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

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ABSTRACT

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

INTRODUCTION

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

Many studies have investigated the roles of regional vs. local factors and their impact on species distributions; however, disagreement exists concerning their relative importance in structuring local communities (Ricklefs, 2004; Soininen, 2014). Disparity over the dominance of regional and local factors in explaining local communities also stems from the differences between study systems in relation to geographic location and habitat. For example, high-latitude regions can exhibit strong regional effects on local communities due to geographic variability in the influence of the past glaciations (Svenning & Skov, 2003; Svenning et al., 2010; Alahuhta et al., 2013). In freshwater ecosystems, variable patterns in the relative importance of regional and local determinants on local communities have strongly depended on the studied biological assemblage (De Bie et al., 2012; Alahuhta & Heino, 2013; Viana et al., 2014; Heino et al., 2015; McCann, 2015). These freshwater examinations have focussed on distinguishing local environmental conditions from regional spatial processes in explaining local communities. However, much less attention is given to actual historical effects, such as the Pleistocene glaciation period, in explaining freshwater communities.

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

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

Besides belonging to different functional plant groups, aquatic macrophytes can also be categorised based on life history strategy (Grime, 1977), in which species are classified as competitive (C), stress-tolerant (S) and ruderal (R). Competitors (C) are plant species growing in areas of low stress and disturbance, thus having good competition capabilities. Stress can be defined as conditions such as lack of light or nutrients, whereas disturbance can be caused by wind or drought. Competitors can outcompete other plants by reserving available resources such as growth area or nutrients. Favourable characteristics of competitors include rapid growth rate, high productivity and wide phenotypic plasticity. The latter property describes highly flexible morphology and reallocation of resources depending on conditions experience by the plant. For example, the large-sized helophyte, *Phragmites australis,* is a typical C-strategist representing aquatic plants. Stress-tolerant plant species (S) occupy areas of high intensity stress and low intensity disturbance, such as in deep-water environments. Species have adapted to this strategy with slow growth rates, long-lived leaves, high rates of nutrient retention, and low phenotypic plasticity. They are adapted to environmental stresses through physiological variability. Typical examples include large isoetids such as *Isoetes lacustris* or *Lobelia dortmanna* with evergreen leaves adapted to lack of nutrients and light. Ruderal plant species (R) are adapted to high-intensity disturbance and low-intensity stress. These species are fast-growing, have short life cycles and vigorous seeds production. Plants that have adapted this strategy are often found colonizing recently disturbed land, and are often annuals. Typical examples are small-sized isoetids like *Ranunculus reptans* and *Elatine hydropiper* occupying the eroded littoral zone.

The overall purpose of our study was to investigate the importance of regional and local factors on aquatic macrophyte communities in 80 Finnish lakes. Firstly (I), we researched the relative roles of post glaciation condition, geographical location, climate characteristics and local water quality in explaining variation in aquatic macrophyte composition of all taxa, helophytes and hydrophytes. Secondly (II), we investigated if aquatic macrophytes categorized as dominant competitive, stress-tolerant and ruderal plant groups, based on the life history strategy classification (Grime, 1977), respond similarly to these four explanatory variable sets. Based on previous findings (Toivonen & Huttunen, 1995; Vestergaard & Sand-Jensen, 2000; Alahuhta et al., 2014), we expected to find that all macrophyte communities respond primarily to local determinants. We also hypothesised that macrophyte communities are affected by regional variables, as latitudinal gradient derived from climatic variation is known to structure macrophytes at regional scales (Heino & Toivonen, 2008; Alahuhta, 2015). In addition, we supposed that glaciation period does not influence macrophyte communities anymore, because many plant species disperse efficiently, have wide range sizes and spatial processes have rarely been important factors controlling macrophytes even at regional scales (Barrat-Segretain, 1996; Claussen et al., 2002; Viana et al., 2014; Alahuhta et al., 2015).

MATERIAL AND METHODS

Study area and supra delineation

We used aquatic macrophyte data from 80 boreal lakes (<100 km^2) distributed across Finland (Fig. 1). Half of the lakes (40) were situated in high-altitude supra-aquatic areas, which were above the maximum water level during the existence of Ancylus Lake in ca. 9 000 BP (Table 1). The Ancylus Lake was the largest post-glacial sea lake in Fennoscandia, covering over 60% of Finland's surface area (Tikkanen & Oksanen, 2002). As the supra-aquatic areas were not enclosed by the Ancylus Lake and terrestrial land surrounded supra-aquatic lakes in a way similar to modern times, aquatic plants established in these 40 lakes have been efficiently spatially isolated from each other by a non-habitable terrestrial matrix and thus limited by dispersal processes. Another 40 lakes were situated in subaquatic areas, which were below sea level during the existence of Ancylus Lake. A sudden rise in water level, when the Ancylus Lake was established, has likely led to the loss of many macrophyte species from their original sites. However, new colonies have probably formed in shallower areas, as species were able to disperse freely throughout the lake. These subaquatic lakes were randomly chosen from a larger set of lakes (see Alahuhta et al., 2012). The separation between supra- and subaquatic areas (Fig. 1) was based on the map found in Tikkanen & Oksanen (2002).

Macrophyte and explanatory variables

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

Macrophyte community composition variables were calculated separately for all taxa, helophytes and hydrophytes. In addition, we separated plant species into dominant plant strategy groups (C, S or R) based on Grime (1977) and Grime et al. (1988). Information on 36 species traits was based on Jalas (1958, 1965, 1980). Aquatic plant strategy properties based on Rørslett (1989) and Murphy et al. (1990) were used to define the dominant strategies for all the studied plants. The list of dominant plant strategy groups for each species is given in Online Resource S1. If species possessed a certain species trait, this was recorded and the cumulative number of species traits over all 36 traits representing each plant strategy group was calculated. Then, a species was classified to that dominant plant strategy group (C, S or R) for which the number of species traits was the highest (e.g. if 4 traits represented C, 2 traits represented S and 6 traits represented R, then the species was grouped as a ruderal (R) species). In some rare cases with same amount of traits for R and C, the final strategy was selected by using the most common strategy of the overall genus. The species were divided into dominant plant strategy groups as follows: 71 competitors, 22 stress-tolerant and 16 ruderal species (Online Resource S1).

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

The explanatory variables consisted of local variables, climate variables, one historical variable indicating post glaciation condition (supra- and subaquatic areas) and spatial structure (geographical coordinates). Local variables were alkalinity in water (mmol/l), total phosphorus in water (µg/l), water colour (mg Pt/l) and lake area (km^2), whereas climate variables were comprised of growing degree days (> 5°C, Pirinen et al., 2012) and January temperature (°C). Alkalinity is related to the ability of some macrophyte species to utilize bicarbonate as a source of carbon, giving these species a competitive advantage over others (Vestergaard & Sand-Jensen, 2000). Total phosphorus reflects lakes trophic conditions (Alahuhta, 2015). Water colour is used to mirror at what water depth species can exist, as availability of light for photosynthesis decreases strongly towards deeper water columns in lakes with high humic content (Toivonen & Huttunen, 1995). Lake area indicates horizontal habitat availability with larger lakes having more different habitats available for macrophyte establishment (Lacoul & Freedman, 2006). Of the climate variables, growing degree days is directly related to the length and intensity of the growing season, whereas the January temperature was used as a proxy for harsh winter conditions, which affect macrophytes through thick ice cover, ice erosion and freezing of sediments (Hellsten, 2001; Lind et al., 2014). Information on local variables was obtained from the Hertta database for the period of 2006–2011 (growing season only), based on mean values of 1 metre surface samples for water quality variables (http://www.syke.fi/en-US/Open_information). Climate variables for lake area were derived from the Finnish Meteorological Institute for the period 1981–2010 with the resolution of 1km (Pirinen et al., 2012). ArcGIS 10 (ESRI, Redlands, CA, US) was used to process both climate variables. Lake coordinates (Y = latitude, X = longitude) were based on centre points from each lake, gathered using ArcGIS.

Statistical analyses

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

Variation explained by each variable group was evaluated with adjusted R^2, which provides unbiased estimates of the explained variation (Peres-Neto et al., 2006). In forward selection, type I errors can be avoided by using adjusted R^2 values, which are also comparable between different models as the number of explanatory variable is taken into account (Blanchet et al., 2008). In addition, utilization of adjusted R^2 values can lead to negative pure fractions in a variation partitioning procedure (Borcard et al., 2011). For joint fractions, negative adjusted R^2 values can also indicate multicollinearity among studied explanatory variables. Following the procedure of Blanchet et al. (2008), forward selection to obtain significant variables for further analysis was based on the Monte Carlo permutation test (999 permutations, $\alpha = 0.05$) and two stopping rules: $p > 0.05$ or the adjusted R^2 value of the reduced model exceeded that of the global model. Explanatory variables showed a variable degree of multicollinearity (total phosphorus and colour: $R_{\text{Spearman}} = 0.74$, $p < 0.001$; latitude and climate variables: $Rs = |0.96\text{-}0.98|$, $p < 0.001$), although this does not impair the variation partitioning procedure used in our study (Oksanen et al., 2012). All pRDAs were performed in the R environment with PACKFOR (S. Dray, Université Claude Bernard Lyon I) and VEGAN packages (Oksanen et al., 2012).

We also considered whether post glaciation condition had created different local environmental conditions between supra- and subaquatic lakes that further affect macrophyte community compositions. To evaluate this, we used structural equation modelling (SEM) to test a) indirect effects of post glaciation condition on water quality variables and macrophyte flora and b) direct effects of water quality on macrophytes. SEM is especially informative in studies of cause-effect relationships by investigating the networks of connections among system components (Grace et al., 2012). A key feature in SEM is to partition relationships among pathways, which traces a route from a predictor to a response representing a distinct mechanism (Grace, 2006). In our study, we built a robust SEM model among the explanatory variables and macrophyte flora that was tested separately for different macrophyte variable groups (Fig. 2). Given the rationale on the hierarchy of factors we analysed, we expected that post glaciation condition indirectly affects local water quality, which in turn directly influences macrophyte communities. We also assumed that water quality variables were linked. We used the first two axis scores of PCA (i.e., PCA1 and PCA1) to represent macrophyte community compositions. In our results, standardized coefficients indicate the strength of the relationship because they are scaled to the same units (Grace et al., 2012). Standardized estimates correspond to effect-size estimates. The goodness of model fit was based on chi-square and the evaluation of parameter estimates on z statistics. The interpretation of model fit is opposite to conventional statistical analysis in SEM (i.e., higher p>0.05 indicates better model based on chi-square), whereas z statistics follow the common interpretations of analysis. Our key purpose was to understand the patterns of correlation among a set of variables (i.e., post glaciation condition, local water quality and macrophyte community composition), not to explain as much of their variance as possible with the model specified. SEM models were constructed in the R environment using LAVAAL (Rosseel, 2012) and SEMPATHS (Epskamp, 2015) packages.

RESULTS

Macrophyte community compositions

Overall variation explained in variation partitioning was 17.5% for all taxa, 17.6% for helophytes and 17.8% for hydrophytes (Table 2). Of the pure fractions, community composition of all taxa (6.6%), helophytes (1.7%) and hydrophytes (10.4%) were best explained by local variables, which was the only statistically significant pure fraction. Other pure fractions had clearly smaller or non-existence importance for all of the three macrophyte community compositions. The joint fraction of climate and geographical location was comparatively high for all taxa (6.7%), helophytes (11.0%) and hydrophytes (4.2%). The joint fraction of geographical location and post glaciation condition also showed some explained variation for all community compositions (0.6–1.6%), similarly to the joint effect of local variables and geographical location (1.2–1.4%). Post glaciation condition and geographical location were quite high compared to other fractions for helophyte community composition. These results suggest that post glaciation condition affects variation in helophyte community composition, because post glaciation condition is clearly dependent on geographical location. A majority of subaquatic lakes are located in central Finland, whereas post glaciation condition lakes span over a large area covering most of the eastern and northern parts of the country (Fig. 1). Similarly, local variables vary between supra- and subaquatic lakes, as colour and total phosphorus gradients are clearly wider in subaquatic lakes (Table 1). In addition, the joint contribution of local variables and climate explained small amount of variation (0.9–1.1%). The number of species varied between supra- and subaquatic lakes for all taxa and helophyte community compositions.

Alkalinity and colour were the most important local variables for community composition of all taxa and hydrophytes, whereas total phosphorus explained most variation for helophytes (Table 3, Fig. 3). Of the hydrophytes, *Potamogeton berctoldii* and *Nuphar pumila* were most positively and *Lobellia dortmanna and Isoetes echinospora* were most negatively associated with alkalinity. *Potamogeton natans* was most positively and *Subularia aquatica* and *Ranunculus peltatus* most negatively correlated with colour. Of the helophytes, *Cicuta virosa* was most distinctly related to total phosphorus. Growing degree days of climate variables had the highest effect on all macrophyte community compositions. *Nuphar lutea* and *Nymphaea tetragona* of the hydrophytes and *Lysimachia thyrsiflora* and *Phragmites australis* of the helophytes were positively associated with the growing degree days, which also negatively influenced the helophytes *Hippuris vulgaris* and the hydrophytes *Potamogeton perfoliatus, Potamogeton gramineus* and *Subularia aquatica*. Of the geographical location, coordinate Y indicating latitudinal variation was the most important variable for all community compositions. Supra-aquatic and subaquatic lakes were quite clearly separated in ordination space for all taxa and helophytes.

Dominant plant strategy groups

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

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

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

Structural equation modelling

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

DISCUSSION

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

The environmental determinant operating at the broadest scale in our study was post glaciation condition. We expected that aquatic macrophytes with efficient dispersal strategies had evenly colonized supra- and subaquatic lakes by now (e.g., Barrat-Segretain, 1996; Sawada et al., 2003), and we indeed found few differences between strongly and poorly dispersing species (Online Resource S2). However, post glaciation condition seems to influence macrophyte community compositions after over 9 000 years. We found support for this outcome from both the variation partitioning and structural equation modelling. Although the pure effect of post glaciation condition showed only a modest contribution to the macrophyte flora, the joint fraction of post glaciation condition and geographical location indicated considerable influence on macrophyte community compositions compared to most of the other joint effects. In addition, the joint contribution of local variables, post glaciation condition and geographical location suggested that these variable groups form a complex interplay with each other that is difficult to distinguish in variation partitioning. For example, the variation in colour is much wider in subaquatic lakes compared to supra lakes, whereas different soil types influence total phosphorus concentrations between the lakes. Finer soil deposits were washed in subaquatic areas but these nutrient-rich soils are often present in supra areas (Ojala et al., 2013) creating better growth conditions for plants in supra areas. On the other hand, current clay soils are typically found in southern and western lowland catchments of Finland as a consequence of subglacial sedimentation, enhancing natural background concentrations of nutrients in subaquatic lakes (Alahuhta et al., 2011). In addition, human pressures are stronger in more populated southern areas of Finland, for which anthropogenic-originated nutrients increase trophic status in many subaquatic lakes (Kanninen et al., 2013b). These confounding and often confronting effects make it difficult to study the effect of post glaciation condition in Finnish lakes, of which most are slightly affected by human pressures.

However, structural equation modelling enabled us to distinguish the effect of post glaciation conditions on local water quality and macrophyte flora. Post glaciation condition indirectly affected macrophyte composition of all taxa, helophytes and competitors. In addition, post glaciation conditions indirectly influenced total phosphorus, which significantly structured ruderals. Helophytes were also contributed by total phosphorus, but not statistically significantly ($p=0.081$). These findings suggest that aquatic macrophyte communities have, in a way similar to terrestrial plants (Skov & Svenning, 2003), not yet reached their full distribution ranges following the last glaciation period. In addition, inorganic phosphorus can be bound in organic matter, the rise of which results in increasing colour values in water (Madsen et al., 1996). This chain of events likely explains why colour was most strongly correlated with total phosphorus (Table 4), further supporting the indirect post glaciation condition effect on macrophytes. It seems colour values vary along the post glaciation condition delineation in our study area. Our findings contradict previous paleolimnological studies (Sawada et al., 2003; Väliranta, 2006; Väliranta et al., 2011), in which aquatic macrophytes were proposed to quickly occupy ice-free areas following deglaciation. Many helophytes and hydrophytes classified as competitors but also stress-tolerants dispersed rapidly to new habitats within a few millennia after ice sheets withdrew in North America. Furthermore, aquatic macrophytes in North America responded little to post-glacial climate changes, as Late-Holocene cooling does not appear to have affected their ranges (Dieffenbacher-Krall & Jacobson, 2001). In our work, however, post glaciation condition affected mostly helophytes, because more than half of the competitive species and half of ruderal species were classified as helophytes. Instead, hydrophytes and stress-tolerants, of which all species were hydrophyte species, were not influenced by either post glaciation condition or total phosphorus. This was also seen in the ordination plots, where supra-aquatic and subaquatic lakes were distinguished from each other for all taxa, helophyte and competitors only. Helophytes often inhabit aquatic-terrestrial ecotones, where growing conditions in many ways resemble that of terrestrial ecosystems (Alahuhta et al., 2011). Thus, it may be that true aquatic macrophytes growing permanently in water are less influenced by post glaciation condition than semi-aquatic helophyte species.

Climate structured aquatic macrophyte communities at the second broadest scale. Latitudinal gradient in climate is strong in the boreal region and previous studies have evidenced a clear variation in species distributions along a changing climate from south to north (Rørslett, 1991; Heino & Alahuhta, 2015; Alahuhta et al., 2016). Climate was equally or more important than other factors for community composition of all taxa, helophytes and competitors. The two regional factors (climate and glaciation) are also linked through latitudinal and altitudinal variation, as supra-aquatic lakes are located in more northern and eastern areas with lower growing degree days and more continental climate conditions (Alahuhta et al., 2011). In addition, supra-aquatic lakes are typically at least 200m above sea level (Tikkanen & Oksanen, 2002), where temperatures are lower compared to lowland areas. Competitive species were generally dominant in sub-aquatic lakes with higher nutrient status, thus supporting the original theory of Grime (1977) regarding resource availability.

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

Local variables contributed to the macrophyte flora at the smallest spatial scale. The high influence of local determinants on macrophyte flora originates from the fact that variation in local gradients is typically very wide in freshwater ecosystems, creating variable habitat conditions even in neighbouring lakes (Elser et al., 2007). Wide water quality gradients have enabled species with different tolerances to local environmental conditions to co-exist in geographically closely-situated habitats, typically resulting in relatively high species turnover among these habitats for aquatic macrophytes (Alahuhta & Heino, 2013; Viana et al., 2014). In addition, regional factors have had a smaller impact on freshwater assemblages due to the sheltering effect of water, which has, for example, moderated the influence of extreme atmospheric temperatures on aquatic species (Lacoul & Freedman, 2006). Although the climate gradient in freshwater ecosystems is not as wide as in terrestrial systems, climatic determinants must be studied alongside local factors when investigating aquatic macrophyte community compositions at the regional scale.

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

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

Finally, the hierarchical nature of regional and local determinants in structuring aquatic macrophyte community compositions found in our study is also related to the accuracy of explanatory variables. Local factors were measured at the lake level corresponding with that of macrophyte surveys. Climate determinants were similarly delineated to lake surface area, but fine-scale variation in climate gradient is modest (Whittaker et al., 2001). Both local water quality and climate factors were long-term averages of multiple measurements, decreasing uncertainty related to yearly changes in these observations. Separation of supra- and subaquatic areas was the least exact based on the modelled scenario, however, the accuracy is well-suited for our regional study scale covering almost 300 000 km^2.

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Table 1. Descriptive statistics of explanatory variables and number of species in supra- and 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 (µg/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 °C)	Mean	1016	1169	1093
	Min.	538	839	538
	Max.	1348	1430	1430
January temperature (°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

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

0.05) pure fractions based on the ANOVA-like permutation test are marked in italics. “-“ indicate negative adjusted R^2 values. C = competitors, S = stress-tolerants, R = ruderals.

	All Taxa	**Helophytes**	**Hydrophytes**	**C**	**S**	**R**
Local	*6.63*	*1.69*	*10.43*	*5.39*	*9.54*	*10.05*
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

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 R^2 and forward selection using the Monte Carlo permutation test (999 permutations; a = 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	0.0129*	Lake area	0.020*
			Area	0.0108*		
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

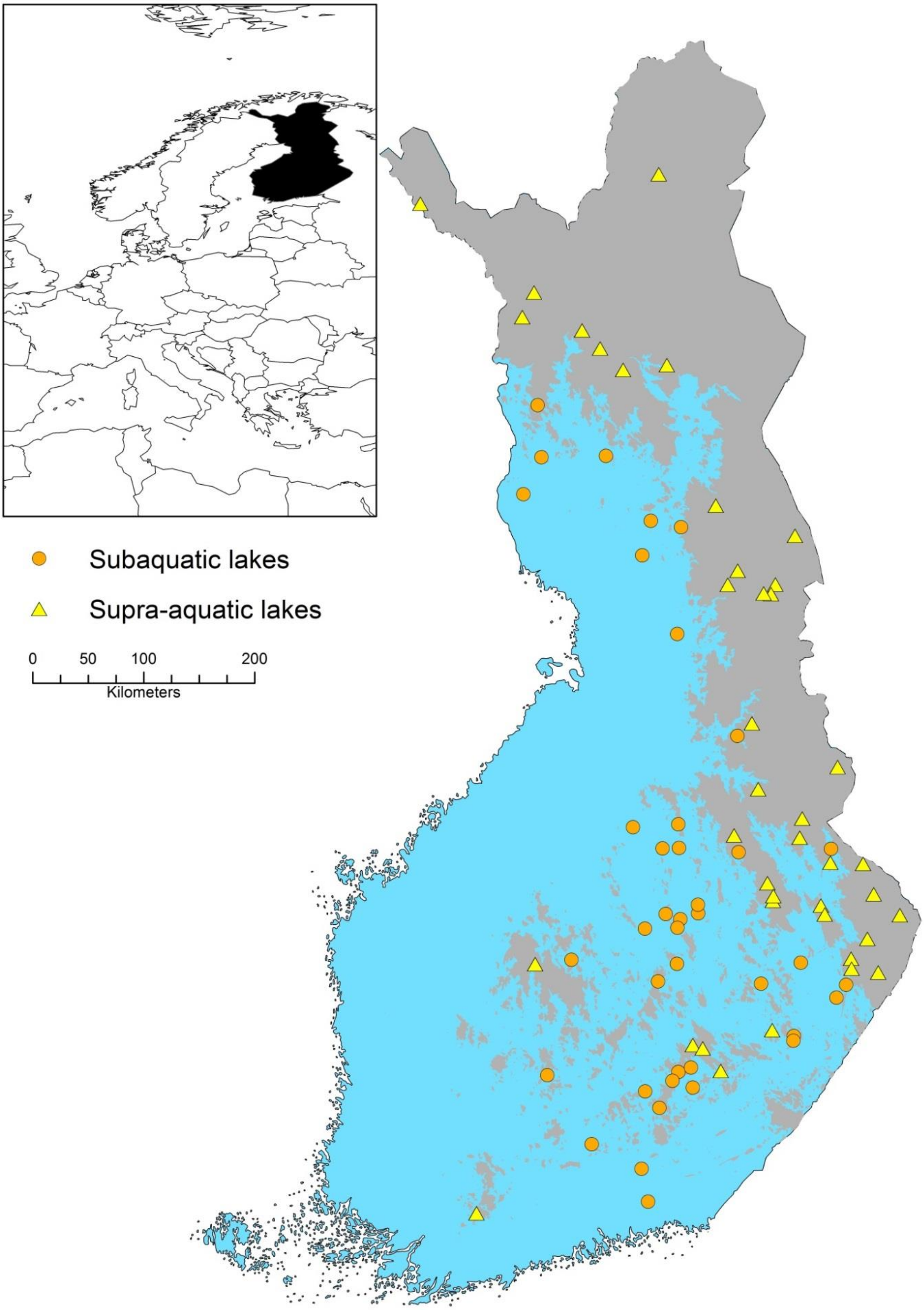

Fig. 1. Location of supra- and subaquatic lakes in Finland.

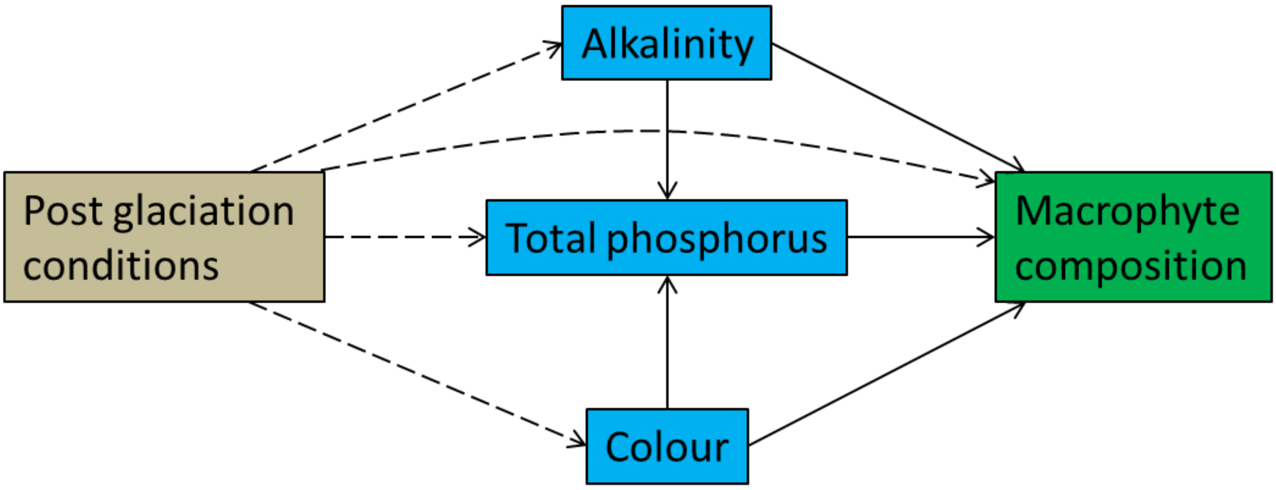

Fig. 2. Conceptual model used to evaluate the influence of post glaciation condition on local variables and macrophyte community composition using structural equation modelling. Dashed lines indicate indirect, endogenous effect, whereas full lines indicate direct influence.

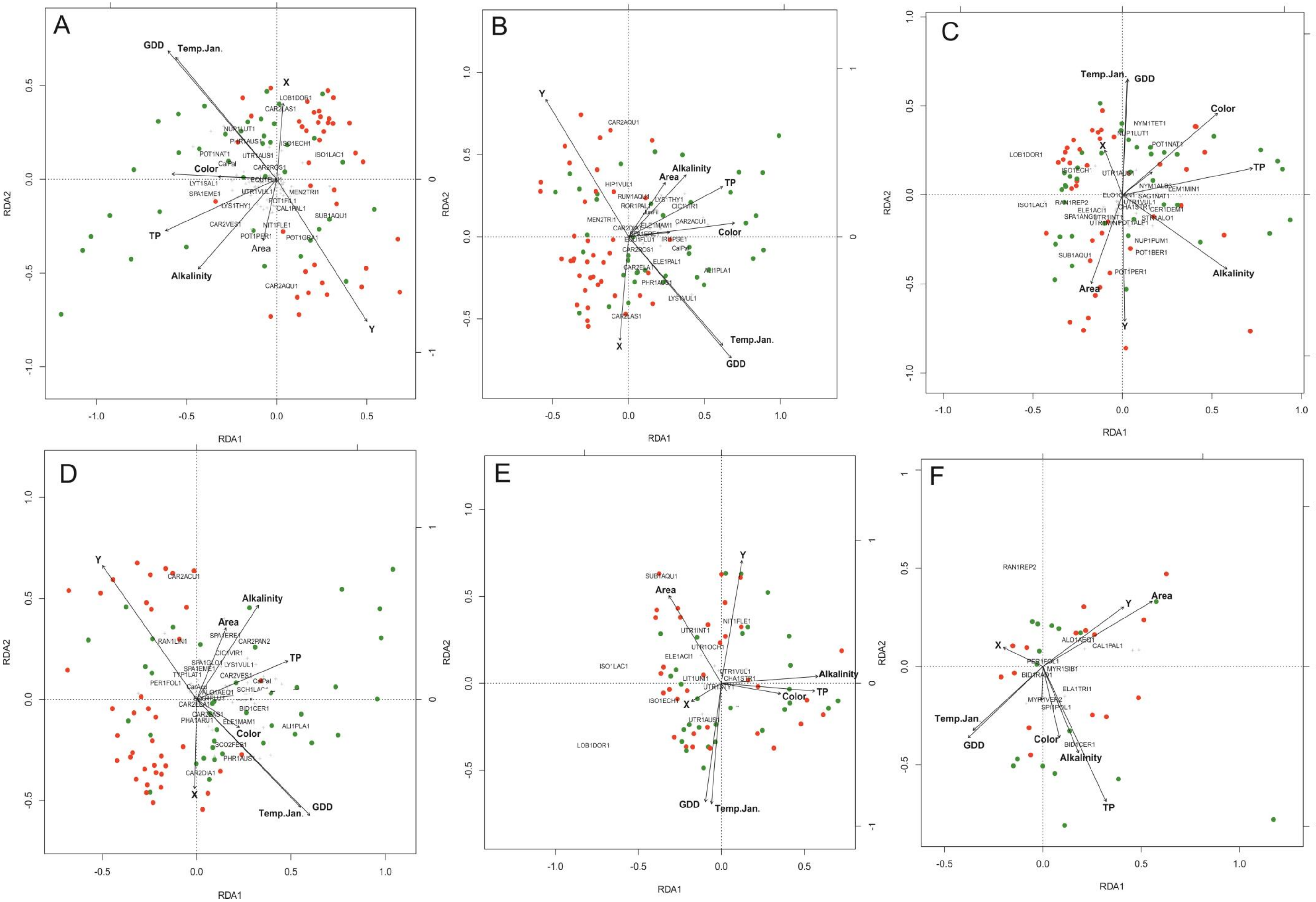
A
GDD
Temp.Jan.
X
Y
Color
TP
Alkalinity
Area
LOB1DOR1
CAR2LAS1
NUP1LUT1
PHR1AUS1
ISO1ECH1
POT1NAT1
CalPal
UTR1AUS1
CAR2ROS1
ISO1LAC1
EQU1FLU1
LYT1SAL1
SPA1EME1
UTR1VUL1
MEN2TRI1
POT1FIL1
LYS1THY1
CAL1PAL1
NIT1FLE1
SUB1AQU1
CAR2VES1
POT1PER1
POT1GRA1
CAR2AQU1
RDA1
RDA2
B
Y
X
Alkalinity
Area
TP
Color
Temp.Jan.
GDD
CAR2AQU1
HIP1VUL1
RUM1AQU1
LYS1THY1
ROR1PAL1
CIC1VIR1
JunFil
MEN2TRI1
ELE1MAM1
CAR2ACU1
CAR2DIA1
SPA1ERE1
IRI1PSE1
EQU1FLU1
CalPal
CAR2ROS1
ELE1PAL1
CAR2ELA1
ALI1PLA1
PHR1AUS1
LYS1VUL1
CAR2LAS1
RDA1
RDA2
C
Temp.Jan.
GDD
Color
X
TP
Area
Alkalinity
Y
NYM1TET1
NUP1LUT1
POT1NAT1
LOB1DOR1
ISO1ECH1
UTR1AUS1
NYM1ALB3
LEM1MIN1
ELO1CAN1
SAG1NAT1
ISO1LAC1
RAN1REP2
UTR1VUL1
ELE1ACI1
CHA1STR1
CER1DEM1
SPA1ANG1
UTR1INT1
STR1ALO1
UTR1MIN1
POT1ALP1
NUP1PUM1
POT1BER1
SUB1AQU1
POT1PER1
RDA1
RDA2
D
Y
Alkalinity
Area
TP
Color
X
Temp.Jan.
GDD
CAR2ACU1
RAN1LIN1
SPA1ERE1
CAR2PAN2
CIC1VIR1
SPA1GLO1
LYS1VUL1
SPA1EME1
TYP1LAT1
CAR2VES1
PER1FOL1
CarAcu
CalPal
ALO1AEQ1
SCH1LAC1
CAR2ELA1
BID1CER1
CAR2LAS1
PHA1ARU1
ELE1MAM1
ALI1PLA1
SCO2FES1
PHR1AUS1
CAR2DIA1
RDA1
RDA2
E
Y
SUB1AQU1
Area
NIT1FLE1
UTR1INT1
UTR1OCH1
ELE1ACI1
ISO1LAC1
UTR1VUL1
CHA1STR1
LIT1UNI1
UTR1MIN1
Alkalinity
TP
Color
ISO1ECH1
X
UTR1AUS1
LOB1DOR1
GDD
Temp.Jan.
RDA1
RDA2
F
RAN1REP2
Y
Area
ALO1AEQ1
CAL1PAL1
X
PER1FOL1
MYR1SIB1
BID1RAD1
ELA1TRI1
MYR1VER2
SPI1POL1
Temp.Jan.
GDD
Color
BID1CER1
Alkalinity
TP
RDA1
RDA2

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.