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PATTERNS OF AQUATIC MACROPHYTES IN THE BOREAL REGION: IMPLICATIONS FOR SPATIAL SCALE ISSUES AND ECOLOGICAL ASSESSMENT
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Abstract

Eutrophication and global warming are increasingly causing deterioration of aquatic ecosystems, and boreal freshwaters are especially vulnerable to these changes. Anthropogenic pressures and landscape characteristics influencing the functioning and structure of ecosystems vary with spatial scale (grain size i.e. study unit and extent i.e. study area). This emphasises that the understanding of spatial scale is a vital element when studying species distribution patterns. Moreover, spatial scale is often neglected in ecological assessments, in which the degree of ecological integrity of an ecosystem is assessed using selected biological groups. One of these groups is aquatic macrophytes. The aims of this thesis were (i) to study the distribution and richness of aquatic macrophytes in the boreal region in Finland at multiple scales and (ii) to evaluate the performance of ecological assessment metrics selected for Finnish lake macrophytes.

The spatial extent at which aquatic macrophytes were studied had an important influence on the patterns found. Climatic factors associated with latitudinal and altitudinal gradient determined macrophytes at broad extent, although the patterns changed at finer regional extent. Moreover, this strong effect of climate could lead to the widening of distribution ranges of helophytes in boreal catchments during the 21st century due to the climate change. Many of these species have already widened their range limits during the previous century and increasing temperatures may create new niches for vegetation to colonize.

Lake macrophyte richness, turnover and quality metrics showed a clear relationship with nutrient concentration in waters at landscape and regional extent. Helophytes and metrics were positively or inversely negatively related to nutrients, whereas species turnover and other life-form groups had a unimodal or non-significant response to nutrient availability. In addition, land use (agricultural and urban areas and forestry ditch drainage) influenced likely macrophytes directly through shore morphology changes and indirectly through water quality. Macrophytes were also explained at various scales by area and depth, which were related to habitat heterogeneity, and aquatic plants responded to water ionic and electrical characteristics (pH, alkalinity and conductivity).

Ecological quality metrics of macrophytes appeared to be scale dependent, since land use adjacent to the lake shoreline had a higher influence on the metrics compared to land use of the whole catchment. However, the scale-related pattern in the effect of land use was not congruent between metrics, as the Trophic Index showed poorer performance compared to the proportion of type-specific species and Percent Model Affinity. This was presumably due to lack of helophytes in the species pool used and to reference values which were defined across lake types in the Trophic Index. Uneven performance of the metrics derived from different biological groups suggests that an approach integrating multiple lines of evidence on ecological status appears most feasible for assessment of the overall lake status.

Keywords: aquatic macrophytes, boreal region, climate change, ecological classification, Finland, GIS, land use, spatial modeling, spatial scale, species distribution, species richness, Water Framework Directive
Tiivistelmä

Vesistöjen rehevöityminen ja ilmastonmuutos heikentävät vesiekoosysteemien laatua, ja boreaaliset sisävedet ovat erityisen alttiita näiden uhkatekijöiden aiheuttamille muutoksille. Ihmistoiminnan aiheuttamien muutosten ja luontaisten maisematekijöiden merkitys vesiekoosysteemien toimintaan ja rakenteeseen vaihtelee mittakaavan (tutkimusyksikön ja -alueen) mukaan. Kuitenkin spatioalaisen mittakaavan merkitys on usein unohdettu ekologisissa arvioinneissa, joissa selviteään ekosysteemin luonnontilaisuutta eri biologisilla lajiryhmillä. Vesikasvit ovat yksi usein käytetty biologinen ryhmä järvien ekologisessa arvioinnissa. Tämän tutkimuksen tarkoitus on (i) tutkia vesikasvien levvinenysystä ja runsautta Suomessa useissa mittakaavoissa, ja (ii) arvioida ekologisten luokittelumuuttujien toimivuutta järvien vesikasveilla eri mittakaavoissa.


Ekologiset luokittelumuuttujat olivat riippuvaisia mittakaavasta, koska rantavöyrykkeen läheisellä maankäyttöllä oli suurempi merkitys muuttujuihin koko valuma-alueen maankäyttöllä. Kuitenkin mittakaavan merkitys vaihteli eri muuttujuihin välillä, kun referenssi-indeksi osiotti heikompaa vastetta maankäyttöön eri mittakaavoissa kuin tyyppilajien suhteellinen osuus ja prosenttiin mallin samankaltaisuus. Tämä luultavasti johtui sitä, että referenssi-indeksissä ilmaan veroiset vesikasvit puuttuvat tutkimattavista lajeista ja referenssiarvot olivat yhteiset riippumatta järviyypistä. Eri biologisiin ryhmin perustuu luokittelujärjestelmä ilmeni hyvin vaihtelevasti ekologista laatua, minkä vuoksi eri muuttujia yhdistävä menetelmä, joka arvioi vesimuodostuman kokonaistilaa, on toteuttamiskelpoinen lähestymistapa boreaalisissa järvissä.

Asiasonat: boreaalinen alue, ekologinen luokittelu, GIS, ilmastonmuutos, lajien levvinenysys, lajirunsaus, maankäyttö, spatioalainen mallintaminen, spatioalainen mittakaava, Suomi, vesikasvit, vesipoliitikan puitedirektiivi
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List of original articles

This thesis is a summary of the following articles, which are referred to in the text by their Roman numerals (I-V):


Contributions

I Miska Luoto (ML) was responsible for the study idea and Janne Alahuhta (JA) together with ML planned the study design. JA processed material and was responsible for hierarchical partitioning analysis, whereas ML performed other statistical analyses. Results were interpreted by JA and ML. JA wrote the first draft of the manuscript, to which contributions were made by ML and Kari-Matti Vuori.

II Miska Luoto (ML) was responsible for the study idea, and Janne Alahuhta (JA) and ML jointly planned the study design. JA processed material and executed statistical analyses. JA and ML jointly interpreted the results. JA wrote the first version of the manuscript, which was commented by ML and Jani Heino.

III Kristian Meissner (KM), Merja Honkanen (MH) and Mikko Mönkkönen (MM) planned the study. Antti Kanninen (AK) provided water quality and aquatic macrophyte data, which was also contributed by Katri Liljeroos (KL). Janne Alahuhta (JA) processed catchment data. MH conducted statistical analyses, mainly interpreted the results and wrote the first draft of the manuscript. JA along with the other authors contributed to interpretation of the results and the manuscript.

IV Janne Alahuhta (JA) was responsible for the study idea. Study design was planned together with JA and Antti Kanninen (AK) and JA also contributed to field surveys. JA processed vegetation and catchment data and AK was responsible for water quality and lake position data. AK performed NMS –analysis and JA conducted all other statistical analyses. The results were interpreted together with JA and AK. The first version of manuscript was jointly written by JA and AK and Kari-Matti Vuori commented the manuscript.

V Janne Alahuhta (JA) and Kari-Matti Vuori (KMV) together came up with the study idea and design. JA planned and conducted aquatic macrophyte sampling, and he was responsible for aquatic macrophyte analyses and interpretation of macrophyte results. KMV and other authors mainly contributed to analyses of other biological groups and interpretation of the results. JA and KMV jointly wrote the first draft of the manuscript, which was commented by the other authors.
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1 Introduction

Biodiversity, integrity and functioning of different ecosystems are facing serious problems on the global scale and freshwaters are one of the most threatened ecosystems (Vitousek et al. 1997, Vörösmarty et al. 2010, Barnosky et al. 2011). Eutrophication, pollution and climate change have already impacted lake and river systems. Boreal regions are especially vulnerable to these threats (Dudgeon et al. 2006, Heino et al. 2009). For example, land use alterations enhance eutrophication and increasing temperatures influence species distributions. Understanding of species distribution changes requires knowledge of heterogeneous ecological processes taking place at different spatial scales, because species and landscape patterns are unevenly distributed across space (Pickett & Cadenasso 1995, Gaston 2000). Modern statistical approaches and improved quality of GIS data have enabled more extensive distribution studies especially at broad spatial scales.

Ecological assessments programs have recently focused increasing attention on spatial scale as a factor determining species responses. Many assessment approaches have adopted regional reference conditions, in which natural variability of water body habitat characteristics along with landscape structure and ecological communities are considered as a part of the assessment system (e.g. European Communities 2000). In addition, spatial scales in which anthropogenic pressures operate need to be considered in assessment procedures and further in the efficient implementation of protection measures (Gaston 2000, Williams et al. 2004). Evaluation of man-made impacts on freshwaters relies on the integrity of community structure of biological groups and on the presence of indicator species that provide information about ecological quality in a water body (Rickert & Hines 1978, Carpenter et al. 2006). Aquatic macrophytes belong to one traditionally studied biological group in ecological assessments. Macrophytes indicate well long-term changes of littoral zone, but reflect poorer rapid changes in water quality (Palmer et al. 1992, Melzer 1999).

Aquatic ecosystems in the boreal region are confronted with harsh environmental conditions, such as cold climate and acidic waters, which limit the distribution and richness of ecological communities. Even small changes in the environmental conditions can have a significant influence on aquatic ecosystems, and environmental determinants of aquatic communities need to be identified at multiple scales. In addition, patterns of predicted environmental changes and their effects on ecosystems can provide early warning signals of possible ecological
deterioration in vulnerable boreal regions. Consequently, ecological assessment programs are urgently being developed around Europe (see European Communities 2000). In Fennoscandia, assessment programs need to take into account the environmental uniqueness of the boreal region, hence putting pressure on finding the most appropriate ecological metrics to indicate anthropogenic stress.

This thesis examines the patterns of aquatic macrophyte distribution and richness at different geographical scales and assesses the macrophyte quality metrics derived from the Finnish ecological classification program.
2 Study background

2.1 Aquatic macrophytes in lake ecosystems

Lakes are open and heterogeneous ecosystems that require a continuous energy input from internal or external sources (Wetzel 2001). The heterogeneity of lake system is hierarchically and temporally structured. This heterogeneity is a result of multiple physical, chemical and biological mechanisms acting at various spatial scales: catchment, terrestrial land adjacent to lake shoreline and lacustrine zones within lake basin (Hutchinson 1967, Naiman & Decamps 1997). Moreover, spatial and temporal scales of physical phenomena taking place in lake ecosystems are in close interaction. The origin of a lake affects its geomorphological and limnological features and also its ecological conditions. Most boreal lakes are of glacial origin, dating back to the last Ice Age 10 000 years ago. Boreal lakes are usually shallow, have a low volume and are still transforming due to continuous land uplift (Kuusisto 2005). The combination of these geomorphological and limnological characteristics with a short growing period has resulted in unique ecological conditions of boreal lakes. Although boreal lakes have typically lower diversity compared to other lakes, they preserve communities and species characteristic to high latitude areas. Moreover, these ecosystems are extremely vulnerable to global warming because they are e.g. adapted to colder temperatures (Heino et al. 2009) and the ecological functioning and diversity of boreal lakes are highly dependent on ecosystem interfaces, such as littoral zones (Wetzel 1990).

Aquatic macrophytes, comprising vascular plants, aquatic bryophytes and macroalgae growing permanently or temporally in aquatic environments (Sculthorpe 1967), are an important component of the littoral zone. Together with microalgae, aquatic plants are responsible for the primary production of lakes (Wetzel 1992, Krause-Jensen & Sand-Jensen 1995). Macrophytes provide shelter and nutrition for macroinvertebrates and zooplankton, whereas epiphytic algae grow on plants (Newman 1991, Tolonen et al. 2001). Macrophyte stands are used for reproduction, shelter and prey areas for fish (Schriver et al. 1995). Waterfowl are dependent on macrophytes for nutrition and habitat (Schmidt et al. 2005). Aquatic macrophytes also diminish littoral erosion, prevent nutrients flowing from terrestrial land to open water and influence the quality and quantity of sediments (Spence 1982, Barko & Smart 1983, Wetzel 1990). Aquatic
macrophytes can be classified based on species structural and environmental adaption (traits) to environment (growth forms) or attachment (life forms). Growth forms are divided to helophytes, nymphaeids, isoetids, elodeids, ceratophyllids, lemnids, bryids and charids (Mäkirinta 1978), whereas rhizophytes (incl. helophytes, isoetids, eloideids, charids) are macrophytes attached to a substrate and pleustophytes (incl. ceratophyllids, lemnids and bryophytes) are free floating species (Sculthorpe 1967). In general, rhizophytes often indicate long term environmental changes, because they mainly take up nutrients and other minerals through their root system, whereas pleustophytes are directly dependent on water quality and respond more rapidly to anthropogenic impacts. However, macrophytes are mainly species-specific in preferring different kinds of nutrient conditions, ranging from oligotrophic to (hyper-)eutrophic (Toivonen & Huttunen 1995). Species also respond differently to other environmental conditions, such as anoxia, water level fluctuations, freezing, flooding and ice erosion (Arts 2002, Lacoul & Freedman 2006).

Many aquatic macrophytes are widely distributed due to their efficient reproduction strategies and good dispersal capabilities (Sculthorpe 1967, Barrat-Segretain 1996, Santamaria 2002). Vegetative and clonal reproduction is a major mechanism for population growth and dispersal of macrophytes, whereas sexual reproduction and genetic recombination are often subordinate strategies (Wetzel 2001). All growth forms expand mainly populations by e.g. plant fragments, rhizomes and winter buds that are dispersed even long distances via wind, water, animals and humans. Some species, often helophytes, combine intensive vegetative growth with wind dispersed seed production resulting to high colonization capability (Barrat-Segretain 1996, Wetzel 2001).

### 2.2 Species distribution models in aquatic ecosystems

Species distribution models (SDM) are empirical models connecting field observations and environmental variables, with emphasis on their spatial entities (Guisan & Zimmermann 2000). SDMs have become an increasingly important tool for studying species-environment relationships since the 1990s (Austin 2002, Guisan & Thuiller 2005, Heikkinen et al. 2006, Elith & Leathwick 2009), and the focus of modelling studies has widened to more applied subjects during recent years, such as conservation biology and climate change research (Parviainen et al. 2008, Beaumont et al. 2011, Thuiller et al. 2011). The majority of SDM studies have been performed in terrestrial ecosystems with equal-sized grid data (Guisan
& Thuiller 2005, Maggini et al. 2006), whereas species-environment relationships have rarely been studied in aquatic ecosystems until very recently (Cheung et al. 2009, Stephenson & Morin 2009, Compton et al. 2010). In freshwaters, fish modelling studies dominate (Joy & Death 2004, Grenouillet et al. 2011), largely due to the available data sets, and aquatic macrophytes are among the less studied biological groups of SDMs (Lehmann 1998, Vis et al. 2007, Heikkinen et al. 2009). Moreover, since lakes in many ways represent islands, study grain size in lake modelling studies must be ecologically justified.

The selection of appropriate environmental variables for species distribution models depends on the ecological and bio-physical processes expected to influence the biota, as well as on the availability of data and the purpose of the model (Austin 2007, Elith & Leathwick 2009). In optimal circumstances all ecologically relevant environmental variables are used, but this is often not possible, and a modeller is forced to utilize a limited number of environmental variables. When selecting ecologically plausible variables, it must be considered whether environmental variables have direct, indirect or resource related effects on species, arranged along a gradient from proximal to distal explanatory variables (Austin 2002). Direct variables with strong causal relationships with plants has a direct physiological influence on plant growth (e.g. temperature for aquatic macrophytes), whereas resource variables are consumed by the plant (e.g. nutrients in water and sediment) (Guisan & Zimmermann 2000, Guisan & Thuiller 2005, Heikkinen et al. 2006). Models using proximal resource and direct gradients are the most robust and widely applicable, whereas indirect distal variables produce models with local usage at best (e.g. Heikkinen et al. 2009). Manipulation of environmental data can be adequately executed with GIS, although it is often difficult to provide GIS coverage for proximal variables (Austin 2002).

Although all relevant explanatory variables should be used to create an ecologically plausible model, increasing the number of variables can also cause problems. A high number of explanatory variables, which indicate congruent ecological responses, can result in multicollinearity between the variables (e.g. Heikkinen et al. 2006, Murray & Conner 2009). Multicollinearity is especially a problem if the aim of a study is to estimate the contributions of individual variables (Legendre & Legendre 1998). As a result of multicollinearity, p values can be misleading and the confidence intervals of the regression coefficients very wide, changing considerably with the addition or exclusion of one explanatory variable.
In addition, under- or overfitting can also distort model performance, when prediction error increases due to a too simple or complex model, respectively (Guisan & Thuiller 2005, Heikkinen et al. 2006). In underfitting, the calibration model is not sufficiently complex to capture all the interferences of the relationships between explanatory variables (interference error), whereas overfitting is a result of random noise caused by a high number of explanatory variables in the model (estimation error). Although models with considerable complexity may appear to give a better fit, the predictions they produce may be poorer (Heikkinen et al. 2006). For obtaining optimal prediction, the remaining interference error and the estimation error dispel the effect of each other, i.e. the number of explanatory variables is in balance.

Species distributions under climate change can be statistically predicted using SDMs, which give ecological estimations of how species distributions will possibly alter in the future (e.g. Thuiller et al. 2011). Predictive accuracy has become the key objective in modelling due to the need for high reliability for species distribution predictions (e.g. Marmion et al. 2008, Elith & Graham 2009). The predictions were previously solely based on climatic variables until the importance of non-climatic variables, e.g. soil and bedrock, in model performance was presented. The suitability of environmental conditions for a given species might result from a variety of factors unrelated to climate, and purely climate-driven models can produce inaccurate predictions of species distributions under climate change (Pearson & Dawson 2003, Thuiller et al. 2004). However, the significance of non-climatic variables for SDMs has mainly been derived from terrestrial ecosystem studies, whereas this methodological aspect has rarely been addressed in studies of aquatic environments.

Spatial autocorrelation is a frequently observed feature in spatially sampled biological data, and can hamper attempts to identify plausible relationships between biota and the environment, especially when using grid data in SDMs (Legendre 1993, Dale & Fortin 2002). Basically in autocorrelation, data lacks independence between pairs of observation at given distance in space or time and, hence, values of particular variables in neighbouring sites are more similar compared to the expected values in the case of a random set of observations (Legendre 1993, Diniz-Filho et al. 2003). Spatial autocorrelation can be derived from endogenous and exogenous processes or from both simultaneously (Legendre & Legendre 1998, Legendre et al. 2002). In the former, the spatial pattern is generated by factors that are an inherent property of the variable itself, for example distance-related biotic processes such as reproduction, dispersal,
speciation, extinction or geographical range extension (Legendre 1993, Diniz-Filho et al. 2003). Autocorrelation can also be independent of the variable of interest (exogenous autocorrelation), e.g. when the processes are spatially structured environmental factors such as geomorphological processes or climatic constraints, which can cause species distributions to be spatially structured (Legendre 1993, Diniz-Filho et al. 2003). Nevertheless, the magnitude and structure of spatial autocorrelation need to be determined in species distribution analyses in order to improve the causality of the outcome.

2.3 Role of scale in determining aquatic macrophyte distributions

Understanding of scale is an essential component in explaining species distributions (Cottenie 2005, Field et al. 2009). Scale refers to a dimension of an object of process and is characterized by grain size (size of the base unit used in sampling and analysis) and extent (size of the study area) (Turner et al. 2001, Whittaker et al. 2001). Each species responds to its environment on a unique range of scale and landscape processes showing different patterns depending on scale (Levin 1992, Pickett & Cadenasso 1995). A single mechanistic ecological process cannot explain population or ecosystem patterns at all scales, because different spatially structured processes are probably relevant at different scales (both extent and grain size), resulting in hierarchical structure of the biotic and abiotic phenomena (Whittaker et al. 2001, Chase & Leibold 2002, Willis & Whittaker 2002, Mykrä et al. 2007). The key question is to find the relevant scale for a specific process and, more importantly, to understand the interaction between simultaneously operating processes at different scales (Fig. 1). A clear pattern operating in one scale may show an opposite gradient in another (Rahbek 2005, Willis & Bhagwat 2009). At each scale, a species can be considered to possess suitable functional traits which are equivalent to the selective characteristics of that scale, before it can potentially exist at lower spatial levels (Poff 1997, Zobel 1997). On the other hand, finer scale processes, such as sudden disturbances, can influence landscape structure and further species distributions on a broader scale (Pickett & Cadenasso 1995, Whittaker et al. 2001, Heino 2011).
Broad-scale processes are related to the life history of species and dynamic mechanisms (e.g. colonization, speciation, dispersal and different metacommunity paradigms) that constrain local species communities despite suitable finer scale habitat conditions (Leibold et al. 2004, Benton 2009, Field et al. 2009). The species distributions generally vary across latitude, altitude, depth and isolation at broad scales (Smith & Brown 2002, Willig et al. 2003, Rahbek 2005). Broad scale processes can also act as statistical surrogates for local scale habitat selective forces, although they cannot explain all local ecological variation due to their averaging nature (Poff 1997). When study extent and grain size become widen at broad scale, details are often lost and patterns become more homogenous. Within these relatively homogenous broad scale patterns operate finer scale biotic
processes derived from heterogeneous habitat conditions, competition and dynamic mechanisms between local species (Levin 1992, Field et al. 2009).

Understanding of the effects of spatial patterns on species distributions has generally increased among terrestrial taxa and some well-studied freshwater and marine biological groups, such as fishes and macroinvertebrates (Cottenie 2005, Hillebrand 2004, Heino 2011). In freshwaters, the main research focus has been on river ecosystems (Mykrä et al. 2007, Soininen et al. 2009, Stephenson & Morin 2009), whereas different spatial patterns affecting lake ecosystems have received less attention (Heino & Toivonen 2008, Akasaka et al. 2010). Because distribution patterns can differ between various biological groups and/or regions (Gaston 2000, Heino 2011), spatial patterns must be studied in different ecological and biogeographical contexts. Boreal areas have been relatively well represented among spatial pattern studies of lake species distributions (Johnson et al. 2004, Soininen & Weckström 2009, Bennett et al. 2010, Sharma et al., in press), but until recently aquatic plants has mostly been neglected in these studies (Heino 2001, Heino & Toivonen 2008, Kosten et al. 2009). For example, species distribution and turnover of different macrophyte functional groups has hardly ever been studied in boreal lakes at broad extent before. In addition, broad-scale studies using lake aquatic macrophytes have often been restricted to smaller spatial extents, although a few regional and continental extent investigations have emphasised the importance of climate derived latitudinal and altitudinal gradients, dynamic mechanisms and also water quality for spatial patterns of species distributions (Heino 2001, Heegaard 2004, Capers et al. 2007, Chambers et al. 2008, Heino & Toivonen 2008, Kosten et al. 2009).


2.4 Ecological assessment and aquatic macrophytes with emphasis on scale

The purpose of ecological assessments is to define the degree of the biological integrity of an ecosystem (Davis & Jackson 2006). In freshwaters, the biological integrity of (nearly) pristine, natural condition is often compared with that of an anthropogenically impacted site, representing a reference condition approach (Stoddard et al. 2006). The degree of deterioration is then defined as a deviation between observed values of the potentially impacted site and expected values of reference conditions. This approach has gained wide acceptance in current assessment procedures, for example in the Water Framework Directive (WFD). An ambitious goal of WFD is to achieve at least good ecological status for all European freshwaters by the year 2015 (European Communities 2000). WFD has adopted a multi-taxon approach, in which different biological groups are assessed in order to evaluate the community integrity of a water body, because the groups respond differently to anthropogenic pressures and environmental conditions in general (Sondergaard et al. 2005, Johnson et al. 2006, Brazner et al. 2007). However, no consensus on how overall water body status should be defined across multiple groups has been reached (Nõges et al. 2009).

In the multi-taxon approach, lakes are typically assessed using aquatic macrophytes, phytoplankton, fishes and macroinvertebrates, along with water chemical properties. Ecological assessments have often relied on indicator species or community metrics derived from these groups (Palmer et al. 1992, Clarke 1993, Beck & Hatch 2009). The principle of indicator species is that they respond measurably to an anthropogenic pressure, e.g. eutrophication or acidification derived from land use alterations. In addition to anthropogenic stressors, several abiotic factors influence the composition and diversity of macrophyte communities (Arts 2002, Lacoul & Freedman 2006). An underlying issue in ecological assessments is the separation of anthropogenic disturbance effects on biota from natural, inherent variation in ecosystems. For example, in the WFD-compliant ecological assessment (European Communities 2000), the natural
variation due to abiotic factors is taken into account through typology, i.e. grouping of naturally similar ecosystems together. However, the typology systems do not necessarily cover all relevant abiotic variation affecting lake biota. To avoid biased assessment accuracy, it is important to measure the residual effect of natural variation on ecological quality metrics of different organism groups.

Spatial scale also has implications for ecological assessments and conservation measures. As lakes are hierarchically structured systems, the spatial scale at which landscape-related anthropogenic stressors operate has an important effect on ecological assessment (Akasaka et al. 2010, Beck et al. 2010). Catchment land use can have a different impact on aquatic ecosystem compared with land use adjacent to lake shoreline, because in long lake chains only a small portion of land use-derived diffuse pollution of the whole catchment reaches lakes lower in the chain (Kratz et al. 1997). Moreover, the terrestrial land adjacent to lake shoreline is in immediate contact with the lake, enabling direct nutrient run-offs to the lake basin. Dense macrophyte stands growing in littoral zones can act as buffers against direct nutrient run-offs to lakes, hence making them prone to reflect land use changes in the direct vicinity of lake shoreline (Wetzel 1990, 1992). However, information on land use processes operating at different scales is often neglected in ecological assessments (Johnson et al. 2006), although it is vital to find the most significant spatial scale relevant to the overall ecological quality of freshwaters (Yater & Bailey 2011).

### 2.5 Main study aims

The main study aims were to investigate regional scale distributions and richness of aquatic macrophytes in boreal catchments and lakes and to evaluate the performance of selected ecological assessment metrics derived from lake macrophytes (Fig. 2). First, we studied the main determinants of helophyte (emergent aquatic macrophyte) distributions in boreal lake catchments by separating the variation between climate, geomorphology and land use (I). Then the significance of individual environmental variables was assessed (I) and the main climatic determinants were used to predict future distribution patterns of helophytes under climate change in the lake catchments (II). In addition, we evaluated whether inclusion of non-climatic variables improves modelling accuracy for aquatic macrophyte predictions (II). In both modelling articles (I, II) we also studied whether applicable ecological assessments can be produced with nationwide data. Secondly, we studied the influence of potential productivity on
aquatic macrophyte species richness and turnover in boreal lakes at regional extent (III). More specifically, relations between macrophyte species richness and richness of different vegetation functional life-forms and three explanatory groups (area, nutrients and non-nutrient related water quality) were uncovered. Furthermore, we determined the relationship between macrophyte species turnover and explanatory variables. Thirdly, we assessed how adequately aquatic macrophyte-based metrics indicate ecological quality in boreal lakes at regional (IV) and landscape (V) scales. Three macrophyte metrics were evaluated by comparing a priori selected reference and impacted lakes (IV, V), and the relationship between the metrics and vegetation community structure and environmental variables was studied (IV). In addition, the influence of spatial extent on the metrics was studied using land use data from four different extents (IV), and a comparison between overall status approaches using different biological groups was performed (V).

Fig. 2. A schematic picture illustrating the study process of aquatic macrophytes in relation to distribution and richness patterns and ecological classification. Roman numbers on the right side boxes refer to individual study articles.
3 Study areas and spatial scales

Study areas were located in Finland (19°–32° E, 60°–70° N), which is situated in Fennoscandia, Northern Europe. Exact geographical position, number of studied areas and study grain size (catchments in I, II and lakes in III, IV, V) varied in different studies (Fig. 3). Study areas generally covered the whole country in articles I, II, IV, whereas the rest of the study lakes were located in two separate regions of eastern Finland (III, V). The study extent varied from regional (I, II, III, IV) to landscape (V; Table 1), following definitions of Willis & Whittaker (2002). Detailed descriptions of study areas are given in articles I-V.

In articles I and II, study areas covered all 848 so-called second size category catchments in hydrological regimes located within Finland (Fig. 2, Table 1). The aquatic macrophyte-derived ecological classification was researched with 110 study lakes (< 40 km², 85 impacted and 25 reference lakes) covering the whole of Finland, excluding the northernmost parts (IV). In article III, the study lakes (67) belonged to the Vuoksi catchment in eastern Finland, and 59 of these lakes were also used in IV. Finally, ecological classification based on aquatic macrophytes and other biological groups was studied in six small humic lakes with high percentages of catchment forest and peatland (> 35% of catchment area) located in the Kainuu region of eastern Finland (V).
Fig. 3. Study areas of different articles located inside Finnish borders, including sea areas (broken line). Left side map represents study catchments and right side map study lakes. Roman numbers after study region refer to individual study articles. The majority of study lakes (59) of the Savo region (III) were also included in study lakes of article IV.
4 Material and methods

4.1 Dependent variables

Aquatic macrophytes were studied using different types of data in the separate articles (Table 1). Ecological classification was investigated on species-level (IV, V), growth form data (helophytes) was utilized in catchment studies (I, II) and both species and life-form data were used in the richness study (III). In addition, other biological groups (phytoplankton, benthic macroinvertebrates and fish) and palaeolimnology were utilized in the lakes of the Kainuu region and detailed descriptions of these variables can be found in article V.

4.1.1 Remote sensing vegetation data (I, II)

Helophytes, occurrence (present/absent) and percentage cover (vegetation cover per each catchment, %), were derived from Finnish CORINE land-cover classification, which has a specific class for this vegetation growth form inhabiting shallow water areas covered with silt deposits, flooded areas and wetlands without peat cover or tree vegetation. CORINE is based on automated interpretation of the Landsat Enhanced Thematic Mapper Plus (ETM+) satellite images (from the years 1999 to 2002) and data integration with existing digital maps (see Luoto et al. 2007). The macrophyte data was acquired with a grain size of 25m x 25m and was averaged to catchment scale. Species-level identification was not possible, but the studied class represented typical helophytes together.

Aerial photograph interpretation in well-studied lakes in southern Finland revealed the presence of 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).

4.1.2 Empirical vegetation data (III, IV, V)

Aquatic macrophytes were surveyed using a main belt transect method (Kuoppala et al. 2008), in which a five meter wide transect is placed in opposite direction to the lake shoreline from the flood border to the last occurrence of vegetation in a lake, or to the middle point of the basin if vegetation extended over the entire lake.
The transect is divided into zones according to the growth form or species and the zones may be overlapping. The number of transects varied according to lake size, larger lakes having more transects (Kuoppala et al. 2008). Ten transects were used in the Kainuu region (V) and the number of transects varied between seven and 26 in the other study lakes (III, IV).

The surveys were performed between June and September 2002–2008 (III, IV) and at the end of August 2005 (V). In addition to true hydrophytes, helophytes and shore plants were also recorded. The total number of species was 56 in the Kainuu region (V), 105 in article III and 137 in article IV. Species richness was studied with five dependent variables (III): 1) total macrophyte species richness, 2) species richness of helophytes, 3) species richness of rhizophytes, 4) species richness of pleustophytes and 5) growth-form group richness. In ecological assessment studies three macrophyte metrics were used as dependent variables (IV, V): 1) the proportion of type-specific taxa (TT50, Kuoppala et al. 2008), 2) Percent Model Affinity (PMA, Novak & Bode 1992) and 3) Trophic Index (TI, Penning et al. 2008b). The metrics were re-scaled so that they were comparable over lake types. An integration approach based on the Finnish ecological classification system was used to re-scale the metrics in the Kainuu region (V; Vuori et al. 2009) and the linear regression method was used in article IV (Hämäläinen et al. 2007).

Table 1. Study frameworks of the individual articles.

<table>
<thead>
<tr>
<th>Article</th>
<th>Study grain size</th>
<th>Study extent</th>
<th>Studied phenomenon</th>
<th>Empirical/Remote sensing macrophyte data (E/R)</th>
<th>Number of study areas</th>
<th>Number of dependent variables</th>
<th>Number of explanatory variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>catchment</td>
<td>regional</td>
<td>distribution</td>
<td>R</td>
<td>848</td>
<td>2</td>
<td>25</td>
</tr>
<tr>
<td>II</td>
<td>catchment</td>
<td>regional</td>
<td>distribution</td>
<td>R</td>
<td>848</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>III</td>
<td>lake</td>
<td>regional</td>
<td>richness, turnover</td>
<td>E</td>
<td>67</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>IV</td>
<td>lake</td>
<td>regional</td>
<td>ecological metrics</td>
<td>E</td>
<td>110</td>
<td>3</td>
<td>13</td>
</tr>
<tr>
<td>V</td>
<td>lake</td>
<td>landscape</td>
<td>ecological metrics</td>
<td>E</td>
<td>6</td>
<td>3 (12*)</td>
<td>-</td>
</tr>
</tbody>
</table>

*Including ecological quality metrics derived from all biological groups.
4.2 Explanatory variables

All CORINE 2000 land cover classes (I) or infrastructure classes (IV) with grain size of 25 m represented land use and cover in Finland (see Luoto et al. 2007, Table 1). More precise information on agricultural areas was obtained from the Field Crop Production Register (year 2008) of the Information Centre of the Ministry of Agriculture and Forestry (IV). Drainage ditch intensity (km/km²) was calculated from a ditch sub-dataset of the Topographic Database (1: 10 000) provided by the National Land Survey of Finland (I, IV). Climate variables downscaled from 10-km grain size to 250 m (mean values) using Kriging interpolation were derived from the Finnish Meteorological Institute for the period 1961–1990 (I, II) or 1971–2000 (III) (Venäläinen & Hämäläinen 2002). In article II, climate scenarios for the years 2051–80 were also obtained from the Finnish Meteorological Institute (Jylhä et al. 2004). In catchment studies, average altitude and altitude range were derived from a digital elevation model (DEM) with grain size of 25 m (I, II), whereas the Hertta-database maintained by the Finnish Environment Institute was used to obtain mean lake altitude (III, IV). Soil and bedrock types (I, II) were derived from digital maps (1:1 000 000) of national Quaternary deposits and pre-Quaternary rocks. In article IV, the influence of spatial extent on ecological classification was studied using four different area definitions: catchment, and buffer zones of 500 m, 300 m and 100 m. Otherwise, data were defined for lake catchment grain size (I, II, III, V).

The lake hydromorphological variables (IV) consisted of lake surface area, mean depth, lake order, shoreline development factor (e.g. Heino 2008) and fetch (e.g. Håkansson 1982). In addition, shoreline length was used to explain the species-area relationship of aquatic macrophyte richness in article III. Water quality variables included total phosphorus (III, IV), total nitrogen (III, IV), pH (III, IV), color (IV), secchi depth (III), conductivity (III) and alkalinity (III). Water quality variables, obtained from the Hertta-database, were median values of surface water (0–2m) samples taken during the growing season (June-September) over the period 2000–2007 (III) or 2000–2008 (IV). In addition, climate related latitudinal gradient was studied with north coordinate (IV), whereas sampling effort was accounted for using total transect length (III) or number of transects (IV) in a lake.
4.3 Statistical and spatial analyses

Statistical analyses utilized in different articles are summarized in Table 2. Mann-Whitney U-test was used to study differences between reference and impacted lakes related to ecological classification (IV, V), and changes in predictions were statistically evaluated with the t-test (II). To limit multicollinearity between individual explanatory variables (III, IV), composite variables were created using Principle Component Analysis (PCA) included in SPSS 16.0 (SPSS Inc., Chicago, Illinois, USA). The relationship between community composition and primary environmental determinants was studied with Nonmetric Multidimensional Scaling (NMS) in article IV, using a macrophyte lake frequency data (proportion of transects in which a species is recorded). NMS was used because this method does not have predefined assumption of data normality or linearity (McCune & Grace 2002). Species occurring in a single lake and having frequencies less than five were excluded from NMS-analysis, which was performed with PC-ORD 4.35 (McCune & Mefford 1999). Species turnover was analysed with Jaccard and Simpson indices, incorporated in the “vegan” package in R (Oksanen et al. 2008). The turnover was studied so that first pair-wise index values were calculated between the lake in concern and four of its nearest productivity neighbours and then these values were averaged to describe mean lake similarity with nearest neighbours along the productivity gradient.

The relations between aquatic macrophytes and explanatory variables were determined using spatial modelling approaches (Table 2): generalized linear models (GLM; I), generalized additive models (GAM; II, IV) and simultaneous autoregressive models (SAR; III). GLMs are mathematical extensions of linear models which can handle non-linear relationships and different types of statistical error distributions (Venables & Ripley 2002). GAMs are semi-parametric extensions of generalized linear models (Hastie & Tibshirani 1990, Guisan et al. 2002) that allow linear and complex additive response shapes or a combination of the two within the same model. Hence, GAMs are more data driven than GLMs. SARs are standard linear regression models, in which spatial autocorrelation structure is included as an additional term (Kissling & Carl 2008). Hence, the SAR models account for patterns in the response variable that are not predicted by explanatory variables, but are instead related to values in neighbouring locations. These models were calculated using R (GLM), S-Plus 6.1 (Insightful Corp., Seattle, WA, USA) with Grasp-interface (GAM; Lehmann et al. 2002) and SAM 3.0 (SAR; Rangel et al. 2010).
In addition to the models, complementary statistical procedures were employed to explore relationships between explanatory variable groups and individual variables. Variation partitioning using partial GLMs (Anderson & Gribble 1998, Heikkinen et al. 2004) was used to decompose variation between three environmental variable groups, whereas hierarchical partitioning (Chevan & Sutherland 1991, Walsh & MacNally 2003) revealed variation explained by individual variables (I). In addition, the significance of single explanatory variables to GAMs was assessed with alone, drop and model contribution in article II (Lehmann et al. 2002). Model-averaged parameter estimates and measure of support (Burnham & Anderson 2002, MacKenzie et al. 2006) were calculated in order to draw further conclusions concerning explanatory variables of species richness (III).

Degree of spatial autocorrelation was estimated by calculating Moran’s I statistics (I, II, III, IV) with the program ROOKCASE (Sawada 1999). In addition, spatiality of macrophyte distribution data was evaluated by inclusion of coordinates in models (I, II).

Table 2. Main statistical and spatial methods utilized in each article.

<table>
<thead>
<tr>
<th>Article</th>
<th>Main statistical methods</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Generalized linear models (GLM), Variation partitioning (VP), Hierarchical partitioning (HP), Spearman correlation, Moran’s I autocorrelogram</td>
</tr>
<tr>
<td>II</td>
<td>Generalized additive models (GAM), t-test, Spearman correlation, Moran’s I autocorrelogram</td>
</tr>
<tr>
<td>III</td>
<td>Simultaneous autoregressive models (SAR), Principle component analysis (PCA), Model-averaged parameter estimates, Measure of support, Moran’s I autocorrelogram</td>
</tr>
<tr>
<td>IV</td>
<td>Generalized additive models (GAM), Nonmetric multidimensional scaling (NMS), Principle component analysis (PCA), Spearman correlation, Pearson correlation, Moran’s I autocorrelogram</td>
</tr>
<tr>
<td>V</td>
<td>Mann-Whitney, Canonical correspondence analysis (CCA)</td>
</tr>
</tbody>
</table>
5 Results and Discussion

5.1 Environmental determinants of aquatic macrophytes at regional extent (I)

Variation partitioning using GLMs revealed that helophytes were mainly explained by the combined effect of climate, geomorphology and land use at broad extent (21–27%, article I: Fig. 4). Land use and climate for macrophyte occurrence and land use and geomorphology for macrophyte percentage cover also accounted for a considerable portion of variation. In addition, climate variables showed the highest individual influence on helophytes based on hierarchical partitioning, followed by altitude and ditch intensity. Climate variables indicated a latitudinal gradient, as macrophyte occurrence and percentage cover increased with increasing latitude (I: Table 2). Latitudinal gradient, commonly associated with macrophytes (Heino 2001, Hillebrand 2004, Chambers et al. 2008), is a surrogate for different historical, geographical, biotic, abiotic and stochastic factors, which vary with space and latitude (Willig et al. 2003). Likewise, altitude is often considered to be a mirror of latitudinal gradient, related to productivity, ambient energy and contemporary climate (Rahbek 2005), and hence aquatic macrophytes are often limited by high altitudes (Rørslett 1991, García et al. 1994). Our macrophyte occurrence and percentage cover increased with increasing altitude, but the gradient levelled off at higher end values. Most of the clay soil catchments are concentrated to lowlands located in southern parts of the country and the proportion of organic soils is also higher in high altitude catchments. In addition, nutrient enrichment of waters due to clay soils probably resulted in a positive relationship between helophyte vegetation distribution and finer grained soils and less acidic bedrocks. Clay soils can promote littoral overgrowth both at the lake and habitat levels in boreal catchments (Partanen et al. 2009). Lake area and helophytes were positively related in small and middle sized lake surfaces. This relationship probably originates from habitat heterogeneity: as larger lakes encompass more microhabitats, more species are able to find a suitable habitat with increasing area (Rørslett 1991, Jones et al. 2003, Heegaard 2004). Surprisingly, our preliminary results, which should be interpreted with caution, suggested that lake area can be a better indicator of species-area relationship than shoreline length for helophytes (see also Møller & Rørdam 1985).
Significant contribution of land use to macrophyte distribution was partly unexpected, because land use generally has a strong influence at finer extents (Luoto et al. 2007, but see also Heino & Toivonen 2008). More importantly, drainage ditch intensity had the highest positive contribution to helophytes, which has not been found at this broad extent before. This relationship was probably caused by the ability of helophytes to tolerate increased leaching of suspended solids and dissolved humic substances from peat soils (see Barko & Smart 1983), where ditching is generally executed to increase tree growth. Increase of nutrient concentrations and decreased light penetration due to drainage ditching can also benefit helophytes over other growth forms (Toivonen & Huttunen 1995). In addition, dispersal of seeds and propagules through ditches can partly explain the positive influence of ditch intensity on helophytes. Ditches may increase within catchment dispersal and indirectly also between catchment dispersal at broad extents. Drainage ditching has been reported to affect water quality and macrophyte occurrence in the boreal region (Ecke 2008), and our study further suggested that silvicultural drainage ditching promotes macrophyte distributions at broad extent. Furthermore, agricultural and urban development areas had a positive effect on macrophytes that was probably related to nutrient leaching from agricultural fields and intersection of geographical position of infrastructure with agricultural areas.

Our ecologically plausible modelling results, congruent with those of other methodologically similar studies (Heikkinen et al. 2004), indicated that nationwide data can reliably be used for first-hand estimations of helophytes. Despite some shortcomings of the dependent variable, such as lack of species-level identification, the clear relationships between aquatic flora and environmental variables suggested that spatial scales of different variables were suitable for this type of cost-efficient catchment study, and that the grain sizes were not too fine or coarse for the analysis.

5.2 Aquatic macrophyte distribution predictions under climate change at regional extent (II)

As a result of climate change, helophytes will widen their distributions in boreal catchments based on GAMs. Aquatic vegetation will colonize new catchments in northernmost Finland, and the cover will become more abundant in all catchments due to climate change (II: Fig. 2). Rosset et al. (2010) found similar pattern with macrophyte richness in Swiss ponds. Boreal species are predicted to lose their
habitat (Virkkala et al. 2008) or widen their distribution ranges (Saetersdal et al. 1998) as a result of increased temperature and precipitation estimations. Our results indicated that helophyte occurrence will increase by more than 10%, and that the percentage cover will increase by approximately 25% (II: Table 3). In boreal freshwaters, stream aquatic vegetation and lake fish distributions were estimated to increase due to increased floods and improved dispersal, respectively (Jeppesen et al. 2003, Ström et al. 2011).

Macrophyte distribution change was mainly temperature-driven, governed by growing degree days (see also Heikkinen et al. 2009). Climatic conditions of northern catchments will become more suitable for vegetation growth and the harshness of the continental climate effect will probably smoothen in inland catchments. Increased nutrient concentrations, derived from diffuse pollution due to increased precipitation in the future (Jylhä et al. 2004), can hinder temperature-driven distribution changes of macrophytes (Rosset et al. 2010). Boreal lakes are typically oligotrophic-mesotrophic concerning productivity and helophytes often benefit from nutrient surplus, hence possible nutrient enrichment may not decrease macrophyte distributions. Moreover, future vegetation distributions probably derive from changing environmental conditions rather than from dispersal. Novel environmental conditions create additional niche space originating from climate change-promoted overgrowth that is filled by helophytes. Communities of helophytes are typically driven by species-sorting processes along environmental gradients, where heterogeneous environmental conditions with associated niche differences and sufficient dispersal determine species distributions (see also Cottenie 2005, Heikkinen et al. 2009).

Botanical museum records showed that many of the studied helophyte species have already increased their distributions during the last decade (Lampinen & Lahti 2009). Especially Phragmites australis and Typha latifolia have become much more abundant in southern Finland, and new observations have also been made beyond the previous northern range limits. In addition, Carex vesicaria has also shown similar distributional changes, and the abundances of Equisetum fluviatile and Carex rostrata are currently increasing evenly throughout the country. Hence, our results suggest that increase in the distributions of these helophyte species will continue in the future.

Inclusion of geomorphological variables to pure climate models clearly improved model performance (II: Table 4). This strengthens previous conclusions that pure climate-driven models often produce incomplete distribution predictions when species depart from equilibrium with climate, owing to a suite of non-

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climatic factors (Pearson & Dawson 2003, Thuiller et al. 2004, Luoto & Heikkinen 2008). In addition, recent studies have emphasized the selection of appropriate environmental variables for species distribution models (Beaumont et al. 2007, Heikkinen et al. 2009). Our final models showed weaker statistical performance compared to excluded models, but growing degree days in the final model was clearly the most significant individual variable for aquatic vegetation in the GAMs. High multicollinearity between climatic variables also prevented their utilization in the models. A priori selection of explanatory variables in the models has been used in a number of bioclimatic modelling studies, when empirical information concerning the physiological limits constraining the geographical distributions of species has been available (see Austin 2002, Heikkinen et al. 2006, Austin 2007, Elith & Leathwick 2009). Moreover, we were able to bypass collinearity and overfitting problems by using a limited number of physiologically meaningful variables (Guisan & Thuiller 2005, Luoto & Heikkinen 2008). Finally, species distribution models provided a useful first-filter estimate for the identification of distributional changes of helophytes in boreal region.

5.3 Macrophyte species richness and turnover at regional extent (III)

Aquatic macrophyte richness was mainly determined by shoreline length, total nutrient concentration (TN and TP) and non-nutrient related water quality (pH, alkalinity and conductivity; PAC), and Secchi depth also affected rhizophytes. The simultaneous autoregressive models of total and helophyte species richness accounted for ca. 70% of the total variation, whereas rhizophyte and pleustophyte richness models explained ca. 40% of the variation (III: Table 3). In addition, growth-form group richness was best explained by nutrient concentration and PAC, which accounted for over 40% of the total variation. Shoreline length and PAC often had strong positive correlation with macrophytes (III: Table 4), in accordance with previous studies (Rørslett 1991, Vestergaard & Sand-Jensen 2000). The relation between macrophytes and PAC was probably due to humic and acid waters, which also influence the form of carbon (e.g. Vestergaard & Sand-Jensen 2000, Borman et al. 2009), hence narrowing the regional species pool. The positive relationship between Secchi depth and rhizophytes was probably related to light availability-dependent habitat heterogeneity for submerged species (Chambers & Kalff 1985, Dennison et al. 1993).
Total nutrient concentration in water had various patterns with species richness: positive with total species richness and growth-form richness, u-shaped with helophytes, non-significant with rhizophytes and unimodal with pleustophytes. For different life-form groups, the non-positive response to nutrient concentration may be related to high humic content of the lakes. Nutrients can be bound to humic substances with high iron content functioning as a phosphorus (phosphate) storage (Wetzel 2001). Bound nutrients are not available for primary production lowering the overall concentration of usable inorganic nutrients. Thus, the total phosphorus and nitrogen content in water may not reflect the true availability of nutrients for rhizophytes and pleustophytes.

Macrophyte species turnover was explained by transect length and nutrient concentration (II: Table 5). Species turnover had a unimodal gradient with nutrient concentration, a result evident for all vegetation variables except for pleustophytes (II: Fig. 4). Basically, lakes with very low and high nutrient concentrations were similar to each other and lakes with intermediate concentrations were more dissimilar in terms of species composition. The model explanations differed substantially, ranging from 11 to 57% total variation. Rhizophyte and pleustophyte models accounted for the highest variation, whereas helophyte models performed the poorest.

The unimodal turnover gradient of aquatic macrophytes was contrary to numerous previous studies (Chase & Leibold 2002, Chase 2010, but see Chalcraft et al. 2004, Donohue et al. 2009). Unimodal species turnover was probably due to increased harshness of the environment (low and high nutrient concentrations), that can act as an environmental filter allowing only species tolerating harsh conditions to persist (Chase 2010). Filtering of species from the regional species pool may have resulted in a lower turnover rate at both ends of the nutrient concentration spectrum. At the high end, the decrease of macrophyte turnover was derived from six lakes with very high levels of nutrient concentrations in water. The proportion of agricultural areas was considerable within river basins of these lakes, probably resulting in significant diffuse pollution of lakes. Hence, studied macrophytes are poorly adapted to these eutrophic conditions, limiting the number of species capable of growing in the nutrient-rich lakes.

Environmental harshness did not decrease local, within-lake species richness, contrary to results of Chalcraft et al. (2008). Depending on the level of nutrient concentration, local species richness may increase, i.e. total number of species in the lake, but the regional species diversity may also decrease due to reduced species turnover within the lakes. Our results indicate that anthropogenic
eutrophication causes regional impoverishment of aquatic macrophyte species diversity.

5.4 Ecological classification of lakes, extent of land use and overall status (IV, V)

Impacted lakes showed a differentiated community structure from reference lakes, that was related to low nutrient concentrations and land use pressure, greater depth and positive climate originated latitudinal gradient of the reference lakes. Similarly, responses of key environmental variables to macrophyte metrics were parallel between impacted and reference lakes based on GAMs. The metrics separated impacted and reference lakes, but the performance varied with individual metric and lake type. The precision of the proportion of type-specific taxa (TT50) and Percent Model Affinity (PMA) was higher than that of Trophic Index (TI), whereas TT50 showed better sensitivity than other metrics (IV: Fig. 3). These patterns were less obvious in humic and shallow lake types, which dominate the studied water bodies, as impacted and reference lakes did not differ in ecological conditions (V) or the status of reference lakes was underestimated (IV). High water colour, acidity, decreased light penetration, reduced habitat availability and organic sediment accumulation all have significant effects on the biological communities of humic and shallow lakes (Spence 1982, Rintanen 1996, Lacoul & Freedman 2006). For example, several eutrophication sensitive taxa are submerged species, with an increasing occurrence probability in deeper waters. Moreover, we found that the influence of depth was not sufficiently included in lake typology, hampering bioassessments using TI (IV). Lake morphology-driven assessment biases have also been found in other taxa-based metrics (Mehner et al. 2007, Jyväsjärvi et al. 2009).

TT50 and PMA are based on the composition of type-specific reference communities and use the whole macrophyte species pool. By contrast, the predetermined indicator values of species in TI are equal across different lake types and the metric utilizes only part of the species pool (hydrophytes). The use of equal reference values across lake types may not account for the natural variability in macrophyte taxonomic composition of different boreal lake types adequately. In addition, disregarding helophytes may also decrease the performance of TI, because this growth form is ecologically important in boreal lake ecosystems (Toivonen & Huttunen 1995, Edvardsen & Økland 2006, Partanen et al. 2009, Sass et al. 2010). Several helophyte species, e.g. Carex
*diandra, Carex pseudocyperus, Glyceria maxima, Typha sp.* and *Iris pseudacorus*, responded to nutrients and land use in our study (IV); hence the role of helophytes cannot be overlooked solely on the basis of their marginal status (e.g. Penning *et al.* 2008a).

The land use of adjacent to the lake shoreline had a clearly higher effect on the ecological status and water quality compared to the anthropogenic pressure of the whole catchment (IV: Table 5). The scale dependency of land use effect may be related to the direct anthropogenic impact on the littoral zone, as well as indirectly to the effects of diffuse pollution on water quality. In long lake chains, nutrients bound to particles are sedimented along the system; thus only a portion of land use-derived diffuse pollution of the whole river basin reaches lakes lower in the chain (Kratz *et al.* 1997). In addition, land use adjacent to the lake shoreline can directly damage the littoral zone through nutrient run-offs and changes in lake morphology, which have immediate negative effects on aquatic macrophytes.

Several sources of spatially structured anthropogenic pressure can damage freshwater ecological quality (Sand-Jensen *et al.* 2000, Rasmussen & Anderson 2005, Partanen *et al.* 2009). Agricultural and urban area adjacent to the lake shoreline was mainly responsible for the harmful effects to aquatic macrophytes in our study (IV), in agreement with other studies (Akasaka *et al.* 2010, but see also Sass *et al.* 2010). However, different metrics did not indicate consistent scale dependency. TT50 and PMA responded more intensively to the land use adjacent to lake shoreline, whereas TI did not show a similar pattern. TI has been developed primarily to indicate the trophic status of water, which is why hydromorphological changes – a common stressor of the littoral zone - probably have little effect on TI.

Overall lake status can be defined using an integrated assessment of different biological quality elements or on the “One-out, All-out” (OoAo) principle, which defines the status according to the weakest element or parameter (Nøges *et al.* 2009). The integrated lake-specific status classifications based on the median status scores indicated good or high status in all the lakes, whereas overall status of lakes was moderate or less according to the OoAo approach (V: Appendix 1). Since anthropogenic stress in lakes seems only moderate based on found biological assemblages and water quality (e.g. Ilmavirta 1982, Rintanen 1996, Rask *et al.* 2000, Willen 2003), the OoAo approach appears to be unrealistic for use in the assessment of these lakes. Moreover, current problems in the classification system, such as the use of BQI in shallow humic lakes (Johnson 1998), insensitivity of some metrics in response to land use changes in this lake
type (Toivonen & Huttunen 1995, Tammi et al. 1999, Moe et al. 2008) and lack of reference conditions (Stelzer et al. 2005), suggest that the integrated classification principle appears to provide more stable and reliable results than the OoAo principle in small boreal humic lakes. The utilization of an integrated, generalized classification principle is well justified when natural variability in metric values is considerable (Søndergaard et al. 2005).
6 Study uncertainties

In general, the study of species-environment relationships leads to many challenges that can bias the ecological causality of observed patterns. Data can suffer from accuracy problems, especially if generalizations are made with limited original data. For example, GIS-derived ice variables were given less reliability than climate variables due to downscaling from scarce data (I). GIS and water quality data are also subjected to possible uncertainties during each preparation phase, from collection to processing and analyzing. In addition, the small number of observations hinders attempts to generalize the obtained results (V).

Empirical species data always faces species identification errors related to different field observers and used sampling methods. Species frequency and abundance estimations are subjectively defined and abundances are especially vulnerable to observer-related differences (Penning et al. 2008a). The main transect sampling method used is a relatively new field procedure applied from the 1990s onwards and especially early samplings may include errors (IV). Changes in taxonomy may also affect quality metrics sensitive to new species (TT50; IV, V). Lack of species-level identification can also weaken the study results to some extent (I, II), although many helophyte responses to explanatory variables were clear and ecologically rational. Nevertheless, relatively coarse accuracy of helophyte percentage cover data (25 m x 25 m) and unmeasured limnological variables probably accounted for most of the unexplained variation.

The ditch drainage intensity tool produced conflicting results when lake grain size quality metrics responded positively to forest ditching (IV), which also promoted helophytes in catchment grain size (I). The relationship between helophytes and ditch drainage can be ecologically plausible due to different grain sizes between the studies (see also Ecke 2008). In addition, the roughness of original stream data (streams and ditches combined over a 30-year period without exclusion of filled ditches etc.) may have decreased utilization of the data, and more detailed data is required in lake grain size studies.

Lack of temporal scale is a frequent problem found in empirical species and water quality data (Rusak et al. 1999, Harmel et al. 2006). However, aquatic macrophytes are less sensitive to short-term annual variations than other aquatic biological groups, and long-term mean values of water quality were used to minimize year-to-year variation.
Spatial models can provide strong indications of species distributions, but projections are subjected to several uncertainties. In addition to appropriate explanatory variables, multicollinearity and fitting problems, uncertainty can be derived from manual vs. automated model selection, sample size, species geographical attributes, used models, model selection criteria, identification and exclusion of outliers and overdispersion (Heikkinen et al. 2006). Automated model selection, such as GRASP, is a time-saving approach for large data sets. Disadvantage of this approach is that critical steps and alternative pathways in model building are not similarly transparent and controllable as in manual model selection. In the worst case, automated model selection can lead to biologically implausible models and selection of irrelevant variables.

In addition, suitable sample size, unbiased samples (temporally and geographically) and inclusion of absences reduce data deficiencies (Elith & Leathwick 2009, Heikkinen et al. 2009). Full range of environmental gradients, including complete future climate coverages, is needed for sustainable species distribution projections (Heikkinen et al. 2009). Species prevalence and level of contiguity may also have influence on model performance, often resulting to poorer modelling performance for widespread species compared to marginal species (Heikkinen et al. 2006). In general, different models produce unequal predictions, and generalized additive models and generalized linear models have generally been the most accurate (Elith et al. 2006, Marmion et al. 2008, Beaumont et al. 2009). Selection algorithms can also influence the model accuracy (Maggini et al. 2006, Parviainen et al. 2008).

Spatial autocorrelation can hamper causality between observed relationships, although autocorrelograms showed modest autocorrelation with model residuals in this study entity. Only Trophic Index suffered from substantial spatial autocorrelation (IV), which may partly explain the weaker performance of this metric in ecological assessment. Inclusion of spatial structure to models, as in simultaneous autoregression models, would better reveal how spatial autocorrelation possibly impairs the performance of TI. Gilbert & Bennett (2010) presented serious accusations against the variation partitioning method using trend surface analysis that may dilute the validity of some results (I).

Lack of reference lakes is a known problem in the development of ecological quality metrics (Stelzer et al. 2005), and a narrow set of reference conditions threatens metric results in some lake types (IV, V). Selection of reference lakes based on low a priori anthropogenic pressure in river basin and water quality is not necessarily an adequate procedure (V). In addition, validation of ecological
quality metrics is obscured if water body typology does not cover relevant natural variables. Moreover, studied metrics do not perform adequately in different water body types due to their inability to indicate anthropogenic pressure and/or separation of the pressure from natural variation.
7 Conclusions

This study examined aquatic macrophyte distributions in boreal catchments at broad extent and assessed ecological classification using aquatic vegetation in boreal lakes. The overall conclusions of this thesis are presented below, in accordance with the study aims and results (Table 3).

1. The spatial extent at which aquatic macrophytes are studied has a significant effect on the patterns found. This study confirmed several known relationships between aquatic macrophytes and environmental variables at broad spatial extent (climate related latitudinal and altitudinal gradient, effect of geology), but also discovered new ones (forestry drainage ditching intensity). In addition, patterns thought to be existing dominantly at finer spatial extent were also found at broad extent (land use, water quality, lake morphology). Spatial extent also had important implications for ecological assessment, as land use adjacent to the lake shoreline affected stronger ecological status metrics compared to the land use of whole catchment.

2. Grain size (catchment vs. lake) did not have a clear influence on aquatic macrophyte responses. In both grain sizes the relationships between aquatic macrophytes and environment were mainly parallel. Response to altitude was the only difference between the grain sizes.

3. Aquatic macrophyte distributions are affected by climate related latitudinal and altitudinal gradients at regional extent (I, II, III, IV). However, the influence of climate on macrophytes declined at finer regional extent (III), emphasising that the latitudinal climate gradient determines aquatic vegetation only at the broadest spatial extents. In addition, latitudinal climate gradient is fairly acknowledged in ecological assessment, as reference lakes appear to be responding to latitudinal gradient (IV).

4. Nutrient availability is the primary determinant of aquatic macrophytes in lake grain size at regional and landscape extent (III, IV, V). The pattern between macrophytes and nutrients varied from positive to non-significant depending on the form of dependent variable (richness, turnover, metric or life-form). Helophytes and metrics showed a strong positive (or inversely negative) response to nutrients (III, IV), whereas species turnover and pleustophytes had a unimodal relationship with nutrient availability at regional extent (III). In addition, species richness and metrics were positively or inversely negatively explained by pH, conductivity and alkalinity (III, IV).
This was probably related to high humic content, water acidity and the form of carbon in water.

5. Macrophyte species richness increased with increasing area showing thus a clear species-area relationship at regional extent. Lake surface area or shoreline length determined especially species richness and turnover in lake grain size (III), but also affected species distribution pattern in catchment and lake grain size (I, II, IV). In addition, macrophytes responded to lake depth-related variables (mean depth and Secchi depth; II, IV). These gradients are related to vertical (depth) and horizontal (area) habitat availability, where species occurrence and percentage cover increase with increasing habitat availability and heterogeneity.

6. Climate change alters aquatic macrophyte distributions at broad extent. Helophytes will widen occurrences northward under climate change and many species have already stretched their distribution ranges during the previous century. However, unimodal pattern between species turnover and nutrient concentration at broad extent (III) suggest that not all macrophyte species positively respond to warmer climate, but increased nutrient concentrations limit distribution changes.

7. Land use impacts aquatic macrophytes regardless of spatial scale. Macrophyte metrics and helophytes had a unimodal or negative gradient with agricultural areas, infrastructure areas and forestry ditch drainage in both catchment and lake grain size. Presumably, land use influences macrophytes directly through shore morphology and indirectly through water quality (I, II, IV).

8. Helophytes are an ecologically and structurally significant growth-form group of the littoral zone, and that alterations in helophyte distributions can indicate wider ecological deterioration of littoral zones and lakes in general (I, II, III, IV). The omission of helophytes from ecological assessment also seriously dilutes the performance of the assessment system (IV, V). In addition, reference values defined across lake types probably also resulted in weaker precision and sensitivity of the TI compared to other metrics (IV). Finally, uneven performance of ecological quality metrics suggests that an integrated approach in defining overall lake status is more justified compared to the One-out-All-out approach, which is based on the weakest assessment metric (V).
9) Lack of proximal explanatory variables did not prevented from discovering ecologically plausible responses between aquatic macrophytes and environment variables in catchment grain size (I, II). Moreover, physiologically relevant variables related to specific spatial scale can help to avoid statistical pitfalls such as multicollinearity and fitting problems, but good statistical fit does not necessarily indicate ecological causality, as found in article II.

Table 3. Potential primary determinants of aquatic macrophytes at regional extent with different response variables in varying grain size. A positive contribution of the explanatory variable is marked with “+”, a negative influence with “-” and an insignificant effect with “#”. Parentheses indicate that the effect was found only for certain life form groups or metrics, not for all studied response variables. NA represents non-availability of the variable for that particular study design. * indicates that urban development and arable land had scale-dependent patterns on ecological metrics compared between catchment and buffer zone land use.

<table>
<thead>
<tr>
<th>Land use</th>
<th>Catchment helophyte distribution</th>
<th>Lake macrophyte richness</th>
<th>Ecological metrics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Urban development</td>
<td>+</td>
<td>NA</td>
<td>-*</td>
</tr>
<tr>
<td>Arable land</td>
<td>+</td>
<td>NA</td>
<td>-*</td>
</tr>
<tr>
<td>Drainage ditch intensity</td>
<td>+</td>
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<td>+</td>
</tr>
<tr>
<td>Geomorphology</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude</td>
<td>+</td>
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<td>#</td>
</tr>
<tr>
<td>Lake cover/shoreline length</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Lake depth</td>
<td>NA</td>
<td>NA</td>
<td>(-)</td>
</tr>
<tr>
<td>Climate</td>
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<tr>
<td>Growing degree days/latitudinal pattern</td>
<td>+</td>
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<td>+</td>
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<tr>
<td>Nutrients</td>
<td>NA</td>
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<td>-</td>
</tr>
<tr>
<td>pH</td>
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<td>NA</td>
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<tr>
<td>Colour/water transparency</td>
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<td>(+)</td>
<td>-</td>
</tr>
<tr>
<td>Spatiality</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autocorrelation</td>
<td>#</td>
<td>#</td>
<td>(+/-)</td>
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</tbody>
</table>
8 Future study needs

This study showed that the distributions of helophytes will widen as a result of climate change, but that the influence of changing climate needs to be investigated for different macrophyte growth forms and species. Increased nutrient concentrations might hinder climate-driven distribution changes of macrophytes, but evidence of this phenomenon is scarce (Rosset et al. 2010). More comprehensive investigation of eutrophication-climate change relationship on aquatic macrophytes is required. Estimations of future macrophyte distributions are also urgently required at continental and global scales.

Moreover, many ecological phenomena, such as species range limits and niche conservatism, have important implications for species biodiversity and conservation in the changing environmental conditions. These theories need to be examined with aquatic macrophyte species, because previous studies rely heavily on terrestrial ecosystem and well-known aquatic groups (Bennett et al. 2010, Grenouillet et al. 2011). Distance decay relationships of aquatic macrophytes also require further evidence from boreal lakes (e.g. Soininen et al. 2007). All in all, understanding of macrophyte scale-related patterns is still incomplete and species-environment relationships in multiple scales must be evaluated within a region (e.g. Astorga et al., in press).

Land use-derived diffuse pollution seriously deteriorates aquatic vegetation, and more detailed estimations of land use stressors of aquatic ecosystems are needed. The influence of forest drainage ditch intensity was studied at regional extent, but the tool needs further development and more exact ditch data sets are required for reliable finer scale investigations. Moreover, information on underdrains used in sub-irrigation of fields would improve the knowledge of agricultural pressure on aquatic macrophytes at local and regional scale.

New insights into land use pressures would also benefit ecological assessment. Aquatic macrophyte-derived ecological quality metrics need further improvement and validation. Although large numbers of metrics were studied in the preliminary phase of development work, at least depth-related metrics require additional research, e.g. maximum colonization depth. Early vegetation samplings lacked depth information, which is why complementary reference and impacted lakes must be included in the national database. Better understanding of the relationship between the quality metrics and macrophyte diversity patterns would also benefit classification system. In addition, due to the poor reference lake situation, experimental investigation of predictive modelling, such as in a
RIVPAC-style application (e.g. Aquiar et al. 2011), is highly recommended in order to establish reference conditions.

Species turnover responded to nutrient concentration with a unimodal gradient, although the number of lakes in the nutrient-rich spectrum was rather limited. An additional set of eutrophic lakes could confirm the observed gradient.

Area showed a positive correlation with aquatic macrophytes, although the species-area relationship was verified with several area-derived variables. Preliminary results also indicated that shoreline length had a stronger influence on helophytes than surface area in catchment grain size at regional extent. A comprehensive study on species-area relationship using different area-related variables and all life-forms at multiple scales would provide more extensive knowledge of this relationship and improve understanding of species-area related hypothesis on aquatic macrophytes.
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Original articles


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 PATTERNS OF AQUATIC MACROPHYTES IN THE BOREAL REGION: IMPLICATIONS FOR SPATIAL SCALE ISSUES AND ECOLOGICAL ASSESSMENT

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