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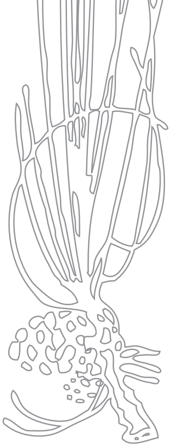
Marja Lindholm



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Contents

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Abstract

To comprehensively understand the impact of anthropogenic activities on biodiversity, we must understand how biodiversity has changed over time and its underlying processes. Regardless of a recent increase in scientific interest towards changes in community composition, i.e. beta diversity, these changes have not been studied comprehensively in lake environments in a spatio-temporal framework. In addition, although biotic homogenisation has gained much attention in recent decades, it is still unclear how this process acts at different levels of biodiversity through time.

The main aim of this thesis is to study temporal and spatial biodiversity patterns of vascular aquatic macrophyte communities in small boreal lakes during a period of 70 years. The focus is on beta diversity-environment relationships and different dimensions of biodiversity, with special attention to functional features. This thesis is based on three separate case studies that all have utilised temporal presence-absence data of vascular aquatic macrophytes from 27 to 28 lakes from the 1940s to the 2010s.

Vascular aquatic macrophyte communities showed only moderately different spatial beta diversity patterns in relation to human impact across decades. The patterns of different dimensions of spatial beta diversity diverged only slightly from each other. The temporal change in aquatic macrophyte communities at the lake level has been modest since the 1940s. Nevertheless, it seems that even relatively modest changes in the environment affect temporal gains and losses of species at the lake level. There were no signs of either biotic homogenisation or biotic differentiation (taxonomic, phylogenetic or functional), but the changes in the environment have affected functional community composition and changes in functional richness to some extent.

By using the spatial and temporal beta diversity perspective, this thesis highlights the fact that even though biotic homogenisation is a pervasive problem globally, it is not an unambiguous process acting similarly at all spatial and temporal scales or in different environments and different organism groups. There are likely five partly interdependent reasons why no signs of biotic homogenisation were detected in the study area during the 70-year study period: the modest changes in the environment from the 1940s to the 2010s, high ecological resilience of the lakes, information on species presence and absence was used instead of abundance data, biotic interactions and complex community-environment relationships together with stochastic processes and climate change.

The results highlight that relying on only one or two survey points in time can result in limited knowledge of the ecological phenomenon under study, and an exceptional year in terms of weather conditions can hinder detecting overall long-term trends in compositional changes, especially under ongoing climate change. The patterns detected in macrophyte beta diversity are likely to represent situations in the extensive boreal and glaciated areas of Eurasia and North America, with largely similar species pools in many regions. Therefore, lakes across the boreal region and areas that have faced glaciation and postglacial processes might be resistant against moderate levels of human pressure.

Keywords anthropogenic impacts, aquatic plants, beta diversity, biodiversity, biodiversity facets, lakes, land use, species phylogeny, species traits, temporal trends

List of original publications

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

I Lindholm, M., Alahuhta, J., Heino, J., & Toivonen, H. (2020). No biotic homogenisation across decades but consistent effects of landscape position and pH on macrophyte communities in boreal lakes. *Ecography*, 43, 294–305. https://doi.org/10.1111/ecog.04757

II Lindholm, M., Alahuhta, J., Heino, J. & Toivonen, H. (2021). Temporal beta diversity of lake plants is determined by concomitant changes in environmental factors across decades. *Journal of Ecology*, 109, 819–832. https://doi.org/10.1111/1365-2745.13508

III Lindholm, M., Alahuhta, J., Heino, J., Hjort, J., & Toivonen, H. (2020). Changes in the functional features of macrophyte communities and driving factors across a 70-year period. *Hydrobiologia*, 847, 3811–3827. https://doi.org/10.1007/s10750-019-04165-1

Original publications are available in the appendices of the printed version of this thesis. Publication I is reprinted under CC BY 3.0 Creative Commons licence. Publication II is reprinted with permission from John Wiley and Sons. Publication III is reprinted under CC BY 4.0 Creative Commons licence.

Author's contributions

In all three studies, the author of this thesis had the principal responsibility for data analyses and writing of the manuscript drafts. The author of this thesis gathered the land use and the phylogenetic data and the trait data in part and participated in the most recent aquatic macrophyte sampling. JHeino, the author of this thesis and JA designed the studies. JA provided the trait data in part. JHjort contributed to the statistical analysis in publication III. HT provided the aquatic macrophyte data from the 1940s to 2000s and contributed to interpretations. All authors contributed to writing of the manuscripts.

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As I was writing these acknowledgements, I received a pic from friends of their new-born baby. That great news was again a good a reminder of what really is important

in life. Even though this thesis project has sometimes been too big a part of my everyday life, these past years have been wonderful due to my dear son Väinö and my husband Tapio. Väinö was one year and two months old, when I started this PhD project. Without the counterbalance to the academic struggles and the joy and love that he has brought to my life, this thesis would not have been completed. And Tapio, your constant support has enabled this all. Thank you both! I love you.

To finish with, I have one message I would like you, the reader of these acknowledgements (as I know that you are probably not going to read this whole thesis), to take home. If you are in a position where you can decide the future of any biodiversity monitoring program, please decide in favour of continuing. Please, say yes to all funding applications that are meant to continue monitoring or to do a re-survey. Please, say no to all actions that threaten to end any long-term field sampling. Even though they are time-consuming and costly, these datasets they produce are priceless. Be the enabler, and the world (i.e. biodiversity change researchers, conservation managers and maybe some future PhD students) will thank you.

January 2021

Marja Lindholm

1 Introduction

"*Everything changes and nothing stands still*", stated the Greek philosopher Heraclitus (attrib.). This statement describes the dynamic character of Nature well. Nature is constantly changing. For example, biological communities are temporally dynamic as they gain and lose species and environments around them change over time (Bengtsson *et al.* 1997; Datry *et al.* 2016). However, in the era of the Anthropocene (Crutzen 2002), human actions have increased these changes by intensifying land use, habitat degradation, introducing new species to ecosystems and altering the climate, especially during the last century (Vitousek 1994; Chapin *et al.* 2000). Due to these actions, humans have seriously impacted ecosystems, leading to a globally declining trend of biodiversity (Barnosky *et al.* 2011; IPBES 2019). Unfortunately, anthropogenic impacts are only predicted to increase and intensify over time (Vitousek 1994; Chapin *et al.* 2000; Sala *et al.* 2000; Heino *et al.* 2020b).

Even though declining biodiversity at the global scale is a commonly accepted phenomenon, biodiversity change at smaller scales is not as straightforward as previously assumed (Hillebrand *et al.* 2018). At landscape and local levels, findings related to declining biodiversity have been controversial, as biodiversity at local sites (i.e. alpha diversity) has been shown to either decline, increase or remain stable over time (e.g. Vellend *et al.* 2013; Dornelas *et al.* 2014; Newbold *et al.* 2015). Despite these contradictory results related to alpha diversity, there is a growing body of evidence of considerable shifts in species composition found at a locality, i.e. community compositions at landscape and local scales through time (i.e. beta diversity; McGill *et al.* 2015). Specifically, studies have shown that even when alpha diversity is increasing or remains stable over time, community composition may be continuously changing (e.g. Larsen *et al.* 2018; Magurran *et al.* 2018; Blowes *et al.* 2019; Finderup Nielsen *et al.* 2019; Hendershot *et al.* 2020). This shows that studying only alpha diversity, usually through species-based metrics such as species richness, is not enough when studying biodiversity change. In this vein, Hillebrand *et al.* (2018) recommended focusing on compositional shifts when local biodiversity change is studied. Also, Gotelli *et al.* (2017) highlighted the need for community-level assessments of temporal trends in biodiversity. Moreover, it has been found that long-term trends are detected more reliably at community-level than population-level (Stuble *et al.* 2020).

When changes in biodiversity are studied, there is a need for temporal approaches. Using temporal ecological datasets, it is possible to investigate the actual changes that human actions have caused. For example, ecological datasets can provide knowledge about the initial state (i.e. baseline) of the ecosystem when studying ecological changes (e.g. Ot'ahel'ová *et al.* 2011). However, the focus in ecological sciences has been on spatial patterns of biodiversity at the expense of temporal ones (Magurran 2011). The reason for this and the main problem with temporal approaches is the lack of reliable and comprehensive spatio-temporal data. Long timeseries of replicated samplings covering several decades are quite rare in all organism groups (Magurran 2011), and monitoring data with frequent sampling usually do not cover long time periods (Dornelas *et al.* 2013). Palaeoecological studies that cover very long time periods differ in their methodology and approaches from studies that utilise historical field data (Sayer *et al.* 2010) as well as using chronosequences and metabarcoding methods. Recently, re-surveying historical datasets has gained increasing attention (Hédl *et al.* 2017), but the limitation with this approach is quite often that these datasets are usually based on only two or three time points, even though the temporal scale can be quite broad in ecological and historical contexts. There can also be temporal decay of quality of historical datasets; for example, there might be missing metadata (Tessarolo *et al.* 2017). Due to these issues, combinations of historical and contemporary datasets that cover several decades and several sampling points are very valuable when biodiversity change is studied, especially for less-investigated ecosystems, such as inland waters.

What is the value of studying changes in biodiversity or compositional shifts of biotic communities in the first place? The simple answer is that humankind is completely dependent on biodiversity in various ways at different temporal and spatial scales (Isbell *et al.* 2017), and understanding preceding changes in biodiversity and community compositions can help us forecast and prevent harmful changes. It can even be said that biodiversity is the foundation of human life, as biodiversity is linked to ecosystem functions and, through these, to ecosystem services, such as the production of renewable resources like food, human disease regulation and protection from natural hazards (Chapin *et al.* 2000; Díaz *et al.* 2006; Cardinale *et al.* 2012; Isbell *et al.* 2017). Biodiversity increases the stability of ecosystem functions through time and, on the other hand, the loss of biodiversity can decrease the ecosystem functioning, for example by impairing the capacity of communities to capture resources, produce biomass and recycle and decompose nutrients (Cardinale *et al.* 2012). Thus, biodiversity is linked to human health and quality of life. However, despite this, humans continue causing changes in biodiversity and altering ecosystem functioning and stability (IPBES 2019).

1.1 Temporal and spatial beta diversity

Biodiversity is a broad concept covering the variety of all living things and ecosystems. Therefore, biodiversity can be viewed from many different perspectives, as the previously mentioned alpha and beta diversities already showed. In recent years, ecological research has shifted focus from exploring only local (alpha diversity) or regional species richness (gamma diversity) patterns to understanding how species composition varies spatially and temporally (beta diversity, i.e. turnover) and which factors may generate such variation (Anderson *et al.* 2011). There are probably three main explanations for why beta diversity has gained increasing attention in recent years in biodiversity studies: 1) Beta diversity patterns can reveal more about ongoing biodiversity change than alpha diversity alone (e.g. Larsen *et al.* 2018; Magurran *et al.* 2018; Blowes *et al.* 2019; Finderup Nielsen *et al.* 2019; Fontana *et al.* 2020; Hendershot *et al.* 2020); 2) Spatial and temporal variation in species composition allows testing hypotheses about the processes that create and preserve biodiversity in ecosystems (Legendre & De Cáceres 2013); 3) Contemporary and future threats, as well as solutions, in the conservation of natural environments occur at several spatial scales (Socolar *et al.* 2016). While many of these threats act at large spatial scales, they affect biota at more local scales. Therefore, beta diversity patterns can provide a useful tool for understanding these multidimensional issues (Socolar *et al.* 2016). However, despite its popularity, beta diversity has not gained an established definition or reached a consensus on how it should be studied and measured in the fields of ecology and biogeography. This manifests itself in a variety of different practices and indices (Anderson *et al.* 2011; Legendre & Condit 2019; Magurran *et al.* 2019) and even nomenclature.

In its simplified form, beta diversity refers to variation in community composition across space or time (Whittaker 1972; Anderson *et al.* 2011). Anderson *et al.* (2011) distinguished two kinds of beta diversity: non-directional variation and directional turnover. Non-directional variation measures the differences in community structure among sample units within a given spatial area, while directional turnover measures the change in community composition along a specific spatial, temporal or environmental gradient (Anderson *et al.* 2011). However, as turnover can also refer to one of the widely used partitioning components of beta diversity introduced by Baselga (2010), only the term beta diversity will be used in the following when compositional change both in space and time are considered, unless otherwise stated.

Basically, beta diversity can be represented either as a spatial or temporal point of view (Fig. 1) or a combination of both. Spatial beta diversity signifies the difference in community composition across sites, while the change in community composition over time can be called temporal beta diversity, i.e. temporal turnover (Legendre & Gauthier 2014; Shimadzu *et al.* 2015). At landscape and local spatial scales and at intermediate timescales, community composition changes are a result of processes such as local colonisation (i.e. gains of species) and local extinction (i.e. losses of species), i.e. changes in species occupancy (Sax & Gaines 2008). These can be driven by dispersal mechanisms across sites (Tilman 1994) or by gradual or abrupt changes in environmental conditions, including anthropogenic impacts such as land use changes (Legendre 2019). Many studies have focused on spatial beta diversity at one time point, while temporal beta diversity (e.g. Cook *et al.* 2018) and spatial beta diversity through time have gained less attention (Winegardner *et al.* 2017; Larsen *et al.* 2018; Wengrat *et al.* 2018).

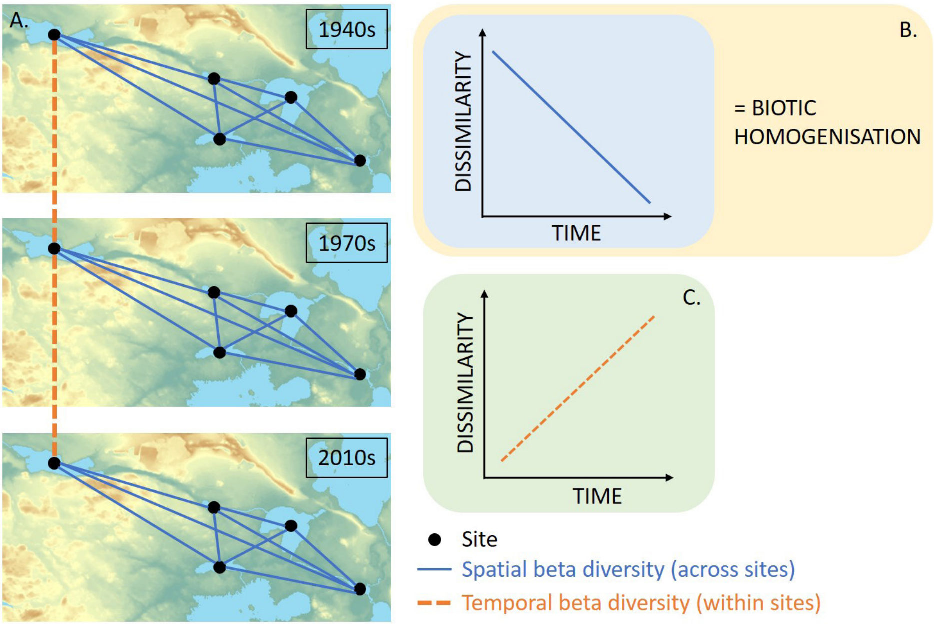

Figure 1. Schematic diagrams of spatial and temporal beta diversity. A) Spatial beta diversity is the difference in diversity across sites at one time point, while temporal beta diversity is the difference in diversity between time points. B) It has been identified that human impact increases similarity across sites over time (i.e. spatial beta diversity decreases) (McGill *et al.* 2015). This process is called biotic homogenisation (Olden & Rooney 2006). C) It has been also identified that human impact decreases similarity within sites over time (i.e. temporal beta diversity increases) (McGill *et al.* 2015).

McGill *et al.* (2015) identified that spatial beta diversity in the Anthropocene has been showing a decreasing trend on all spatial scales due to human impact, and an increasing trend in temporal beta diversity at local scales (Fig. 1). However, they also noted that temporal patterns in spatial beta diversity have been highly context-dependent, and local temporal beta diversity is not measured empirically often enough to clearly show definite trends (McGill *et al.* 2015). Despite that notion, there is still a growing body of evidence indicating that variation in temporal beta diversity is unexpectedly high at local scales (Dornelas *et al.* 2014; McGill *et al.* 2015), a phenomenon which subsequent studies have also confirmed (Gotelli *et al.* 2017; Blowes *et al.* 2019). As both temporal and spatial beta diversity trends are unclear and there is no solid consensus on direction and intensity of the trends, these issues should be studied more with different organism groups and in various environments.

Spatial beta diversity can be decomposed into two different components that can provide further insights into spatial variation in community composition (Legendre 2014). There are basically two different approaches to be used in the context of this decomposition: the method by Podani and Schmera (2011) and Carvalho *et al.* (2012) and the method by Baselga (2010). In the former method, total beta diversity is decomposed into replacement and richness difference components (Podani & Schmera 2011; Carvalho *et al.* 2012), while in the latter method, it is decomposed into turnover and nestedness components (Baselga 2010). One community may include a larger number of species than another, which is called richness difference. Nestedness denotes if the species at a site are a strict subset of the species at a richer site and, therefore, it is only a specific type of richness difference (Legendre 2014; Brittain *et al.* 2020). There has been a lot of discussion on which method is the better one, and quite recently Schmera *et al.* (2020) recommended not using Baselga's (2010) turnover component (which Schmera *et al.* (2020) called replacement component).

One outcome of decreasing spatial beta diversity due to human actions is called biotic homogenisation (Fig. 1). It is one of the major negative consequences of anthropogenic impacts on biodiversity through time. In the biotic homogenisation process, ecosystems lose their biological uniqueness and genetic, taxonomic and functional similarity between communities increases (McKinney & Lockwood 1999; Olden & Rooney 2006). Biotic homogenisation was first defined by McKinney and Lockwood (1999) as "the replacement of local biotas with non-indigenous species". Afterwards, Olden and Rooney (2006) emphasised the multidimensional and multifaceted nature of this process occurring between two or more locations over a specified time interval, due to which ecosystems lose their biological uniqueness in space. Biotic homogenisation can be the result of, for example, the removal of natural dispersal barriers (McKinney & Lockwood 1999), promotion of habitat generalists (Devictor *et al.* 2008) or reductions of the length of natural environmental gradients (Groffman *et al.* 2014) due to anthropogenic land use. The opposite process to biotic homogenisation is called biotic differentiation. In that process, in accordance with its name, similarity among communities decreases (Olden & Poff 2003).

It has been argued that we are heading towards an era called the 'Homogocene', as many studies have shown that human actions are causing increasing biotic homogenisation in different environments (Olden *et al.* 2018). In addition, as there are several studies showing that homogenisation is acting particularly strongly in aquatic environments (e.g. Rahel 2002; Donohue *et al.* 2009; Petsch 2016; Padial *et al.* 2020), the term 'Aquatic Homogocene' has also been introduced. Studies concerning aquatic homogenisation have focused mainly on fish (e.g. Villéger *et al.* 2014; Castaño-Sánchez *et al.* 2018; Kuczynski *et al.* 2018; Richardson *et al.* 2018; Budnick *et al.* 2019; Cazelles *et al.* 2019) and macroinvertebrates (e.g. Donohue *et al.* 2009; Cook *et al.* 2018; Bertoncin *et al.* 2019; Budnick *et al.* 2019; Zhang *et al.* 2019), while other organism groups, such as aquatic macrophytes, have received only little attention.

1.2 Taxonomic, phylogenetic and functional dimensions of biodiversity

Traditionally, biodiversity research has been conducted by using only taxonomic approaches, i.e. concentrating on the species level, which does not take into account how species are related to each other nor does it consider species' ecological differences. Therefore, analyses focusing only on taxonomic data are inherently limited (McGill *et al.* 2006), and recent studies have shown that using the taxonomic, phylogenetic and functional dimensions (i.e. facets) of beta diversity together can give better insights into biodiversity patterns than the taxonomic approach alone (Heino & Tolonen 2017; Teichert *et al.* 2018; Perez Rocha *et al.* 2019). The use of phylogenetic and functional approaches can provide additional insights on ecological and historical processes that are behind the biodiversity patterns (Webb *et al.* 2002; Meynard *et al.* 2011). As phylogenetic and functional diversities can contribute to the resilience of ecosystems by enhancing the ability to generate ecological solutions in response to environmental changes (Yachi & Loreau 1999), these aspects should be studied together with taxonomic aspects in a rapidly changing world (Devictor *et al.* 2010). The use of different biodiversity dimensions (i.e. taxonomic, phylogenetic and functional) can also reveal different aspects of biotic homogenisation and different mechanisms associated with these aspects of biodiversity (Alahuhta *et al.* 2019). This emphasises the fact that these different dimensions should be explored simultaneously, even though most studies concerning biotic homogenisation have also focused only on taxonomic distinctiveness (e.g. Budnick *et al.* 2019), which refers to loss or replacement of native species (Olden *et al.* 2004).

Phylogenetic beta diversity measures the phylogenetic distance between communities (Graham & Fine 2008). Anthropogenically-driven loss of phylogenetic beta diversity, i.e. phylogenetic homogenisation, can occur independently from taxonomic and functional homogenisation (Graham & Fine 2008). In the phylogenetic homogenisation process, endemic or rare species are lost, resulting in a decrease of among-species genetic differentiation (e.g. Winter *et al.* 2009; Harrison *et al.* 2018; Liang *et al.* 2019). Loss of evolutionary diversity is a primary conservation concern (Vamosi & Wilson 2008; Frishkoff *et al.* 2014). This can be studied through species phylogenetic relationships, e.g. using phylogenetic trees that take into account the evolutionary history of species. The idea behind this is that the more time has passed since two species shared a common ancestor, the higher the probability that they are also ecologically diverged (Schulze *et al.* 2019).

Functional diversity can be seen as a subset of biodiversity driving the functioning of ecosystems and their responses (Legras *et al.* 2018). In its simplest form, it refers to the variation of species' morphological, physiological, and ecological traits between organisms (Petchey & Gaston 2006; Carmona *et al.* 2016). More specifically, it refers to the 'distribution of the species and abundance of a community in niche space' that can be divided into three major components: functional richness, functional evenness and functional divergence (Mason *et al.* 2005). In the functional homogenisation process, specialised species or entire functional groups are lost (Olden *et al.* 2004). This is directly linked to ecosystem functions and indirectly to ecosystem services through the loss of functional diversity (Clavel *et al.* 2011). The maintenance of multiple functions in an area thus needs multiple species with a variety of traits. Functional traits (e.g. specific leaf area) are any morphological, physiological or phenological feature that can impact an organism's fitness indirectly via their effect on growth, reproduction and survival (Violle *et al.* 2007). They reflect the processes of evolution as well as abiotic and biotic environmental constrains and determine how primary producers respond to environmental factors and influence other trophic levels and ecosystem functions and services (Díaz *et al.* 2004; Garnier & Navas 2012). Thus, changes in the environment may be reflected in traits and traits may respond differently to, for example, intensifying temperatures than the species themselves (Lamanna *et al.* 2014; Lenoir & Svenning 2015). Therefore, a trait-based approach may allow better generalisations to be made in understanding and predicting ecosystem functioning than species-based approaches (Lavorel & Garnier 2002; Swenson 2013). The importance of functional traits and niche processes has been acknowledged for a relatively long time (e.g. McGill *et al.* 2006), but they are not studied much in the temporal context, at least in freshwater environments (e.g. Sand-Jensen *et al.* 2018).

1.3 Lake environments under global change

Fresh waters hold a very large proportion of total global biodiversity in relation to their small areal extent (Strayer & Dudgeon 2010). Fresh waters also provide many essential ecosystem services for humans such as drinking water and food. As other ecosystems, also freshwater ecosystems are threatened by numerous, simultaneously operating anthropogenic stressors (Ormerod *et al.* 2010; Birk *et al.* 2020). Changes in freshwater ecosystems globally, and especially in lake environments, are mainly due to biotic exchange, anthropogenic land use (hereafter, land use) and climate change (Sala *et al.* 2000; Dudgeon *et al.* 2006; Reid *et al.* 2019; Smol 2019). Scientists have recently warned that lake environments are facing a severe biodiversity crisis and are thus losing much of their biodiversity (Albert *et al.* 2020). This degradation of biodiversity is more rapid in fresh waters than in terrestrial or marine ecosystems (WWF 2016; Albert *et al.* 2020). Therefore, to be able to prevent further loss, it is important to advance our understanding of temporal and spatial shifts in communities in lake environments.

Lakes vary in the degree of connectedness to other ecosystems, and the spatial organisation of lake districts is largely a result of an area's geomorphological history (Riera *et al.* 2000). Heino *et al.* (2020) emphasised that lakes are not isolated from other freshwater ecosystems or their surrounding terrestrial environments, thereby stating that lakes should be generally viewed as 'meta-systems'. One way to take these connections into account is via the lake's position in the landscape. Position in the landscape can reflect both the hydrologic connectivity and physical features of a lake and the landscape, which are strongly related to lake water chemistry (Johnson *et al.* 1997; Martin & Soranno 2006). Many characteristics of lake environments follow a pattern with the lake landscape position (Kratz *et al.* 1997; Riera *et al.* 2000). Thus, the lakes in one lake district can be very different regarding the abiotic characteristics and the biota. For example, the lakes lower in the landscape are typically larger, are more connected to the drainage system, and tend to have higher pH and ionic concentrations than the headwater lakes (Heino & Muotka 2006; Martin & Soranno 2006). Additionally, species richness is generally higher in lakes lower in the landscape (Lewis & Magnuson 2000). Moreover, despite the changes occurring in lake environments, lake landscape position can remain stagnant through time and rarely changes within short time periods. Therefore, it is possible that lake landscape position can override, for example, changes in land use through time when biodiversity of lake biota is considered.

Lakes are generally more stable environments with less temporal variation in water chemistry and smaller water level fluctuations compared to lotic environments. However, there is strong research-based evidence that land use has an effect on the water chemistry of lake environments (e.g. Carpenter *et al.* 1998; Taranu & Gregory-Eaves 2008; Jamoneau *et al.* 2020), and therefore indirect influence on the biodiversity of lake biota (e.g. Akasaka *et al.* 2010). Land use can also cause habitat loss, fragmentation and physicochemical stress, which all can influence biodiversity (Budnick *et al.* 2019). Anthropogenic activity and land use changes have led to nutrient enrichment, i.e. cultural eutrophication in many freshwater lakes across the world (Smith *et al.* 1999). Further, a recent study revealed that eutrophication is the most relevant stressor affecting several lakes in Europe (Birk *et al.* 2020). The main reason for this is the increased intensity of agricultural production and fertilisation (Durand *et al.* 2011). Fertilization is especially related to nitrogen-phosphorus ratios (Arbuckle & Downing 2001) and total phosphorus (Taranu & Gregory-Eaves 2008; Ecke 2009). In Europe in general, the amount of used fertilisers has increased notably from the 1940s to the 1990s, after which it has slightly decreased (Van Grinsven *et al.* 2015). However, fertilisers can be stored in the ground and ground water for decades, still negatively affecting water quality after the area of agricultural land has decreased (e.g. Stålnacke *et al.* 2003; Hart *et al.* 2004).

In addition to agriculture, urbanization can be a substantial source of nutrients, pollutants and other substances in water (e.g. Hatt *et al.* 2004; Paul & Meyer 2008). Chemical effects of urbanization depend on the type and extent of urbanization (residential vs. commercial/industrial), presence of wastewater treatment plants, effluent and/or combined sewer overflows and the extent of stormwater drainage (Paul & Meyer 2008). However, Ecke (2009) found that drainage ditching rather than land use itself could affect water quality. Forest and peatland drainage for agricultural use and forestry affect water chemistry through the leaching of nutrients from soil to water causing eutrophication in agricultural and urban areas. In peatland areas, ditching increases the humus content of water and thus influences water transparency (Prévost *et al.* 1999; Holden *et al.* 2004; Peltomaa 2007; Ecke 2009). In addition, artificial ditches can act as dispersal corridors for aquatic species (Soomers *et al.* 2010; 2013). As water chemistry is one of the key factors that affect lake biota, it is important to study historical changes in land use and their relationships to lake communities.

1.4 Aquatic macrophytes

A recent global assessment stated that aquatic vegetation in lake environments is facing accelerating losses in terms of area or cover (Zhang *et al.* 2017). Freshwater macrophytes[1] are globally threatened for the same reasons as lake environments generally, including eutrophication, land use changes, algal blooms, aquaculture cultivation and global climate change (Zhang *et al.* 2017). This is concerning, as aquatic macrophytes have essential functional and structural roles in lakes. They are one of the key primary producers, as they are an important food source for a variety of organisms, such as

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[1] Aquatic macrophytes refer to macroscopic forms of aquatic photosynthetic organisms, which live and grow permanently or seasonally in water environments (Chambers *et al.* 2008). Macrophytes include a diverse group of angiosperms, ferns, mosses, liverworts and some freshwater macroalgae submerged below, floating on or growing up through the water surface (Chambers *et al.* 2008). In this thesis, the focus is on vascular aquatic macrophytes.

amphibians, birds, fish, invertebrates and mammals (Carpenter & Lodge 1986; Lodge 1991; Lodge *et al.* 1998; Bakker *et al.* 2016). They generate three-dimensional habitat and shelter structures for other lake-dwelling organisms and therefore create spatial structure in lakes (Gasith & Hoyer 1998; Dibble *et al.* 2006; Padial *et al.* 2009; Choi *et al.* 2014). They are also a part of cycles of substances, like nutrients and sediments (Carpenter & Lodge 1986; Chambers & Prepas 1994; Jeppesen *et al.* 1998; Sand-Jensen 1998; Vermaat *et al.* 2000; Marion & Paillisson 2003), and they can maintain water transparency by absorbing nutrients and sediment from the water column, and reduce phytoplankton biomass (Scheffer 1999). In addition, aquatic macrophytes can be used as valid surrogates for wider biodiversity in lake environments (Law *et al.* 2019), and they are one of the biological quality elements when assessing the ecological status of surface waters, for example, in the European Water Framework Directive (European Commission 2000). Due to these reasons, aquatic macrophytes constitute a good and important model group for examining long-term changes in lake communities and ecosystems. Moreover, as there are challenges in conservation and management of both aquatic macrophytes and their ecosystems (O'Hare *et al.* 2018), it is crucial to understand how aquatic macrophyte communities have changed due to anthropogenic impacts to be able to predict and prevent harmful changes in the future.

Lake macrophyte diversity and distribution across the landscape are influenced by variations of several environmental factors acting at different spatial and temporal scales (Lacoul & Freedman 2006). Climatic and hydrologic conditions, geomorphology and catchment properties all affect abiotic factors such as light, temperature, water nutrient content, substrate characteristics, water movements and different kinds of disturbances. All these interact spatially and temporally to varying degrees (Lacoul & Freedman 2006) and have a strong influence on macrophyte species' occurrence, life-history traits and community dynamics (Lacoul & Freedman 2006; Bornette & Puijalon 2011). Additionally, biological interactions (Lacoul & Freedman 2006) and historical factors (Jamoneau *et al.* 2020) can modify species communities via several mechanisms. Moreover, anthropogenic actions, such as disturbance and pollution, have a strong influence on macrophyte communities both directly and indirectly (Zhang *et al.* 2017). As land use in the lake watershed has an effect on water chemistry, and especially on nutrient loading, it has been shown to have an indirect influence on lake macrophyte diversity (e.g. Jennings *et al.* 2003; Cheruvelil & Soranno 2008; Papastergiadou *et al.* 2008; Akasaka *et al.* 2010; Ot'ahel'ová *et al.* 2011; Alahuhta *et al.* 2014; Joniak *et al.* 2017; Sun *et al.* 2018; 2019). Land use has been shown to be related to variation in macrophyte community composition (e.g. Alahuhta *et al.* 2012), species richness (e.g. Azzella *et al.* 2014) and abundance (e.g. Sass *et al.* 2010). However, the relationships between land use changes and macrophyte beta diversity are understudied in a temporal context (e.g. Zhang *et al.* 2018). Also, historical land use has been shown to influence taxonomic richness and community composition of macrophytes (Jamoneau *et al.* 2020). Thus, it is important to study the temporal dynamics of macrophytes in relation to land use changes.

As human actions have had a strong impact especially on fresh waters (Sala *et al.* 2000; Dudgeon *et al.* 2006; Vörösmarty *et al.* 2010; Woodward *et al.* 2010; Vilmi *et al.* 2017), temporal aquatic macrophyte datasets can help to investigate the changes that anthropogenic actions have caused. However, the problem with temporal aquatic macrophyte research is also the lack of reliable and comprehensive spatio-temporal data. Thus, there are few long-term studies of aquatic macrophytes (e.g. Sand-Jensen *et al.* 2000; 2008; 2018; Davidson *et al.* 2005; Azzella *et al.* 2013; Murphy *et al.* 2018), and only a handful of studies have been specifically concentrating on beta diversity or biotic homogenisation and differentiation (Baastrup-Spohr *et al.* 2017; Salgado *et al.* 2018; Zhang *et al.* 2018). These studies have used different approaches and have examined a variety of diversity measurements and are based on historical datasets and re-surveying the same sites (e.g. Baastrup-Spohr *et al.* 2017; Zhang *et al.* 2018) or palaeoecological methods (e.g. Salgado *et al.* 2018). Other-than-temporal studies have also found contradicting results, showing either biotic homogenisation or no signs of it (e.g. Lougheed *et al.* 2008; Johnson & Angeler 2014; Elo *et al.* 2018). These studies have also been conducted in different freshwater environments and using distinct analytical frameworks with several beta diversity indices.

Aquatic macrophyte species differ widely in terms of anatomy, life-history traits, physiology and ability to tolerate stressors (Lacoul & Freedman 2006). Traditionally, when these functional dimensions of biodiversity have been studied in aquatic macrophyte research, various types of categorical divisions derived mainly from life and growth forms have been used (e.g. Vermaat *et al.* 2000). But more recently, species traits have been used to an increasing extent in macrophyte studies (Dalla Vecchia *et al.* 2020). However, investigations have not been done extensively in a spatial and temporal framework and considering the whole aquatic macrophyte community. Only recently has there been an increase in studies using functional traits in a temporal context of community change (e.g. Sand-Jensen *et al.* 2018). Functional and phylogenetic homogenisation and differentiation of aquatic macrophyte communities have received even less attention than taxonomic ones (Zhang *et al.* 2018; Kim & Nishihiro 2020). Furthermore, functional changes in aquatic macrophyte communities at the species level are also understudied (see however Fu *et al.* 2020). Fu *et al.* (2020) tested, by using an individual trait variance partitioning framework, whether within-lake and among-lake filtering effects on submersed macrophytes occurred at individual or species level.

2 Aims of the thesis

Regardless of the recent increase in scientific interest towards beta diversity, it has not been studied comprehensively in lake environments and in a spatio-temporal framework. In addition, although biotic homogenisation has gained much attention in recent decades (e.g. Castaño-Sánchez *et al.* 2018; Richardson *et al.* 2018), it is still unclear how this process is acting in different dimensions of biodiversity through time. This is especially the case in the lake-rich boreal region which has been under the last glaciation, covers large areas across the Northern Hemisphere and is only moderately impacted by human activities compared to many other regions and ecosystems across the world. Also, functional similarity and uniqueness have only recently received more attention (e.g. Gámez-Virués *et al.* 2015; Liang *et al.* 2019), and the role of beta diversity in ecosystem functioning is still not clear (Mori *et al.* 2018). In this thesis, I will seek new insights on these issues.

In this thesis, my main aim is to study temporal and spatial biodiversity patterns of vascular aquatic macrophyte communities in small boreal lakes during a period of 70 years. The focus is on beta diversity-environment relationships and different dimensions of biodiversity with special attention to functional features (Fig. 2). This thesis is based on three studies, all of which have utilised temporal presence-absence data of vascular aquatic macrophytes from 27 to 28 lakes from the 1940s to the 2010s. Through these studies, I am seeking answers to the following four research questions and testing nine hypotheses:

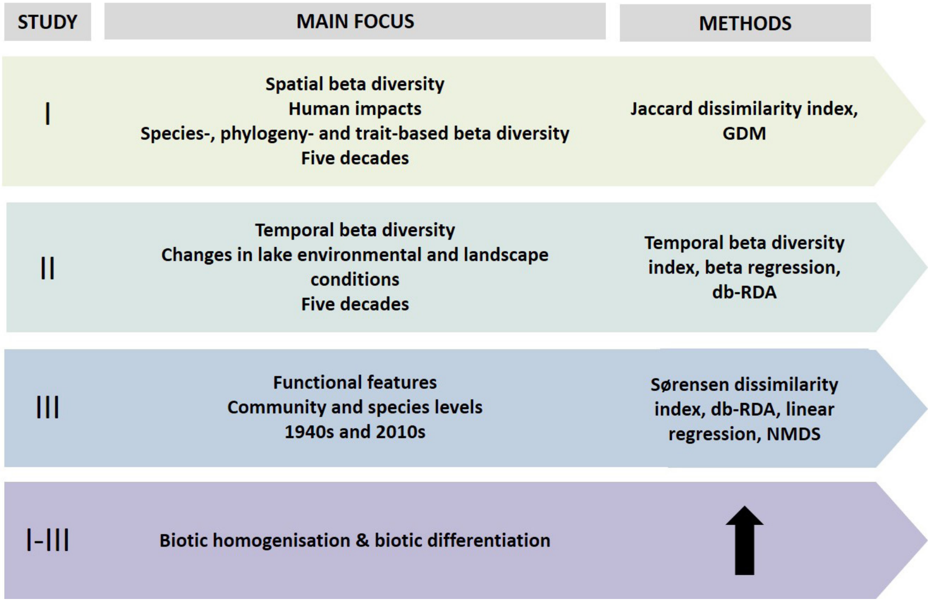
Q1 Do vascular aquatic macrophyte communities show different patterns in *spatial* beta diversity (i.e. across sites) in relation to human impacts between decades or between species-, phylogeny- and trait-based beta diversity? (Study I; hypotheses H1–H3)

Q2 Do vascular aquatic macrophyte communities show different patterns in *temporal* beta diversity (i.e. within sites) in relation to concomitant changes in lake environmental and landscape conditions across decades? (Study II; hypotheses H3, H4)

Q3 Have functional features of vascular aquatic macrophytes changed at the community and species levels after a period of 70 years? (Study III; hypotheses H5–H7)

Q4 Has there been biotic homogenisation or differentiation in vascular macrophyte communities from the 1940s to the 2010s due to anthropogenic impacts? (Studies I–III; hypotheses H8, H9)

First, I hypothesised that the patterns in spatial beta diversity are different in relation to human impacts in different decades (H1) (Petsch 2016). Second, the patterns in spatial beta diversity are different for different dimensions of beta diversity (H2) (e.g. Heino & Tolonen 2017). Third, the strong landscape position gradient might overcome the effects of human land use change (e.g. Alexander *et al.* 2008) in driving both spatial and temporal beta diversity patterns (H3). Fourth, there has



STUDY	MAIN FOCUS	METHODS
I	Spatial beta diversity Human impacts Species-, phylogeny- and trait-based beta diversity Five decades	Jaccard dissimilarity index, GDM
II	Temporal beta diversity Changes in lake environmental and landscape conditions Five decades	Temporal beta diversity index, beta regression, db-RDA
III	Functional features Community and species levels 1940s and 2010s	Sørensen dissimilarity index, db-RDA, linear regression, NMDS
I-III	Biotic homogenisation & biotic differentiation	⬆

Figure 2. Relationship between the studies, the focus and the used methods. GDM = Generalised dissimilarity modelling, db-RDA = Distance-based redundancy analysis, NMDS = Non-metric multidimensional scaling.

been variation in temporal losses and gains of species across the landscape (H4) (e.g. Winegardner *et al.* 2017). I based my fourth hypothesis on the assumption of Socolar *et al.* (2016) that in the areas where urbanization has prevailed through time, the dominant process would be the loss of species, and in areas where agricultural field area has decreased, the dominant process would be the gain of species. Fifth, different environmental variables explain functional community composition between decades (H5). Sixth, changes in functional richness are linked to changes in the environment across decades (H6) (e.g. Zhang *et al.* 2018). Seventh, declining species (i.e. 'losers') have different functional traits than increasing (i.e. 'winners') or stable species (H7) (e.g. Steffen *et al.* 2013).

It has been recognised that human impact generally is causing a temporally decreasing trend in spatial beta diversity and an increasing trend in temporal beta diversity at local scales (Fig. 1; McGill *et al.* 2015). As decreasing spatial beta diversity can reflect biotic homogenisation, I also have a hypothesis related to this issue: The aquatic macrophyte communities have become more similar among lakes (biotic homogenisation), i.e. spatial beta diversity decreases due to human impact over time (H8). My last hypothesis also follows McGill *et al.* (2015): Temporal beta diversity in each lake will show increasing degrees of change through time (H9).

3 Study area

Twenty-seven lakes were studied in publications I and II, and 28 lakes were studied in publication III, all of which are located in the river Kokemäenjoki drainage basin in southern Finland (Fig. 3). This area belongs to the Northern Baltic Drainages freshwater ecoregion (Abell *et al.* 2008). The study lakes are near the city of Tampere, in the area between the two large lakes Roine and Pyhäjärvi. The study area belongs to the southern boreal climate zone (Ahti *et al.* 1968) and had a mean annual temperature of 4.4 °C and a mean annual precipitation of 598 mm during the normal period 1981–2010 (Pirinen *et al.* 2012). The winter ice cover period lasted approximately 150–170 days during the period 1961–2000 (Korhonen 2005), and the length of the thermal growing season (>5 ºC) was approximately 175–185 days during the period 1981–2010 (Finnish Meteorological Institute 2019). From the 1940s onward, the mean annual temperature in the study area has increased approximately over 1 ºC (Fig. 4). The underlying bedrock consists mainly of gneiss and diorites, and the soil mainly of sand moraine and peat formations, and at lower elevations in the study area, of clay (Geological Survey of Finland 2018).

Boreal environments have experienced glacial and postglacial processes, and these have resulted in a diverse, small-scale geomorphological landscape with a large number of small lakes and ponds (Seppälä 2005). Many of the study lakes are situated in small chains of lakes and streams and have brown, humic water. Both of these features are typical to small Finnish lakes. Naturally, more eutrophic lakes are located at lower elevations and are mainly surrounded by agricultural land or settlements (Fig. 5). Smaller and more oligotrophic lakes at higher elevations in the landscape are less affected by human activity and are mainly influenced by peatland drainage and use of summer cottages (Fig. 5; Toivonen & Huttunen, 1995). This is mainly due to glacial and postglacial processes – fine-grained sediments with nutrients have been washed along the elevational gradient in the landscape (Seppälä 2005). Therefore, changes in lake environmental conditions occur along a relatively low elevation gradient (77 to 131 m a.s.l.) in the study area. Key characteristics of these lakes are given in Table 2.

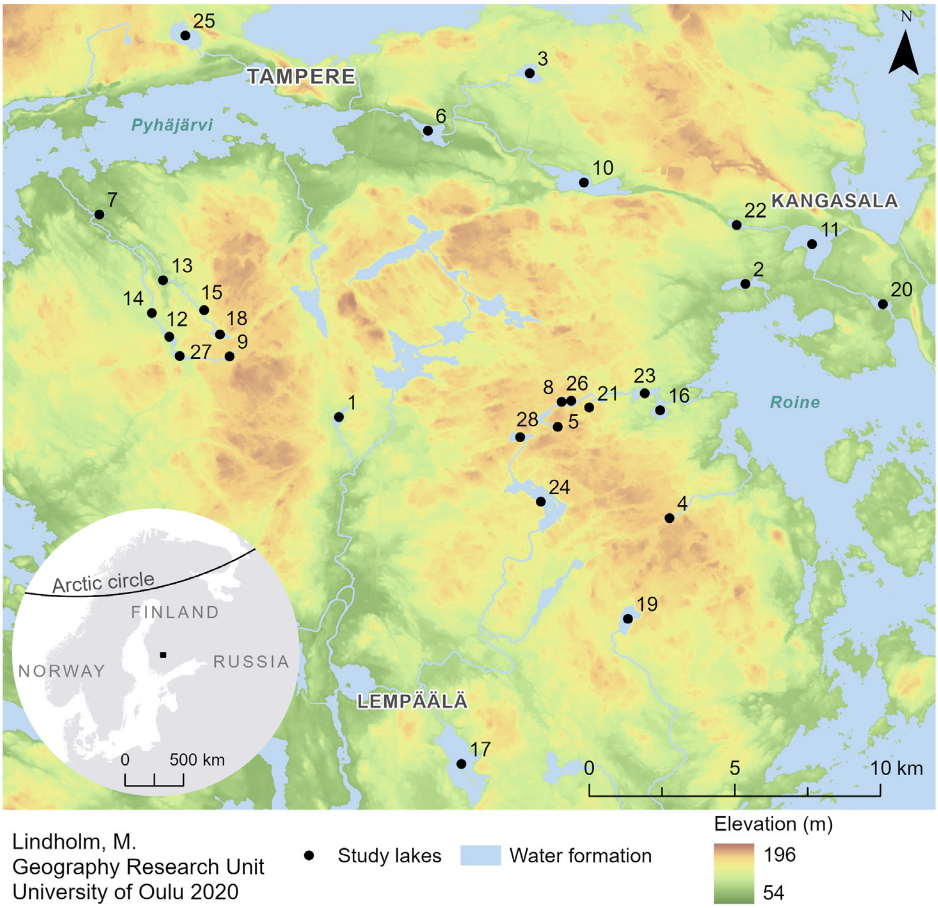


Figure 3. Map showing the location of the study area and the lakes (N=28) studied. Lake number 9 was not included in studies I and II (Water formations: Finnish Environment institute 2014; Elevation model: National Land Survey of Finland 2015).

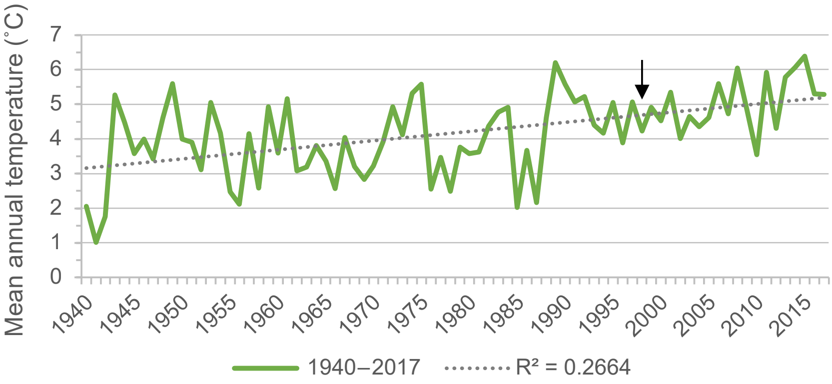


Figure 4. Mean annual temperature between 1940 and 2017. The observation station is located in the northern part of the study area, near the city of Tampere. The arrow in the diagram represents the year 1998 when the observation station (Tampere, Härmälä) was moved slightly, but the estimated difference is below 0.1 °C (Finnish Meteorological Institute 2020a).

Figure 5. The study lakes are under different anthropogenic pressures: A) urban built area, B) summer cottages, C) agriculture (crop production) and D) agriculture (pasture). E) Lakes at higher elevations are surrounded mainly by forests and peatland. Pictures: Marja Lindholm, 2017.

4 Materials and methods

4.1 Aquatic macrophytes

Aquatic macrophytes were sampled from 28 lakes during five different decades. The first macrophyte survey was conducted in 1947–1950 by U. Perttula (Perttula 1954 unpublished) and reinvestigated using similar methods in 1975–1978 (Toivonen & Huttunen 1995), 1991–1993, 2005–2008 and in 2017. For clarity, these surveys are referred to as 1940s, 1970s, 1990s, 2000s and 2010s. An aquascope and two different types of rakes were used in surveying aquatic macrophytes in the whole lake area. Macrophyte identification was done to the lowest possible taxonomic level. Species classified traditionally as aquatic vascular plants in Finland (Linkola 1933) and, in addition, seven tall species growing in the water from the sedge genus *Carex* were included. Hybrids (e.g. *Typha* x *glauca*) and taxa identified to genus level (e.g. *Isoëtes* sp.) were not included in analyses. However, some species were combined to species complexes due to identification differences between the five decades. Unfortunately, there was a lack of species information from one lake from the 1990s. Therefore, information from 27 lakes was used in study I and II. Thus, in total, 66 vascular macrophyte taxa were included in study I and II, and 65 taxa in study III. The focus was on presence-absence data, as with historical datasets focusing on the whole lake area, presence-absence data are usually more reliable sources of information compared to coverage information or other information representing abundance in macrophyte studies. Species richness values and descriptive statistics for five decades can be found in Table 2.

Due to the unavailability of a true phylogeny covering all macrophyte species in the data, taxonomic distances based on the Linnaean hierarchy were used as a proxy for phylogenetic relationships of macrophyte species. A similar approach has been used in previous studies dealing with phylogenetic diversity (e.g. Ruhí *et al.* 2013; Heino & Tolonen 2017). However, this can only be considered as a coarse proxy of true phylogeny. Equal branch lengths and five taxonomic levels above species level (genus, family, order, class and subdivision) were used. Taxonomic information was collected from the open online source Catalogue of Life (Roskov *et al.* 2018).

To represent functional diversity of aquatic macrophytes in study I and III, four functional traits were used: growth form, normal method of propagation (degree of vegetative propagation in study III), perennation and potential size (Fig. 6). These are important traits of aquatic macrophytes (Willby *et al.* 2000; Göthe *et al.* 2017) and they affect where species can live, how they reproduce and what kind of life cycle they

Figure 6. Examples of the species with different functional traits. A) *Subularia aquatica* L., the growth form of which is isoetid. It propagates by seed, is both annual and biennial/short lived perennial and its maximum potential length is 8 cm. It has had stable distribution during the study period in the study area. B) *Potamogeton crispus* L., the growth form of which is elodeid. It propagates mostly vegetatively but also by seed, is perennial and its maximum potential length is 100 cm. It has increased its distribution during the study period in the study area. Pictures: Marja Lindholm, 2017

have. Growth form division consists of the following classes: ceratophyllid, elodeid, helophyte (incl. tall *Carex*), isoetid, lemnid and nymphaeid (Toivonen & Huttunen 1995). Only the main growth form of species was considered. Normal method of propagation (Klotz *et al.* 2002) consists of five ranked classes: 1) by seed, 2) mostly by seed but also vegetatively, 3) by seed and vegetatively, 4) mostly vegetatively and also by seed and 5) vegetatively. Perennation consists of three ranked classes: 1) annual, 2) biennial/short lived perennial and 3) perennial. Perennation information was mainly collected from Willby et al.'s (2000) attribute-based data, where some species had an attribute present in two categories. In such cases, the species obtained a value in between the ranked categories (i.e. 1.5 and 2.5), following Göthe *et al.* (2017). However, value 2, which indicates the presence of the attribute, was weighted at the expense of value 1, which indicates the occasional, but not general exhibition of the attribute. Perennation information was not available in this source for all species. In such cases, data was complemented by information from other literature sources and databases (e.g. Ecological Database of the British Isles: *http://ecoflora.org.uk*). Potential size information (cm) is a continuous trait from Hämet-Ahti *et al.* (1998) complemented from Mossberg and Stenberg (2012) for a few species. It represents the potential length of an individual omitting the root or rhizome length (Bornette *et al.* 1994; Doledec & Statzner 1994). In study II, species were divided into helophytes (i.e. emergent species including species from the genus *Carex*) and hydrophytes (i.e. true aquatic plants including ceratophyllids, elodeids, isoetids, lemnids and nymphaeids), following Toivonen & Huttunen (1995), to see if there would be differences in lake macrophyte functional groups.

4.2 Biodiversity metrics

A summary of the used metrics of biodiversity can be found in Table 1. In study I, the amount of total beta diversity was calculated among pairwise comparisons of lakes for taxonomic, phylogenetic and functional data and for different time periods separately based on Jaccard's dissimilarity index (BAT package; Cardoso *et al.* 2015; 2017). The total beta diversity was decomposed into replacement and richness difference components following the partitioning framework developed by Podani and Schmera (2011) and Carvalho *et al.* (2012). The richness difference component was applied (Podani & Schmera 2011) instead of the nestedness component (Baselga 2010), because overall difference in species richness was the subject of interest (Brittain *et al.* 2020). Recently, Schmera, Podani, & Legendre (2020) also recommended not using Baselga's (2010) turnover component (which Schmera *et al.* (2020) called replacement component). In study III, the amount of functional beta diversity (reflecting both functional replacement and loss/gain) was calculated among all pairwise comparisons of lakes for the two time periods separately. The Gower distance (Gower 1971) and a hierarchical cluster analysis (stats package; R Core Team 2017) were used to produce a trait tree. Then, using the trait tree and macrophyte presence-absence data (site-by-species matrix), both the average and the variance of functional beta diversity was calculated based on the Sørensen dissimilarity index (BAT package; Cardoso *et al.* 2015; 2018).

Three different pairwise dissimilarity matrices based on total beta diversity were generated in study I: dissimilarity matrix based on the aquatic macrophyte species presence–absence data (hereafter taxonomic dissimilarity matrix), phylogenetic dissimilarity matrix and functional dissimilarity matrix. The taxonomic dissimilarity

Table 1. A summary of the used biodiversity metrics.

Study	Biodiversity metric and facet	Index
I	Taxon, phylogenetic, functional beta diversity	Jaccard dissimilarity
	Replacement and richness difference components	
	Taxon, phylogenetic, functional dissimilarity matrix	Jaccard dissimilarity
II	Temporal beta diversity	Sørensen dissimilarity
	Species losses and gains	
	Taxon dissimilarity matrix	Sørensen dissimilarity
III	Functional beta diversity	Sørensen dissimilarity
	Functional dissimilarity matrix	Sørensen dissimilarity
	Functional richness	Fric

matrix was formed based on Jaccard's dissimilarity index (BAT package; Cardoso *et al.* 2015; 2017). Taxonomic distances between aquatic macrophyte species were calculated (vegan package; Oksanen *et al.* 2018) and hierarchical cluster analysis was utilised to produce a taxonomic tree for the species (stats package; R Core Team 2017). Using the taxonomic tree along with the aquatic macrophyte absence-presence data, the phylogenetic dissimilarity matrix based on Jaccard's dissimilarity index was formed (BAT package; Cardoso *et al.* 2015; 2017). To obtain the functional dissimilarity matrix between sites, the species-by-species distance matrix based on Gower (1971) (dis)similarity coefficient was first generated using the trait data (FD package; Laliberté & Legendre 2010; Laliberté *et al.* 2014). Similar to phylogenetic dissimilarity, hierarchical cluster analysis was utilised to produce a trait tree. Then, using the trait tree and aquatic macrophyte presence-absence data, a functional dissimilarity matrix was generated. Also in study II, a dissimilarity matrix based on the Sørensen dissimilarity index was formed using an aquatic macrophyte matrix including all sites (BAT package; Cardoso *et al.* 2015; 2020) and a square-root transformation was used to euclidify the dissimilarities. This was done separately to the whole community, hydrophytes and helophytes. In study III, a dissimilarity matrix was formed based on the same trait tree and the site-by-species matrix as mentioned above. The functional dissimilarity matrix based on the Sørensen dissimilarity index was generated (BAT package; Cardoso *et al.* 2015; 2018).

Temporal beta diversity indices (TBIs) are dissimilarity indices that measure temporal beta differentiation, i.e. the change in community composition from one time point to a subsequent time point (Legendre 2019). This index varies from zero (community compositions at two time points are exactly the same) to one (communities have no shared species). In study II, TBIs were calculated for each lake based on Sørensen dissimilarity (adespatial package; Dray *et al.* 2019). As this index is limited to measuring only two survey time points, changes between separate survey pairs were measured: the 1940s and 1970s, the 1970s and the 1990s, the 1990s and the 2000s, and the 2000s and 2010s. Also changes from the oldest survey (1940s) to the most recent survey (2010s) were measured to observe the long-term trend in the study period. The p-values (based on 9 999 random permutations) were corrected for multiple testing, as several lakes were tested simultaneously (Legendre 2019). The TBIs were decomposed into beta diversity explained by either species temporal losses or temporal gains.

In study III, the functional richness index (FRic) of Villéger, Mason and Mouillot (2008) was used, as the total functional range covered by the community (Legras *et al.* 2018) was the focus of interest. FRic was calculated based on raw data with square root correction (FD package; Laliberté & Legendre 2010; Laliberté *et al.* 2014) to each lake for the 1940s and 2017, respectively.

4.3 Predictor variables

There is only a limited amount of environmental information available from the 1940s, and thus the focus was on environmental variables that are widely identified to be key variables for aquatic macrophytes: lake area (ha), maximum depth (m), pH and Secchi depth (m) (Lacoul & Freedman 2006). These environmental variables represent a larger complex of ecologically important factors for lake flora and correlate with other water chemistry and hydromorphological variables which were not available for all study periods (e.g. Kosten *et al.* 2009). Water transparency (m) was measured using a Secchi disk at the same time as the macrophyte sampling. Measurements of pH were done in the 1940s in the summertime, while in the 1970s both in the summertime and during the fall overturn and in the other decades during the fall overturn. Water transparency is related to colonization depth and minimum light requirements of aquatic macrophytes (Middelboe & Markager 1997).

To study the effect of lake landscape position, four different proxy variables were determined: elevation of the lake (m), watercourse distance to the main lake (m), lake order and lake network number. These four variables characterise the position of a lake along the watershed upland-lowland gradient and therefore are a proxy for connectivity and variation in physical, hydrological and ecological characteristics of the lake in the landscape (Kratz *et al.* 1997; Quinlan *et al.* 2003). Based on Spearman's correlation test, all these landscape position variables were statistically significantly correlated with each other. Therefore, the modelling in study I was done by including other environmental variables and only one landscape position variable at a time in the models. As the general patterns in models with each lake landscape variable were similar, a decision was made to focus only on elevation, as models that included it best explained variation in the compositional dissimilarity among lakes. Elevation was used also in the later studies II and III to maintain coherency between the studies. The importance of different factors (e.g. land use) can vary across elevational gradients in relation to establishment of freshwater macrophyte communities (Sun *et al.* 2019). At lower elevations, land use can be a more important predictor, while at higher elevations, natural variation in nutrient concentrations or soil properties can become more important (e.g. Fernández-Aláez *et al.* 2018).

In addition, land use variables from 200 m buffer zones (Pedersen *et al.* 2006) derived from the base maps for each decade (National land survey of Finland 2017; 2018) were used as a proxy for human impact. Studies have shown that land use on relatively narrow buffer zones adjacent to lake shoreline has the strongest impact on lake macrophytes (Pedersen *et al.* 2006; Akasaka *et al.* 2010; Alahuhta *et al.* 2012; Sun *et al.* 2018). Three land use variables proportional to the buffer area were calculated: agriculture area (i.e. field and pasture area), built area and amount of ditches. These land use types are key ones that have changed most over the past decades in this study area. In addition, these land use types influence water chemistry and other physical characteristics of lakes. The agricultural land within a watershed is strongly related, for example, to total phosphorus (e.g. Taranu & Gregory-Eaves 2008), the information that is not available

Table 2. Key characteristics of the study lakes, species richness values and descriptive statistic over five decades (N=27). Minimum (min), maximum (max) and mean (mean) values, standard deviation (SD) and coefficient of variation (CV).

	Variables	**Min**	**Max**	**Mean**	**SD**	**CV**
1940s	Elevation (m)	77.1	130.9	102.1	15.7	15.4
	Depth (m)	1.8	21.0	7.0	4.9	69.8
	Area (ha)	0.3	209.2	39.8	55.5	139.5
	pH	5.4	8.5	6.8	0.8	12.1
	Secchi (m)	0.2	5.1	2.1	1.3	63.5
	Agriculture (%)	0.0	71.6	28.8	24.7	85.9
	Built area (%)	0.0	4.1	0.8	0.9	123.9
	Ditches	0.0	6.3	1.0	1.4	136.3
	Species richness	5	42	21.7	11.9	54.6
1970s	Elevation (m)	77.2	131.0	102.2	15.8	15.4
	Depth (m)	1.5	21.0	7.7	5.2	66.5
	Area (ha)	0.3	209.0	39.8	55.5	139.6
	pH	5.2	7.2	6.2	0.5	8.7
	Secchi (m)	0.2	4.3	1.7	1.1	63.1
	Agriculture (%)	0.0	64.1	23.3	22.4	96.2
	Built area (%)	0.0	5.2	1.4	1.5	105.9
	Ditches	0.0	5.6	1.2	1.2	98.1
	Species richness	7	43	24.9	11.5	46.2
1990s	Elevation (m)	77.2	131.0	102.2	15.8	15.4
	Depth (m)	1.5	21.0	7.7	5.2	66.5
	Area (ha)	0.4	209.0	39.8	55.5	139.7
	pH	5.6	7.8	6.8	0.6	9.1
	Secchi (m)	0.4	4.2	2.1	1.2	56.6
	Agriculture (%)	0.0	63.4	18.8	20.6	109.3
	Built area (%)	0.0	6.7	1.7	2.0	115.2
	Ditches	0.0	7.1	1.4	1.4	101.5
	Species richness	6	44	25.7	12.0	46.7
2000s	Elevation (m)	77.2	131.0	102.2	15.8	15.4
	Depth (m)	1.5	21.0	7.7	5.2	66.5
	Area (ha)	0.3	215.1	40.1	56.2	140.3
	pH	4.7	7.6	6.8	0.7	10.0
	Secchi (m)	0.3	6.5	2.2	1.5	68.4
	Agriculture (%)	0.0	61.1	15.2	19.3	126.8
	Built area (%)	0.0	6.8	1.7	2.0	116.2
	Ditches	0.4	10.6	2.3	2.0	87.1
	Species richness	7	44	25.4	11.3	44.4

Table 2. *Continues...*

	Variables	Min	Max	Mean	SD	CV
2010s	Elevation (m)	77.2	131.0	102.2	15.8	15.4
	Depth (m)	1.5	21.0	7.7	5.2	66.5
	Area (ha)	0.3	215.8	40.1	56.3	140.6
	pH	4.7	7.7	6.7	0.7	10.6
	Secchi (m)	0.5	6.5	1.8	1.3	73.4
	Agriculture (%)	0.0	60.7	14.3	18.8	131.7
	Built area (%)	0.0	7.1	1.8	2.1	121.4
	Ditches	0.0	10.6	2.1	1.9	93.3
	Species richness	6	37	21.1	10.5	49.7

from the 1940s. Built area represents the human settlements, the level of urbanization and general human impact, which are often related to non-native species distribution (McKinney 2006). Ditches in lake catchments have an effect on water chemistry (Ecke 2009) and dispersal of macrophytes.

Additionally, geographical coordinates of lakes' centres were used. Climatic variables were also considered. However, reliable climate data from this small study area were not available for the whole study period. In addition, considering the quite small study area, there would have been only minor changes between the lake-specific climate variables.

The Wilcoxon signed rank test was used to detect differences in environmental variables between the decades. The temporal change in pH units, water transparency, agriculture area, urban area and ditches between survey decade pairs was calculated, and these metrics of changes were used in the analyses in study III. The change was calculated by subtracting the earlier decade's values from the later decade's values (i.e. 1970-1940). Measurements of pH were done in the summertime for the 1940s data. Thus, summertime pH values from the 1970s were used when the changes in pH units were calculated between these two decades. In other decades, measurements were conducted during the fall overturn. Thus, fall pH values from the 1970s were used when the changes in pH units were calculated between the 1970s and 1990s. However, due to data availability, using summertime pH values from the 1940s and fall pH values from the 2010s was unavoidable, thus limiting the strict comparability between these decades. In addition, elevation values, which represent the lake landscape position, were used from an earlier decade's values, i.e. in the survey decade pair 1940s–1970s, values from the 1940s were used.

4.4 Data analysis

A schematic diagram showing the methodology used in the three studies can be found in Figure 7. Data analyses in study I and III were conducted in R version 3.4.3 (R Core Team 2017) and study II in R version 3.6.2 (R Core Team 2019). All preliminary and basic statistical procedures were done using the package *stats* (R Core Team 2017; 2019). Preliminary examinations included tests of normality, boxplots, scatter plots and Spearman correlation tests.

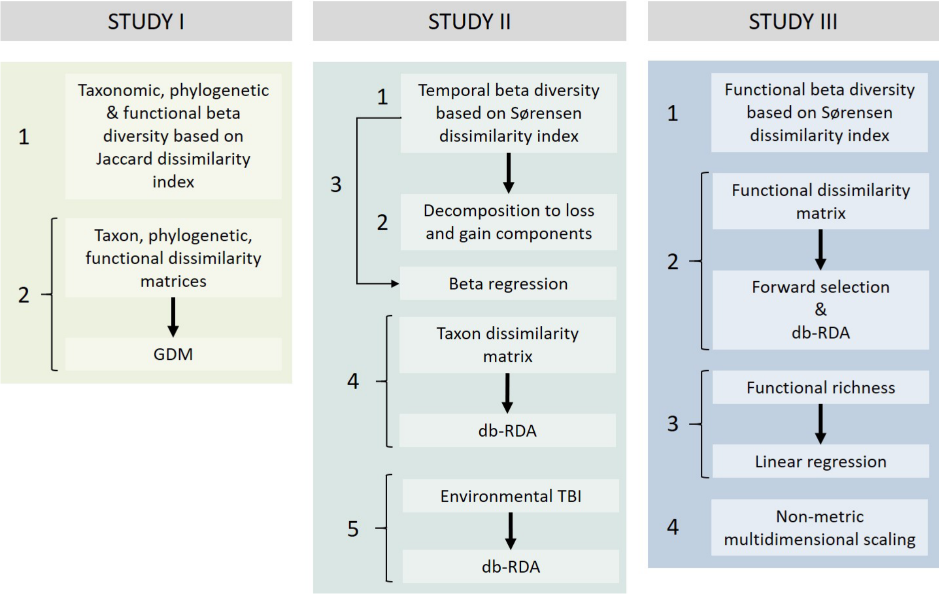


Figure 7. A schematic diagram showing the methodology used in the three studies. Numbers indicate the complementary analyses conducted in each study.

4.4.1 Study I

To study the spatial beta diversity and biotic homogenisation and to answer Q1 and Q4, the amount of total beta diversity for taxonomic, phylogenetic and functional data and for different time periods were inspected, and generalised dissimilarity modelling (GDM) was used to analyse spatial patterns in different dimensions of beta diversity in relation to environmental and geographical gradients (Ferrier *et al.* 2002; 2007).

To run GDM, three pairwise dissimilarity matrices based on total beta diversity were used: taxonomic dissimilarity matrix, phylogenetic dissimilarity matrix and functional dissimilarity matrix. Each dissimilarity matrix and the environmental data were converted to site-pair format (gdm package; Manion *et al.* 2018). Then, the GDM model was fitted to tabular site-pair data and the variable importance in the GDM model was estimated. The spatial autocorrelation was controlled in GDM by using geographical distances as predictors among other variables. The full set of variables was tested, because the relative effects of these variables were particularly the focus of interest. This also facilitates comparing the impacts of different predictor variables with different beta diversity dimensions across all decades. In addition, the significance of each variable was estimated using the boot-strapped p-value. The modelling was independently conducted for different time periods and different dimensions of beta diversity (i.e. taxonomic, phylogeny and functional).

4.4.2 Study II

To study the temporal beta diversity and answer the Q2 and Q4, the temporal beta diversity indices (TBI), beta regression and distance-based redundancy analysis (db-RDA) were used between the survey decade pairs: the 1940s and 1970s, the 1970s and the 1990s, the 1990s and the 2000s, and the 2000s and 2010s. To see if there were differences in lake plant functional groups, analyses were performed for all taxa, hydrophytes (i.e. true aquatic plants) and helophytes (i.e. emergent species).

Species temporal losses or temporal gains were tested for significance by using parametric and permutational paired t-tests. The TBIs and dominant process (gains or losses) were visualised on maps, as identifying sites that have changed in exceptional ways was a point of interest. The lakes were divided into two groups according to whether they were above or below 100 meters above sea level. The cut-off level 100 meters is approximately the midpoint of the elevation gradient of study lakes (77 to 131 m a.s.l.). Then, the loss and the gain components were visualised (Legendre 2019) to see if the loss and the gain components follow this elevation division.

To model variation in TBI values across lakes, beta regression (Ferrari & Cribari-Neto 2004) was conducted with a log link function (betareg package; Cribari-Neto and Zeileis 2010). The changes in the environment and lake landscape position were the predictor variables. The same set of variables was used to enable comparison between the survey decade pairs. Beta regression is suitable when the response variable is constrained between 0 and 1. However, as some of the TBI values were exactly zero, the constant value 0.00000001 was added to the TBIs and their components. The models were tested (lmtest package; Zeileis and Hothorn 2002) and the model residuals checked to see if there was spatial autocorrelation. This was done by calculating Moran's I coefficients based on the lake centre's geographical coordinates using five distance classes (pgirmess package; Giraudoux 2018). In addition, overall dissimilarity in community composition was inspected by conducting db-RDA (Legendre & Andersson 1999; vegan package; Oksanen *et al.* 2019a), and constraining the sites by a factor representing the five survey decades.

To identify lakes where the changes in environmental conditions had been the most important, the same approach was used as with the community data. The environmental variable data were transformed into non-negative and standardised (Legendre 2019, Appendix S2). TBIs were calculated with the standardised Euclidean distances (adespatial package; Dray *et al.* 2019) and a test of significance was conducted using 9 999 permutations. Aquatic macrophyte TBIs were related to environmental TBIs by conducting beta regression with a log link function (betareg package; Cribari-Neto and Zeileis 2010).

4.4.3 Study III

To study the changes in functional features and to answer Q3 and Q4, four complementary approaches were used with the time periods 1940s and 2017. In these approaches, the vascular aquatic macrophyte presence-absence data and the functional trait data were utilised.

To examine functional community-environment relationships separately for the decades, db-RDA (Legendre & Andersson 1999) was used with the functional dissimilarity matrix as a dependent variable. This method works with any type of distance matrix as a response matrix (Legendre & Legendre 2012). Predictor variables were selected for the model using the forward selection procedure with two stopping rules (Blanchet *et al.* 2008; vegan package; Oksanen *et al.* 2019b). The db-RDA was run with the lingoes correction to avoid negative eigenvalues, and the model significance was tested by 999 permutations (vegan package; Oksanen *et al.* 2019b).

The temporal change in functional richness (i.e. the proportion of the functional space filled by community) was examined to reveal how it is linked to the changes in the environment. The change in FRic was calculated between the two time periods (from now on FRic_c). Environmental variables were divided into 'stable' and 'non-stable' variables to see if changes in FRic_c are related to concomitant changes in the environment or environmental factors that are considered to be stable through decades. The change was calculated in non-stable environmental variables (pH, water transparency, agricultural area, built area and ditches) between the 1940s and 2017. For clarity, these changes are referred to with a subscript $_c$. Values from the 1940s were used with the more or less stable variables (east and north coordinates, elevation, lake area and depth). The relationship between FRic_c and all environmental variables was modelled using linear regression (LR). FRic_c was log-transformed to normalise distribution. Collinearity was tested by variance inflation factor (VIF) and the LR optimization was based on Akaike's Information Criterion (AIC) (Burnham & Anderson 2004). In addition, commonality analysis was executed to decompose the linear regression R^2 to unique and common components of explanatory variables (yhat package; Nimon *et al.* 2013). Unique components indicate how much variance is uniquely accounted for by a single variable, and common components indicate how much variance is common to a variable set. To further disentangle the relationship of functional richness to the environment, FRic was examined in the 1940s and 2017 separately. Four predictor variables based on the previous LR model of FRic_c were forced into both LR models, as the purpose was to compare the same predictor variables between the time periods.

To see if species with certain sets of traits (growth form, normal method of propagation, perennation and potential size) become more common or rare during the study period, each species was observed in functional space. The Gower distance (Gower 1971) was used to calculate between-species distances based on the trait data (FD package; Laliberté & Legendre 2010; Laliberté *et al.* 2014). Then, ordination was used by non-metric multidimensional scaling (NMDS) (vegan package; Oksanen *et al.* 2019b). In the produced functional space, species were plotted based on NMDS with two dimensions (final stress level = 0.179). The species were represented with different symbols based on whether the species have (1) declined, (2) remained the same (stable) or (3) increased in distribution during the study period in the study area (i.e. differences in the number of localities between two different decades). A species was considered declining when its occurrence decreased by two or more lakes, and vice versa for increasing species. Stable species declined or increased in a maximum of one lake (i.e. from -1 to 1) between the time periods. Permutational multivariate ANOVA (PERMANOVA; Anderson 2001) was used to test for significant differences between these three species groups with 999 permutations (vegan package; Oksanen *et al.* 2019b). NMDS species scores were also associated with each trait by conducting the Kruskal–Wallis rank sum test (stats package; R Core Team 2017) and by plotting the relationships between the NMSD axes and the four traits.

5 Results and discussion

In this chapter, I will discuss the main outcomes of the three studies to answer the research questions (Q1–4) and assess the contribution of this thesis to biodiversity research. First, I briefly go through the main changes found in environmental conditions during the last 70 years in the study area, and shortly describe the changes in gamma and alpha diversity in aquatic macrophyte communities for the background information. Next, I will discuss spatial and temporal beta diversity through studies I and II. After that, I will consider the functional changes in aquatic macrophyte communities through study III. Then, I will synthesise the findings in relation to biotic homogenisation. Finally, I will evaluate the limitations in temporal studies and datasets and identify future study needs. A summary of the results can be found in Figure 8.

5.1 Changes in environmental conditions during the last 70 years

The study area has faced only modest changes in land use from the 1940s to 2010s when compared globally (e.g. Zhang *et al.* 2018). Generally, agricultural areas (i.e. fields and pasture) have declined in most lake shore areas (Fig. 9). Therefore, the amount of harmful substances from the agricultural areas has probably decreased. Urbanization and drainage ditching have increased through time (Fig. 9). For the most part in Finland, the most intensive period of forest drainage ditching has been from the beginning of the 1960s to the 1980s (Peltomaa 2007). Even though built area has increased during the whole study period, phosphorus removal from industrial and municipal wastewaters was started in the mid-1970s in Finland (Räike *et al.* 2003).

Human-caused nutrient input is a crucial process causing temporal changes in lake environments (Birk *et al.* 2020). Unfortunately, as there is no nutrient information available from the 1940s, other factors that are closely related to increasing nutrient input, such as land use variables (Soranno *et al.* 2015) and water transparency (Wetzel 2001), have to be relied on. For example, usually when the amount of nutrients increases, water transparency decreases (Wetzel 2001). Water transparency (m) has increased in the lakes near urban areas during the study period. The lakes where water transparency has declined most are located at higher elevations in the landscape, are less affected by human activity and are surrounded by coniferous forest and peatlands. In these lakes, decreasing water transparency can be due to long-term increases in dissolved organic carbon and the brownification it can cause (Evans *et al.* 2005; Kritzberg *et al.* 2020). The changes in pH across the decades have been mixed. When considering water chemistry data from 1970s onwards, water colour and total nitrogen have increased clearly, while total phosphorus increased towards the 1990s and declined after that (Fig. 10).

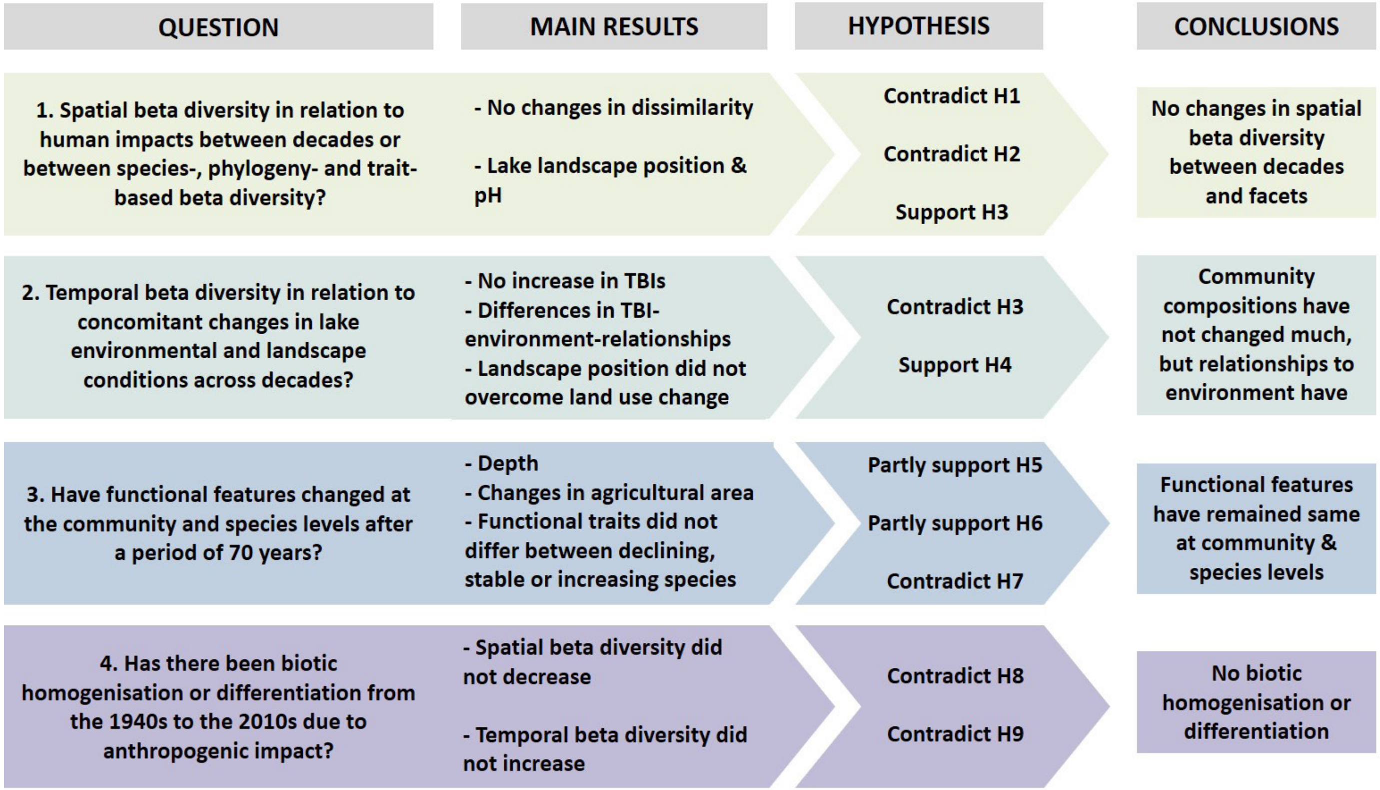
Based on the TBI values for environmental variables between the survey pair decades, there were no significant changes in the environmental conditions between the survey decades. Exceptional changes in environmental conditions had been observed in only a few lakes surrounded by urban areas (Table S2 in study II). Based on the db-RDA biplot, the lakes in all decades have had quite similar environmental conditions (Fig. S3 in study II).

There have also been some lake-specific changes during the study period. Especially during the period between the 1940s and 1970s, water level has been lowered in some lakes and grazing in shore areas has ended. One somewhat challengingly measurable factor has been the introduction and subsequent spread of the muskrat (*Ondatra zibethicus*) to this area and its population dynamics. After the 1980s, muskrat population sizes have decreased for yet unknown reasons (Nummi 2020).

5.2 Changes in gamma and alpha diversity

Gamma diversity has remained relatively stable in the study area between the decades. In the 1940s there were 61 species, and the number of species increased by one per time point until the 2000s, and in the 2010s there were 63 species.

Alpha diversity (the median species richness) has slightly increased from the 1940s until the 1990s and has decreased after the 1990s (Appendix 5 in study I). After the



QUESTION	MAIN RESULTS	HYPOTHESIS	CONCLUSIONS
1. Spatial beta diversity in relation to human impacts between decades or between species-, phylogeny- and trait-based beta diversity?	- No changes in dissimilarity - Lake landscape position & pH	Contradict H1 Contradict H2 Support H3	No changes in spatial beta diversity between decades and facets
2. Temporal beta diversity in relation to concomitant changes in lake environmental and landscape conditions across decades?	- No increase in TBIs - Differences in TBI-environment-relationships - Landscape position did not overcome land use change	Contradict H3 Support H4	Community compositions have not changed much, but relationships to environment have
3. Have functional features changed at the community and species levels after a period of 70 years?	- Depth - Changes in agricultural area - Functional traits did not differ between declining, stable or increasing species	Partly support H5 Partly support H6 Contradict H7	Functional features have remained same at community & species levels
4. Has there been biotic homogenisation or differentiation from the 1940s to the 2010s due to anthropogenic impact?	- Spatial beta diversity did not decrease - Temporal beta diversity did not increase	Contradict H8 Contradict H9	No biotic homogenisation or differentiation

Figure 8. Summary of the research questions, found results and those relationship to hypotheses and conclusions.

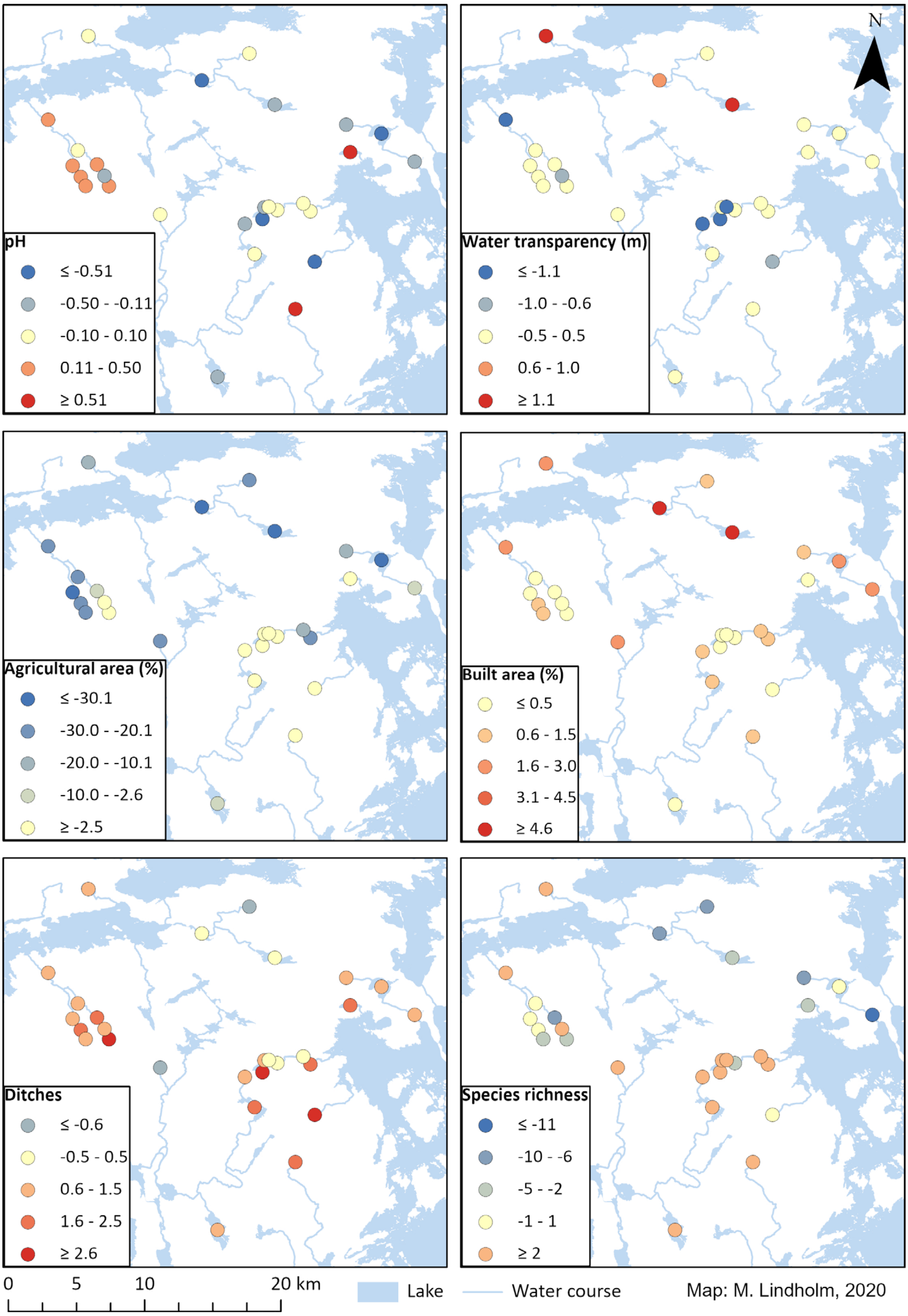


Figure 9. Changes in environmental conditions and species richness between the 1940s and the 2010s.

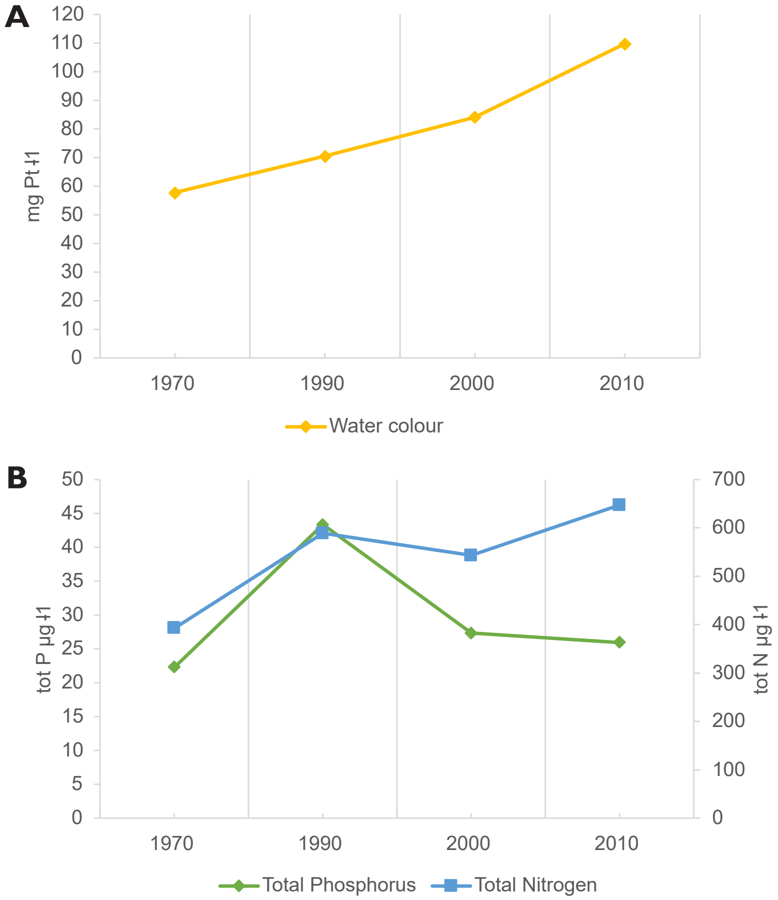


Figure 10. Water chemistry changes from the 1970s to the 2010s in the study lakes. Water chemistry is based on single samples taken during macrophyte sampling. A) Mean water colour. B) Mean total phosphorus and total nitrogen.

1940s, some new species have dispersed to the study lakes, such as *Glyceria maxima*, *Juncus bulbosus*, *Potamogeton compressus* and *Rumex hydrolapathum*. Some species, such as *Iris pseudacorus* and the invasive *Elodea canadensis* have increased their occupancy in the study lakes. For example, in the 1940s, *E. canadensis* was found only in one lake, Mäyhäjärvi, but in the 2010s it was found in ten lakes. Two species that were found in the 1940s, *Acorus calamus* and *Limosella aquatica*, have disappeared from the study lakes: *A. calamus* by the 1990s and *L. aquatica* by the 1970s.

5.3 Spatial beta diversity (Q1)

In study I, the aim was to explore if vascular aquatic macrophyte communities show different patterns in *spatial* beta diversity in relation to human impacts between decades or between species-, phylogeny- and trait-based beta diversity. A short answer to this intricate question is that mainly they do not. During the past 70 years, vascular aquatic macrophyte communities showed only slightly different spatial beta diversity patterns in relation to human impact (Fig. 11; contradicting H1). Similar findings were found in all different dimensions of beta diversity, i.e. taxonomic, phylogenetic and functional, and the patterns of different dimensions of beta diversity diverged only slightly from each other (Fig. 11; contradicting H2). With the taxonomic and the phylogenetic spatial beta diversity, the explained deviance was clearly lower in the 1940s than in the later decades, when it was relatively high. In every decade, explained deviance for functional total beta diversity was lower than for the taxonomic and phylogenetic models (Table 2 in study I). Elevation, representing lake landscape position, and pH were the most important variables in each decade, while land use was not particularly important in shaping spatial beta diversity patterns (contradicting H1, supporting H3). In addition, geographical distance between lakes was a weak predictor of the compositional dissimilarity in each decade.

Taxon and phylogenetic dimensions of beta diversity followed the same patterns overall. The most notable differences were found in functional beta diversity, even though the differences between functional and taxonomic or phylogenetic beta diversity were quite small as well. Also, Zhang *et al.* (2018) found that functional diversity did not add any particular value compared to taxonomic diversity. However, studies focusing on other organisms have shown that even using these kinds of quite coarse proxies of phylogenetic and trait information can provide additional information to taxon-based information (Heino & Tolonen 2017; Perez Rocha *et al.* 2018; Richardson *et al.* 2018). Naturally, using true phylogeny could possibly provide a different picture from taxonomic distances based on the Linnaean hierarchy.

Several studies have shown that pH has a major influence on aquatic macrophyte communities (reviewed by Lacoul & Freedman 2006). Thus, it was not surprising that it was an important predictor variable also for the compositional dissimilarity across the lakes. In the 1940s, and also in the 2000s, pH had a lower influence on spatial beta diversity than in other decades (Fig. 12). Despite the fact that pH is a commonly used measure, it is important to note that the pH values are based on only single measurements per lake and per time period, thus undermining their reliability. Additionally, summer pH values are sensitive to variation in primary production of phytoplankton and submerged plants during the growing season (Kirk 2011), which

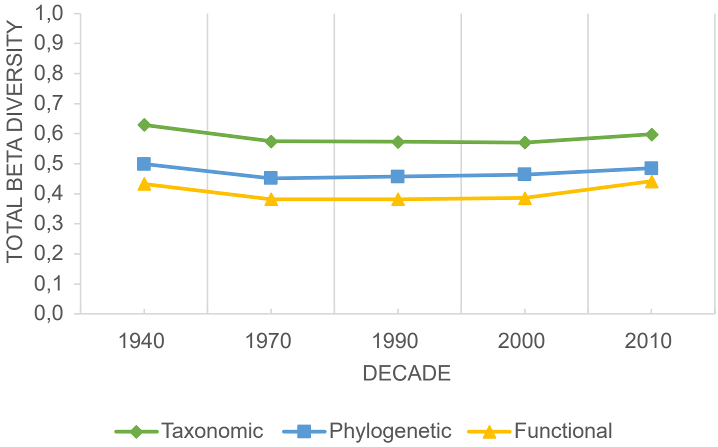


Figure 11. The average of the total beta diversity for the taxonomic, phylogenetic and functional dissimilarity between the lakes in each decade.

concern the pH values from the 1940s. However, as the patterns of pH related to compositional dissimilarities were strong and quite consistent between other decades (Fig. 12), it suggests that this should not be a major issue.

Lake landscape position was another important variable, especially in the 1940s, explaining the compositional dissimilarities of taxonomic, phylogenetic and functional dimensions. It is possible that lake landscape position has overdriven the changes in land use through time. However, it was also notable that the importance of elevation decreased through time while urbanization in the study area has increased. Alexander *et al.* (2008) suggested that landscape position affects which species are present within a lake, but human development has an effect on the abundance of macrophytes. Lougheed *et al.* (2008), using Sørensen similarity index, found that the macrophyte communities were significantly more similar among wetlands in forested landscapes than among sites in agriculturally-dominated landscapes in Michigan, U.S.A. The study area, the Muskegon River catchment, was also dominated by forest in the upstream regions and agricultural and small urban areas downstream (Lougheed *et al.* 2008),

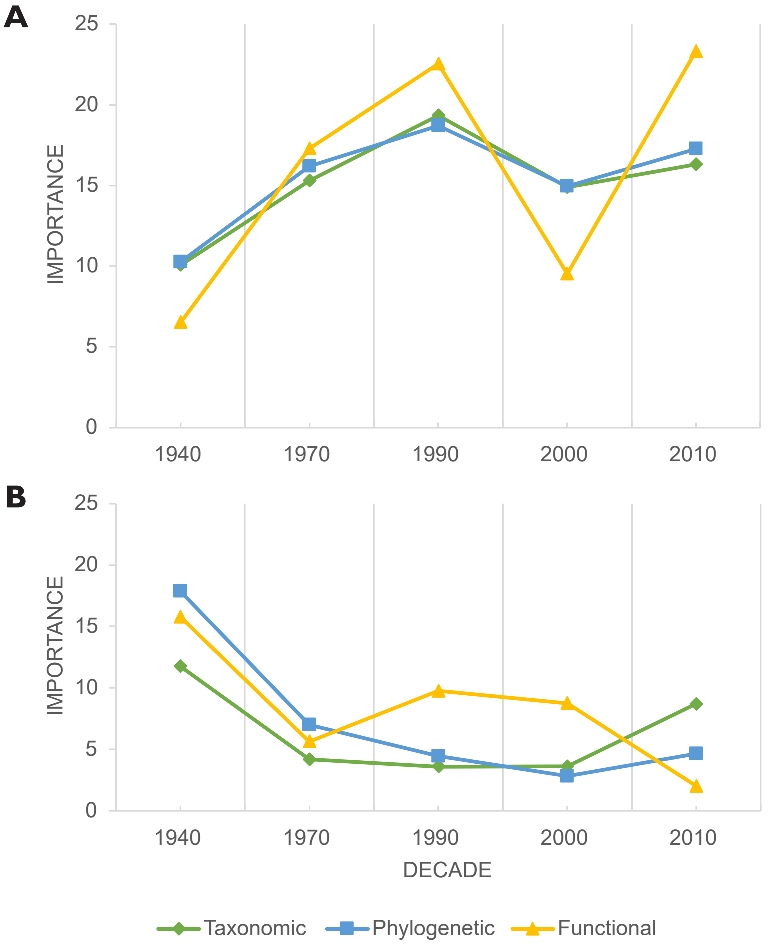


Figure 12. The relative importance of pH (A) and elevation (B) for the taxonomic, phylogenetic and functional dissimilarity based on generalised dissimilarity modelling in each decade.

supporting the importance of lake landscape position in relation to macrophyte communities at the landscape level in glaciated areas. Heegaard *et al.* (2001) also suggested that the relationship of lake macrophyte species to the altitudinal gradient is a response to local conditions in the lowlands in Northern Ireland, where farming has resulted in eutrophication. Moreover, Sun *et al.* (2019) found that turnover (component of spatial beta diversity) in macrophyte composition between upland lakes in Britain was lower than in other lake types, indicating a more specialist flora and increased potential for exchange of propagules due to spatial aggregation and higher hydrologic connectivity. It has also been found that lake landscape position can affect macrophyte species composition if it is strongly related to some important chemical property of water, such as alkalinity (Alexander *et al.* 2008). It should also be noted that as lake landscape position reflects hydrologic connectivity and physical features of a lake and the landscape (Kratz *et al.* 1997; Riera *et al.* 2000), it is inevitably linked to other environmental variables. For example, in the study area, soil is linked to lake landscape position as the clay areas are more or less located at lower elevations and the sand moraine areas are situated in higher elevations (Geological Survey of Finland 2018). Moreover, landscape characteristics, especially bedrock and soil, have a strong impact on pH values of lakes (Quinlan *et al.* 2003).

Land use was not particularly important in explaining the compositional dissimilarity across the lakes in the study area. Of the land use variables, only ditches in the 1940s and built area in the 2010s had a clear impact on taxonomic dissimilarity across the lakes. The built area, representing human settlements and level of urbanization, however, has showed a small increase in importance in explaining compositional dissimilarity after the 1990s. At the same time, the amount of urbanization has increased near the study lakes. Nevertheless, studies conducted in Denmark have found that improved treatment of domestic sewage has reduced the annual phosphorus input to fresh waters substantially from the 1970s, bringing input close to the pre-eutrophication level (Sand-Jensen *et al.* 2008; 2017). Ditches were an important variable for phylogenetic dissimilarity in the 1940s as well. Previous studies have shown a strong connection between land use and macrophyte community composition (e.g. Sun *et al.* 2019). Thus, it is interesting that there was no such connection in compositional differences across the study lakes and land use. A recent study showed that historical land use can have stronger impacts than present land use on both water chemistry and macrophyte taxonomic richness and composition (Jamoneau *et al.* 2020). This time-delayed response of the vegetation to land use change and anthropogenic pressure could partly explain the results found, and this issue will require further research in the future. However, it is important to note that the land use variables are based on basic maps and therefore do not necessarily represent exactly the same time point as macrophyte sampling. It is also good to remember that these land use variables represent only land use in shore areas of the lake, not the land use in the whole watershed. However, several studies have shown that land use on relatively narrow buffer zones adjacent to lake shoreline has the strongest impact on lake macrophytes (Pedersen *et al.* 2006; Akasaka *et al.* 2010; Alahuhta *et al.* 2012; Sun *et al.* 2018). Additionally, studies have shown that smaller waterbodies should have a more direct exchange with nearby terrestrial ecosystems (e.g. Declerck *et al.* 2006). As the study lakes are quite small, the lack of watershed land use should not be an issue.

In addition to pH, other water quality metrics such as nutrients play a prominent role for aquatic macrophytes (Lacoul & Freedman 2006). Thus, these findings may be somewhat limited by the fact that there was no nutrient information available (from the 1940s). However, as pH, land use and nutrient concentrations are closely related (Johnson *et al.* 1997; Taranu & Gregory-Eaves 2008; Ecke 2009), this should not be a critical issue. For example, increase in pH is often associated with enhanced nutrient status in lakes (Wetzel 2001). In addition, it has been argued that ecological communities show delayed responses to environmental change as the response of local diversity to environmental changes often requires time (Tilman *et al.* 1994). Also, for macrophytes, it has been found that historical land use influences taxonomic richness and community composition of macrophytes more than recent land use (Jamoneau *et al.* 2020). Therefore, this phenomenon related to legacy effects might be acting in these study lakes, and that also could partly explain the weak relationship found between spatial beta diversity and land use.

5.4 Temporal beta diversity (Q2)

In study II, the aim was to find if vascular aquatic macrophyte communities show different patterns in *temporal* beta diversity in relation to concomitant changes in lake environmental and landscape conditions across decades. Based on comparisons of the TBI dissimilarities between adjacent sampling periods, the compositions of vascular aquatic macrophyte communities have not changed much through the decades in the lakes across the landscape under modest anthropogenic impacts (Figs. 13 & 14). Nevertheless, it seems that during the study period, hydrophyte assemblages have changed more than helophyte assemblages. This finding was expected, as these two macrophyte groups partly respond differently to environmental gradients (e.g. Alahuhta & Heino 2013). Significant between-decade changes in community composition occurred only in a few lakes (Table S1 in study II). However, based on beta regression results, aquatic macrophyte communities showed differences in relationships between TBI and changes in environmental conditions across decades (Table 1 in study II). There was no evidence that strong landscape position gradient had overcome the effects of anthropogenic land use change (e.g. Alexander *et al.* 2008) in driving temporal beta diversity patterns (Fig. 3 in study II) (contradicting H3).

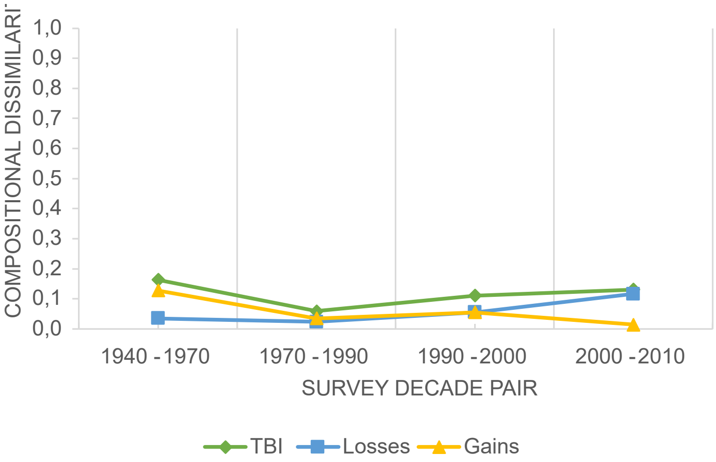


Figure 13. Changes in vascular aquatic macrophyte community compositional dissimilarity (TBI) and its gains and losses components between the survey decade pairs: the 1940s and the 1970s, the 1970s and the 1990s, the 1990s and the 2000s, and the 2000s and the 2010s.

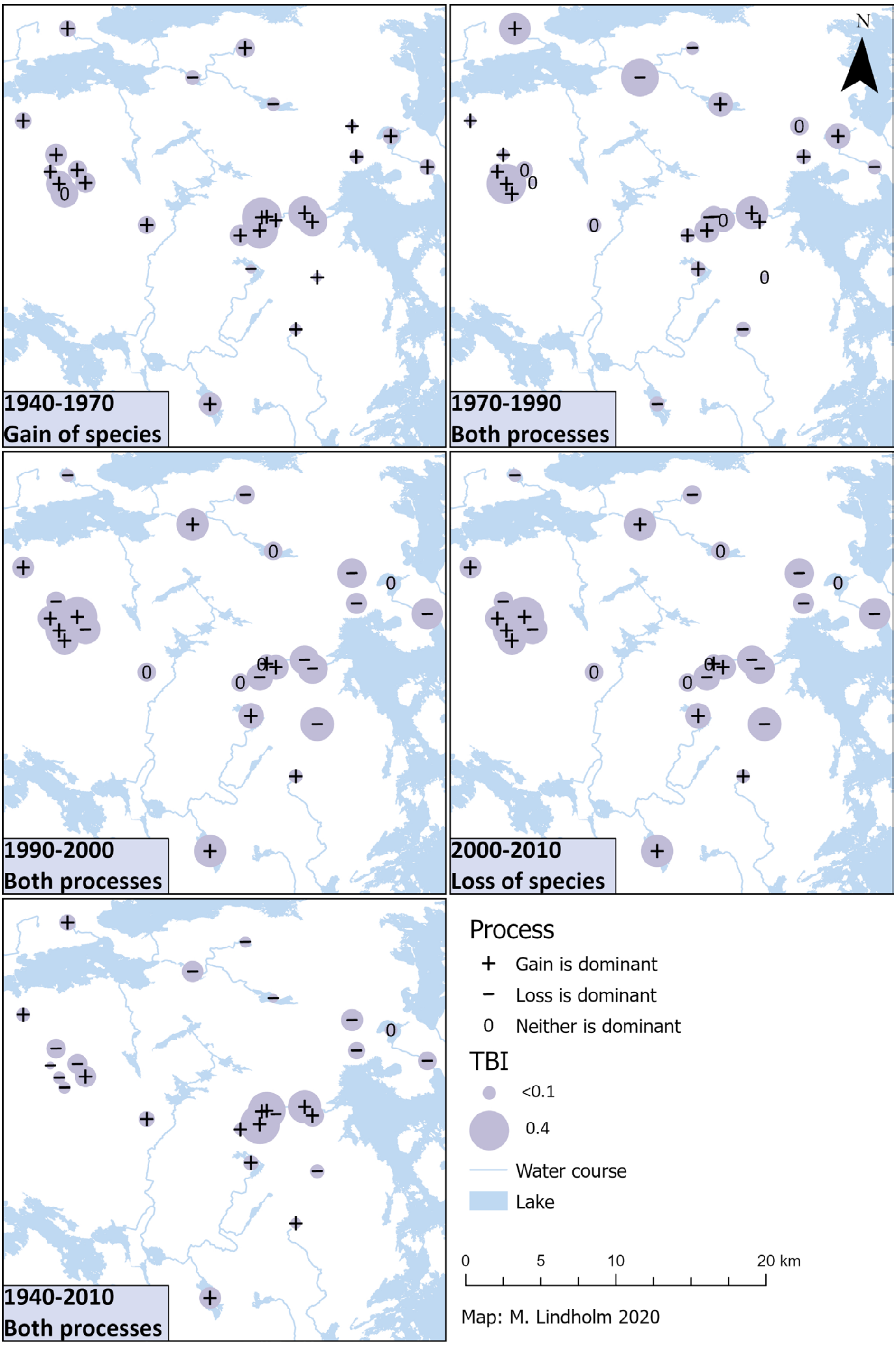


Figure 14. Maps showing the losses and gains computed from the species occurrence data between the aquatic macrophyte surveys. The sizes of the points are proportional to the TBI indices (Sørensen D). The plus (+) sign indicates that the gains of species is dominant and the minus (–) sign the loss of species. The dominant processes in the landscape between the survey decade pairs are shown as written.

When observing the mean TBI and its gain and loss components of all the lakes, there does not seem to be much change between decade pairs (Fig. 13). Also, when observing the whole study period from the 1940s to the 2010s, species gains and species losses seem to be in equilibrium (Fig. 14). However, consecutive decade pairs reveal a more detailed picture of the species losses and gains when observing these at the lake scale. The main changes in temporal beta diversity have occurred from the 1940s to the 1970s, when the gain of new species has been the dominant process in the lakes throughout the landscape. Following that period, the temporal losses and gains of species have been quite stable at the landscape level. However, from the 2000s to the 2010s, the dominating process was, on the contrary, the loss of species. Additionally, even though there were clear main patterns in temporal losses and gains of species at the landscape level, there still has been variation in temporal losses and gains of species in the lakes across the landscape (Fig. 14; supporting H4). In the areas where urbanization has prevailed through time, the dominant process has been the loss of species. On the other hand, in areas where agricultural field area has decreased, the dominant process has been the gain of species, in accordance with Socolar *et al.* (2016). On average, changes in helophyte and hydrophyte assemblages' compositional dissimilarities and their gain and loss components between the pairs of survey decades followed similar patterns as the whole community, but there was, on average, more intensive loss of hydrophytes compared to helophytes (Table S6 in study II).

Temporal changes in environmental conditions played a key role in explaining the TBI. TBIs were related to changes in water transparency, pH and land use. However, none of the variables explained the TBI from the 1940s to the 1970s. From the 1970s to the 1990s, all changes in environmental conditions included in the model were important. In contrast, from the 1990s to the 2000s, only the stable elevation variable, which represents the lake landscape position, explained significant variation in the TBI (Table 1 in study II). It seems that during that period, the changes in the environment did not influence TBI. However, there was no clear pattern with elevation (i.e. lake landscape position) in temporal gains or losses of species, when the lakes were divided into two groups according to whether they are above or below 100 meters above sea level (Fig. 3 in study II; contradicting H3).

In most of the study lakes, water transparency has decreased from the 1940s to the 1970s, when temporal gains have been dominant, and after this period, changes in water transparency have been more sporadic. It is highly likely that between the 1940s and the 1970s, the amount of nutrients has increased in these lakes. The increase of nutrients is also supported by the fact that the increased species in the study lakes benefit from eutrophication (Toivonen 1985; Toivonen & Huttunen 1995). Some of those species (*Typha latifolia*, *Elodea canadensis* and *Potamogeton crispus*) have become dominant macrophytes forming large stands in some lakes (Toivonen 2009). Generally hydrophytes are expected to respond more directly to eutrophication than helophytes, and they are sensitive to anthropogenic impacts (Sand-Jensen *et al.* 2000). As the changes in the hydrophyte assemblage composition and the loss of hydrophytes were higher than those of the helophytes, these findings further support the interpretation of increased nutrients. Johnson and Angeler (2014) found that in lowland European streams macrophyte alpha diversity decreased with elevated nutrients, but beta diversity remained high. Moreover, Sass *et al.* (2010) found that agricultural development explained more of the variation in macrophyte species richness and abundance than urban land use in lakes in Wisconsin, U.S.A. However, in northern and naturally oligotrophic fresh waters, macrophyte species richness at the local scale usually increases with increase of nutrients, i.e. from oligotrophic to slightly eutrophic conditions (Rørslett 1991; Rintanen 1996). Another study also conducted in central Finland found that species turnover (i.e. beta diversity) was related to changes in agriculture between the 1930s and 1996, and the number of new aquatic macrophyte species increased in the same areas where the agricultural areas decreased (Hilli *et al.* 2007). Thus, it seems that some aquatic macrophyte species benefit from a decrease in agricultural area with declining nutrient input in small boreal lakes (e.g. Hilli *et al.* 2007).

As mentioned earlier, several studies have shown that pH has a strong influence on aquatic macrophyte communities (reviewed by Lacoul & Freedman 2006). Usually photosynthetic actions of algae cause the increase in pH values, thus indicating increasing nutrient concentrations (Kirk 2011). However, pH has both decreased and increased when the gain of species has been the prevailing process in the study lakes (i.e. between the 1940s and the 1970s). Thus, it is difficult to say with certainty what could be the relationship of decreasing pH and the gains of species in the study lakes. As pH scale is logarithmic, calculating the temporal change in pH units between the survey decade pairs and using these metrics of changes in the analysis, affects the reliability. However, the calculated changes of pH values can be seen as an index of the real pH changes. This should not have an effect on the direction of the change, or the main patterns found (Grogono 1980), albeit the mathematical basis of calculating change in pH units is not entirely correct. In addition, when comparing the 1940s and the 1970s, pH measurements were based on the summertime values, as there were no fall pH measurements available from the 1940s. And as already mentioned, summer pH values are sensitive to variation in primary production of phytoplankton and submerged macrophytes during the growing season (Kirk 2011), thus further affecting reliability of pH values.

Other studies that have utilised TBI have found inconsistent patterns related to gains and losses (Kuczynski *et al.* 2018; Brice *et al.* 2019). Moreover, studies that have used different indices have found distinct patterns: species gains overriding species losses at regional scale in Denmark (Finderup Nielsen *et al.* 2019) and roughly balanced extinctions and colonisations in 158 assemblages across the globe (Dornelas *et al.* 2019). However, it is important to note that this study is mainly based on comparing adjacent sampling periods, while these previous studies are based on reference to a single baseline time period. Nevertheless, it seems that the temporal losses and gains of species are highly context dependent, probably depending on both temporal and spatial scales, as well as the intensity of anthropogenic disturbance.

There are only a couple of studies focusing on the temporal beta diversity of aquatic macrophytes covering several decades and several sites, and these studies have found changes in community composition through time using other metrics and indices (e.g. Virola *et al.* 1999; 2001; Hilli *et al.* 2007; Baastrup-Spohr *et al.* 2017). Studies that have concentrated on only one lake have found shifts from submergent-dominated to emergent-dominated floras (e.g. Egertson *et al.* 2004). This shift has also been detected in a few of the study lakes of this thesis (Ranta & Toivonen 2008) that have been affected more strongly by humans, and this can also be seen in a slightly higher loss of hydrophyte species compared to helophytes. Studies have also found declining trends in temporal beta diversity of macroinvertebrate and fish communities in stream environments (Cook *et al.* 2018; Kuczynski *et al.* 2018; Larsen *et al.* 2018). It is possible that some stream-dwelling organism groups are more exposed to anthropogenic pressure compared to lake macrophytes (Korhonen *et al.* 2010). Fish and most macroinvertebrates have to rely on only spatial dispersal to re-colonise sites (Heino *et al.* 2015), but lake macrophytes can also restore their occupancy by germination from a seed bank or by re-growth from belowground rhizomes and roots (Harwell & Havens 2003). This kind of re-colonisation could be called "*dispersal in time*" (Buoro & Carlson 2014).

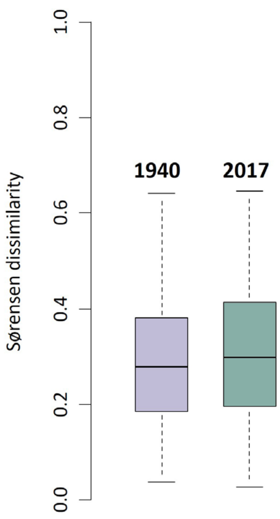
In the study lakes, there have been some lake-specific changes during the study period, and especially during the period between the 1940s and 1970s. Lowering the water level in some lakes and the end of grazing in shore areas have probably had effects on temporal changes in aquatic macrophyte occupancy. It is also highly likely that some species which have increased their occupancy in certain lakes, such as *Iris pseudacorus*, have been planted in the lakes deliberately due to their aesthetic values. These kinds of changes are quite hard to detect. The dynamics of muskrat populations have probably caused changes in species abundances due to their grazing and housing behaviour. Especially, muskrats have had impacts on dominant macrophyte species, for example, by grazing more nutrient-rich species such as *Schoenoplectus lacustris*, *Equisetum fluviatile* and *Nymphaea alba* ssp. *candida*, which again has contributed to the increase of *Typha latifolia* in these lakes (Toivonen & Meriläinen 1980). In addition, as muskrat's feeding habits can create patches in vegetation and thus create different succession stages and the increase of small herbaceous helophytes and other weak competitors, this might be one reason for the gain of species from the 1940s to the 1970s. After the 1980s, population sizes of muskrat have decreased (Nummi 2020). Interestingly, these changes are not visible in the presence-absence data, but this might be the reason behind the variation in temporal losses and gains of species across the landscape.

5.5 Functional changes (Q3)

In study III, the aim was to answer the question of whether functional features of vascular aquatic macrophytes have changed or remained the same at the community and species levels after a period of 70 years. There were no drastic changes in the functional features, even though some changes were detected. Mean functional beta diversity was almost the same in the 1940s and 2017 based on Sørensen dissimilarity index (Fig. 15). However, there have been changes in functional community-environment relationships, as partly different environmental variables explained functional community composition between the decades (Fig. 15). Only depth of the lake explained the spatial variation in functional community composition in both decades (partly supporting H5). Furthermore, the changes in functional richness were partly linked to changes in the environment across decades, as changes in agricultural area were related to changes in functional richness (partly supporting H6). Nonetheless, there was no clear pattern of species with certain sets of traits becoming more common or rare during the study period (Fig. 15; contradicting H7).

In the 1940s, the variables that best accounted for the variation in functional community composition were elevation (representing lake landscape position), depth of the lake and the amount of ditches. In 2017, pH, depth of the lake and lake area were the most important variables (Fig. 15). The amount of explained variation (adj. R^2) in both time periods was almost the same: 19.9 % in the 1940s and 20.4 % in 2017. The relative strength of competitive interactions in a specific functional niche can vary with water depth in macrophyte communities (Fu *et al.* 2014b). Colonisation depth and minimum light requirements vary with macrophyte growth forms (Middelboe & Markager 1997), which was one of the functional traits. In the study area, elevation represents lake landscape position and is temporally a very stable variable and many environmental characteristics are related to this gradient. In other glaciated areas,

A



B

	Estimate	Std error	t	P
Intercept	–606.8	182.5	–3.325	0.003
Agricultural area$_c$	–0.029	0.012	–2.495	0.020
Area	0.006	0.002	2.853	0.009
Elevation	–0.043	0.01	–4.338	0.000
North coordinate	0	0	3.324	0.003

C

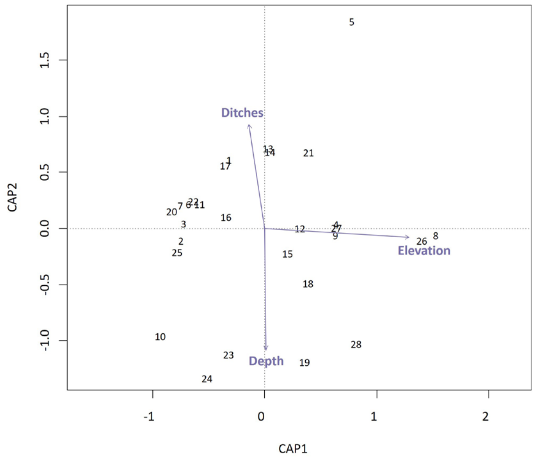


Figure 15. A) Variation in functional beta diversity based on Sørensen dissimilarity index in the 1940s and 2017. N = 28 lakes in both 1940s and 2017. B) Summary of the results of linear regression analysis (response variable = change in functional richness index between the 1940s and 2017). Plots of distance-based redundancy analysis of functional composition of aquatic macrophyte communities in the 1940s (C) and in 2017 (D). The significant environmental variables are shown as arrows in the plots. E, F) Non-metric multidimensional scaling (NMDS) plots of species distribution in functional space. In plot E, species abbreviations are shown, and in plot F, the lines connect each species to its group centroid. Purple = stable species, green = increased species and blue = decreased species.

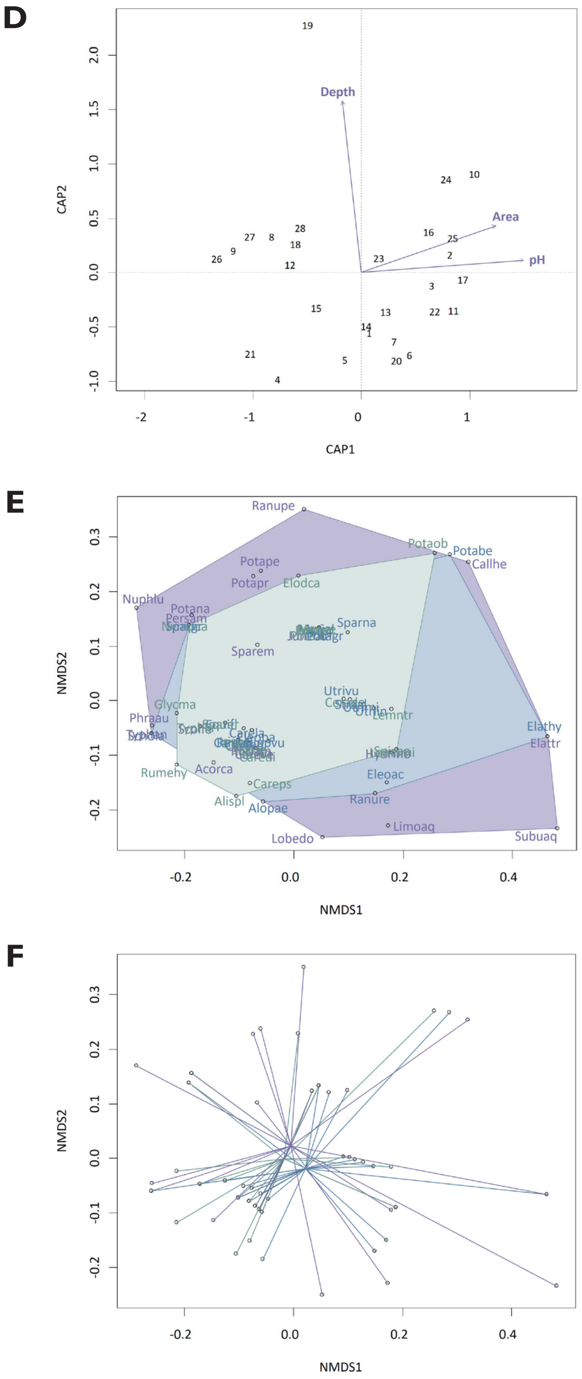


Figure 15. *Continues...*

macrophyte taxonomic community composition has been found to differ along the lake landscape position gradient (Alexander *et al.* 2008). Thus, it was not a surprise that this gradient was also important to functional composition of macrophyte communities.

Ecke (2009) found that drainage ditching rather than land use itself could affect water quality and occurrences of macrophytes. Thus, it was interesting to note that the amount of ditches was an important variable explicitly in the 1940s, as the amount of ditches has increased towards 2017. It is thus possible that ditching has already had effects on macrophyte communities early on, and further ditching did not have additional impacts. With pH, there are similar issues as mentioned earlier. In contrast, in 2017, lake size and pH explained the spatial variation in functional community composition. Larger lakes sustain different functional composition than smaller lakes. Thus, it can be assumed that larger lakes harbour contrasting habitats for biologically and ecologically different macrophyte species, thereby showing functional composition differing from that in small forest lakes. Findings of studies on lake macroinvertebrates have shown that functional composition changes from small to large lakes along with concomitant changes in habitat structural features (Heino 2008).

FRic in the 1940s was generally higher than in 2017. The final LR model included only one non-stable variable, agricultural area$_c$, and three stable variables: lake area, elevation and north coordinate (Fig. 15). The LR model explained 67 % of the variation in the change of the FRic (adj. R^2 value). The lakes at lower elevation in the landscape have had more changes in functional richness between the time points than the lakes in the upper parts of the landscape, further highlighting the importance of lake landscape position in the study area. The changes in functional richness were higher in the larger lakes, even though the pattern was not as clear as with elevation. Zhang *et al.* (2018) also found that functional richness of lake macrophytes was related to environment, as it decreased with the habitat loss from before the 1970s to after the 2000s. Additionally, they found functional differentiation of macrophyte assemblages instead of homogenisation, even though their study area in the Yangtze River floodplain has faced strong human impacts for a long time (Zhang *et al.* 2018). Kim and Nishihiro (2020) found that sexual and pollination traits of lake macrophytes showed noticeable responses to precipitation and land use in Japan from the early 1900s to the 2000s. On the other hand, in stream environments, macrophyte species loss has been associated with change in species traits, as species with traits representing higher mechanical stress tolerance become more abundant (Steffen *et al.* 2013).

This study is based on the assumption that traits should vary more between species than within species (McGill *et al.* 2006; Messier *et al.* 2010). The chosen traits indicate the mean species characteristics revealing the function of the species at the community scale. Therefore, intraspecific trait variability should not be a large issue (Fu *et al.* 2014a; García-Girón *et al.* 2019; Dalla Vecchia *et al.* 2020), even though studies have found that intraspecific trait variability has a role, for example, in mediating relationships of stability-environmental gradients (e.g. Fu *et al.* 2018). It is also important to note that these results are based on four specific traits and other patterns could arise with other traits. The selection of traits was still to some degree limited because there is a lack of high-quality trait information in many cases with more northern and oligotrophic species. However, the used traits were essential and quite robust related to these issues studied, as quite broad trait classes and size categorization were used. In addition, such trait divisions have been used repeatedly with aquatic macrophytes to represent functional diversity (e.g. Zhang *et al.* 2018).

Jarzyna and Jetz (2018) found that temporal functional diversity patterns are scale dependent. Nevertheless, in lake environments, functional diversity patterns should be seen particularly at the landscape level (e.g. Heino 2008). Therefore, spatial scale is probably not a concern in this thesis. Furthermore, the time period covered (~70 years) is enough to observe significant trends in aquatic macrophyte functional changes in case they existed. Nevertheless, van der Plas *et al.* (2020) recently showed that while plant traits can be strongly linked to ecosystem functions within years, they alone are poor predictors of long-term ecosystem functioning. Variability across years, for example differing in weather conditions, limit the ability to predict levels of multiple ecosystem functions (van der Plas *et al.* 2020). Thus, using traits in temporal context seems to be quite complex and needs more investigation.

5.6 Biotic homogenisation (Q4)

The purpose of the fourth research question was to examine if there has been biotic homogenisation or differentiation in vascular macrophyte communities from the 1940s to the 2010s due to anthropogenic impact. There were no signs of a declining trend in spatial beta diversity, i.e. there has been no biotic homogenisation in aquatic macrophyte communities (contradicting H8). Also, temporal beta diversity in each lake did not show increasing degrees of change through time (contradicting H9). Both of these results differ from other studies conducted in marine environments (e.g. Richardson *et al.* 2018), in fresh waters for other organisms (e.g. Donohue *et al.* 2009; Castaño-Sánchez *et al.* 2018; Zhang *et al.* 2019) and studies conducted with aquatic macrophytes (Salgado *et al.* 2018).

McGill *et al.* (2015), who identified the declining trend of spatial beta diversity, proposed that the patterns were unclear and that there were strong influences of context dependency among studies. This seems to be the case in later studies as well, as the results related to spatial beta diversity have been mixed (Winegardner *et al.* 2017; Larsen *et al.* 2018; Wengrat *et al.* 2018). There are only a few studies of temporal changes in spatial beta diversity (Winegardner *et al.* 2017; Larsen *et al.* 2018; Wengrat *et al.* 2018) and even fewer considering aquatic macrophytes. Winegardner *et al.* (2017) did not find changes in spatial beta diversity of lake diatoms between 1850 and 2007, even though they examined a longer time period compared to this thesis. Similarly, Larsen *et al.* (2018) did not find signs of biotic homogenisation when they studied stream macroinvertebrates in 10 streams during 30 years. However, Wengrat *et al.* (2018) found a decreasing trend in spatial beta diversity of diatom assemblages, but only when they studied eutrophic reservoirs instead of the whole set of reservoirs over the past 60–100 years. Thus, it seems that temporal changes in spatial beta diversity patterns are difficult to detect.

Zhang *et al.* (2018) studied temporal (before 1970s compared to after 2000s) changes in compositional dissimilarities of freshwater macrophyte assemblages across the floodplain lakes of the Yangtze River in China. Instead of homogenisation, they found mainly taxonomic and functional differentiation of macrophyte assemblages concomitant to a general decrease in species richness, even though their study area has faced strong and increasing human impacts for a long time (Zhang *et al.* 2018). Similarly, there were no signs of biotic differentiation in the study lakes of this thesis either. Baastrup-Spohr *et al.* (2017) studied lakes in Denmark around 1990 and again around 2010. Using the Sørensen similarity index, they found that similarity of species composition among lakes increased over the study period, resulting in homogenised macrophyte communities (Baastrup-Spohr *et al.* 2017). Salgado *et al.* (2018) studied a combination of contemporary and palaeoecological lake macrophyte data in Northern Ireland. By using Bray-Curtis dissimilarities, they also found within- and among-lake assemblage homogenisation after the 1960s (Salgado *et al.* 2018). On the other hand, and also using Bray-Curtis dissimilarity, Johnson and Angeler (2014) found that aquatic macrophytes did not become homogenised with increasing disturbance in lowland European streams.

In many geographical areas and organism groups, the functional homogenisation process has been noticed to occur, thereby seriously affecting ecosystem functioning (e.g. Bergeron *et al.* 2019). It has even been suggested that the decline of specialist species could cause global functional homogenisation (Clavel *et al.* 2011) and that biotic homogenisation is connected with ecosystem multifunctionality (e.g. Hautier *et al.* 2018). However, there were no changes in species relatedness or functional similarity of communities across decades, suggesting that neither phylogenetic (Winter *et al.* 2009) nor functional homogenisation (Clavel *et al.* 2011) are occurring in the study area. Study III confirmed that there are no signs of functional homogenisation or, on the other hand, functional differentiation, as the multiple-site functional beta diversity remained almost unchanged.

There are probably five partly interdependent main reasons why there were no signs of taxonomic, phylogenetic or functional homogenisation in the study area during the 70-year study period. First, compared to the other areas in the world where biotic homogenisation has been observed (Finderup Nielsen *et al.* 2019; Zhang *et al.* 2019), the changes in environment have been quite modest from the 1940s to the 2010s. Also using Sørensen's dissimilarity index, Elo *et al.* (2018) did not find signs of biotic homogenisation in relatively oligotrophic lakes in Eastern Finland, where human impact is similarly quite low compared to many other areas worldwide. Instead, they detected changes in mean community composition, but they also found early signs of homogenisation as beta diversity in lakes with moderate ecological status was smaller than expected on the basis of the main environmental characteristics shaping community composition (Elo *et al.* 2018). Moreover, earlier studies have found that macrophytes can maintain their abundances and endure at a local site, if environmental changes are small (Sand-Jensen *et al.* 2008). This is probably the reason behind their endurance in the study lakes as well.

Second, despite the ecological stressors in the study lakes, one reason for the small changes in beta diversity can be the high ecological resilience of the lakes (Holling 1973), which is in accordance with the idea that species can keep pace with changes in the environment (for lakes, see a review by Heino *et al.* 2020a). Due to high phenotypic plasticity, both morphological and ecological (Lacoul & Freedman 2006), macrophyte species can probably adapt to modest changes in the environment. Additionally, connectivity is essential for the resilience of freshwater biota and environments (Heino *et al.* 2017). The study lakes have high connectivity to other small lakes and, more importantly, to the two largest water bodies in the area, lakes Roine and Pyhäjärvi (Fig. 3), which can act as colonisation sources for macrophyte species. Because of the high dispersal capacity of aquatic macrophytes by seed and vegetative propagules, and owing to flexible reproductive systems (Eckert *et al.* 2016), spatial connectivity might enhance landscape-level ecological resilience (Allen *et al.* 2016). Moreover, as primary producers, macrophytes can have greater landscape-level resilience than consumers (Johnson & Angeler 2014). Johnson and Angeler (2014) found that macrophyte assemblages did not become homogenised with increased disturbance, although fish and macroinvertebrates did so. This issue is probably related to re-colonisation ability of macrophytes, as mentioned above.

Third, it is possible that the used measures are not the best ones to detect biotic homogenisation. Studies that have found clear signs of biotic homogenisation for aquatic macrophytes are either considering other biodiversity measurements or beta diversity measures or are based on palaeoecological methods (e.g. Salgado *et al.* 2018). However, the used methods have been proved to be efficient in detecting changes in community composition in other systems (e.g. Legendre & Condit 2019). But it is likely, for example, that TBI is more suitable to study shifts is community composition after drastic environmental change (e.g. Legendre & Salvat 2015). However, a more likely reason for the patterns found is the absence of abundance information. Using only binary coefficients, i.e. those based on presence-absence data, instead of quantitative forms of the indices can produce less-sensitive results (Legendre 2014). Hillebrand *et al.* (2018) stated that presence-absence data should not be exclusively relied on when studying biodiversity change. Using only presence-absence data can overemphasise the role of rare species in ecosystem function, while common and dominant species have a strong role when using abundance information (Anderson *et al.* 2011). Also, it is likely that there have been changes in a species' abundance long before this species is completely lost from the site. Ot'ahel'ová *et al.* (2011) found during a 34-year time period that macrophyte species richness did not change much in floodplain lake ecosystems, although the abundance of macrophytes fluctuated over the years. Therefore, the use of abundance data would reveal a more detailed picture of temporal biodiversity change. It is also possible that relatively modest changes in land use in the study area do not result in altered beta diversity based on presence-absence data. Even though changes in spatial and temporal beta diversity patterns were not found, it is possible that there have been changes in species abundances. For example, there could be a loss of functional beta diversity due to more specialised species becoming rare but not extinct in some lakes.

Fourth, in this thesis, biotic interactions of aquatic macrophytes are not considered. Recently, different types of biotic interactions have received more attention also in a spatial context, and their effects on spatial variation in community composition are gaining evidence (e.g. García-Girón *et al.* 2020a). In addition, preliminary results indicate that in these study lakes, biotic interactions have an important role, as historical contingency via priority effects seems to counteract environmental change across decades (García-Girón *et al.* 2020b). Moreover, it has been found that native submerged and floating-leaved aquatic macrophyte species may resist invasion at small spatial scales in communities where competition among individuals contributes to community structure (Capers *et al.* 2007).

Fifth, all the issues mentioned above combined with multiple interacting lake-scale stressors, the complex community-environment relationships and stochastic processes might also explain why there were no signs of biotic homogenisation and the relationships to anthropogenic changes were weaker than expected. In addition, when the possible effects of climate change (current warming trend; Heino *et al.* 2009) are added to the list of these factors, a quite multidimensional puzzle is created.

5.7 Limitations of temporal studies and datasets

To comprehensively understand the impact of anthropogenic activities on biodiversity, we must understand how biodiversity has changed over time and what are the underlying processes. However, as with all temporal biodiversity studies (Dornelas *et al.* 2013), there are some issues related to data used in this thesis that can have an effect on the interpretation of its findings. The most common limitations with temporal studies are related to temporal extent, as long time series are often unavailable. The dataset used in this thesis covers a wide temporal extent, including five different decades, but whether the major changes in community dynamics and environment have taken place between the specific survey periods (e.g. during the 1960s or the 1980s) is unknown. Moreover, as the baseline was the 1940s, the full range of impacts of major anthropogenic pressures are probably underestimated (Mihoub *et al.* 2017). Another general issue in temporal studies is the sampling variation (Magurran 2011). It is possible that there is some sampling variation between the surveys done in the 1940s and after. Thus, it is possible, for example, that the changes in temporal beta diversity between the 1940s and 1970s are in some degree due to this sampling variation. After the 1940s, this is hardly an issue as the same person has participated in and instructed the field work. Closely related to sampling variation is the precision of data. Only presence-absence data were used in this thesis, as with historical datasets focusing on the whole lake area, presence-absence data are a more reliable source of information compared to coverage information representing abundance.

Another common limitation in temporal studies is the lack of environmental information. This issue can be overcome by using different kinds of proxy variables. In this thesis, there is a lack of some important environmental variables, such as nutrients and sediment characteristic. Using land use variables derived from basic maps and leaning on the water transparency variable, this issue can be overcome at least in part. In addition, in this thesis, the environmental variables and species information are based on the whole lake. There is probably variation inside lakes both in environmental conditions and species distribution, but unfortunately this issue cannot be overcome.

In addition, conditions in a survey point can affect the quality of sampling and can thus hinder detecting overall long-term trends in community compositional changes. In 2017, (2010s) the spring and early summer were relatively cold and the thermal growing season was slightly late compared to the 2000s sampling period (Finnish Meteorological Institute 2020a; 2020b). Late-maturing species that are challenging to identify in their early phases, such as species from the genus *Sparganium*, were not necessarily properly developed during the field work. However, inter-annual variations in aquatic macrophytes' occupancy are probably not that sensitive to short-term variation in annual weather conditions, as macrophytes can endure at a local site if environmental changes are small (Sand-Jensen *et al.* 2008), improving the reliability of the findings (e.g. Stuble *et al.* 2020). But still, the delay in thermal growing season can be one reason why the temporal loss of species was prominent in the lakes from the 2000s to the latest sampling period. It is thus possible that one exceptional year regarding weather conditions can hinder detecting overall long-term trends in community compositional changes (e.g. McCain *et al.* 2016; Stuble *et al.* 2020). van der Plas *et al.* (2020) also brought up the issue of differing weather conditions when plant traits are used to predict levels of ecosystem functions across years. As climate change has been predicted to cause more extreme weather conditions (Seneviratne *et al.* 2012), this issue may become even more relevant in the future and affect studies based on only a single field season. Moreover, if only the first (1940s) and the last (2010s) sampling decades were looked at, it would have seemed that both temporal losses and gains of species had been equally present. However, inspecting decades within this 70-year-long time period, a more detailed picture of temporal beta diversity patterns was gained. These issues further highlight the fact that relying only on one or two survey points in time can result in limited knowledge of the ecological phenomenon under study.

5.8 Recommendations for further research

There is an urgent need for information on how biodiversity is changing in time. Future studies should try to utilise data from several decades to overcome the typical limitations of temporal information (Dornelas *et al.* 2019; Stuble *et al.* 2020). Additionally, as spatial and temporal beta diversity seem to be highly context depended, there is a need to study these in several geographical areas as well as at different temporal and spatial scales. There is a need to understand the more stable environments under ongoing global change, and spatial and temporal beta diversity should be studied with different levels of anthropogenic impacts.

There is also an urgent need for a comprehensive database of aquatic macrophyte traits, species-specific multi-trait data, which covers not only species from oligotrophic and northern environments, but also species that are not traditionally included in macrophyte studies, for example species in the genus *Carex*. As macrophytes can restore their occupancy by re-growth from belowground root and rhizomes or by germination from a seed bank (Harwell & Havens 2003), root and rhizomes traits would add an interesting aspect to temporal lake studies (Dalla Vecchia *et al.* 2020). Moreover, future studies should take into account intraspecific trait variability, especially in studies focussing on aquatic macrophytes. There is also a shortage of true phylogeny for many aquatic macrophyte species. This information is needed if we really want to understand the loss of evolutionary diversity and the factors causing it.

As lakes are not completely isolated islands in 'the sea of land' (Heino *et al.* 2020a), lake position in the landscape, reflecting both natural connectivity and lake characteristics, should be taken into account in lake biodiversity studies to increase our understanding of landscape-scale biodiversity-environment relationships. This should also be considered in conservation and management planning. Moreover, recent findings related to the importance of biotic interaction in lake environments (García-Girón *et al.* 2020a; 2020b) highlight that much remains to be studied in order to understand comprehensively temporal and spatial patterns in aquatic macrophyte communities in boreal lakes.

6 Concluding remarks

The main goal in this thesis was to study spatial and temporal biodiversity patterns of vascular aquatic macrophyte communities in small boreal lakes during a period of 70 years. The focus was on beta diversity-environment relationships and different dimensions of biodiversity with specific attention to functional features. This thesis increases our knowledge on often-neglected temporal biodiversity patterns in lake environments. The findings help to understand how vascular aquatic macrophyte communities respond to changes in the environment across decades and may unravel the functional stability of macrophyte communities and driving factors at the landscape level.

Based on the results of this thesis, eight main concluding remarks can be made:

- Vascular aquatic macrophyte communities showed only moderately different spatial beta diversity patterns in relation to human impact across decades. The patterns of different dimensions of spatial beta diversity diverged only slightly from each other. Lake position in the landscape, reflecting both natural connectivity and lake characteristics, explained the patterns found in spatial beta diversity, probably because the study area has faced only modest changes in land use from the 1940s to 2010s when compared globally, and there is a strong lowland-upland gradient due to postglacial processes.

- The temporal change in aquatic macrophyte communities at the lake level has been modest through the decades. Nevertheless, it seems that even relatively modest changes in the environment affect temporal gains and losses of species at the lake level. For example, aquatic macrophyte species, especially hydrophytes, seem to benefit from the decrease in agricultural area with declining nutrient input into small boreal lakes.

- Even though there were no signs of functional homogenisation or differentiation, the changes in the environment have affected functional community composition and changes in functional richness to some extent.

- Although the focus of this thesis was on a single lake district, the patterns detected in macrophyte beta diversity within and across decades are likely to represent situations in the extensive boreal and glaciated areas of Eurasia and North America, with largely similar species pools in many regions. Therefore, lakes across the boreal region and areas that have faced glaciation and postglacial processes might be resistant against moderate levels of human pressure.

- By using the spatial and temporal beta diversity perspective, this thesis highlights the fact that even though biotic homogenisation is a pervasive problem globally (Reid *et al.* 2019), it is not an unambiguous process acting similarly at all spatial and temporal scales or in different environments and different organism groups. However, it is also important to emphasise that the results presented in this thesis do not imply that biotic homogenisation across a longer time period is not possible.

- When comparing the results of this thesis to other studies, it is clear that when studying beta diversity patterns and biotic homogenisation, the context dependency, the degree of human pressures, the scale of the study (both spatial and temporal), the organism group studied, as well as the measurements of beta diversity are important when results are interpreted.

- Relying only on one or two survey points in time can result in limited knowledge of the ecological phenomenon under study, and an exceptional year in terms of weather conditions can hinder detecting overall long-term trends in compositional changes, especially under the ongoing climate change. This should also be taken into account in conservation planning.

- Albeit studying biodiversity patterns in a temporal context is full of uncertainties, temporal studies and long-term monitoring programmes are needed to comprehensively understand the impact of anthropogenic activities on biodiversity. However, when biodiversity changes are studied, the quality of temporal datasets should always be considered carefully.

As aquatic macrophytes have crucial functional and structural roles in lake environments, preserving diversity of functional features in aquatic plant communities should be taken into account in land use planning and conservation actions. Understanding temporal and spatial trends has important implications for biodiversity conservation. Therefore, community composition should be taken into account, especially in the protection of landscape-level and local biodiversity (Socolar *et al.* 2016, Hillebrand *et al.* 2018). In addition, long-term monitoring programmes of lake biota are needed if we want to forecast and prevent harmful changes or restore lake environments judiciously and accurately. And, finally, it is worth remembering that there is no single measure of biodiversity (Gaston & Spicer 2004). As species and communities can respond in various ways to different anthropogenic pressures, different metrics and indicators are needed to understand biodiversity change and to plan effective conservation programmes (WWF 2018; Secretariat of the Convention on Biological Diversity 2020).

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