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Environmental and spatial correlates of community composition, richness and status of boreal lake macrophytes

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ABSTRACT

We assessed the relative roles of natural covariates, human disturbance (water quality and catchment land use) together with geography in driving variation in aquatic macrophyte community composition, richness and status among 101 lakes in southern and central Finland. In addition to all species together, we studied different growth forms (i.e. emergent and submerged macrophytes and aquatic bryophytes) separately. Partial redundancy analysis (taxonomic composition) and partial least-squares regression (species richness and status index) were employed to display the share of variability in macrophyte assemblages that was attributable to the environmental factors (both natural and human-affected) and the spatial filters generated through principal coordinates of neighbor matrices (PCNM).

Macrophyte community composition, richness and status were explained by natural covariates, together with joint effects of human disturbance variables and space. The contributions of pure fractions of human disturbance and space were mostly modest, albeit variable among macrophyte groups and status indices. Alkalinity, historical distributions, colour, dynamic ratio and lake area were most important natural covariates for macrophytes. Of those variables influenced by human, macrophytes were mostly explained by conductivity, total phosphorus, turbidity and chlorophyll-*a*.

Our results demonstrate, as expected, that macrophytes are dominantly affected by local environmental variables, whereas dispersal-related processes seem not to be important at regional extent. Response of macrophyte growth forms to environment and space, however, varied significantly. Community composition and richness of emergent macrophytes showed congruent response to natural covariates and human disturbance. Aquatic bryophytes, which are rarely studied along lake macrophytes, responded stronger than other growth forms to human disturbance. Contrary to our expectations, ecological indices were not affected by dispersal-related processes, but were mainly explained by natural covariates. This study is the first to investigate spatial patterns in aquatic macrophytes derived bioassessment. Geographical structuring of environmental variables and regional extent negatively affected indices, suggesting that ecological status assessment needs further development.

1. Introduction

Improving our understanding of the spatial scales of ecological processes and patterns has been an important aim in ecology for past few decades (Levin, 1992) and remains as an essential challenge in bioassessment (Hering et al., 2010; Heino, 2012). As communities are structured by the interaction of species with their biotic and abiotic environment at different spatial scales (Benton, 2009; Field et al., 2009; Alahuhta and Heino, 2013), ecological assessment systems have also faced the many questions related to spatial structuring of species distributions and environment (Hering et al., 2010; Poikane et al., 2011; Heino, 2012). For example, the spatial extent, representing the geographic area under investigation, influences the species pool and width of environmental gradients (Rahbek, 2005; Bennett et al., 2010; Alahuhta and Heino, 2013). In a sound bioassessment system these variations are accounted for, but the methodology of the system

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may affect how well they can be incorporated (Aroviita et al., 2009).

Multi-metric and predictive modelling approaches form the basis of freshwater bioassessment systems which are based on the reference condition approach (Beck and Hatch, 2009; Friberg et al., 2011). In the multi-metric approach, biological communities are described by a number of metrics, which combine information on species richness, abundance and composition (Johnson et al., 2006; Alahuhta et al., 2009; Kanninen et al., 2013a). This approach normally relies on lake and stream typologies and on comparison between reference and impacted sites for determining ecological quality status. Water bodies, similar in their natural character, are grouped together and compared with each other as a control for natural background variability or the influence of natural covariates (sensu Wickham et al., 1997), which is essential for the performance of a bioassessment system (Hering et al., 2006; Vuori et al., 2009). However, categorical typology systems cannot cover all the relevant abiotic variation affecting biota, which may seriously dilute assessment reliability (Nõges et al., 2009). Abiotic variables can also be geographically structured, which makes establishment of reference conditions challenging at large extents. In addition, the consideration of spatial processes in multi-metric systems depends on how they are taken into account when establishing reference conditions. The identification of changes principally caused by local anthropogenic activities has been the key purpose of bioassessment. Therefore, local natural community drivers have been the main focus of bioassessment research, whereas other possible factors affecting community variability – such as spatial processes and scale – have received less attention (Frimpong and Angermeier, 2010; Gray and Arnott, 2011).

Aquatic macrophytes are considered good indicators of long-term changes of lake ecosystems, as they respond to reduced light availability, increased sedimentation and nutrient concentrations and hydromorphological changes, often originating from anthropogenic activities (Beck and Hatch, 2009; Bornette and Puijalon, 2011). Moreover, macrophytes have an essential functional role in freshwater ecosystems, as they provide habitat and shelter, breeding areas and food resources for other aquatic and terrestrial species (Carpenter and Lodge, 1986; Schmidt et al., 2005). However, traits vary among different macrophyte functional groups (growth forms) potentially influencing their responses to environmental gradients and obviously their functional roles in the ecosystem. Direct connection to aerial carbon and oxygen, improved light availability and wind dispersal make emergent macrophytes efficient competitors and dispersers compared to other macrophytes (Santamaria, 2002; Boedeltje et al., 2003; Soons, 2006). Emergent macrophytes have also been considered important in boreal lake bioassessment due to their position at the water land interface (Alahuhta et al., 2012; but see also Kanninen et al., 2013a; Dudley et al., 2013). Furthermore, compared to both emergent and submerged macrophytes, free-floating aquatic species are more directly dependent on water quality and exposure driven factors (Karttunen and Toivonen, 1995; Glime, 2007).

Our general purpose was to study how different macrophyte variables respond to environmental and spatial variables. More specifically, we first studied the relative importance of natural covariates, human disturbance (water quality and land use) and spatial variables in explaining among-lake variation of community composition, species richness and ecological status of macrophytes at a regional scale. We expected natural covariates and variables related to human disturbance to be important for macrophyte community composition and richness, along with spatiality. The importance of spatiality is often expected to increase with increasing extent (Bennett et al., 2010; Sharma et al., 2011), however, the relative importance of local variables has been documented to be high for macrophytes even at regional extents (Capers et al., 2010; Mikulyuk et al., 2011; Alahuhta and Heino, 2013). Macrophyte ecological status indices should respond primarily to human influences on water quality and to anthropogenic land use, as the indices have been specifically adjusted to detect man-made changes; whereas natural variability has been attempted to be accounted for by a lake typology. Secondly, we investigated whether functional groups (emergent and submerged macrophytes and aquatic bryophytes) differ in their response to natural covariates, human disturbance and space. We hypothesized that emergent plants show a weaker relationship than submerged macrophytes and aquatic bryophytes to water quality and land use variables. Thirdly, we studied if there is geographical structuring in environmental variables (natural covariates and human disturbances) affecting the performance of macrophyte status assessment. We assumed, based on previous studies (Vuoristo, 1998; Räike et al., 2003), that there will be geographical patterns in environmental variables that may have negative influences on the performance of status indices.

2. Materials and methods

2.1. Data

We used aquatic macrophyte data from 101 boreal lakes ($A < 40\,km^2$) in southern and central Finland (Appendix A in Supporting Information). Macrophytes were surveyed using a transect method ('main belt transect method'), in which a 5-m-wide transect from the upper eulittoral to the outer limit of vegetation (or to the deepest point of the basin if vegetation covers the entire lake) was examined (Kanninen et al., 2013b). The transect was divided into zones according to the dominant growth-form or species. Macrophytes were observed by wading or by boat, with assistance of rakes and hydroscopes. The number of transects varied between seven and 26 depending on lake size and securing proper view of species composition (Kanninen et al., 2013b). The surveys were carried out between July and September 2002–2008. The recorded species (134 in total) included emergent (incl. shore species) and submerged macrophytes and aquatic bryophytes (Table 1, Appendix A in Alahuhta et al., 2012).

Macrophyte community composition variables and species richness were calculated separately for all taxa, emergent and submerged macrophytes and aquatic bryophytes. Ecological status was based on the Finnish national typology and ecological classification scheme (Alahuhta et al., 2009; Vuori et al., 2009). Three metrics – proportion of type-specific taxa, Percent Model Affinity and Trophic Index – were used to define the status of the macrophyte vegetation in the study lakes (see Alahuhta et al., 2012 for details). The three metrics were re-scaled according to Mykrä et al. (2012) to allow for a meaningful comparison and averaging across the metrics. The average of the re-scaled metrics was used as a composite status index.

Three sets of explanatory variables were used: (i) natural covariates, (ii) human disturbances (human affected water quality and land use) and (iii) spatial variables (Table 1). Natural covariates (sensu Wickham et al., 1997) included lake order (categorical variable), mean altitude of lake (m.a.s.l.), modelled amplitude of water level fluctuation (m, Keto et al., 2008), lake surface area (ha), shoreline development factor (Alahuhta et al., 2012), dynamic ratio (Håkanson, 1982), mean depth (m), alkalinity ($mmol\,l^{-1}$), colour ($mg\,PT\,l^{-1}$) and pH. The latter water quality variables were included, because colour is assumed to be relatively inert to human influences reflecting peat land portion of drainage basin and is used in the national lake typology system. pH – along with its counterpart alkalinity – also primarily indicates natural background variation. Natural background variation primarily overrides anthropogenic impacts on these water quality variables in the boreal region (Mannio and Vuorenmaa, 1995). For example,