pRDAs
245 were performed in the R environment with PACKFOR (S. Dray, Université Claude Bernard Lyon I)
246 and VEGAN packages (Oksanen et al., 2012).

247

248 We also considered whether post glaciation condition had created different local environmental
249 conditions between supra- and subaquatic lakes that further affect macrophyte community
250 compositions. To evaluate this, we used structural equation modelling (SEM) to test a) indirect
251 effects of post glaciation condition on water quality variables and macrophyte flora and b) direct
252 effects of water quality on macrophytes. SEM is especially informative in studies of cause-effect
253 relationships by investigating the networks of connections among system components (Grace et al.,
254 2012). A key feature in SEM is to partition relationships among pathways, which traces a route
255 from a predictor to a response representing a distinct mechanism (Grace, 2006). In our study, we
256 built a robust SEM model among the explanatory variables and macrophyte flora that was tested
257 separately for different macrophyte variable groups (Fig. 2). Given the rationale on the hierarchy of
258 factors we analysed, we expected that post glaciation condition indirectly affects local water

259 quality, which in turn directly influences macrophyte communities. We also assumed that water
260 quality variables were linked. We used the first two axis scores of PCA (i.e., PCA1 and PCA1) to
261 represent macrophyte community compositions. In our results, standardized coefficients indicate the
262 strength of the relationship because they are scaled to the same units (Grace et al., 2012).
263 Standardized estimates correspond to effect-size estimates. The goodness of model fit was based on
264 chi-square and the evaluation of parameter estimates on z statistics. The interpretation of model fit
265 is opposite to conventional statistical analysis in SEM (i.e., higher $p > 0.05$ indicates better model
266 based on chi-square), whereas z statistics follow the common interpretations of analysis. Our key
267 purpose was to understand the patterns of correlation among a set of variables (i.e., post glaciation
268 condition, local water quality and macrophyte community composition), not to explain as much of
269 their variance as possible with the model specified. SEM models were constructed in the R
270 environment using LAVAAL (Rosseel, 2012) and SEMPATHS (Epskamp, 2015) packages.

271

272 **RESULTS**

273

274 **Macrophyte community compositions**

275 Overall variation explained in variation partitioning was 17.5% for all taxa, 17.6% for helophytes
276 and 17.8% for hydrophytes (Table 2). Of the pure fractions, community composition of all taxa
277 (6.6%), helophytes (1.7%) and hydrophytes (10.4%) were best explained by local variables, which
278 was the only statistically significant pure fraction. Other pure fractions had clearly smaller or non-
279 existence importance for all of the three macrophyte community compositions. The joint fraction of
280 climate and geographical location was comparatively high for all taxa (6.7%), helophytes (11.0%)
281 and hydrophytes (4.2%). The joint fraction of geographical location and post glaciation condition
282 also showed some explained variation for all community compositions (0.6–1.6%), similarly to the

283 joint effect of local variables and geographical location (1.2–1.4%). Post glaciation condition and
284 geographical location were quite high compared to other fractions for helophyte community
285 composition. These results suggest that post glaciation condition affects variation in helophyte
286 community composition, because post glaciation condition is clearly dependent on geographical
287 location. A majority of subaquatic lakes are located in central Finland, whereas post glaciation
288 condition lakes span over a large area covering most of the eastern and northern parts of the country
289 (Fig. 1). Similarly, local variables vary between supra- and subaquatic lakes, as colour and total
290 phosphorus gradients are clearly wider in subaquatic lakes (Table 1). In addition, the joint
291 contribution of local variables and climate explained small amount of variation (0.9–1.1%). The
292 number of species varied between supra- and subaquatic lakes for all taxa and helophyte community
293 compositions.

294

295 Alkalinity and colour were the most important local variables for community composition of all
296 taxa and hydrophytes, whereas total phosphorus explained most variation for helophytes (Table 3,
297 Fig. 3). Of the hydrophytes, *Potamogeton berctoldii* and *Nuphar pumila* were most positively and
298 *Lobellia dortmanna* and *Isoetes echinospora* were most negatively associated with alkalinity.
299 *Potamogeton natans* was most positively and *Subularia aquatica* and *Ranunculus peltatus* most
300 negatively correlated with colour. Of the helophytes, *Cicuta virosa* was most distinctly related to
301 total phosphorus. Growing degree days of climate variables had the highest effect on all macrophyte
302 community compositions. *Nuphar lutea* and *Nymphaea tetragona* of the hydrophytes and
303 *Lysimachia thyrsiflora* and *Phragmites australis* of the helophytes were positively associated with
304 the growing degree days, which also negatively influenced the helophytes *Hippuris vulgaris* and the
305 hydrophytes *Potamogeton perfoliatus*, *Potamogeton gramineus* and *Subularia aquatica*. Of the
306 geographical location, coordinate Y indicating latitudinal variation was the most important variable

307 for all community compositions. Supra-aquatic and subaquatic lakes were quite clearly separated in
308 ordination space for all taxa and helophytes.

309

310 **Dominant plant strategy groups**

311 The total explained variation was 18.9% for competitive, 14.8% for stress-tolerant and 13.0% for
312 ruderal species (Table 2). Local variables were clearly the most significant pure fraction
313 contributing to all of the plant strategy groups (C: 5.4%, S: 9.5%, R: 10.1%). Post glaciation
314 condition affected, and the number of species clearly varied, between supra- and subaquatic lakes
315 only for competitors. Of the joint fractions, climate and geographical location influenced
316 competitive (8.1%), stress-tolerant (4.2%) and ruderal (2.1%) species. For competitors, joint effects
317 of local variables and geographical location (1.7%), local variables and climate (1.3%) and
318 geographical location and post glaciation condition (1.8%) also had an effect on this plant group.

319

320 Colour and alkalinity were the most important local variables for competitive species, whereas total
321 phosphorus had the highest effect on stress-tolerant and ruderal species (Table 3, Fig. 3). Among
322 competitive species, *Eleocharis mamillata* and *Alisma plantago-aquatica* were most positively and
323 *Menyanthes trifoliata* and *Persicaria foliosa* most negatively correlated with colour. Competitor
324 *Carex paniculata* was positively associated with alkalinity. The relationship with total phosphorus
325 was positive for ruderal *Bidens cernua* and negative for stress-tolerant *Isoetes lacustris* and ruderal
326 *Ranunculus reptans*. Of climate variables, growing degree days contributed most to competitive and
327 stress-tolerant species, and January temperature was the only climate variable selected for ruderal
328 species. Competitors *Phragmites australis* and *Scolochloa festucacea*, and stress-tolerant
329 *Utricularia australis* were positively associated with the growing degree days and January
330 temperature. A negative relationship with these climate variables was found for competitors

331 *Ranunculus lingua*, stress-tolerant *Nitella flexilis* and ruderal *Alopecurus aequalis*. Coordinate Y of
332 geographical location (i.e., latitude) was the most important variable for all plant strategy groups.
333 Post glaciation condition distinguished supra-aquatic and subaquatic lakes two their own groups for
334 competitors.

335

336 **Structural equation modelling**

337 The overall fit of our model was relatively poor (minimum function test statistics = 4.803, df = 1, p
338 = 0.028). However, we were able to compare relationships among the set of observed variables.
339 Concerning intercorrelation structure among post glaciation condition and water quality variables,
340 total phosphorus was affected by alkalinity, colour and post glaciation condition, whereas post
341 glaciation condition had no statistical influence on alkalinity and colour (Table 4). For all taxa,
342 alkalinity, colour and post glaciation condition were statistically positively significantly related to
343 macrophytes represented by the PCA2. Post glaciation condition was negatively associated with
344 helophytes in the PCA2, whereas both alkalinity (PCA1 and PCA2) and colour (PCA1) were
345 negatively correlated with hydrophytes. For competitive species, colour negatively and alkalinity
346 and post glaciation condition positively contributed to this plant group in the first and second axes,
347 respectively. Stress-tolerant plants were positively correlated with alkalinity and colour in the
348 PCA1.

349

350 **DISCUSSION**

351

352 The main purpose of our work was to investigate the relative importance of regional and local
353 determinants in explaining community composition of different macrophyte groups in high-latitude

354 lakes. We found that local water quality and habitat factors greatly structured all macrophyte
355 groups. However, climate showing a strong latitudinal gradient (through joint effect of climate and
356 geographical location) was equally or more important for macrophyte community compositions.
357 These findings suggest that macrophyte communities are primarily filtered by local determinants
358 together with regional characteristics at the studied spatial scale. This finding was further supported
359 by the (indirect) influence of post glaciation condition on local water quality variables, which in
360 turn (directly) contributed to the macrophyte communities. We thus agree with the previous
361 investigations (Whittaker et al., 2001; McGill, 2010; Alahuhta, 2015) that regional determinants
362 interact with local-scale abiotic factors in explaining macrophyte community patterns and
363 examining only regional or local factors is not sufficient for understanding how aquatic macrophyte
364 communities are structured locally and regionally.

365

366 The environmental determinant operating at the broadest scale in our study was post glaciation
367 condition. We expected that aquatic macrophytes with efficient dispersal strategies had evenly
368 colonized supra- and subaquatic lakes by now (e.g., Barrat-Segretain, 1996; Sawada et al., 2003),
369 and we indeed found few differences between strongly and poorly dispersing species (Online
370 Resource S2). However, post glaciation condition seems to influence macrophyte community
371 compositions after over 9 000 years. We found support for this outcome from both the variation
372 partitioning and structural equation modelling. Although the pure effect of post glaciation condition
373 showed only a modest contribution to the macrophyte flora, the joint fraction of post glaciation
374 condition and geographical location indicated considerable influence on macrophyte community
375 compositions compared to most of the other joint effects. In addition, the joint contribution of local
376 variables, post glaciation condition and geographical location suggested that these variable groups
377 form a complex interplay with each other that is difficult to distinguish in variation partitioning. For
378 example, the variation in colour is much wider in subaquatic lakes compared to supra lakes,

379 whereas different soil types influence total phosphorus concentrations between the lakes. Finer soil
380 deposits were washed in subaquatic areas but these nutrient-rich soils are often present in supra
381 areas (Ojala et al., 2013) creating better growth conditions for plants in supra areas. On the other
382 hand, current clay soils are typically found in southern and western lowland catchments of Finland
383 as a consequence of subglacial sedimentation, enhancing natural background concentrations of
384 nutrients in subaquatic lakes (Alahuhta et al., 2011). In addition, human pressures are stronger in
385 more populated southern areas of Finland, for which anthropogenic-originated nutrients increase
386 trophic status in many subaquatic lakes (Kanninen et al., 2013b). These confounding and often
387 confronting effects make it difficult to study the effect of post glaciation condition in Finnish lakes,
388 of which most are slightly affected by human pressures.

389

390 However, structural equation modelling enabled us to distinguish the effect of post glaciation
391 conditions on local water quality and macrophyte flora. Post glaciation condition indirectly affected
392 macrophyte composition of all taxa, helophytes and competitors. In addition, post glaciation
393 conditions indirectly influenced total phosphorus, which significantly structured ruderals.
394 Helophytes were also contributed by total phosphorus, but not statistically significantly ($p=0.081$).
395 These findings suggest that aquatic macrophyte communities have, in a way similar to terrestrial
396 plants (Skov & Svenning, 2003), not yet reached their full distribution ranges following the last
397 glaciation period. In addition, inorganic phosphorus can be bound in organic matter, the rise of
398 which results in increasing colour values in water (Madsen et al., 1996). This chain of events likely
399 explains why colour was most strongly correlated with total phosphorus (Table 4), further
400 supporting the indirect post glaciation condition effect on macrophytes. It seems colour values vary
401 along the post glaciation condition delineation in our study area. Our findings contradict previous
402 paleolimnological studies (Sawada et al., 2003; Väliänta, 2006; Väliänta et al., 2011), in which
403 aquatic macrophytes were proposed to quickly occupy ice-free areas following deglaciation. Many

404 helophytes and hydrophytes classified as competitors but also stress-tolerants dispersed rapidly to
405 new habitats within a few millennia after ice sheets withdrew in North America. Furthermore,
406 aquatic macrophytes in North America responded little to post-glacial climate changes, as Late-
407 Holocene cooling does not appear to have affected their ranges (Dieffenbacher-Krall & Jacobson,
408 2001). In our work, however, post glaciation condition affected mostly helophytes, because more
409 than half of the competitive species and half of ruderal species were classified as helophytes.
410 Instead, hydrophytes and stress-tolerants, of which all species were hydrophyte species, were not
411 influenced by either post glaciation condition or total phosphorus. This was also seen in the
412 ordination plots, where supra-aquatic and subaquatic lakes were distinguished from each other for
413 all taxa, helophyte and competitors only. Helophytes often inhabit aquatic-terrestrial ecotones,
414 where growing conditions in many ways resemble that of terrestrial ecosystems (Alahuhta et al.,
415 2011). Thus, it may be that true aquatic macrophytes growing permanently in water are less
416 influenced by post glaciation condition than semi-aquatic helophyte species.

417

418 Climate structured aquatic macrophyte communities at the second broadest scale. Latitudinal
419 gradient in climate is strong in the boreal region and previous studies have evidenced a clear
420 variation in species distributions along a changing climate from south to north (Rørslett, 1991;
421 Heino & Alahuhta, 2015; Alahuhta et al., 2016). Climate was equally or more important than other
422 factors for community composition of all taxa, helophytes and competitors. The two regional
423 factors (climate and glaciation) are also linked through latitudinal and altitudinal variation, as supra-
424 aquatic lakes are located in more northern and eastern areas with lower growing degree days and
425 more continental climate conditions (Alahuhta et al., 2011). In addition, supra-aquatic lakes are
426 typically at least 200m above sea level (Tikkanen & Oksanen, 2002), where temperatures are lower
427 compared to lowland areas. Competitive species were generally dominant in sub-aquatic lakes with

428 higher nutrient status, thus supporting the original theory of Grime (1977) regarding resource
429 availability.

430

431 Of individual climate variables, growing degree days had the greatest influence on the community
432 composition of all taxa, helophytes, hydrophytes, competitors and stress-tolerants. Similar findings
433 have been evidenced for aquatic macrophytes in other studies (Alahuhta et al., 2011; Alahuhta et
434 al., 2016). Coordinate Y, which similarly to growing degree days mirrors broad-scale latitudinal
435 variation in climate, contributed most to all community compositions. The species associated most
436 strongly with latitudinal climate gradient (*Nuphar lutea*, *Lysimachia thyrsiflora* and *Phragmites*
437 *australis*) are absent from the most northern parts of Finland (Lampinen et al., 2015). The
438 relationship was negative for the hydrophytes *Subularia aquatica* and *Potamogeton gramineus*,
439 which have more northern distributions (Lampinen et al., 2015). On the other hand, January
440 temperatures affected most ruderals but also all taxa, helophytes and competitors. The influence of
441 harsh winter conditions on macrophytes is difficult to distinguish from the latitudinal climate
442 gradient, however, as the temperature of January and growing degree days were highly correlated.
443 Harsh winter conditions, such as ice erosion and freezing of littoral sediments, should especially
444 structure stress-tolerant species, of which many large-sized isoetids are vulnerable to these harmful
445 phenomena (Lind et al., 2014). However, ice effect is most obvious in lakes with regulated water
446 level, and therefore not visible in research lakes, where distribution of large sized isoetids is
447 determined by water quality (Hellsten, 2001).

448

449 Local variables contributed to the macrophyte flora at the smallest spatial scale. The high influence
450 of local determinants on macrophyte flora originates from the fact that variation in local gradients is
451 typically very wide in freshwater ecosystems, creating variable habitat conditions even in

452 neighbouring lakes (Elser et al., 2007). Wide water quality gradients have enabled species with
453 different tolerances to local environmental conditions to co-exist in geographically closely-situated
454 habitats, typically resulting in relatively high species turnover among these habitats for aquatic
455 macrophytes (Alahuhta & Heino, 2013; Viana et al., 2014). In addition, regional factors have had a
456 smaller impact on freshwater assemblages due to the sheltering effect of water, which has, for
457 example, moderated the influence of extreme atmospheric temperatures on aquatic species (Lacoul
458 & Freedman, 2006). Although the climate gradient in freshwater ecosystems is not as wide as in
459 terrestrial systems, climatic determinants must be studied alongside local factors when investigating
460 aquatic macrophyte community compositions at the regional scale.

461

462 Alkalinity of individual local variables was the most important local variable for community
463 composition of all taxa and hydrophytes. Competitors were also greatly affected by alkalinity. The
464 effect of alkalinity is related to the different forms of carbon used by aquatic plants in
465 photosynthesis. Concentrations of carbon dioxide are typically low in water; however, some
466 macrophyte species, which are mostly hydrophytes, can utilize bicarbonate as a source of carbon
467 (Capers et al., 2010; Alahuhta & Heino, 2013). We found that hydrophytes *Potamogeton*
468 *berchtoldii* and *Nuphar pumila* were most positively associated with alkalinity. Vestergaard &
469 Sand-Jensen (2000) categorized *P. berchtoldii* to be present in alkaline lakes and *N. pumila* and *C.*
470 *vesicaria* is related to mesotrophic-eutrophic waters, where alkalinity is connected to lake
471 productivity (Toivonen & Huttunen, 1995). Colour was an equally important local peatland
472 richness-related variable for all taxa and hydrophyte compositions, as also reported for other boreal
473 hydrophyte community compositions (Alahuhta et al., 2013; Kanninen et al., 2013b). Colour
474 mirrors water transparency and growth of submerged macrophytes is limited to shallow littoral
475 areas in dark-water, humic lakes (Toivonen & Huttunen, 1995; Hellsten, 2001). In our work,
476 *Subularia aquatica* and *Ranunculus peltatus* were most greatly limited by lower water transparency.

477 For helophytes, total phosphorus reflects trophic status in lakes, with *Cicuta virosa* and *Carex acuta*
478 most greatly benefitting from increased nutrient concentrations. *Lemna minor* also had a positive
479 relationship with total phosphorus, whereas *Ranunculus reptans* and *Isoetes lacustris* were
480 negatively associated with phosphorus concentration. *Lemna* species favour lakes with high trophic
481 status and isoetids are known to suffer from an enrichment of nutrients in water, which further
482 results in lowered light availability and increased organic sedimentation (Rorslett, 1991; Borman et
483 al., 2009).

484

485 Finally, the hierarchical nature of regional and local determinants in structuring aquatic macrophyte
486 community compositions found in our study is also related to the accuracy of explanatory variables.
487 Local factors were measured at the lake level corresponding with that of macrophyte surveys.
488 Climate determinants were similarly delineated to lake surface area, but fine-scale variation in
489 climate gradient is modest (Whittaker et al., 2001). Both local water quality and climate factors
490 were long-term averages of multiple measurements, decreasing uncertainty related to yearly
491 changes in these observations. Separation of supra- and subaquatic areas was the least exact based
492 on the modelled scenario, however, the accuracy is well-suited for our regional study scale covering
493 almost 300 000 km².

494

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504

505

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672 Table 1. Descriptive statistics of explanatory variables and number of species in supra- and
673 subaquatic lakes.

		Supra	Sub	Total
Environmental (local) variables				
Alkalinity (mmol/l)	Mean	0.16	0.19	0.18
	Min.	0.02	0.04	0.02
	Max.	0.88	0.68	0.88
Total phosphorus ($\mu\text{g/l}$)	Mean	14.1	26.5	20.3
	Min.	4.0	2.6	2.6
	Max.	39.1	131.2	131.2
Colour mg (Pt/l)	Mean	72	83	77
	Min.	14	3	3
	Max.	155	270	270
Lake area (km^2)	Mean	9.3	8.4	8.9
	Min.	0.5	0.7	0.5
	Max.	55.9	85.6	85.6
Growing degree days ($>5\text{ }^\circ\text{C}$)	Mean	1016	1169	1093
	Min.	538	839	538
	Max.	1348	1430	1430
January temperature ($^\circ\text{C}$)	Mean	-11.1	-9.5	-10.3
	Min.	-13.8	-13.1	-13.8
	Max.	-5.4	-6.3	-5.4
Number of species				
All taxa	Mean	22.6	28.4	25.5
	Min.	9	14	9
	Max.	39	55	55
Hydrophytes	Mean	13.3	14.1	13.7
	Min.	4	5	4
	Max.	25	25	25
Helophytes	Mean	9.3	14.3	11.8
	Min.	2	6	2
	Max.	18	30	30
Competitors	Mean	15.7	21.8	18.7
	Min.	2	10	2
	Max.	27	43	43
Stress-tolerant	Mean	5.3	4.8	5.1
	Min.	0	1	0
	Max.	10	10	10
Ruderal	Mean	1.5	1.8	1.7
	Min.	0	0	0
	Max.	5	7	7

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676 Table 2. Results of variation partitioning as percentage value (*100) based on adjusted R^2 values
677 and forward selection using the procedure of Blanchet et al. (2008). Statistically significant ($p <$

678 0.05) pure fractions based on the ANOVA-like permutation test are marked in italics. “-“ indicate
 679 negative adjusted R² values. C = competitors, S = stress-tolerants, R = ruderals.

	All Taxa	Helophytes	Hydrophytes	C	S	R
Local	<i>6.63</i>	<i>1.69</i>	<i>10.43</i>	<i>5.39</i>	<i>9.54</i>	<i>10.05</i>
Climate	-	0.38	0.06	0.23	0.12	0.05
Supra	0.01	0.08	0.34	0.02	0.00	0.00
XY	-	0.47	-	0.07	0.05	-
Local+Climate	1.05	0.87	0.92	1.27	0.71	0.33
Local+Supra	-	-	-	-	0.00	0.00
Local+XY	1.38	1.17	1.31	1.65	1.10	0.55
Climate+Supra	0.90	0.96	0.66	1.28	0.00	0.00
Climate+XY	6.77	11.03	4.18	8.09	4.17	2.07
Supra+XY	1.30	1.62	0.56	1.83	0.00	0.00
Local+Climate+Supra	0.63	1.03	0.48	0.68	0.00	0.00
Local+Climate+XY	-	-	-	-	-	0.11
Local+Supra+XY	0.71	1.36	0.46	0.74	0.00	0.00
Climate+Supra+XY	-	-	0.07	-	0.00	0.00
All four groups	-	-	-	-	0.00	0.00

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Table 3. The most important explanatory variables explaining aquatic macrophyte communities of all taxa, helophytes and hydrophytes and three plant strategy groups (competitors, stress-tolerant and ruderal) derived from Grime's categorization. The variables were selected based on adjusted R² and forward selection using the Monte Carlo permutation test (999 permutations; $\alpha = 0.05$). GDD = growing degree days, Y = latitude, X=longitude. Statistical level of significance: * <0.05 ; ** <0.01 ; *** <0.001 .

Community composition						
	All taxa		Helophytes		Hydrophytes	
	Variable	adj. R ²	Variable	adj. R ²	Variable	adj. R ²
Local variables	Alkalinity	0.039***	Total phosphorus	0.028***	Alkalinity	0.056***
	Colour	0.038***	Lake area	0.010*	Colour	0.056***
	Lake area	0.011***			Lake area	0.011**
Climate variables	GDD	0.067***	GDD	0.089***	GDD	0.053***
	Temp. of January	0.010**	Temp. of January	0.024***		
Geographical location	Y	0.068***	Y	0.091***	Y	0.054***
	X	0.017***	X	0.036***		
Supra-and subaquatic delineation	dummy variable	0.023***		0.029***		0.013**
Dominant plant strategy group						

	Competitive		Stress-tolerant		Ruderal	
	Variable	adj. R ²	Variable	adj. R ²	Variable	adj. R ²
Local variables	Colour	0.036***	Total phosphorus	0.052***	Total phosphorus	0.061***
	Alkalinity	0.032***	Alkalinity	0.0285***	Alkalinity	0.030**
	Lake area	0.011**	Colour Area	0.0129* 0.0108*	Lake area	0.020*
Climate variables	GDD	0.078***	GDD	0.041***	Temp. of January	0.026**
	Temp. of January	0.017***				
Geographical location	Y	0.079***	Y	0.044***	Y	0.027**
	X	0.023***				
Supra- and subaquatic delineation		0.029***				

Table 4. Standardized parameter estimates as weighted edges from structural equation modelling (SEM) among post glaciation condition (supra), local water quality and macrophyte community composition of different variable groups, which were represented by the first two axis scores of principal redundancy analysis (PCA1 and PCA2). A suggested guideline for interpreting the influence of standardized path coefficients with absolute values is that less than 0.10 indicates a small effect, values around 0.30 indicate a medium effect and values greater than 0.50 indicate a large effect (e.g., Grace, 2006). The a priori hypothesized model is given in Fig. 2. “→”: direct effect, “(→)”: indirect effect, TP: total phosphorus, PGC: post glaciation condition originated from the delineation between supra- and subaquatic lakes. Statistical level of significance: *<0.05; **<0.01; ***<0.001.

	PCA1					
Interactions	All taxa	Helophytes	Hydrophytes	Competitors	Stressors	Ruderals
Alkalinity→TP	0.444***	0.444***	0.444***	0.444***	0.444***	0.444***
Color→TP	0.650***	0.650***	0.650***	0.650***	0.650***	0.650***
PGC(→)TP→Macrophytes	0.167** -0.158	0.167** -0.186	0.167** 0.109	0.167** 0.166	0.167** 0.110	0.167** 0.379***
PGC(→)Alkalinity→Macrophytes	0.096 -0.258	0.096 -0.146	0.096 0.458***	0.096 0.173	0.096 0.454***	0.096 0.206
PGC(→)Color→Macrophytes	0.101 0.216	0.101 0.177	0.101 0.558***	0.101 -0.374*	0.101 0.367**	0.101 -0.022
PGC(→)Macrophytes	0.104	0.022	0.001	-0.100	-0.038	-0.107
	PCA2					
Alkalinity→TP	0.444***	0.444***	0.444***	0.444***	0.444***	0.444***
Color→TP	0.650***	0.650***	0.650***	0.650***	0.650***	0.650***
PGC(→)TP→Macrophytes	0.167** 0.145	0.167** -0.280	0.167** 0.095	0.167** 0.131	0.167** 0.055	0.167** -0.119
PGC(→)Alkalinity→Macrophytes	0.096 0.472***	0.096 -0.141	0.096 0.462***	0.096 0.328**	0.096 0.059	0.096 0.073
PGC(→)Color→Macrophytes	0.101 0.354***	0.101 -0.045	0.101 -0.233	0.101 0.138	0.101 0.209	0.101 0.267
PGC(→)Macrophytes	0.309***	-0.382***	-0.090	0.516***	0.042	0.173

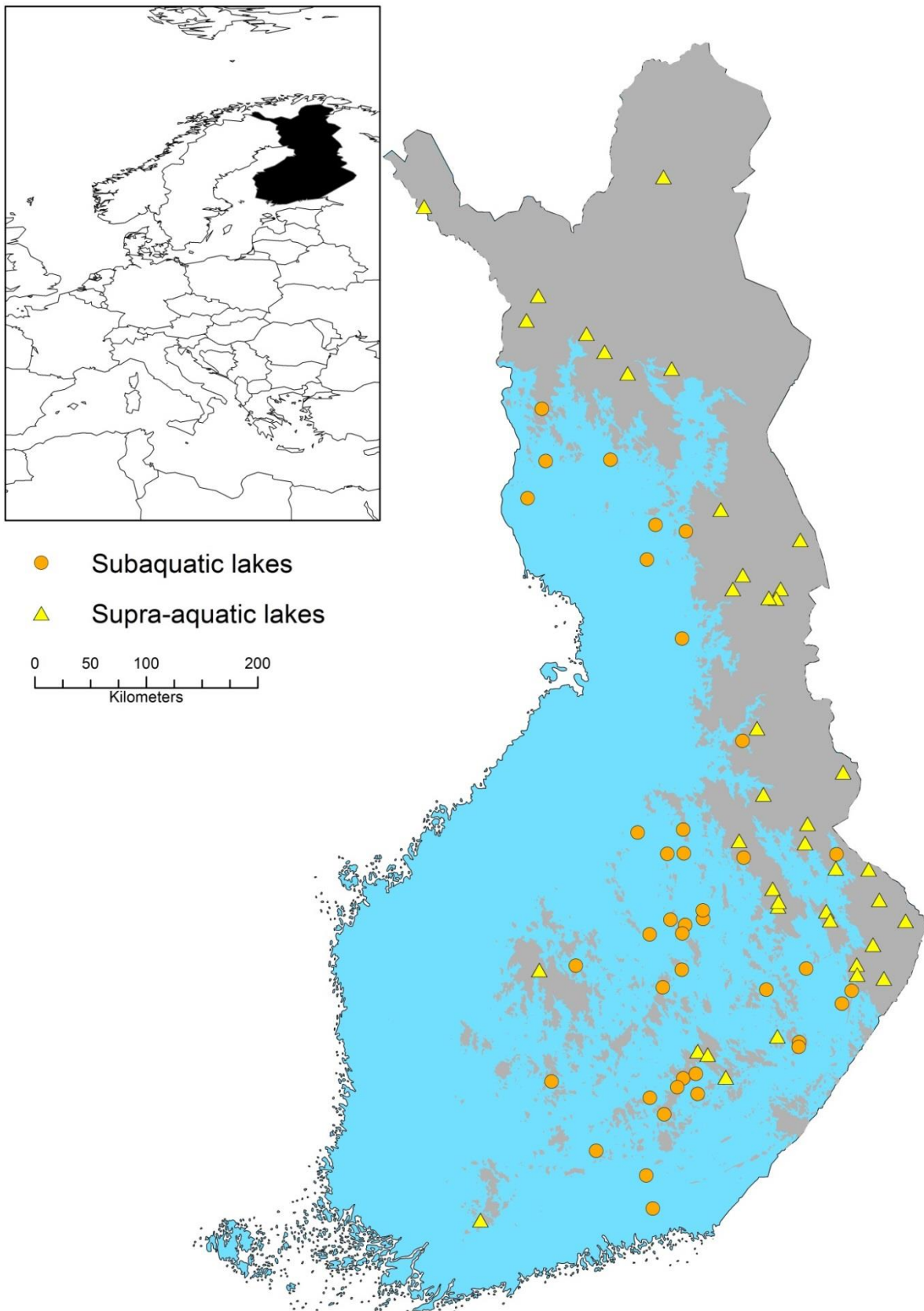


Fig. 1. Location of supra- and subaquatic lakes in Finland.

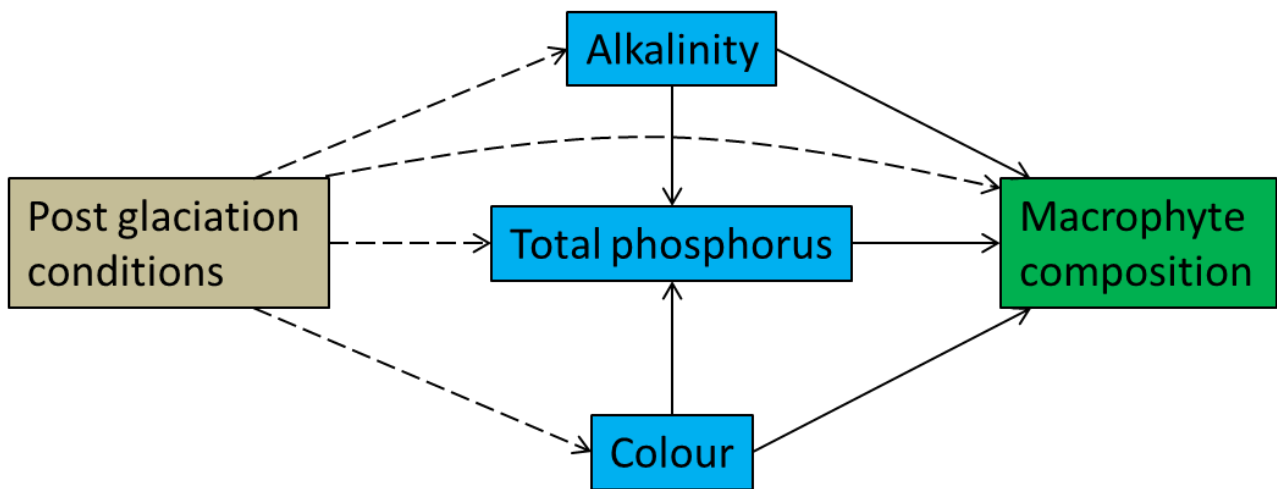


Fig. 2. Conceptual model used to evaluate the influence of post glaciation condition on local variables and macrophyte community composition using structural equation modelling. Dashed lines indicate indirect, endogenous effect, whereas full lines indicate direct influence.

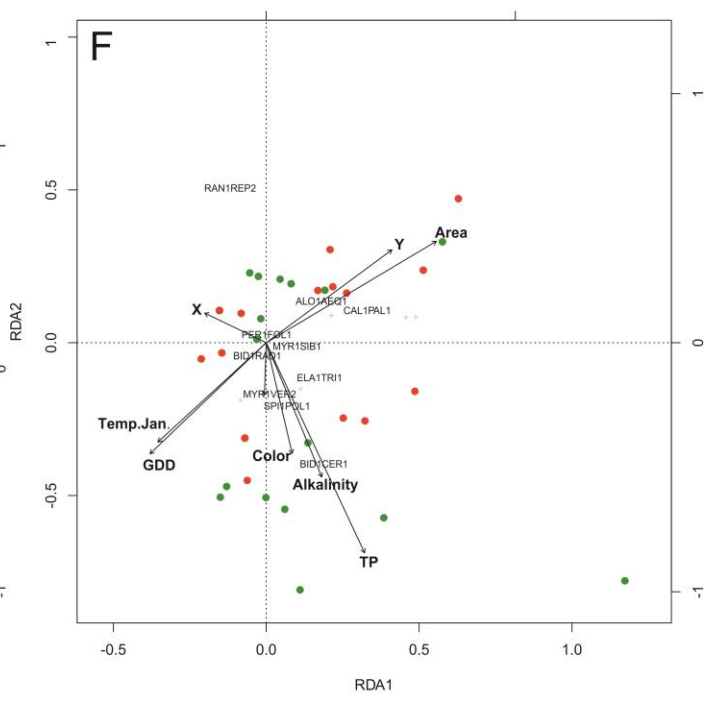
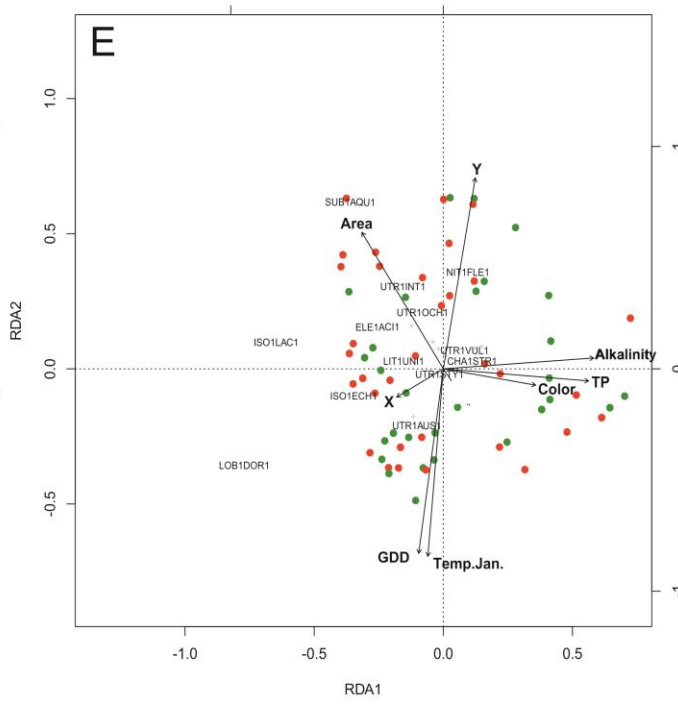
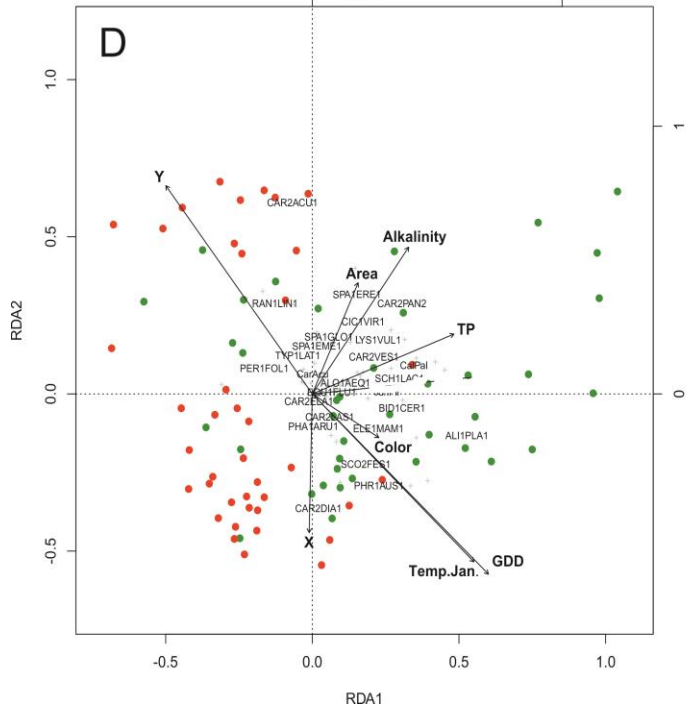
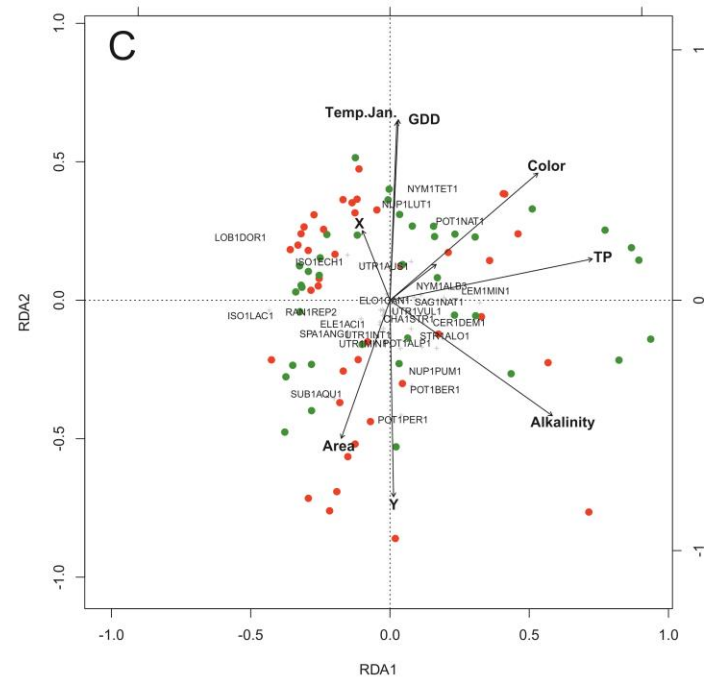
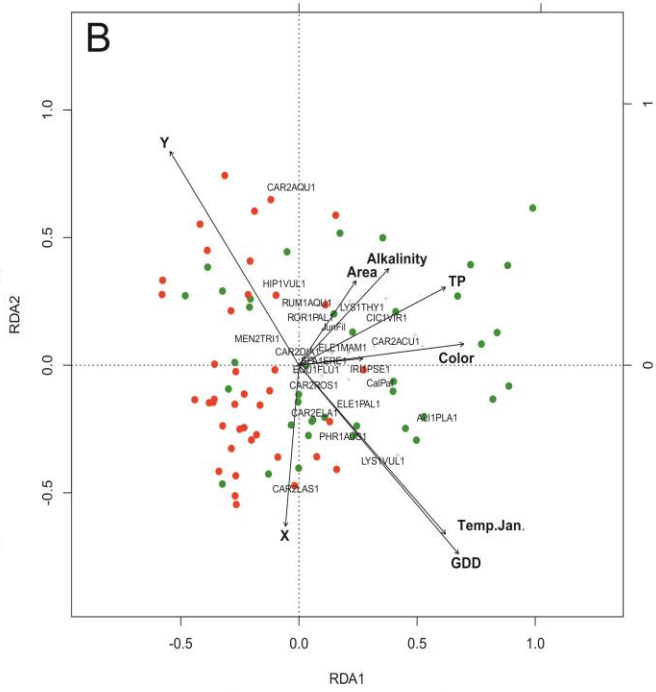
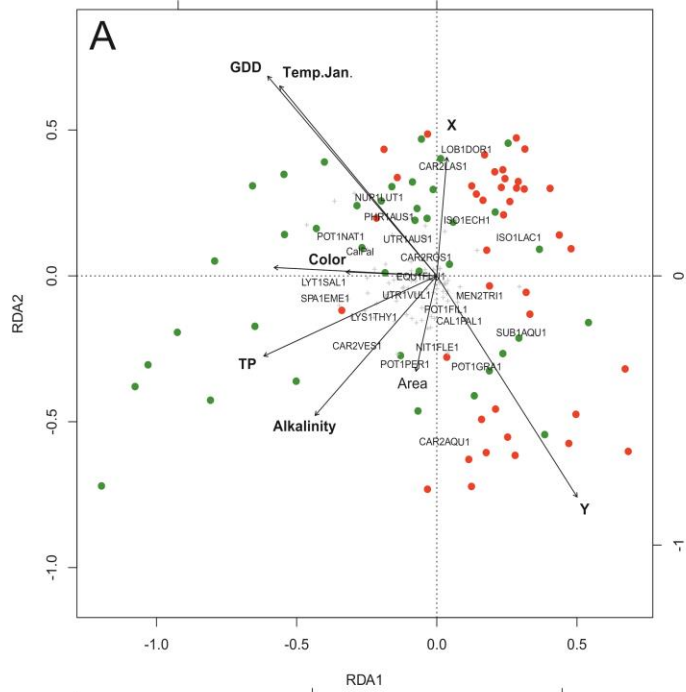


Fig. 3. RDA ordination plots of the environmental gradients for community composition of (A) all macrophytes, (B) helophytes, (C) hydrophytes, (D) competitors, (E) stress-tolerants, and (F) ruderals. Supra-aquatic lakes are shown in red and subaquatic lakes in green. Text will be used for species names with higher priority if labels overlap based on ORDITORP in Vegan. Area: Surface area, GDD: Growing degree days, Supra: Delineation between supra- and subaquatic lakes, Temp.Jan.: Temperature of January, TP: Total phosphorus. Species abbreviations are based on the first three letters of genera and species names. Species abbreviations with full names are found in the Online Resources.

