

# Land use, geomorphology and climate as environmental determinants of emergent aquatic macrophytes in boreal catchments

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We studied the distribution patterns of emergent aquatic macrophytes in relation to land use, geomorphology and climate variables throughout Finland, using data collected from 848 catchments. Our results confirmed previous findings on climatic factors as major determinants of macrophyte distribution, but also catchment land-use, especially drainage ditch intensity, appear to be significant. Drainage ditch intensity had equal or higher contribution to emergent aquatic macrophytes as compared with that of geomorphology variables. To our knowledge this is the first analysis to show that ditch intensity increases emergent aquatic macrophytes at the national level. Overall, our results demonstrate that neither overgrowth problems nor natural distribution patterns of emergent aquatic macrophytes can be understood without analyzing the joint effects of land use, climate and geomorphology.

## Introduction

Environmental determinants of a biotic community structure are typically hierarchical, so that large-scale biogeographic processes and constraints interact with biotic and abiotic factors at the regional and local scales. Ecological mechanisms operating in regional extent may overstep local-scale patterns in species distributions (Cottenie 2005). Hence, identification of large-scale processes affecting communities is often prerequisite for understanding variation in species distributions at local scales. Large extent studies of species distributions in terres-

trial ecosystems are numerous (Parviainen *et al.* 2009, Powney *et al.* 2010), but congruent spatial studies on aquatic ecosystems are mostly lacking (however, *see* Huidobro *et al.* 2006, Blanck and Lamouroux 2007, Heino and Toivonen 2008, Heikkinen *et al.* 2009).

Aquatic–terrestrial ecotones are considered to be the most productive and diverse of the aquatic ecosystems (Wetzel 1990, Mitsch and Gosselink 2000). Emergent aquatic macrophyte zones are scenically and ecologically important components of this ecotone. Emergent macrophytes provide shelter, breeding areas and food resources for other terrestrial and aquatic species (Perrow

*et al.* 1999, Schmidt *et al.* 2005). Emergent aquatic vegetation also traps nutrients, diminishes erosion and influences quality and quantity of sediments (Spence 1982, Pieczynska 1990, Lacoul and Freedman 2006), which in turn potentially buffers against wide scale deterioration of water quality and ecological status of aquatic ecosystems. Emergent aquatic macrophytes indicate in general changes in hydromorphological conditions, such as shoreline structure and water level fluctuations (Hellsten 2001 and references therein, van Geest *et al.* 2005). Water quality changes affect emergent aquatic macrophyte stands indirectly, e.g. via enhanced sedimentation of organic and inorganic matter (Toivonen and Huttunen 1995, Partanen *et al.* 2009). Response of different species varies greatly. For example, *Phragmites australis* often benefits from delayed spring floods and eutrophication, whereas most of the *Carex* species and *Equisetum fluviatile* suffer from water level fluctuations (van den Brick *et al.* 1995, Partanen *et al.* 2006). However, due to high seed production capacity, *Carex rostrata* seems to benefit from a fluctuating water level and can stand longer submersion than other *Carex* species (Hellsten 2001). In addition, *Typha latifolia* favours eutrophic conditions (Toivonen and Huttunen 1995). Because of these varying responses to boreal environmental conditions, emergent aquatic macrophytes are used in Finnish ecological status assessments according to the EU Water Framework Directive (European Communities 2000).

Emergent aquatic macrophyte cover expansions (overgrowth) may occur due to natural succession or anthropogenic factors related to land-use practices. The overgrowth process of boreal lakes and wetlands includes filling up of the littoral areas with plant remains. Consequently, the vegetation cover slowly expands over larger areas. Overgrowth can be classified as bottomward, surfaceward and within the water column (Segal 1971). Overgrowth is often accelerated by anthropogenic impacts derived from different land-use activities such as agriculture, forestry, lake regulation and infrastructure (Spence 1982, Pieczynska 1990, Lacoul and Freedman 2006). Land-use changes result in increased nutrient and suspended solids concentrations, siltation and physical disturbances of

the littoral area (Mensing *et al.* 1998, Arts 2002). One of the most significant sources of nutrient leaching and siltation is ditch drainage (Åstrom *et al.* 2001, Holden *et al.* 2004), which is traditionally executed on peat soils in boreal regions. As a consequence, species composition changes and vegetation cover increases (Spence 1982, Sand-Jensen *et al.* 2000, Heegaard *et al.* 2001, Loughheed *et al.* 2008). Emergent aquatic macrophyte overgrowth, when due to anthropogenic sources, may cause deterioration of the ecological status of lakes.

Ecological assessments have been increasingly performed with GIS applications (Aspinall and Pearson 2000, Zhou *et al.* 2008). Improved data sets have enabled time-saving GIS-based assessments on different spatial scales. In order to capture ecologically plausible causal relationships in these assessments, appropriate study scales must be addressed (Decamps and Naiman 1990, Dermars and Harper 2005). In the case of emergent aquatic macrophytes, studies have generally been performed in relatively small lakes or wetlands of one region and/or with small datasets (e.g. Mäemets and Freiberg 2004, Partanen and Luoto 2006). Novel GIS applications and sophisticated statistical procedures may enable more profound understanding of causal relationships between emergent aquatic macrophyte growth and environmental variables on larger spatial scales. In addition, these large scale assessments can provide first hand cost-efficient estimation of changes of emergent aquatic macrophyte distribution and point out research needs at more local scales. Moreover, changes in the aquatic-terrestrial ecotone can indicate wider ecological deterioration of aquatic ecosystems such as eutrophication or loss of biodiversity that should be taken into consideration in ecosystem management planning.

We studied the occurrence and percentage cover patterns of emergent aquatic macrophytes, and their spatial structure, in relation to land-use, geomorphology and climate variables throughout Finland, using data recorded in 848 catchments in an area of ca. 250 000 km<sup>2</sup>. We used GIS data considered to represent emergent aquatic macrophyte overgrowth or large continuous stands that are about to become expanded (*see* Material and methods). We hypothesized that climate pri-

marily controls distribution patterns of emergent aquatic macrophytes at this national level and that also geomorphology influences macrophyte distribution (Crow 1993, Heino and Toivonen 2008). Responses of individual explanatory variables should indicate that factors known to control vegetation, such as growing degree days and ice cover duration, show clear latitudinal gradient (Hellsten 2001). We further anticipated that altitude limits vegetation distribution in high altitude catchments (Gacia *et al.* 1994) and large lake-surface area provides more available habitats for emergent macrophytes as compared with low lake cover (Rørslett 1991). Furthermore, we expected that land use in general may not have high contribution to distribution patterns of emergent aquatic vegetation at this spatial scale, though high proportions of agricultural land might stimulate distribution due to nutrient leaching (Sand-Jensen *et al.* 2000). However, based on previous findings (Ecke 2009) and the fact that the Finnish catchments are very intensively drained, we assumed that drainage ditches might also have some positive effect on emergent aquatic macrophyte distribution even at the national level. Finally, we tested the applicability of GIS modelling techniques for a cost-efficient country-scale ecological assessment and expected our analysis to show good modelling performance at this large spatial scale.

## Material and methods

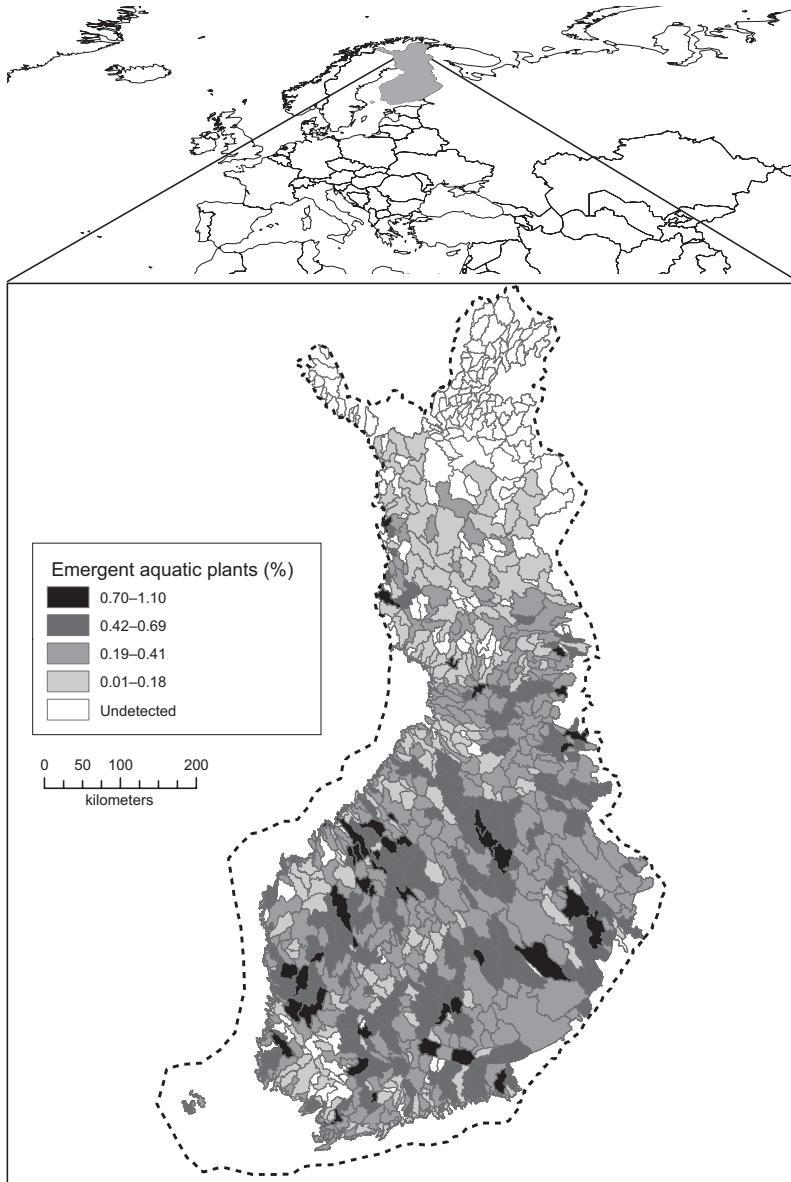
### Study area

Finland is located in northern Europe (19°–32°E, 60°–70°N) and it belongs to the taiga zone characterized by landscapes dominated by coniferous forests with sparse settlements and agricultural areas usually close to waters. The annual average temperature varies from +5 °C in southern Finland to –3 °C in northern Finland (Atlas of Finland 1988). The most common rocks are granite and granite gneiss, and moraine is the dominant landform type (Atlas of Finland 1990). The country is hydrologically divided into lentic-rich inland areas situated in central and eastern Finland and lotic-rich parts in coastal areas and northern Finland. A total of 10% of the surface

area is covered by aquatic ecosystems. Wetlands constitute 30% of the surface area, but nowadays two thirds of wetlands are drained for forestry and peat production, and also dried for agricultural use (Peltomaa 2007). We studied 848 catchments representing second division size category (1.33–4263.52 km<sup>2</sup>) in the Finnish hydrological regime (Fig. 1). These catchments consist predominantly of inland catchments. Coastal land areas and those of the main Åland islands were also included, but the smaller archipelagos were not.

### Emergent aquatic macrophyte and explanatory data

Emergent aquatic macrophyte occurrence (present/absent) and percentage cover (emergent aquatic macrophyte cover per each catchment, %) were derived from the Finnish CORINE land cover classification, which is based on automated interpretation of Landsat ETM satellite images (from the years 1999–2002) and data integration with existing digital maps (*see* Luoto *et al.* 2007). The macrophyte variables have also been introduced elsewhere (Alahuhta *et al.* 2011). The Finnish CORINE data includes a specific class for the emergent aquatic macrophytes growing in shallow water areas covered with silt deposits, flooded areas and wetlands without peat cover or tree vegetation. This class consists predominantly of typical emergent aquatic macrophytes, mainly common reed (*Phragmites australis*), water horsetail (*Equisetum fluviatile*), cattail (*Typha latifolia*), common club rush (*Schoenoplectus lacustris*) and several large sedges such as *Carex rostrata*, *Carex lasiocarpa* and *Carex vesicaria* (Virkkala *et al.* 2005). However, species-level identification was not possible in the CORINE classification, but the studied class represented these emergent aquatic macrophyte species together. Emergent aquatic macrophytes constitute a growth form representing same kind of structural characteristics and adaption to the environment (*see* Spence 1982, Lacoul and Freedman 2006). According to the botanical records of the Finnish Museum of Natural History, all these species occur in entire Finland, except for *Typha latifolia* and *Schoenoplectus*



**Fig. 1.** The studied catchments representing the so-called second division size category (1.33–4263.52 km<sup>2</sup>) in the Finnish hydrological regime, altogether 848 catchments, and percentage cover of emergent aquatic macrophytes in these catchments. Cover classes are based on the natural groupings inherent in the data (natural breaks), where the break points are identified by picking the class breaks that best group similar values and maximize the differences between the classes. The broken line indicates the national borders of Finland, including sea areas.

*lacustris* (Lampinen and Lahti 2009). These two species have latitudinally limited distribution patterns as their northern distribution limits are at 66°N and 68°N, respectively. *Phragmites australis*, *Carex lasiocarpa* and *Carex vesicaria* also show uneven abundances especially in northern Finland. The studied species occur in diverse aquatic macrophyte communities and many of them do not indicate any particular trophic status (Toivonen and Huttunen 1995). However, *Carex vesicaria* and *Typha latifolia* grow in meso-eutrophic waters, whereas *Carex lasiocarpa* pre-

fers oligo-mesotrophic conditions. *Phragmites australis* has also been reported to benefit from eutrophication (Mäemets and Freiberg 2004, Partanen et al. 2009).

Based on distributions and structural characteristics of these species, we considered that *Phragmites australis* primarily dominates in the CORINE class along with *Carex rostrata*. According to Mossberg and Stenberg (2006), *Phragmites australis*, which has broad leaves ( $\leq 3$  cm wide), grows 1–4 m high and forms often continuous, dense stands along littoral

zones in boreal region. *Carex rostrata* can also form continuous stands though its detectability is less obvious from satellite images due to smaller size (leaves  $\leq 8$  mm wide and stem  $\leq 1$  m high) as compared with that of *Phragmites australis*. Despite wide distributions, narrow habitus prevents the detectability of *Equisetum fluviatile* from the images unless stands are considerable. In addition, *Typha latifolia* and *Carex vesicaria* probably contribute to the class in the southern catchments. Especially *Typha latifolia* can grow extensive formations in boreal lakes. Contributions of *Carex lasiocarpa* and *Schoenoplectus lacustris* to the emergent aquatic macrophytes class seem to be minor due to limited distribution patterns and low detectability from satellite images. The emergent aquatic vegetation indicative CORINE class has a resolution of  $25 \times 25$  m. In order to detect the emergent aquatic macrophytes from the satellite images at this resolution the vegetation stands must be continuous and large. Thus, we considered that the class represents overgrowth or stands that are about to become expanded. The GIS-based delineation of the emergent aquatic macrophyte areas was made by using a topographic database and a digital elevation model together with the areas interpreted to present vegetation in water (digitized water mask). Hence, our vegetation data basically describe emergent aquatic macrophyte cover in aquatic littoral areas and wetlands. Determination of the emergent aquatic macrophytes was empirically verified against aerial photograph interpretations of well-investigated lakes in southern part of Finland where the emergent macrophyte species mentioned above were identified (Virkkala *et al.* 2005). The CORINE-based emergent aquatic macrophyte data were chosen because we wanted to assess their capability to represent emergent aquatic macrophytes and because they spatially cover entire Finland.

CORINE derived from the years 1999–2002 was also used to obtain land-cover data. The original data were reclassified to nine land-cover classes used as explanatory variables for emergent aquatic macrophyte occurrence and percentage cover (Table 1). These included infrastructure (all 12 infrastructure classes combined, ranging from residential and industrial areas to dumping sites and urban parks), agricul-

tural areas (arable land, pastures and agricultural mosaic areas), forest areas (coniferous and deciduous forest) and sparse vegetation areas (sparse vegetation, open mire and peat excavation). Land-use variables were calculated as percentage covers for each catchment. In addition, ditch intensity ( $\text{km km}^{-2}$ ) was calculated from a ditch sub-dataset of the Topographic Database (1:10 000) provided by the National Land Survey of Finland. The dataset consisted of combined new and restored ditches executed over the last 30 years and they represented mainly silvicultural ditches as 97% of them were located in forests. Forests with peat soils are commonly drained to increase forest growth in boreal regions (Peltomaa 2007), so these ditches were assumed to be in organic soils.

Two altitude variables (mean altitude and altitude range within a catchment area) were derived from the digital elevation model (DEM) at the 25-meter resolution. DEM is calculated from the contour lines and coastline elements of the basic map by triangulation network interpolation into a grid model. Basically, in interpolation, unknown values are predicted from observed data at known locations. In addition, we obtained four soil and landform types and three reclassified bedrock types from digital maps (1:1 000 000) of national Quaternary deposits and pre-Quaternary rocks (Atlas of Finland 1990). The soil and landform variables used in the analysis were: (1) moraine, (2) rock, (3) clay and (4) sand and gravel. Bedrock types were reclassified from the original data according to acidity: acidic, intermediate and calcareous. Proportion of lake cover was used as a hydrological variable and a surrogate for lake surface cover in the evaluation of occurrence of emergent aquatic macrophytes.

Climate data with a 10-km resolution (mean values) from the period 1961–1990 were obtained from the Finnish Meteorological Institute (Venäläinen and Hämäläinen 2002). This dataset was downscaled from the original resolution to the 0.5-km (25 ha) resolution by kriging interpolation. Considering these notions, we calculated the following climatic variables: (1) growing degree days ( $> 5$  °C), (2) mean temperature (°C) of the coldest month (January), and (3) mean annual precipitation (mm). In addition,

ice-derived variables — duration of the ice cover period (days) and ice cover thickness (mm) in March — were employed in the analysis. Ice variables were interpolated by kriging from the data of 50 lakes (mean values) to the resolution of 25 m from the review period 1961–2000 (Korhonen 2005). As the ice variables were significantly correlated with the climatic variables, they were grouped with climatic variables.

All the data sets were prepared using ArcView ver. 9.2. (ESRI 1991), and a new, programmed ditch intensity extension tool for ArcView was also utilized. The empirically validated ditch intensity tool separates natural brooks, streams and rivers from artificial drainage ditches. A stream is classified as a man-made ditch if it has fewer than 25 curves per kilometer and the curves do not exceed 45°. The accuracy

of this tool improved with high artificial ditch intensities (V. Leppänen unpubl. data). At high percentages of natural brooks and streams (ca. 20% of the total proportion of lotic features) the correctness of the tool was over 70% and at low percentages of natural brooks and streams (ca. 3%) over 90%.

## Statistical analyses

Statistical analyses were performed using the R statistical package (R Development Core Team 2004). Generalized linear models (GLMs) are mathematical extensions of linear models which can handle non-linear relationships and different types of statistical error distributions, such as Gaussian, Poisson, Binomial and Gamma (Vena-

**Table 1.** Descriptive statistics of the land use, geomorphology and climate variables in the studied catchments.

Variable	Unit	Minimum	Maximum	Mean	SD
<b>Land use</b>					
Infrastructure	%	0	68.3	4.0	5.5
Arable	%	0	56.7	7.9	10.0
Pasture	%	0	7.7	0.2	0.4
Agriculture mosaic	%	0	3.8	0.7	0.6
Coniferous forest	%	0	74.8	46.3	12.5
Deciduous forest	%	0	45.8	5.1	5.4
Sparse vegetation	%	3.9	96.0	20.9	10.9
Open mire	%	0	1.1	0.04	0.1
Peat excavation	%	0	9.3	0.4	0.9
Drainage ditch intensity	%	0	3.1	0.9	0.7
<b>Geomorphology</b>					
<i>Topography</i>					
Altitude mean	m	4.3	840.9	144.0	97.0
Altitude range	m	0	1310	150.0	108.2
<i>Soil/Landform</i>					
Moraine	%	0	94.5	51.4	19.2
Rock	%	0	63.3	11.6	12.4
Clay	%	0	73.6	10.2	15.4
Sand and gravel	%	0	87.8	9.5	10.4
<i>Rock type</i>					
Acidic	%	0	100.0	29.5	41.3
Intermediate	%	0	100.0	58.1	45.3
Calcareous	%	0	100.0	1.4	9.2
<i>Hydrology</i>					
Lake cover	%	0.0	51.0	6.2	8.1
<b>Climate</b>					
Ice thickness	cm	41.6	78.7	57.0	8.5
Duration of ice period	days	143.3	226.2	180.3	21.1
Degree growing days (> 5 °C)	°C	165.9	1335.2	978.3	222.0
Temperature of the coldest month	°C	-17.5	-4.5	-11.1	3.0
Mean annual precipitation	mm	416.5	639.8	564.4	53.5

bles and Ripley 2002). In this work, we built GLM models using a full stepwise approach, in which explanatory variables are included or excluded from the full model according to their statistical significance. In the model building, the variable selection criterion ( $p < 0.05$ ) was based on the  $F$ -ratio test for the inclusion or exclusion of predictors. We also examined the possibility of curvilinear relationships between explanatory and dependent variables by entering the quadratic terms of the variables in the models (Austin 2002).

The variation partitioning (VP) approach was used to divide the variation in emergent aquatic macrophyte occurrence and percentage cover among the three groups of predictors: land use, geomorphology and climate. Variation in occurrence and percentage cover of emergent aquatic vegetation was partitioned using a series of partial regression analyses with GLMs (Borcard *et al.* 1992, Heikkinen *et al.* 2004). In the first step, within each of the three groups of predictors, selection of predictor variables was performed to include variables that contributed significantly to the explained variation. The goodness-of-fit for each added variable was measured by the deviance statistics and the change in deviance (Venables and Ripley 2002). Detailed description of variation partitioning with three explanatory matrices can be found elsewhere (Anderson and Gribble 1998, Heikkinen *et al.* 2004). Here, it leads to eight fractions: (a) pure effect of land use, (b) pure effect of geomorphology, (c) pure effect of climate; combined variation due to the joint effects of (d) land use and geomorphology, (e) land use and climate, (f) geomorphology and climate, and (g) the three groups of explanatory variables; and finally (h) unexplained variation. Several fractions, or groups of fractions, can be obtained directly by a (partial) GLM run such as a + d + e + g: explained variation by land-use variables; b + d + f + g: variation by geomorphology variables; c + e + f + g: variation by climate variables; and a + b + d: variation by land use and geomorphology variables. The total explained variation in the data (a + b + c + d + e + f + g) was obtained by regressing the dependent variables using the selected statistically significant variables of the three groups of explanatory variables together ('full model').

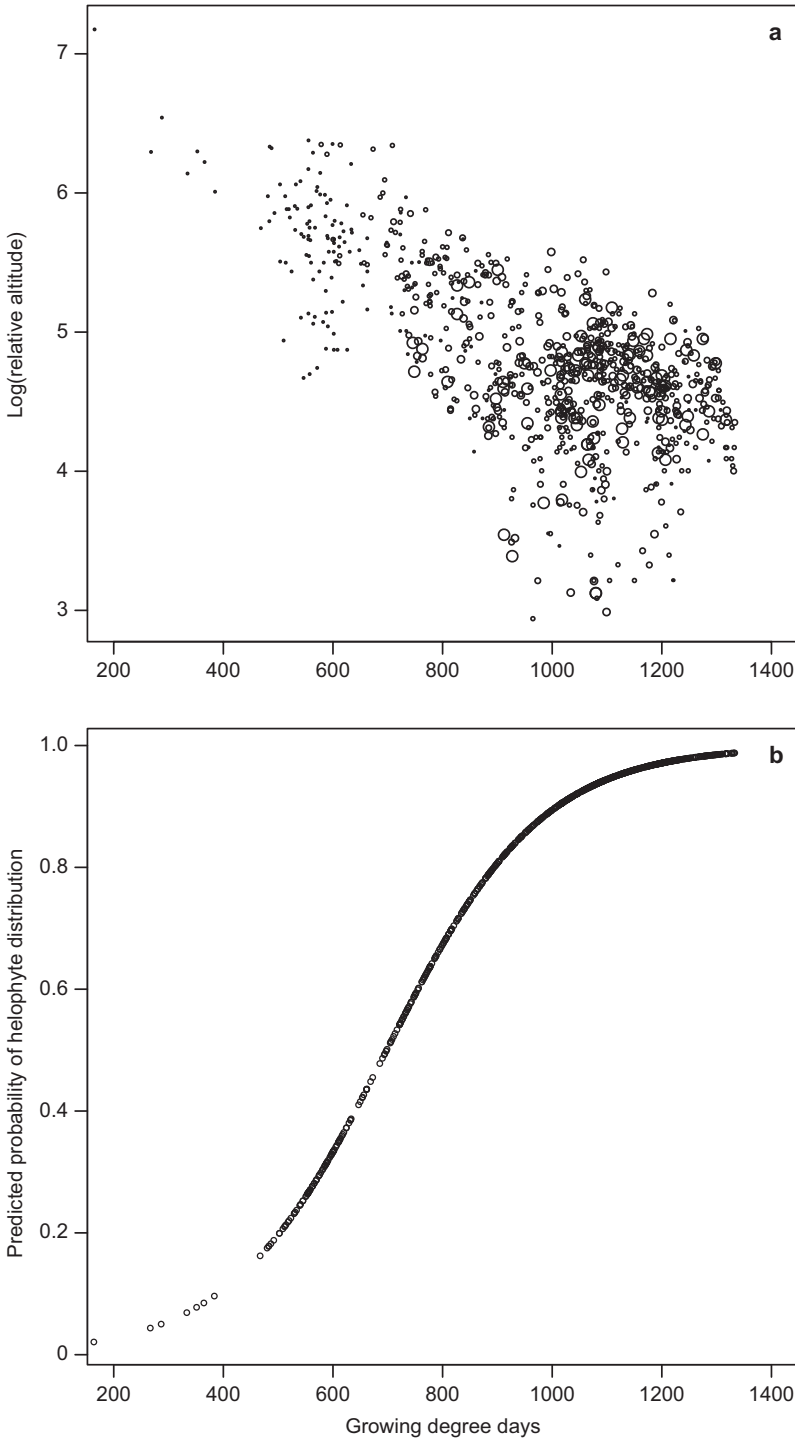
Hierarchical partitioning (HP, Chevan and Sutherland 1991) using ordinary GLMs was performed in order to study the effects of individual explanatory variables on emergent aquatic macrophytes. In the hierarchical analysis, all the possible combinations of explained variance are calculated, thus enabling assessment of the proportion of variation explained independently by each variable. The calculation process was conducted with R (R Development Core Team 2004) and the 'hier.part' package 1.0 therein (Walsh and MacNally 2003). We selected the variables that were the most significant based on VP ( $p$ ), and represented a wide range of different environmental features.

Autocorrelation is a frequently observed feature in spatially sampled biological data that can hamper attempts to identify plausible relationships between biota and the environment (Legendre 1993). Due to spatial autocorrelation, values of particular variables in neighboring sites are rather similar to the expected values in the case of random set of observations. We studied the role of spatial autocorrelation in the data sets by calculating spatial correlograms (Moran's  $I$ ) for emergent aquatic macrophytes, land use, geomorphology and climate variables using the program ROOKCASE (Sawada 1999). Ten inter-sample distance classes were formed using a lag of 10 km (Legendre and Fortin 1989). Moran's  $I$  ranges between  $-1$  and  $+1$ , where  $+1$  means the strongest positive spatial autocorrelation,  $-1$  the strongest negative autocorrelation, and  $0$  no correlation or random distribution. Positive spatial autocorrelation is exhibited when neighboring areas are similar or the same. A checkerboard is a good example of negative spatial autocorrelation (Luoto and Hjort 2006).

## Results

### Descriptive statistics

Percentage covers of emergent aquatic macrophytes were highest in southern Finland and undetected from the 68th latitude northward and from the catchments with average altitude exceeding 300 m (Fig. 1). Because the data resolution of the studied macrophyte class was



**Fig. 2.** (a) Percentage covers of emergent aquatic macrophytes in relation to number of growing degree days and logarithmic transformed altitude range in catchments representing the second division size category in the Finnish hydrological regime, and (b) fitted probability of emergent aquatic vegetation occurrence in relation to growing degree days. The sizes of five different circles follow percentage covers of emergent macrophyte values from the largest to the smallest: between 100% and 95%, between 95% and 75%, between 75% and 50%, below 50% and absent, respectively.

25 × 25 m, vegetation in the northern and high altitude catchments was undetected though higher resolution would probably reveal presence of this growth form. Moreover, emergent

aquatic macrophytes were present in the catchments when the mean January temperature was above  $-15^{\circ}\text{C}$  and the cumulative growing degree temperatures were at least 700 (Fig. 2b).



It was also typical that emergent aquatic macrophytes were absent if catchments did not have any clay soils or agricultural areas.

The proportion of different land-use types and the values of other environmental variables varied considerably among the 848 studied catchments (Table 1). In general, forests and sparse vegetation dominated. Ditch intensity was the highest in the western and central parts of the country. Climatic variables showed latitudinal and altitudinal gradient, as for example growing degree days correlated negatively (Spearman:  $r_s \leq -0.7$ ) with relative altitude in all but the largest emergent aquatic vegetation covers (Fig. 2a).

The explanatory variables correlated with each other and many of the relationships were self-evident. Some land-use variables, such as infrastructure, arable land and agricultural mosaic areas, were negatively correlated with altitude ( $r_s \leq -0.556$ ) and positively with growing degree days ( $r_s \geq 0.631$ ). Moreover, infrastructure positively correlated with arable land ( $r_s = 0.846$ ; Fig. 3a), agricultural mosaic areas ( $r_s = 0.704$ ) and clay soils ( $r_s = 0.796$ ). Agricultural areas were also concentrated on clay soils ( $r_s \geq 0.589$ ). Mixed forests and open mire were positively inter-correlated ( $r_s = 0.513$ ) and both variables were situated in catchments with lower temperatures ( $r_s \leq -0.629$ ). Drainage ditches had some correlation with peat excavation areas ( $r_s = 0.486$ ), sparse vegetation ( $r_s = 0.301$ ) and intermediate bedrock ( $r_s = 0.369$ ). Ditch intensity also correlated positively with infrastructure in the largest helophyte covers (Fig. 3b).

## Variation partitioning

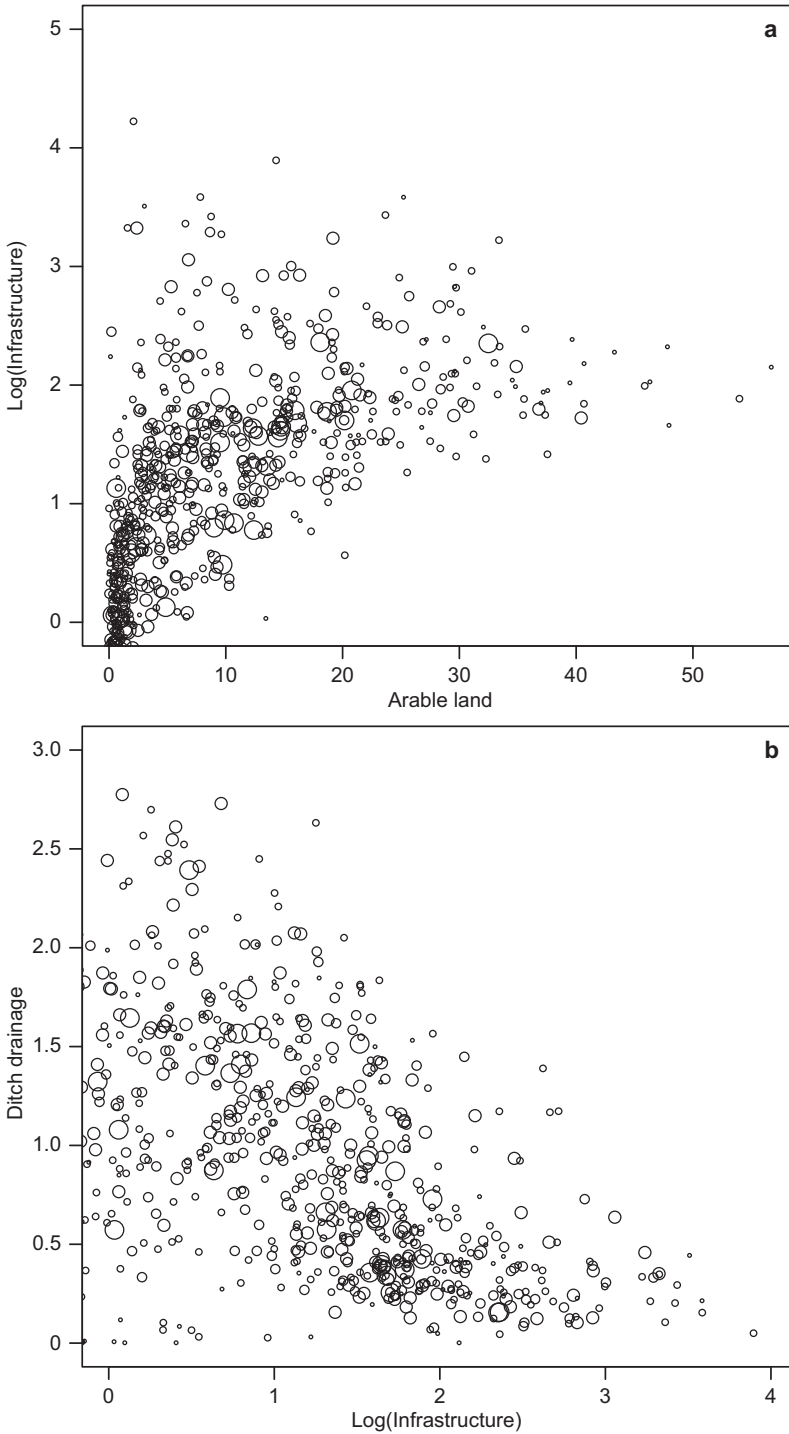
Both occurrence and percentage cover of the emergent aquatic macrophytes in the Finnish catchments were negatively related to moraine and rocky soils, duration of ice cover period and ice thickness and acidic bedrock, and positively to growing degree days, mean altitude, cover of arable land, peat excavation and drainage ditch intensity.

A summary of the selected explanatory variables for emergent aquatic macrophyte occurrence and percentage cover from the three variable groups is presented in Table 2. The results

of variation partitioning for the occurrence and percentage cover of the emergent aquatic macrophytes in terms of the fractions of variation explained are shown in Fig. 4. For the occurrence of the emergent aquatic vegetation, the amount

**Table 2.** The significance of the linear (L) and quadratic (Q) terms for the land use, geomorphology and climate variables selected and used in the variation partitioning procedures. Generalized linear regression models with full stepwise selection of statistically significant ( $p < 0.05$ ) variables were calculated separately for each variable group and for the emergent aquatic macrophyte occurrence (binomial distribution of error) and percentage cover data (Poisson distribution of error). Jan = January, NS = not selected; L = linear term; Q = quadratic term; \* for  $p < 0.05$ , \*\* for  $p < 0.01$ , \*\*\* for  $p < 0.001$ . The variables set in boldface were selected for hierarchical partitioning analysis of emergent aquatic macrophytes.

	Occurrence	Cover (%)
<b>Land use</b>		
Infrastructure	+L***-Q***	+L*-Q*
Arable	+L*-Q***	+L*-Q**
Pasture	+L***	NS
Agriculture mosaic	+L***-Q***	NS
Coniferous forest	+L** <b>-Q**</b>	+L*
Deciduous forest	-L***	NS
Sparse vegetation	+L** <b>-Q**</b>	-L*
Open mire	-L*	NS
Peat excavation	+L*-Q*	+L*
Drainage ditch intensity	+L*** <b>-Q**</b>	+L***
<b>Geomorphology</b>		
<i>Topography</i>		
Altitude mean	+L*** <b>-Q**</b>	NS
Altitude range	-L*	-L***
<i>Soil/Landform</i>		
Moraine	-L*+Q*	NS
Rock	-L***	-L*
Clay	+L** <b>-Q***</b>	+L*-Q*
Sand and gravel	+L*-Q*	
<i>Rock type</i>		
Acidic	-L***+Q*	NS
Intermediate	+L***	NS
Calcareous	NS	NS
<i>Hydrology</i>		
Lake cover	+L*** <b>-Q*</b>	-L**
<b>Climate</b>		
Duration of ice period	-L***	-L*
Ice thickness	-L***+Q***	-L***+Q**
Growing degree days (> 5 °C)	+L*** <b>-Q**</b>	+L** <b>-Q**</b>
Temperature of coldest month (Jan)	+L**	NS
Mean annual precipitation	NS	NS



**Fig. 3.** Percentage covers of emergent aquatic macrophytes in Finland in relation to (a) covers of arable land and logarithmically transformed infrastructure, and (b) ditch density and logarithmically transformed infrastructure inside the catchments representing the second division size category in the Finnish hydrological regime. The sizes of five different circles follow emergent macrophyte abundance values from the largest to the smallest: between 100% and 95%, between 95% and 75%, between 75% and 50%, below 50% and absent, respectively.

of variation captured by all selected environmental variables was 59.3%, and 44.8% for percentage cover of the emergent aquatic macrophytes. The decomposition of the variation showed that

the largest fractions of the variability in emergent macrophyte occurrence were mainly accounted for by the joint effect of land use, geomorphology and climate variables (fraction *g* in Fig. 4;

26.7%). Similarly, the largest fractions of the variability in emergent aquatic macrophyte percentage cover were accounted for by the joint effect of land use, geomorphology and climate variables (fraction g; 21.2%). Additionally, the joint effect of geomorphology and climate variables was considerable for macrophyte occurrence (fraction e; 13.0%). The pure effects of land use (fraction a), geomorphology (fraction b) and climate variables (fraction c) varied between 1.2% and 6.7% in both occurrence and percentage cover of the emergent aquatic macrophytes.

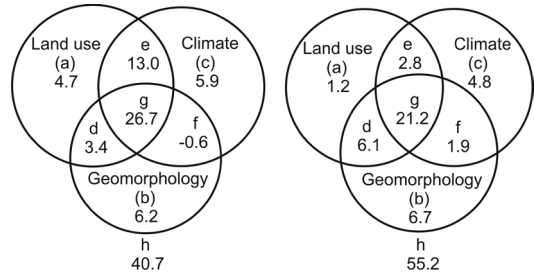
The joint contribution of geomorphology and climate was negatively related to emergent aquatic macrophyte occurrence. A negative joint contribution of two variable groups indicates that these groups are multicollinear, and therefore less variation is explained when the two groups of variables are included together than is expected on the basis of their effects in isolation (e.g. Chevan and Sutherland 1991).

### Hierarchical partitioning (HP)

The HP analysis revealed that climate had the highest explanatory value in occurrence and percentage cover of emergent aquatic macrophytes (growing degree days 19.2% and 15.0%, respectively). In the case of macrophyte occurrence, ditch intensity together with mean altitude had the second highest effect (12.1%), whereas relative altitude (10.1%) and ditch intensity (9.0%) were the next highest contributors to the percentage cover of emergent aquatic vegetation (Table 3).

### Spatial autocorrelation

In the emergent aquatic macrophyte percentage cover data, a clear spatial structure was revealed and Moran's correlograms indicated a positive autocorrelation for small-distance categories. Spatial autocorrelation in the residuals was reduced considerably after including the environmental variables in the final model (statistically non-significant,  $p > 0.05$ ) (Fig. 5). Clearly the highest autocorrelation occurred in the first distance class (10 km), where it was



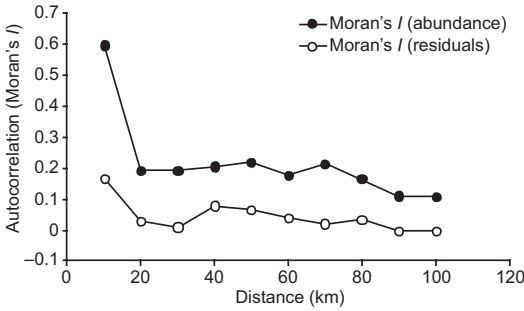
**Fig. 4.** Results of variation partitioning for the occurrence (left) and percentage cover (right) of emergent aquatic macrophytes, in terms of the proportions of variation explained. Variation of the species data matrix is explained by three groups of explanatory variables: land use (a), geomorphology (b) and climate (c), which denote the unique effects of these factors, whereas the categories d–g are the percentages indicating the joint effects of land use and geomorphology (d), land use and climate (e), geomorphology and climate (f) and land use, geomorphology and climate together (g), respectively. Category h represents unexplained effect.

reduced from 0.60 (original response variable) to 0.17 (residuals of the final model) in the emergent aquatic macrophyte data. In the distance class of 60 km or longer, autocorrelation was less than 0.05 in the residuals of the final model. Furthermore, we tested the effect of geographical location on the modelling results. Inclusion of east and north co-ordinates in the final models improved the amount of explained deviance only marginally for the emergent aquatic macrophyte percentage cover data (0.9%).

## Discussion

### Relations between emergent aquatic macrophytes and environmental variables

Together, the three groups of explanatory variables captured the variation in occurrence (59.3%) and percentage cover (44.8%) of emergent aquatic macrophytes quite well. The emergent aquatic vegetation was mostly explained by spatially structured climate and geomorphology variables as expected. Considering the spatial scale of this study, climatic conditions vary considerably with latitude, which is also relevant to aquatic macrophytes (Crow 1993, Hillebrand



**Fig. 5.** Spatial correlograms for emergent aquatic macrophyte data. Filled symbols present original abundance data and open symbols present residuals after environmental variables were included in the final GLM model. Only the correlogram of abundance data is statistically significant ( $p < 0.01$ ) after Bonferroni correction, i.e. at least one of the coefficients was significant at the Bonferroni-corrected level  $0.01/10 = 0.001$ .

**Table 3.** Proportion of explained variance according to hierarchical partitioning. The analyzed variables were selected on the basis of the significance of the variables in the variation partitioning procedures ( $p$ ) and representation of a wide range of different environmental features.

	Occurrence	Cover (%)
<b>Land use</b>		
Infrastructure	5.9	4.2
Arable	–	4.8
Pastures	4.9	–
Agriculture mosaic	9.6	–
Coniferous forest	7.1	4.7
Deciduous forest	–	–
Sparse vegetation	5.4	5.9
Peat excavation	–	4.5
Drainage ditch intensity	12.1	9.0
<b>Geomorphology</b>		
<i>Topography</i>		
Altitude mean	12.1	–
Altitude range	–	10.1
<i>Soil/Landform</i>		
Rock	5.6	5.7
Clay	5.5	5.0
<i>Rock type</i>		
Intermediate	7.7	–
<i>Hydrology</i>		
Lake cover	5.2	–
<b>Climate</b>		
Duration of ice period	–	18.0
Ice thickness	–	13.2
Growing degree days (> 5 °C)	19.2	15.0

2004, Chambers *et al.* 2008). Moreover, climate directly or indirectly influences geomorphology and land cover (Spence 1982), which is a plausible reason for the fact that geomorphology has the highest pure effect on emergent aquatic macrophytes. The pure explanation effect of land use was lower as compared with that of climate and geomorphology. However, joint effects of climate and land use in occurrence and geomorphology and land use in the percentage cover of emergent aquatic macrophytes were considerable.

It was not surprising that emergent macrophyte distribution increased with increasing growing degree days. In addition, in boreal regions aquatic vegetation is limited by harsh winter conditions including thick ice cover and freezing of bottom sediments, and for example, *Phragmites australis* is sensitive to ice erosion (Hellsten 2001). Indeed, the emergent aquatic macrophytes in our data were restricted by the temperature of January, duration of ice period and ice cover thickness.

Another anticipated response was that emergent aquatic macrophytes were limited by high altitudes (Rørslett 1991, Gacia *et al.* 1994). The distribution of emergent aquatic vegetation increased with altitude, but at a certain altitude this effect leveled off, which is illustrated by the saturation of the quadratic term (*see* Heikkinen *et al.* 2004). In Northern Ireland, the aquatic macrophyte correlation with altitude was related to hard water, nutrient-rich lakes situated in lowlands (Heegaard *et al.* 2001). The situation is much the same in Finland, as the clay soil catchments are concentrated to lowlands located in southern parts of the country. On the other hand, the proportion of organic soils is higher in high altitude catchments. High altitudes of northern catchments are also characterized by nutrient-poor alpine lakes that provide poor conditions for colonization (Virola *et al.* 2001).

In addition, nutritious and finer-grain soils promoted vegetation covers, and the distribution of emergent aquatic macrophytes also increased with nutritious bedrocks. Emergent macrophytes generally favour inorganic sediments (Spence 1982, Weisner 1991) and Partanen *et al.* (2009) found clay soils to be the primary factor controlling littoral overgrowth both at the lake and habitat levels in boreal catchments. Clay soils

are nutrient-rich and their erosion by waves and further by wind and rainfall from catchments increases nutrient background concentrations in water bodies. Because clay sediments can provide only few rooting microsites and the dominant *Phragmites australis* prefers sandy and oxygen-rich sediments (Lacoul and Freedman 2006, Partanen *et al.* 2009), we considered the positive effect of clay soils to be related primarily to nutrient enrichment of water bodies. Of the emergent aquatic macrophytes in our study, at least *Typha latifolia* and *Carex vesicaria* grow in more nutrient rich waters and *Phragmites australis* benefits from nutrient surplus in oligotrophic water bodies (Toivonen and Huttunen 1995, Partanen *et al.* 2009).

Our results supported the previous findings that large lake-surface area is often associated with higher macrophyte species richness and distribution as compared with small lake-surface area (Rørslett 1991). Occurrence of emergent aquatic macrophytes and lake surface area were positively related in small and mid-sized lake-surface areas, but the gradient levelled off in large lake-surface areas. Emergent macrophytes are more exposed to wave action than submerged macrophytes, and the exposure generally increases with the lake area (Spence 1982, Lacoul and Freedman 2006). To our surprise, the descriptive results indicated that the relationship between shoreline length and vegetation occurrence was weaker than that of lake-surface area and vegetation occurrence. Shoreline length is considered a better indicator of new habitats for macrophytes because vegetation often grows in fringe or marginal habitats represented evidently in shoreline length (Rørslett 1991, Thomaz *et al.* 2003). However, in Danish ponds, a positive relationship was also found between lake-surface area and richness of emergent plants, despite the lack of correlation with other growth forms (Møller and Rørdam 1985). This suggests that lake-surface area may be a better indicator of new habitat for emergent macrophytes than shoreline length. Other growth forms are more restricted by light limitation (Thomaz *et al.* 2003) and thus shoreline length might be a suitable surrogate of habitat diversity for them. However, this conclusion is somewhat tentative, because we do not know whether catchments consisted of many

small water bodies or a single large one, and a detailed analysis might have revealed complex curvilinear relationship between shoreline length and emergent aquatic macrophytes not indicated in the descriptive analysis.

### **Land use affecting emergent aquatic macrophytes**

Response of emergent aquatic macrophytes to land use appeared significant, which was somewhat surprising considering the scale of our study. Effect of land use is generally low at large spatial scales (Luoto *et al.* 2007, but *see also* Heino and Toivonen 2008). Here, land-use variables affected emergent aquatic macrophytes equally or more than natural geomorphological variables with drainage ditch intensity impact being the highest (Table 3). Other land-use types affecting emergent aquatic vegetation included agriculture and infrastructure. Several studies conducted at a water-body scale have reported acceleration of emergent aquatic macrophyte overgrowth in northern Europe due to anthropogenic pressures (Sand-Jensen *et al.* 2000, Andersson 2001, Brinson and Malvarez 2002, Mäemets and Freiberg 2004, Partanen *et al.* 2009). Emergent aquatic vegetation overgrowth can lead to dominance of a few species, hindering the diversity and ecological functioning of the littoral zone (Lougheed *et al.* 2008). Our results indicate that the overgrowth problem in boreal catchments is related especially to drainage ditching, but with a strong mediating effect of the prevailing climatic and geomorphological conditions.

Emergent aquatic macrophytes had an overall positive response to drainage ditching. To our knowledge this is the first analysis to show that ditch intensity promotes emergent aquatic macrophytes at a wide, national level. Ditching is generally executed in low-altitude areas, where the soil is saturated with water and emergent aquatic macrophytes have often naturally wider distributions. Therefore, altitude might explain the positive influence of ditch intensity on emergent aquatic vegetation. However, we treated drainage ditches and altitude as separate variables, also recognizing possible inter-correlations. The negative correlation between drainage

ditch intensity and altitude was weak, probably because altitude differences were minor between majority of the catchments and the extreme values of drainage ditching and altitude did not meet. Drainage ditches were concentrated in the western and central parts of the country, whereas high altitude catchments were located in northern Finland. We consider that these variables probably show a clearer relationship at a more local scale where environmental differences between areas are more pronounced. Thus, our results highlight the importance to study environmental determinants of biotic community structures at different hierarchical levels.

Drainage ditches were mainly located in peat soils. Hence, the positive influence of ditch intensity on emergent aquatic macrophytes is probably related to the ability of vegetation to tolerate increased leaching of suspended solids (both organic and inorganic) and dissolved humic substances, which is a typical consequence of peatland drainage (Åstrom *et al.* 2001, Holden *et al.* 2004). One competition advantage of emergent aquatic macrophytes over the submerged ones includes better tolerance to toxicants and anoxic sediments (Barko and Smart 1983). For example, *Phragmites australis* can favor moderate accumulation of organic sediments (Mäemets and Freiberg 2004). Another mechanism favoring emergent macrophytes in drained catchments is an increase in nutrient concentrations and decreased light penetration inhibiting growth of submerged macrophytes due to eutrophication (Toivonen and Huttunen 1995). However, excess eutrophication can lead to a decrease in emergent aquatic macrophyte stands (Arts 2002, Lacoul and Freedman 2006). Siltation also expands the area of low water level, which is favorable for many emergent aquatic plants with good colonization capability (e.g. Santamaria 2002).

Dispersal of seeds and propagules through ditches can partly explain the positive influence of ditch intensity on emergent aquatic macrophytes. Aquatic macrophytes are known for their broad distributions due to their efficient growth strategies and high dispersal capacities (Barrat-Segretain 1996, Brochet *et al.* 2010). Ditches probably disperse seeds and propagules between water bodies and wetlands within a catchment, but ditches do not directly affect between catch-

ment dispersal. Catchments are individual entities that are usually connected to each other via a single outlet stream. Thus, at a regional scale ditches may increase within catchment dispersal and indirectly also between catchment dispersal, though actual between catchment dispersal happens via waterfowl, stream flows and wind, depending on species ecological characteristics.

Ecke (2009) found that the covers of agricultural and forest land could not explain either water quality or occurrence of aquatic macrophytes in boreal lakes in Sweden, but that drainage ditching of these land-use areas accounted for both water quality and aquatic macrophytes. This study suggested that drainage ditches in agricultural areas increased emergent macrophyte occurrence through nutrient leaching and erosion of fine, inorganic clay to littoral areas. Further, Ecke (2009) stated that forestry ditching and emergent macrophyte occurrence were also positively related, although the correlation was not statistically significant. Our results also strongly suggested that silvicultural drainage ditching promotes both occurrence and percentage cover of emergent aquatic macrophytes.

It was conservatively hypothesized that agricultural areas might stimulate emergent aquatic macrophytes. Agricultural areas are primary sources of nutrient leaching to water bodies due to fertilization and increased erosion that further lead to deterioration of community structure of aquatic macrophytes (Penning *et al.* 2008). Despite the large spatial scale of our study, agricultural areas had clear positive effect on emergent aquatic macrophyte distribution. Nutrient enrichment from agricultural areas is particularly high, because drainage ditching of cultivation-rich clay soils increases remarkably nutrient erosion, leaching and transport. In water bodies with a higher trophic status, nutrient availability is no longer a limiting factor, but in eutrophic-hypertrophic lakes intense primary production limits emergent aquatic plant growth and distribution (Arts 2002). This fact may have caused the leveling off of the positive influence of agricultural areas in our data.

We could not foresee that infrastructure promotes emergent aquatic macrophytes, which is in contrast to what was reported in some previous studies (Partanen and Luoto 2006, Mäemets

and Freiberg 2004). Infrastructure was positively correlated with agricultural areas, suggesting that these land-use forms are geographically intersected. Hence, influence of infrastructure is most probably related to the presence of agricultural areas close to rural settlements. The positive effect of infrastructure levelled off when the proportion of infrastructure increased within a catchment in densely populated urban areas.

### **Applicability of GIS modelling in ecological assessment**

GIS-data-derived ecological assessments have been increasingly popular due to improved data sets and cost-efficient execution of these analyses (Aspinall and Pearson 2000, Zhou *et al.* 2008). Our cost-efficient assessment of emergent aquatic macrophytes produced ecologically plausible results and the explanation power of the models were comparable to those reported in other methodologically similar studies (e.g. Heikkinen *et al.* 2004, Demars and Harper 2005, Partanen and Luoto 2006). Introduction of a quadratic term, which represents curvilinear relationships between variables, improved the ecological rationality of our results. This has also been recognized in other studies (Austin 2002, Heikkinen *et al.* 2004). Curvilinear response curves were ecologically more plausible as compared with pure linear relationships.

As a caution measure, we placed more reliability on some independent variables over others (pure climate variables over ice cover variables) due to downscaling of the data with denser empirical observations. In addition, temporal variability of different data may have had some impact on the modeling performance. Nevertheless, we recognize that our explanatory data had many limitations, such as lack of species-level identification and general roughness. These shortcomings may, to some extent, weaken causality of our results, although many relationships between emergent aquatic macrophytes and explanatory variables were very clear and ecologically rational. More explicit explanatory data should be used in studies addressing interrelations of land use, catchment characteristics and climate and local macrophyte distributions.

However, good performance of our models indicated that spatial scales of different variables were suitable for this type of cost-efficient catchment study, and that the resolutions were not too fine or coarse for the analysis (Legendre 1993, Luoto and Hjort 2006).

The unexplained contributions in our models can be explained by the accuracy of percentage cover data (25 × 25 m) and unmeasured environmental variables (Austin 2002). However, we consider that the unexplained effect is more related to unmeasured limnological and hydrological variables, as was also demonstrated elsewhere (Partanen and Luoto 2006, Partanen *et al.* 2009). Characteristics specific to each water body and wetland probably determine the majority of percentage cover of emergent aquatic macrophytes. Exposure, sediment quality, light penetration, water quality, lake and wetland topography, water level fluctuations and permanent lowering of lake water level affect the growth and distribution of emergent aquatic vegetation (Wetzel 1990, Mitsch and Gosselink 2000). Despite the lack of limnological variables, the proportion of agricultural and urban land in catchments is a significant predictor of water quality (Johnson *et al.* 1997, Crosbie and Chow-Fraser 1999, Uuemaa *et al.* 2007). Moreover, emergent aquatic macrophyte species respond differently to various limnological and hydrological variables (Arts 2002).

In summary, our results demonstrate that neither overgrowth problems nor natural distribution patterns of emergent aquatic macrophytes can be understood without analyzing the joint effects of land use, climate and geomorphology. As emergent aquatic vegetation was strongly related to climate and land use, distribution patterns of this plant growth form will probably change due to global warming and deteriorative effects of land use. More specific studies focusing on the emergent aquatic macrophyte species and related environmental characteristics (including limnology, hydrology and climate change projections) in different water body and wetland types are needed in order to develop predictive tools for assessment of land use and climate change impacts on littoral ecotones. This study gave a good first hand knowledge of the national distribution pattern of emergent aquatic

macrophytes, which need to be carefully monitored in ecosystem management planning in order to avoid further deterioration of this scenically and ecologically important ecotone.

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## References

- Alahuhta J., Heino J. & Luoto M. 2011. Climate change and the future distributions of aquatic macrophytes across boreal catchments. *J. Biogeogr.* 38: 383–393.
- Andersson B. 2001. Macrophyte development and habitat characteristics in Sweden's large lakes. *Ambio* 30: 503–513.
- Anderson M.J. & Gribble N.A. 1998. Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Aust. J. Ecol.* 23: 158–167.
- Arts G.H.P. 2002. Deterioration of atlantic soft water macrophyte communities by acidification, eutrophication and alkalisation. *Aquat. Bot.* 73: 373–393.
- Aspinall R. & Pearson D. 2000. Integrated geographical assessment of environmental condition in water catchments: Linking landscape ecology, environmental modelling and GIS. *J. Environ. Manage.* 59: 299–319.
- Åström M., Aaltonen E.K. & Koivusaari J. 2001. Impact of ditching in a small forested catchment on concentrations of suspended material, organic carbon, hydrogen ions and metals in stream water. *Aquat. Geochem.* 7: 57–73.
- Atlas of Finland 1988. *Biogeography, nature conservation*. National Board of Survey and Geographical Society of Finland, Helsinki.
- Atlas of Finland 1990. *Geology*. National Board of Survey and Geographical Society of Finland, Helsinki.
- Austin M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Mod.* 157: 101–118.
- Barko J.W. & Smart R.M. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. *J. Ecol.* 71: 161–175.
- Barrat-Segretain M.H. 1996. Strategies of reproduction, dispersion, and competition in river plants: a review. *Végétation* 123: 13–37.
- Blanck A. & Lamouroux N. 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. *J. Biogeogr.* 34: 862–875.
- Borcard D., Legendre P. & Drapeau P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.
- Brinson M.M. & Malvarez A.I. 2002. Temperate freshwater wetlands: types, status, and threats. *Environ. Conserv.* 29: 115–133.
- Brochet A.-L., Guillemain G., Fritz H., Gauthier-Clerc M. & Green A.J. 2010. The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. *Ecography* 32: 919–928.
- Chambers P.A., Lacoul P., Murphy K.J. & Thomaz S.M. 2008. Global diversity of aquatic macrophytes in freshwater. *Hydrobiologia* 595: 9–26.
- Chevan A. & Sutherland M. 1991. Hierarchical partitioning. *Amer. Statistician* 45: 90–96.
- Cottenie K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* 8: 1175–1182.
- Crosbie B. & Chow-Fraser P. 1999. Percentage land use in the watershed determines the water and sediment quality of 22 marshes in the Great Lakes basin. *Can. J. Fish. Aquat. Sci.* 56: 1781–1791.
- Crow G.E. 1993. Species diversity in aquatic angiosperms: latitudinal patterns. *Aquat. Bot.* 44: 229–258.
- Decamps H. & Naiman R.J. 1990. Towards an ecotone perspective. In: Naiman R.J. & Decamps H. (eds.), *The ecology and management of aquatic-terrestrial ecotones*, Man and the Biosphere Series of Unesco vol. 4, The Parthenon Publishing Group, pp. 1–6.
- Demars B.O.L. & Harper D.M. 2005. Distribution of aquatic vascular plants in lowland rivers: separating the effects of local environmental conditions, longitudinal connectivity and river basin isolation. *Freshw. Biol.* 50: 418–437.
- Ecke F. 2009. Drainage ditching at the catchment scale affects water quality and macrophyte occurrence in Swedish lakes. *Freshw. Biol.* 54: 119–126.
- ESRI 1991. *ARC/INFO user's guide. Cell-based modelling with GRID. Analysis, display and management*. Environment Systems Research Institute Inc., Redlands, CA.
- European Communities 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000, establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities* 327: 1–72.
- Gacia E., Ballesteros E., Camarero L., Delgado O., Palau A., Riera J.L. & Catalan J. 1994. Macrophytes from lakes in the eastern Pyrenees: community composition and ordination in relation to environmental factors. *Freshw. Biol.* 32: 73–81.
- Heegaard E., Birks H.H., Gibson C.E., Smith S.J. & Wolfe-Murphy S. 2001. Species–environment relationships of aquatic macrophytes in Northern Ireland. *Aquat. Bot.* 70: 175–223.
- Heikkinen R.K., Luoto M., Virkkala R. & Rainio K. 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *J. Appl. Ecol.* 41: 824–835.
- Heikkinen R.K., Leikola N., Fronzek S., Lampinen R. & Toivonen H. 2009. Predicting distribution patterns and recent northward range shift of an invasive aquatic plant: *Elodea canadensis* in Europe. *BioRisk* 2: 1–32.



- Heino J. & Toivonen H. 2008. Aquatic plant biodiversity at high latitudes: patterns of richness and rarity in Finnish freshwater macrophytes. *Boreal Env. Res.* 13: 1–14.
- Hellsten S. 2001. Effects of lake water level regulation on aquatic macrophyte stands in northern Finland and options to predict these impacts under varying conditions. *Acta Bot. Fennica* 171: 1–47.
- Hillebrand H. 2004. On the generality of the latitudinal diversity gradient. *Am. Nat.* 163: 192–211.
- Holden J., Chapman P.J. & Labadz J.C. 2004. Artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration. *Prog. Phys. Geog.* 28: 95–123.
- Huidobro L., Morrone J.J., Villalobos J.L. & Alvarez F. 2006. Distributional patterns of freshwater taxa (fishes, crustaceans and plants) from the Mexican Transition Zone. *J. Biogeogr.* 33: 731–741.
- Johnson L.B., Richards C., Host G.E. & Arthur J.W. 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. *Freshw. Biol.* 37: 193–208.
- Korhonen J. 2005. Ice conditions in lakes and rivers in Finland. *Suomen ympäristö* 751: 1–146. [In Finnish with English abstract].
- Lacoul P. & Freedman B. 2006. Environmental influences on aquatic plants in freshwater ecosystems. *Environ. Rev.* 14: 89–136.
- Lampinen R. & Lahti T. 2009. *Plant Atlas of Finland 2008*. University of Helsinki, The Finnish Museum of Natural History, Botanical Museum, Helsinki.
- Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659–1673.
- Legendre P. & Fortin M.J. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107–138.
- Lougheed V.L., McIntosh, M.D., Parker C.A. & Stevenson R.J. 2008. Wetland degradation leads to homogenization of the biota at local and landscape scales. *Freshw. Biol.* 53: 2402–2413.
- Luoto M. & Hjort J. 2006. Scale matters — a multi-resolution study of the determinants of patterned ground activity in subarctic Finland. *Geomorphology* 80: 282–294.
- Luoto M., Virkkala R. & Heikkinen R.K. 2007. The role of land cover in bioclimatic models depends on spatial resolution. *Global Ecol. Biogeogr.* 16: 34–42.
- Mensing D.M., Galatowitsch S.M. & Tester J.R. 1998. Anthropogenic effects on the biodiversity of riparian wetlands of a northern temperate landscape. *J. Environ. Manage.* 53: 349–377.
- Mitsch W.J. & Gosselink J.G. 2000. *Wetlands* 3rd ed. John Wiley & Sons, Hoboken, NJ.
- Mossberg B. & Stenberg L. 2006. *Suuri Pohjolan kasvio*. Kustannusosakeyhtiö Tammi, Helsinki.
- Mäemets H. & Freiberg L. 2004. Characteristics of reed on Lake Peipsi and the floristic consequences of their expansion. *Limnologia* 34: 83–89.
- Møller T. & Rørdam C. 1985. Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark. *Oikos* 45: 8–16.
- Partanen S. & Luoto M. 2006. Environmental determinants of littoral paludification in boreal lakes. *Limnologia* 36: 98–109.
- Partanen S., Keto A., Visuri M., Tarvainen A., Riihimäki J. & Hellsten S. 2006. The relationship between water level fluctuation and distribution of emergent aquatic macrophytes in large, mildly regulated lakes in the Finnish Lake District. *Verh. Internat. Verein. Limnol.* 29: 1160–1166.
- Partanen S., Luoto M. & Hellsten S. 2009. Habitat level determinants of emergent macrophyte occurrence, extension, change in two large boreal lakes in Finland. *Aquat. Bot.* 90: 261–268.
- Parviainen M., Marmion M., Luoto M., Thuiller W. & Heikkinen R.K. 2009. Using summed individual species models and state-of-the-art modelling techniques to identify threatened plant species hotspots. *Biol. Cons.* 142: 2501–2509.
- Peltomaa R. 2007. Drainage of forests in Finland. *Irrig. Drain.* 56: 151–159.
- Penning W.E., Mjelde M., Dudley B., Hellsten S., Hanganu J., Kolada A., van den Berg M., Poikane S., Phillips G., Willby N. & Ecke F. 2008. Classifying aquatic macrophytes as indicators of eutrophication in European lakes. *Aquat. Ecol.* 42: 237–251.
- Perrow M.R., Jowitt A.J.D., Stanfield J.H. & Phillips G.L. 1999. The practical importance of the interactions between fish, zooplankton and macrophytes in shallow lake restoration. *Hydrobiologia* 395/396: 199–210.
- Pieczynska E. 1990. Lentic aquatic–terrestrial ecotones: their structure, functions and importance. In: Naiman R.J. & Decamps H. (eds.), *The ecology and management of aquatic–terrestrial ecotones*, Man and the Biosphere Series of Unesco vol. 4, The Parthenon Publishing Group, pp. 103–140.
- Powney G.D., Grenyer R., Orme C.D.L., Owens I.P.F. & Meiri S. 2010. Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Global Ecol. Biogeogr.* 19: 386–396.
- Rørslett B. 1991. Principal determinants of aquatic macrophyte richness in northern European lakes. *Aquat. Bot.* 39: 173–193.
- Sand-Jensen K., Riis T., Vestergaard O. & Larsen S.E. 2000. Macrophyte decline in Danish lakes and streams over the past 100 years. *J. Ecol.* 88: 1030–1040.
- Santamaria L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecol.* 23: 137–154.
- Sawada M. 1999. ROOKCASE: an Excel 97/2000 Visual Basic (VB) add-in for exploring global and local spatial autocorrelation. *Bull. Ecol. Soc. Am.* 80: 231–234.
- Schmidt M.H., Lefebvre G., Poulin B. & Tschamtké T. 2005. Reed cutting affects arthropod communities, potentially reducing food for passerines. *Biol. Conserv.* 121: 157–166.
- Segal S. 1971. Principles on structure, zonation and succession of aquatic macrophytes. *Hydrobiologia* 12: 89–95.
- Spence D.H.N. 1982. The zonation of plants in freshwater lakes. *Adv. Ecol. Res.* 12: 37–125.
- Thomaz S.M., Souza D.C. & Bini L.M. 2003. Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir, Brazil): the

- influence of limnology and morphometry. *Hydrobiologia* 505: 119–128.
- Toivonen H. & Huttunen P. 1995. Aquatic macrophytes and ecological gradients in 57 small lakes in southern Finland. *Aquat. Bot.* 51: 197–221.
- Venables W.N. & Ripley B.D. 2002. *Modern applied statistics with S*, 4th ed. Springer, New York.
- Venäläinen A. & Heikinheimo M. 2002. Meteorological data for agricultural applications. *Phys. Chem. Earth* 27: 1045–1050.
- van den Brink F.W.B., van der Velde G., Bosman W.W. & Coops H. 1995. Effects of substrate parameters on growth responses of eight helophyte species in relation to flooding. *Aquat. Bot.* 50: 79–97.
- van Geest G.J., Wolters H., Roozen F.C.J.M., Coops H., Roijackers R.M.M., Buijse A.D. & Scheffer M. 2005. Water-level fluctuations affect macrophyte richness in floodplain lakes. *Hydrobiologia* 539: 239–248.
- Virkkala R., Luoto M., Heikkinen R.K. & Leikola N. 2005. Distribution patterns of boreal marshland birds: modeling the relationships to land cover and climate. *J. Biogeogr.* 32: 1957–1970.
- Virola T., Kaitala V., Lammi A., Siikamäki P. & Suhonen J. 2001. Geographical patterns of species turnover in aquatic plant communities. *Freshw. Biol.* 46: 1471–1478.
- Walsh C. & MacNally R. 2003. *Hierarchical partitioning: R Project for statistical computing*. Available at <http://cran.r-project.org/>.
- Weisner S.E.B. 1991. Within lake pattern in depth penetration of emergent vegetation. *Freshw. Biol.* 26: 133–142.
- Wetzel R.G. 1990. Land-water interfaces: metabolic and limnological regulators. *Verh. Internat. Verein. Theor. Angew. Limnol.* 24: 6–24.
- Uuemaa E., Roosaare J. & Mander U. 2007. Landscape metrics as indicators of river water quality at catchment scale. *Nord. Hydrol.* 38: 125–138.
- Zhou D.M., Gong H.L. & Liu Z.L. 2008. Integrated ecological assessment of biophysical wetland habitat in water catchments: linking hydro-ecological modelling with geo-information techniques. *Ecol. Mod.* 214: 411–420.