Variable response of functional macrophyte groups to lake characteristics, land use, and space: implications for bioassessment

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Abstract We investigated how land use at multiple scales affects functional macrophytes groups and ecological status index in the boreal region. We employed a variance partitioning analysis to quantify the relative role of lake characteristics, multiple-scaled land use (catchment, buffer zones of 100, 300 and 500 m), and space in explaining the composition and richness of functional macrophyte groups (emergent and submerged macrophytes and hydrophytes) and ecological status of macrophytes in 110 Finnish lakes. Partial redundancy analysis (community composition) and partial linear regression (richness and status index) revealed that macrophyte community composition, richness, and status index were mostly explained by the pure effect of lake characteristics, which dominated over space for most macrophyte variables. Land use adjacent to shoreline had a higher effect on emergent macrophytes and status index compared to the land use of the whole catchment. Our findings suggest that emergent macrophytes can indicate changes in water quality and hydro-morphology originated from the close vicinity of the littoral zone. Ecological quality assessment based on emergent macrophytes only is probably not sufficient, but including emergent species in the assessments is recommended, especially in the species-poor boreal region.

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Introduction

Anthropogenic pressures influence the structure and functioning of ecosystems at multiple scales and land use processes operating at different spatial scales can affect ecological systems unevenly (Akasaka et al., 2010; Mikulyuk et al., 2011; Marzin et al., 2012). In aquatic ecosystems, the hierarchical structuring of these processes is linked to differences between the topographic catchment and terrestrial land adjacent to a water body (i.e., a buffer zone). Nutrients and suspended solids derived from anthropogenic land use are transported to a water body from the topographic catchment in the drainage system. However, only a portion of all deteriorative substances leaching from the catchment reaches a given water body (Kratz et al., 1997). The fraction of loading reaching lakes situated at lower part of a lake chain depends on the hydraulic retention capacity of the water bodies above (Brett & Benjamin, 2008). Therefore, for instance the trophic status of a lake is not directly determined by the geology and human land use of the whole drainage basin. Natural catchment properties and human disturbances adjacent to the water body have the potential to more directly affect aquatic—especially littoral—habitats and may hence be more influential to the ecosystem (Alahuhta et al., 2012; Marzin et al., 2012).

While scale-related patterns in species richness have been increasingly studied, research on the scale dependency of the relations between land use and indices used in the ecological status assessment of lakes is scarce (see Pedersen et al., 2006; Beck et al., 2010). The condition of lake ecosystems is increasingly assessed and monitored by biological properties (Beck and Hatch, 2009; Rask et al., 2010; Søndergaard et al., 2010), as demanded by legislations such as the Clean Water Act in the USA (U.S. Congress, 2002) and the Water Framework Directive in the EU (European Communities, 2000). A key question in ecological assessments is the identification and quantification of the effects of anthropogenic disturbance on biota. The majority of human disturbances declining the ecological quality of freshwaters are driven by changes in catchment land use, resulting e.g., in increased diffuse loading of nutrients, and consequently, eutrophication (Brett & Benjamin, 2008; Sand-Jensen et al., 2000). However, only a handful of studies have investigated whether ecological status of lakes is influenced by land use pressures at multiple scales (e.g., Beck et al. 2010; Alahuhta et al., 2012).

Aquatic macrophytes are considered good indicators of long-term changes in water quality, hydromorphology, and ecosystem functioning. However, there are differences among functional plant groups in their response to environmental alterations (Akasaka & Takamura, 2011; Netten et al., 2011). Functional plant groups, which neither are connected to nutrient storage in the sediment nor have access to atmospheric carbon dioxide, are often considered to be the most efficient indicators of water quality changes. Emergent macrophytes fail in both criteria, as they are the only functional plant group with high number of species in the boreal region, which use nutrients from sediments and carbon dioxide from atmosphere. However, water quality changes affect emergent macrophytes indirectly, e.g., via enhanced sedimentation of organic and inorganic matter (Toivonen & Huttunen, 1995; Partanen et al., 2009). In addition, emergent species respond to changes in hydro-morphological conditions, such as shoreline structure and water level fluctuations (Partanen et al., 2009; Mjelde et al., 2013). Emergent macrophytes inhabiting the water-land interface may also have a more immediate response to anthropogenic pressures within the catchment than do other macrophytes (Alahuhta et al., 2012).

Inclusion or exclusion of emergent macrophytes from the European bioassessment procedures depends on the vegetation typical for the region and the indices used to assess ecological quality. Alahuhta et al. (2012) found indirect support for inclusion of emergent macrophytes in a boreal classification system, as an index (i.e., Trophic Index) using only hydrophytes seemed to perform poorer than indices which included emergent plants. They further found that the indices including emergent plants had a stronger response to near-shore land use than the Trophic Index. Similarly, presence of emergents in the species pool improved the performance of nitrogen-related status index in a European-scale study (Kolada et al., 2011). However, Kanninen et al. (2013a) did not find clear differences between boreal lake assessment metrics when emergents were included or excluded, although they

suggested inclusion of emergent species in ecological assessments important due to their value for biodiversity and ecosystem functioning. A European-scale study with limited number of lakes did not find any additional value to include emergent macrophytes on indices, because they did not respond to the effects of nutrient pressures efficiently (Dudley et al., 2013). Despite the strong, cumulative evidence of the significance of emergent macrophytes in the functioning of freshwater ecosystems (e.g., Rørslett, 1991; Wetzel, 1990; Alahuhta et al., 2011), it remains unresolved how this functional plant group should be treated in ecological classification.

Our overall objective was to assess the role of functional macrophyte groups in bioassessment. The specific aims of our work were to study whether (1) the community composition and richness of all taxa and functional plant groups (i.e., emergent and submerged macrophytes and hydrophytes) and ecological status of macrophytes respond similarly to lake characteristics (i.e., water quality and hydro-morphology), land use and spatial structure, and (2) the land use at different scales impacts the community composition and richness of all taxa and functional plant groups and ecological status of macrophytes congruently. We anticipated that submerged macrophytes and hydrophytes (both community composition and richness) show more variation than emergent plants with lake characteristics, because these plant groups are more dependent on water quality than emergent flora. We also expected that community composition and richness of emergent macrophytes to respond stronger than other macrophytes to the land use adjacent to lake shoreline based on the findings from Alahuhta et al. (2012). We also hypothesized that the macrophyte ecological status index responds primarily to both lake characteristics (mostly water quality) and land use, as it has been specifically designed to detect anthropogenic changes and the spatial variation has been partly accounted for by lake typology.

Materials and methods

Data

We used aquatic macrophyte data from 110 boreal lakes covering most of Finland (see Alahuhta et al., 2012). Majority of the lakes were shallow, small humic lakes (lake area <40 km², mean depth 3.6 m) and two thirds of the lakes were impacted mainly by anthropogenic pressures (i.e., agriculture and urban development). Macrophytes were surveyed using a 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 covered the entire lake) was examined (Kanninen et al., 2013b). The transect was divided into zones according to the dominant life-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 25 (mean = 14, SD = 4.2) depending on lake size. The surveys were carried out between July 2002 and September 2008. The recorded species consisted of aquatic bryophytes and all aquatic vascular plants, including emergent macrophytes (see Appendix A in Alahuhta et al., 2012).

Macrophyte community composition variables and richness, estimated as the number of species, were calculated separately for all taxa, emergent and submerged (i.e., elodeids) macrophytes and hydrophytes (Table 1). The strict definition of aquatic macrophytes excludes emergent plants (including shore species); these so called true aquatic macrophytes are referred as hydrophytes (see Toivonen & Huttunen, 1995). Ecological status was based on the Finnish national typology and ecological classification scheme (Rask et al., 2010). Three macrophyte indices of the Finnish ecological assessment system were used to define the status of the macrophyte vegetation in the study lakes: the proportion of type-specific taxa (TT50), Percent Model Affinity (PMA), and Trophic Index (TI). TT50 is based on probability of occurrence of taxa in reference conditions and species is considered to be type-specific, when it occurs in more than half of all reference sites of the lake-type. PMA is based on the comparison of each observed taxon relative abundance (RA) to the expected taxon RA under reference conditions. TI is based on division of hydrophytes to tolerant, indifferent, and sensitive species based on their occurrence probabilities along a phosphorus gradients. Details of the quality indices can be found from Penning et al. (2008), Alahuhta et al. (2012), and Kanninen et al. (2013a). The three indices were re-scaled according to Mykrä et al. (2012) and the mean of the re-scaled indices was used as an ecological status index. The mean status index was used because it is a robust assessment tool with

Table 1 Descriptive statistics of macrophyte richness and status index along with lake and land use variables for 110 lakes

	Mean	Minimum	Maximum	SD
Macrophytes variables				
Species richness				
All taxa	29.7	10.0	59.0	9.3
Emergent plants	14.9	6.0	30.0	5.6
Submerged plants	2.7	0.0	10.0	2.2
Hydrophytes	14.8	2.0	34.0	5.9
Status index	0.7	0.3	1.2	0.2
Explanatory variables				
Lake variables				
Lake order	1.4	0.0	4.0	1.4
Altitude (m.a.s.l.)	106.1	11.9	228.9	43.5
Turbidity (FTU)	6.7	0.3	81.0	12.0
Amplitude of water level fluctuation (m)	0.79	0.10	2.49	0.37
Lake area (ha)	6.9	0.2	219.5	21.6
Shoreline development factor	3.1	1.2	13.5	1.8
Dynamic ratio	1.2	0.2	5.0	0.9
Mean depth (m)	3.6	0.4	20.0	3.0
Alkalinity ($\mu g\ l^{-1}$)	0.2	0.0	0.9	0.2
Color (mg PT l^{-1})	102.0	5.0	375.0	67.7
Secchi depth (m)	1.7	0.2	7.3	1.3
Chlorophyll-*a*	21.3	1.4	137.5	21.1
Total phosphorus	38.0	3.0	180.0	32.7
Total nitrogen	688.0	220	2,500.0	387.4
Conductivity (mS m^{-1})	5.4	1.5	16.0	3.6
pH	6.9	5.5	8.8	0.6
Land use				
Agriculture (%)	8.9/17.7/ 18.2/15.8	0.0/0.0/ 0.0/0.0	53.4/90.2/ 85.6/84.4	11.0/20.1/ 20.1/19.3
Urban development (%)	4.0/8.3/9.8/15.7	0.0/0.0/0.0/0.0	18.2/31.8/34.8/46.3	3.8/7.2/8.0/11.9

Land use variables are given in the following order: catchment, 500, 300, and 100 m

fewer falsely classified indicators than in individual quality indices (Alahuhta et al., 2013).

Three sets of explanatory variables were used: lake, land use, and spatial variables (Table 1). Lake characteristics included lake order, altitude (m.a.s.l.), turbidity (FTU), 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}), color (mg PT l^{-1}), Secchi depth (m), chlorophyll-*a* ($\mu g\ l^{-1}$), total phosphorus ($\mu g\ l^{-1}$), total nitrogen ($\mu g\ l^{-1}$), conductivity (mS m^{-1}), and pH. Water quality variables were median values of surface water samples (sampling depth 1 m for all variables except a 0–2 m composite sample for

chlorophyll-*a*) taken during the growing season (June–September) over the period 2000–2008. We assembled the data from the Hertta database at the Finnish Environment Institute. In addition, we included the number of transects studied in each lake to account for sampling effect for macrophytes (see e.g., Beck et al., 2010; Kanninen et al., 2013b).

Land use variables comprise proportions of agricultural and urban land use determined separately for four different spatial scales: the whole topographic catchment and buffer zones with distances of 100, 300, and 500 m from the lake shoreline (Table 1). The agricultural land use data were obtained from Field Crop Production database of Information Centre of the Ministry of Agriculture and Forestry (TIKE, year

2008). Urban land use data were compiled from CORINE land cover database (year 2006). The land use variables were prepared using ArcGIS 9.2 (Esri Corp., Redlands, CA, USA).

Spatial structure was studied using the analysis of principal coordinates of neighbor matrices (PCNM; Borcard & Legendre, 2002), which are a special form of Moran's Eigenvector Map eigenfunctions. They are obtained from a spectral decomposition of a truncated distance matrix of the spatial relationships among sampling locations. We used geographic coordinates of lake centers to calculate Euclidean distances between lakes, and only positive eigenvectors were employed. We were unable to use hydrological connections, because most of lakes were not connected to each other and few lakes were completely isolated without any hydrological connections to any other lentic water body. In addition, PCNMs using overland distances instead of watercourse distances have been found to be equally good in capturing complex spatial patterns for passively dispersing aquatic organisms (Beisner et al., 2006, Landeiro et al., 2011). Spatial structure was studied to account for possible geographic-related patterns, such as latitudinal (climate-derived) gradient in species richness often found for boreal macrophytes (Heino & Toivonen, 2008). PCNMs can also detect small scale spatial patterns, which may be originated from spatial autocorrelation or dispersal. PCNMs were constructed using the PCNM package in the R software.

Statistical analyses

Partial redundancy analyses (pRDA) and partial linear regression (pLR) were employed to distinguish the relationships between variation in macrophytes and explanatory variable groups. For community compositions, pRDAs were used with Hellinger transformed species data prior to the analyses (Legendre & Gallagher, 2001) and species frequency data (i.e., proportion of transects in a lake with the species recorded) were utilized. We employed pLRs for species richness and status index analyses. In pRDAs and pLRs, we followed the procedure of Borcard et al. (1992), in which the total variation in macrophyte community composition, richness, and status index was partitioned into eight fractions. The fractions consists of the pure effect of (1) lake characteristics, (2) land use, and (3) spatial variables, along with combined variation due to the joint effects of (4) lake characteristics and land use, (5) lake characteristics and spatial variables, (6) land use and spatial variables, and (7) the three groups of explanatory variables. The final fraction shows unexplained variation (8). The detailed processes that are required to estimate these fractions are explained in Legendre & Legendre (1998) and Legendre et al. (2005). Non-percentage explanatory variables were log-transformed prior to the analysis if the transformation improved normality. Variance partitioning procedure was done separately for each macrophyte variables and land use scales, resulting to 36 variance partitioning models altogether (nine macrophyte variables × four land use scales). For example, variance was partitioned separately at four land use scales for status index so that spatial dependency of land use on status index can be compared across catchment and three buffer zones.

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 error can be avoided 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). Following the procedure of Blanchet et al. (2008), forward selection was carried out only if a global test using all explanatory variables in a variable set was significant. Forward selection using the Monte Carlo permutation test (1,000 permutations, $\alpha = 0.05$) was then used to obtain significant variables for further analysis. Land use variables were selected separately for each land use scale. In addition, we calculated bivariate correlations between multiple-scaled land use and macrophyte richness and status index. For lake and spatial variables which did not change across land use scales, we selected the variables at catchment scale and used them also at buffer zones scales. All pRDAs and pLRs were performed in the R environment with Packfor and Vegan packages (Oksanen et al. 2012).

Results

Variance partitioning among functional groups at catchment scale

Community composition

Total variation of macrophyte community composition explained was 34% for all taxa, 36% for

emergents, 20% for submerged, and 32% for hydrophytes (Table 2). The fraction explained by lake variables was equal for both all taxa (14%) and the three functional groups (emergents: 13%, submerged: 10%, and hydrophytes: 13%), while the pure effects of land use and space were significantly lower (1–2%). Similarly to pure land use effect, spatial variables contributed only modestly to macrophyte community

Table 2 Pure fractions of variation in macrophyte community composition using redundancy analyses, richness using partial least-squares regression and—derived quality index using partial least-squares regression explained by lake characteristics (LC), land use variables (LU), and spatial variables (SV)

	CC: all taxa	CC: emergents	CC: submerged	CC: hydrophytes	S: all taxa	S: emergents	S: submerged	S: hydrophytes	Index
Catchment									
LC	0.14	0.13	0.10	0.13	0.35	0.32	0.19	0.11	0.32
LU	0.01	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00
SV	0.03	0.03	0.02	0.03	0.01	0.01	0.04	0.14	0.04
LC + LU	0.06	0.05	0.06	0.07	0.03	0.10	0.07	0.00	0.24
LC + SV	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.24	0.00
LU + SV	0.05	0.06	0.03	0.05	0.09	0.10	0.05	0.00	−0.01
LC + LU + SV	0.05	0.06	−0.01	0.03	0.06	0.20	0.04	0.00	0.08
Unexplained	0.66	0.64	0.80	0.68	0.46	0.26	0.62	0.51	0.32
BZ 500 m									
LC	0.12	0.09	0.09	0.13	0.27	0.19	0.23	0.11	0.20
LU	0.00	0.01	0.02	0.01	0.00	0.03	0.00	0.00	0.00
SV	0.03	0.03	0.02	0.03	0.00	0.01	0.03	0.14	0.04
LC + LU	0.08	0.10	0.07	0.08	0.13	0.23	0.03	0.00	0.37
LC + SV	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.24	0.00
LU + SV	0.05	0.04	0.03	0.05	0.06	0.02	0.05	0.00	0.00
LC + LU + SV	0.05	0.08	0.00	0.03	0.06	0.28	0.05	0.00	0.07
Unexplained	0.67	0.65	0.78	0.68	0.48	0.24	0.61	0.51	0.32
BZ 300 m									
LC	0.11	0.09	0.09	0.13	0.28	0.19	0.24	0.13	0.19
LU	0.01	0.01	0.02	0.01	0.00	0.02	0.00	0.00	0.00
SV	0.03	0.03	0.02	0.03	0.01	0.01	0.04	0.09	0.04
LC + LU	0.09	0.10	0.07	0.08	0.10	0.23	0.02	0.00	0.37
LC + SV	0.00	0.01	0.00	0.00	0.00	0.01	−0.01	0.26	0.00
LU + SV	0.04	0.04	0.03	0.05	0.04	0.02	0.04	0.00	0.01
LC + LU + SV	0.06	0.08	0.00	0.03	0.10	0.27	0.05	0.00	0.06
Unexplained	0.66	0.65	0.78	0.68	0.47	0.25	0.61	0.52	0.32
BZ 100 m									
LC	0.12	0.10	0.08	0.13	0.28	0.25	0.23	0.13	0.23
LU	0.01	0.01	0.03	0.01	0.00	0.00	0.00	0.00	0.01
SV	0.03	0.03	0.02	0.03	0.00	0.01	0.04	0.09	0.05
LC + LU	0.08	0.08	0.07	0.08	0.11	0.18	0.03	0.00	0.34
LC + SV	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.26	−0.01
LU + SV	0.05	0.04	0.02	0.05	0.09	0.07	0.05	0.00	0.04
LC + LU + SV	0.05	0.07	0.00	0.02	0.02	0.23	0.04	0.00	0.03
Unexplained	0.67	0.65	0.77	0.68	0.48	0.26	0.61	0.52	0.31

Analyses were done separately for all taxa, emergent macrophytes, submerged macrophytes and hydrophytes (i.e., true aquatic plants)

composition across functional groups (2–3%). Joint fraction of lake characteristics and land use had influence on all functional groups (5–7%), whereas the joint effect of land use and spatial variables was noticeable for all taxa (5%), emergent (6%), and hydrophytes (5%). Contrary, lake characteristics and space did not show joint contribution to the variation at all.

Total nitrogen was the most significant lake variable for community composition of all taxa and hydrophytes, whereas chlorophyll-*a* and altitude were the most important lake variables for emergent and color together with alkalinity for submerged macrophytes (Table 3; Table S1 in Supporting Information). Agriculture was by far the most significant land use variable for community composition, but urban development also had a contribution to macrophytes across functional groups (Table 4). The spatial structure of community composition was explained mostly by large eigenvalues (SV1–SV5) indicating the influence of large spatial scale.

Species richness

Overall variation in species richness explained was 54% for all taxa, 74% for emergents, 38% for submerged taxa, and 49% for hydrophytes (Table 2). Lake characteristics had the highest contribution in explaining the richness of all taxa (35%) and emergents (32%), whereas they explained 19 and 11% of submerged and hydrophyte richness, respectively. Land use had no influence on any of the richness

variables. The pure fraction of space was considerable for hydrophytes (14%), but space had a minor influence on the richness of all taxa and emergents. All joint effects were considerable for emergent richness (10–20%), excluding the explained fraction shared by lake characteristics and space (0%), which in turn jointly explained a considerable amount of variation for hydrophyte richness (24%). In addition, the joint fractions of land use and space and all three explanatory variable groups had some contribution to all taxa and submerged plants.

Alkalinity and lake area were the most important lake characteristics for total taxa richness while conductivity and dynamic ratio contributed most to emergent richness (Tables 3; S1). Submerged macrophytes were mostly affected by alkalinity and turbidity. Number of sampled transects was the most significant variable for hydrophyte richness. Agriculture alone was important for all taxa and emergent richness (Table 4; Fig. 1), whereas urban development influenced submerged macrophytes. Large and small spatial eigenvalues were most essential for macrophyte richness.

Status index

Total variation explained was 68% for the status index. The lake characteristics alone explained 32% and jointly with land use additional 24% of the total variation (Table 2). Pure fractions of land use and space were non-existence or modest (0 and 4%, respectively). Total nitrogen was clearly the most

Table 3 Single most important lake and spatial variables based on adjusted R^2 values in the forward selection by Blanchet et al. (2008)

	Lake characteristics	Adj. R^2 (p)	Spatial variables	Adj. R^2 (p)
Community composition				
All taxa	Total nitrogen	0.13 (0.001)	SV1	0.04 (0.001)
Emergent	Chlorophyll-*a*	0.13 (0.001)	SV1	0.04 (0.001)
Submerged	Color	0.12 (0.001)	SV2	0.03 (0.005)
Hydrophytes	Total nitrogen	0.13 (0.001)	SV1	0.04 (0.001)
Richness				
All taxa	Alkalinity	0.26 (0.001)	SV12	0.06 (0.011)
Emergent	Conductivity	0.47 (0.001)	SV1	0.09 (0.002)
Submerged	Alkalinity	0.17 (0.001)	SV22	0.05 (0.006)
Hydrophytes	Number of transects	0.15 (0.001)	SV13	0.06 (0.005)
Ecological status				
Status index	Total nitrogen	0.50 (0.001)	SV1	0.08 (0.002)

Table 4 The significance of land use variables on community composition, richness, and status index of aquatic macrophytes across four different spatial scales (catchment, buffer zones of 500, 300, and 100 m) demonstrated by adjusted R^2 (P values in parenthesis) and forward selection using the Monte Carlo permutation test (1,000 permutations, $\alpha = 0.05$)

Land use variable	Catchment	BZ 500 m	BZ300 m	BZ100 m
Community composition				
All taxa				
Agriculture	0.10 (0.001)	0.13 (0.001)	0.13 (0.001)	0.10 (0.001)
Urban dev.	0.01 (0.010)	–	0.01 (0.006)	0.02 (0.001)
Emergent				
Agriculture	0.12 (0.001)	0.16 (0.001)	0.16 (0.001)	0.12 (0.001)
Urban dev.	0.01 (0.032)	0.01 (0.012)	0.01 (0.005)	0.03 (0.001)
Submerged				
Agriculture	0.07 (0.001)	0.08 (0.001)	0.07 (0.001)	0.07 (0.001)
Urban dev.	0.02 (0.008)	–	–	0.01 (0.045)
Hydrophytes				
Agriculture	0.08 (0.001)	0.10 (0.001)	0.10 (0.001)	0.09 (0.001)
Urban dev.	0.01 (0.026)	–	–	0.01 (0.006)
Richness				
All taxa				
Agriculture	0.09 (0.002)	0.19 (0.001)	0.18 (0.001)	0.11 (0.001)
Urban dev.	–	–	0.02 (0.046)	0.04 (0.014)
Emergent				
Agriculture	0.31 (0.001)	0.48 (0.001)	0.47 (0.001)	0.30 (0.001)
Urban dev.	–	0.05 (0.001)	0.06 (0.001)	0.12 (0.001)
Submerged				
Agriculture	–	0.08 (0.004)	0.07 (0.002)	0.06 (0.004)
Urban dev.	0.11 (0.003)	–	–	–
Hydrophytes				
Agriculture	–	–	–	–
Urban dev.	–	–	–	–
Ecological status				
Status index				
Agriculture	0.32 (0.001)	0.41 (0.001)	0.41 (0.001)	0.34 (0.001)
Urban dev.	–	0.03 (0.014)	0.03 (0.013)	0.02 (0.030)

Analyses were done separately for all taxa, emergent macrophytes, submerged macrophytes and hydrophytes (i.e., true-macrophytes)

*BZ* buffer zone, *urban dev.* urban development

significant lake variable for the status index (Table 3), and agriculture the most important land use variable (Table 4; Fig. 2). SV1 of the spatial components had the highest effect on macrophyte status.

Comparison of results among land use scales

There were no differences in the explained total variation among the four scales of land use. Neither did we find any divergences in the pure effects of land use or spatial variables among the scales. However, clear differences between the total catchment and buffer zones were discovered for the pure contribution of lake characteristics and the joint effect of lake characteristics and land use (Table 2). The pure influence of lake characteristics decreased from catchment scale to buffer zones (from 35 to 27% for all taxa richness, from 32 to 19% for emergent richness, and from 32 to 20% for status) simultaneously with increasing joint contribution of lake
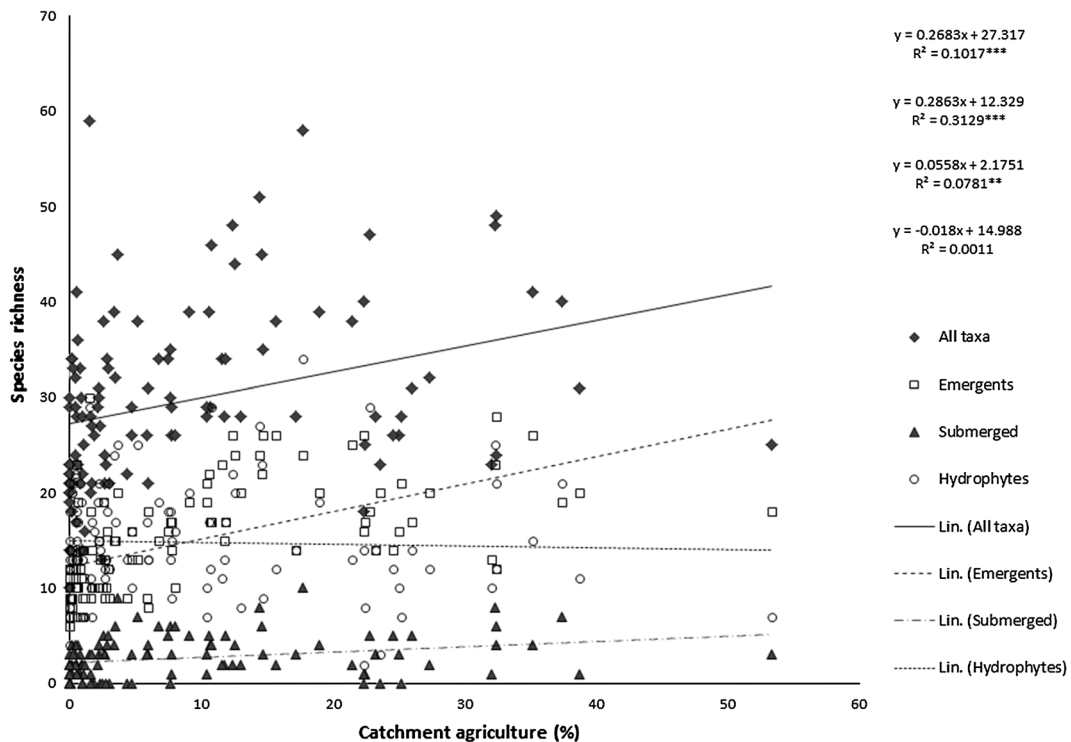
Fig. 1 Scatter plot illustrating the relationship between macrophyte species richness (all taxa, emergents, submerged, and hydrophytes) and catchment agriculture (%). Significance levels: ***<0.001, **<0.01, *<0.05

characteristics and land use (from 3 to 13% for all taxa richness, from 10 to 23% for emergent richness, and from 14 to 37% for status). In addition, a similar but weaker pattern was noticeable for emergent community composition (from 13 to 9% and from 5 to 10%, respectively). No parallel trend was found for the other macrophyte variables.

The same pattern was among land use scales for species richness and status index in bivariate correlations (Table S2). Correlations increased from catchment scale to buffers for the richness of all taxa (from 0.46 to 0.52), emergent (from 0.70 to 0.76), and status index (from −0.65 to −0.70). For urban development, the similar trend was even stronger than for agriculture ($S_{all\ taxa}$: from 0.38 to 0.43, $S_{emergents}$: from 0.59 to 0.67, and status index: from −0.50 to −0.60). It was also found that the relationship between submerged richness and urban development was the highest at catchment scale.

The influence of agriculture also increased from catchment scale to buffer zones (300 and 500 m) in forward selection (Table 4). The boost in adjusted R^2 values was found for all agriculture responses, except

for submerged and hydrophyte richness. Most considerable differences in adjusted R^2 values were noticed for emergent richness (from 0.31 to 0.49) and status (from 0.32 to 0.41). Simultaneously, urban development was selected among the important variables at buffer scales for emergent richness and status.

Discussion

Variation in macrophyte functional groups and status at catchment scale

Macrophyte functional groups react differently to both natural gradients and variables associated with anthropogenic influence (Toivonen & Huttunen, 1995; Vestergaard & Sand-Jensen, 2000; Alahuhta & Heino, 2013). Submerged plants and majority of growth forms of hydrophytes growing under the water column are more dependent than emergent flora on water transparency and concentrations of nutrients and carbon in water. On the contrary, emergent macrophytes are only influenced by low light availability in

the early stage of development and can utilize carbon dioxide from air. Emergent species can also obtain nutrients from sediment, being less directly connected with water quality. For these reasons, submerged species and hydrophytes were expected to react stronger than emergents to lake characteristics. However, there were no differences in the structuring of community composition among functional plant groups at catchment scale, as all the functional groups (both community composition and richness) were primarily affected by lake characteristics. O'Hare et al. (2012) and Alahuhta et al. (2013)—using identical statistical procedures—also found no significant differences in variation explained by environment and space between emergent and submerged macrophyte communities in Scotland and southern Finland, respectively.

Dispersal is less often a limiting factor for aquatic macrophytes, because all growth forms reproduce vegetative and clonal organs that are dispersed even long distances via wind, water, animals, and humans (Santamaria, 2002; Viana et al., 2013). Spatial variables, proxy for dispersal, were not important for majority of macrophyte groups related to both community composition and richness. However, hydrophyte richness was rather strongly associated with spatial variables. This finding was surprising, as hydrophytes (including submerged plants) were expected to respond more strongly than emergent macrophytes to water chemistry (Rørslett, 1991; Vestergaard & Sand-Jensen, 2000). The results suggest that some important environmental variable for hydrophytes is not included in the study or hydrophytes are dispersal limited. Both of these possibilities seem unconvincing, because submerged macrophyte did not show a congruent pattern with space. Submerged plants respond mostly rather alike than other hydrophytes to environmental gradients and share similar reproduction and dispersal strategies with hydrophytes (Toivonen & Huttunen, 1995; Santamaria, 2002). However, different reference conditions defined for northern and southern lakes may complicate how the response of macrophytes to spatial variables should be explained, as submerged plants were relatively strongly affected by space in southern Finland (Alahuhta et al., 2013).

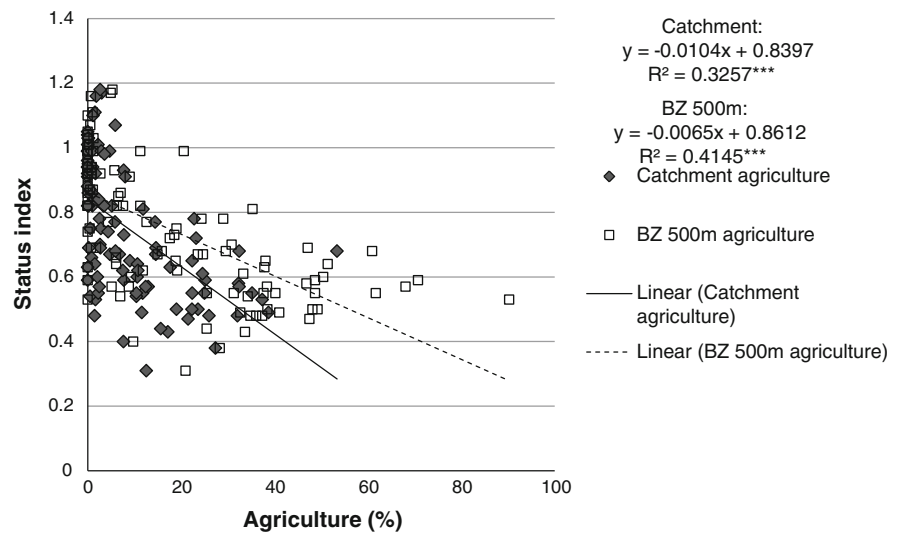The macrophyte status index was highly controlled by the lake characteristics and land use, as pure effect of lake characteristics and joint contribution of lake variables and land use explained the majority of total variation. As expected, spatial structuring (pure or joint fractions) showed minimal contribution compared to lake characteristics and land use confirming the basic performance of status indices (see also Kanninen et al., 2013a). The highest total explained variation of all macrophyte responses suggested that macrophyte status assessment may perform relatively well, although the establishment of reference conditions for macrophytes probably needs adjustment (Alahuhta et al., 2013). Lack of spatially structured contribution also implied that all relevant environmental variables for the index were included in the study.

Functional plant groups were influenced by a variety of individual lake characteristics, which showed little consistence among the groups. In both community composition and richness, there was no single lake variable that was among the most important ones for all functional groups. When functional groups are compared to all taxa, the most significant variables shared were found for all taxa and hydrophytes in community composition (conductivity and dynamic ratio) and for all taxa and emergent macrophytes in richness (total nitrogen). Conductivity and dynamic ratio reflect both fertility and lake area affecting significantly on species composition (e.g., Rørslett, 1991), whereas excess of nitrogen increases emergent macrophyte expansion on the littoral zone (Kankaala et al., 2002).

Influence of land use at different catchment scales

Our results suggested that land use adjacent to a lake's shoreline had a stronger effect on macrophyte richness and ecological status compared to the land use of the whole topographic catchment. This pattern seemed to apply primarily to emergent macrophytes (both richness and community composition), whereas submerged macrophytes and hydrophytes seemed to be independent of the scale effect of land use. Hence, we believe that the scale dependency of the response of macrophyte status to land use was due to emergent species. Recently, Alahuhta et al. (2012) found similar scale dependency for ecological quality indices, as two indices (the proportion of type-specific taxa and Percent Model Affinity) seemed to respond more strongly to the land use adjacent to lake shoreline than in the whole catchment. However, they did not use statistical methods, such as variance partitioning,

Fig. 2 Scatter plot illustrating the relationship between averaged status index and agriculture (%) in catchment and buffer zone of 500 m scales. BZ 500 m = buffer zone of 500 m. Significance levels: ***<0.001, **<0.01, *<0.05

Catchment:
y = -0.0104x + 0.8397
R² = 0.3257***

BZ 500m:
y = -0.0065x + 0.8612
R² = 0.4145***

◆ Catchment agriculture

☐ BZ 500m agriculture

—— Linear (Catchment agriculture)

----- Linear (BZ 500m agriculture)

which could exclusively distinguish the effects of land use from other gradients.

Land use is often used as a proxy for anthropogenic-derived nutrient increase in waters (Alahuhta et al., 2011; Varanka & Luoto, 2012), whereas nutrients affect macrophytes in situ (Lacoul & Freedman, 2006; Bornette & Puijalon, 2011). Alahuhta et al. (2012) found—with the same land use data as in this study—that water quality was also more strongly affected by the land use of adjacent buffer zones than of the whole catchment. In the current study, we noticed that the significance of agriculture, in terms of adjusted R^2 values, bivariate correlations and linear regression (see Fig. 2), was higher for buffer zones than for the whole catchment. Moreover, the pure fraction of lake characteristics decreased simultaneously as the joint fraction of lake characteristics and land use increased in variance partitioning. Thus, the scale dependency of the land use effect may be related to both direct anthropogenic impact on the littoral zone and the indirect effects of diffuse pollution on water quality.

Many mechanisms can possibly explain the detected scale dependency in the joint effect of lake characteristics and land use. Nutrients are sedimented and stored along the hydrological system in long lake chains, and, thus, only a small portion of substances originated from remote parts of the catchment may reach lower lakes (Kratz et al., 1997; Varanka & Luoto, 2012). On the other hand, direct impacts of land use on water bodies are only possible in the terrestrial land adjacent to a lake's shoreline. Land use adjacent to a lake's shoreline also has the potential to directly

deteriorate the habitat quality of aquatic macrophytes (Bornette & Puijalon, 2011; Marzin et al., 2012). Dudley et al. (2013) noted that a macrophyte survey focusing on depths between 0 and 1 m indicated a higher trophic status compared to a survey covering the whole littoral. This surprising result is largely explained by the more diverse habitat structure in and direct nutrient input to the shallow littoral.

Many studies have found little or no evidence for the importance of buffer zones over catchment land use (Jennings et al., 2003; Sass et al., 2010). However, our findings receive support from irrigation ponds (Akasaka et al., 2010), in which macrophyte richness was affected by spatially structured land use. Akasaka et al. (2010) similarly discovered that the land use of a 500 m buffer zone had the greatest impact on total macrophyte richness. In addition, they found species richness of submerged and floating-leaved macrophytes to be best explained by relatively small scales (250 m) compared to richness of emergent macrophytes (1,000 m). In our lakes, emergent plant richness was best explained by the land use of 300 and 500 m buffers, whereas land use did not affect submerged and hydrophyte richness.

Our findings demonstrated, accordant with Marzin et al. (2012), that we may lose important information if the evaluation of human pressures impacting water bodies is limited to one spatial scale, e.g., land use at whole catchment scale. Alahuhta et al. (2013) studied the influence of anthropogenic pressures (i.e., land use and nutrient content indicating water quality variables together) on multiple individual quality status indices in

southern Finland and found that the pressures were spatially structured at catchment scale. However, they did not investigate the scale dependency of land use on the indices. The dependence of water quality on land use is complex and anthropogenic development at buffer and catchment scales may have a synergistic effect on aquatic assemblages. Thereby either catchment- or buffer-scale disturbances alone explain less variation in aquatic communities than both together (see Mikulyuk et al., 2011; Marzin et al., 2012). Thus, multiscaled management measures are needed to mitigate complex synergistic impacts of anthropogenic pressures on the biological integrity of freshwaters and to reduce harmful effects of land use most efficiently. Our findings can be utilized in river basin planning, where most cost efficient water course protection should be focused on the nearby zone of lake.

Implications for bioassessment

Use of emergent macrophytes in lake bioassessment has been under intense debate recently (Kolada et al., 2011; Alahuhta et al., 2012; Dudley et al. 2013; Kanninen et al., 2013a). Numerous national bioassesments in central and southern Europe include only hydrophytes (e.g., Stelzer et al., 2005; Penning et al., 2008; Søndergaard et al., 2010), mainly because emergent macrophytes are considered to have suffered from high variation in taxa composition caused by soil characteristics and shore morphology (Penning et al., 2008; Poikane et al., 2011). As opposed to temperate regions—where hydrophyte flora dominates—the aquatic flora of the boreal region has a high proportion of emergent macrophytes (Duarte et al., 1986; Andersson, 2001; Partanen et al., 2006). For example, in dystrophic lakes emergent macrophytes can comprise the major proportion of a flora consisting of only a few species (Ilmavirta & Toivonen, 1986; Rintanen, 1996). The high spring floods in boreal lakes, fed by snow melt, also favor emergent flora and the formation of littoral zonation. Exclusion of emergent macrophytes from boreal bioassessment can drastically limit the species pool on which bioassessment is based.

Our results indicate that land use adjacent to lake's shoreline had higher influence on emergent macrophytes (including status index) than catchment land use. It may be that indices based on both emergent plants and

hydrophytes respond stronger to anthropogenic pressures geographically close to the littoral zone, but if catchment land use is used in quantifying the anthropogenic pressure gradient, inclusion of emergent macrophytes does not necessarily improve index performance. This can explain the surprising results from boreal lakes, in which the performance of neither stressor-specific indices nor indices based on taxonomic composition in relation to catchment land use was improved by including emergent macrophytes to the overall species pool in addition to hydrophytes (Kanninen et al., 2013a). In addition, a pan-European study of 28 lowland clearwater lakes and four different macrophyte status indices concluded that indices based on only emergent macrophytes yielded significantly poorer results compared to only submerged macrophytes (Dudley et al., 2013). However, we think that the results of Dudley et al. (2013) should be treated with caution due to limited amount of emergent species in the central- and southern-European lakes. The utilized survey method based on small quadrats is also not valid for recording emergent species covering several habitats of the littoral. A transect-based method with a several meter wide area investigated—5 m in the Finnish inventory—and covering all littoral habitats enables the detection of a large number of emergent species (Kanninen et al., 2013b). In our study, we found using the transect-based method relatively high emergent species richness, which responded stronger than other functional groups to agriculture across catchment scales.

In conclusion, while emergent flora is a scenically and ecologically valuable component of boreal lakes, they also have an important role in the current ecological classification work. In high latitudes, these plants form a considerable proportion of aquatic macrophytes and can efficiently detect anthropogenic pressures across catchment scales, but especially in the close vicinity of lake shoreline. A bioassessment tool of boreal lake systems utilizing emergent plants will most likely better indicate ecological changes resulting from multiple-scaled land use and hydromorphological pressures than a system omitting this plant group.

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