Multi-scale effects of hydrological and landscape variables on macrophyte richness and composition in British lakes

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STATEMENT OF ORIGINALITY

I hereby confirm that this PhD thesis is an original piece of work conducted independently by the undersigned and all work contained herein has not been submitted for any other degree.

All research material has been duly acknowledged and cited.

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Date: 31st of August 2016

GENERAL ABSTRACT

Macrophytes are an integral component of lake littoral zones and play an irreplaceable role in maintaining the ecological balance of wetlands. Recent research has highlighted the role of lake-scale environmental factors (or “filters”) and catchment- and/or landscape-scale processes in explaining variation in macrophyte communities across different scales. In this work, the effects of land-use and connectivity on macrophyte communities were explored at two contrasting spatial scales (i.e. *local catchment* scale and *topographic catchment* scale).

At the *local catchment* scale, the results revealed strong scale-dependency. The effects of land use on macrophyte richness were most apparent at fine spatial scales (within 0.5 to 1 km) and significantly outweighed the importance of hydrology. In terms of growth form composition, the effects of hydrological connectivity were stronger than those of land use, with the greatest effect observed at an intermediate distance (~ 5 km) from the lake.

The study on the hydrologically-connected lake pairs indicated that environmental filters were more influential in explaining species turnover than lake connectivity. Interestingly, geographical connectivity explained more of the variability in species turnover than hydrological connectivity. Moreover, the relative importance of environmental filters and lake connectivity to species turnover was very sensitive to the degree of human disturbance.

The multi-scale interaction analyses indicated the effect of lake alkalinity on macrophyte composition is strongly influenced by catchment scale variables including hydrological features and land use intensity. The turnover in macrophyte composition in response to variability in alkalinity was stronger in catchments with low lake and stream density and weaker in catchments with a more highly developed hydrological network. Lake abiotic variables were found to have more influence on macrophyte composition in lowland catchments with a higher intensity of human disturbance. Moreover, the catchment-scale factors promoting the establishment of different communities were found to vary between catchments depending on lake type, the degree of environmental heterogeneity and hydrological connectivity.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

KEY CONCEPTS

Local catchment: Also called lake riparian zones or lake marginal zones are advocated as environment tools to reduce the effect of anthropogenic activity on lake water quality and aquatic vegetation (Parkyn, 2004).

Topographic catchment: A basin-shaped area of land that drains surface and sub-surface water with sediments and other materials to a receiving body of water.

Freshwater ecoregion: A ecological unit including homogenous freshwater systems and the surrounding terrestrial systems (Omernik, 1987).

Landscape buffer: Concentric buffers extending from the lake shoreline at different spatial distances.

Catchment buffer: A series of the combined zones which are represented by the intersection of the *landscape buffers* and the *topographic catchment* boundary.

Landscape connectivity: The degree to which the landscape facilitates or impedes movement among resource patches.

Geographical connectivity: The Euclidean distance between the centroids of any two paired lakes.

Hydrological connectivity: The length of water courses between two connected lakes using a two-dimensional vector map of the stream network.

Lake-scale environmental filter: A set of lake physico-chemistry variables that influence that ability of organisms to colonise and persist in new habitats.

Broad-scale processes: Refers collectively to the environmental and ecological processes (such as dispersal) that occur at the catchment and/or landscape scale.

Meta-community: A set of interacting communities which are linked by the dispersal patterns of multiple and potentially interacting species.

Chapter 1 – General Introduction

1.1 General background

Lakes make up two percent of the Earth's surface area and provide 85% of the planet's freshwater (Gleick, 1993). As an aquatic species gene pool, lakes are one of the ecosystems most vulnerable to anthropogenic disturbance anywhere, yet play an important role in regulating the impacts on catchment perturbation on downstream water resources. In addition, lakes provide fundamental ecosystem services and there is an increasing awareness of their importance in biogeochemical cycling (Bastviken et al., 2011).

Pollution from point (i.e. Industry and sewage treatment works) and diffuse (i.e. agricultural runoff) sources continues to impact on lakes in many regions due to long-term land use change and agricultural intensification. Nutrients carried into rivers through runoff, are disembogued into the lakes. This can disrupt the ecological balance of lakes and cause eutrophication. Lake eutrophication results in the degradation of submersed macrophytes and an increase in the intensity of phytoplankton blooms. It reduces ability of lakes to self-purify and can lead to a collapse in the structure and function of lake ecosystem (Makkay et al., 2008).

Macrophytes are aquatic vascular plants and algae. Table 1.1 summarises the different growth forms of aquatic vascular plants and provides examples of common species. Submersed macrophytes are adapted to survive in environments with very low oxygen and light; the former is obtained through the aerenchyma. Other growth forms, such as emergent and free-floating macrophytes, have their leaves in direct contact with the atmosphere to obtain sufficient oxygen.

Table 2.1 Introduction of macrophyte based growth forms

Growth forms	Features	Example species
Emergent	The plant is rooted in substrate, while the upper part is out of the water.	*Sparganium, Ranunculus*
Free-floating	The whole plant is floating on the water with its specific organizational structure adapting to the floating environment.	*Lemna.minor, Lemna.trisulca*
Floating-leaved	The plant is rooted in substrate, with plant leaves in direct contact with the atmosphere.	*Nuphar.lutea, Nymphaea.exotics.*
Submersed	The whole plant is growing below the water surface and is rooted in the substrate with leaves floating in the water.	*Utricularia, Potamogeton*

Macrophytes provide numerous ecosystem services for the lakes such as sediment stabilization and the sequestration of pollutants, release of oxygen into water through photosynthesis and providing habitat for fish and other aquatic organisms. In addition, macrophytes has been used as a key bio-indicator for the assessment of lake ecological status by EU Water Framework Directive (2000/60/EC).

Macrophytes can uptake nutrients (e.g. nitrogen and phosphorus) from the sediment or lake water. The ability of macrophytes to store nutrients and pollution in a short-term makes them a useful tool to control eutrophication, particularly if their biomass is harvested annually. Many techniques have been developed for the *in situ* restoration of lakes and other water bodies through manipulating and managing macrophyte communities (Gumbricht, 1993; Sooknah & Wilkie, 2004; Hu et al., 2010).

The biogeographical distribution patterns of macrophytes in freshwater habitats (e.g. lake, pond, stream) have been previously investigated (Barendregt & Bio, 2003; Feldmann & Noges, 2007; Weithoff et al., 2010; Keruzore & Willby, 2014; Steffen et al., 2014). The distribution patterns of macrophyte assemblages differ in lakes and streams due to differences in nutrient availability, mean depth and flow. Generally speaking, individual macrophyte species have a restricted pattern of distribution in freshwater systems because of the following three factors:

- Ecological traits, including the ability to disperse, are important in determining whether or not the species can arrive and survive in any given site. Species may fail to arrive at the site because of the restricted power of dispersal. Ecosystems that occur either in isolation or at large distances from the original source have a significant influence on the dispersal of the species;
- Lake physico-chemistry is fundamentally important to the distribution patterns of macrophyte (e.g. as an environmental filter). Macrophyte species can have very broad or highly specific environmental tolerances and this often determines whether a species is commonly found over a wide environment gradient or restricted to a more limited range (e.g. clear, low alkalinity waters).
- Lake connectivity describes the degree of spatial connection between individual water bodies. Water bodies may be connected geographically if they are located in close proximity (relative to the ability of species to disperse) or hydrologically if they are connected by temporary or permanent flow of water between sites. Lake connectivity can significant affect the ability of macrophyte species to disperse and colonise new sites.

1.2 Scientific background and objectives

1.2.1 Catchment Ecology (or Watershed Ecology)

The catchment (sometimes also referred to as the watershed) is defined as the region that drains water, sediment and dissolved materials into a receiving water body or outlet. It is a functioning natural system with a variety of resources (e.g. biotic and abiotic components) interacting with each other in order to perform processes (e.g. transporting sediment and water) and generate products (e.g. biological communities).

Catchment hydrology is the science of water in its various forms (solid, gas and liquid) in the land area of a catchment including its distribution, circulation, chemistry and physical properties. The unidirectional flow generated by gravity in streams and rivers, connects the lakes within the catchment. The characteristics of water flow include stream density, water velocity, and stream discharge and turbulence. Stream density, for example, defined as the total length of streams divided by the total area within the catchment, which is influenced by the climate and physical features of the drainage basin. The degree of stream density development is related primarily to geology. For example, impermeable ground and exposed bedrock result in an increase of surface water runoff as well as a higher stream density. Catchments with steep topography tend to have a higher stream density than those with more gentle topography. Catchments with a high stream density have a shorter response time to precipitation events and flooding.

However, degraded catchments often have lost some of their ecological function and, therefore, provide fewer environmental and societal benefits. It is clear that recognizing and protecting vital components (such as stream connectivity, nature vegetation) and functions of natural system is a priority for maintaining the health of freshwater ecosystems.

1.2.2 Human disturbance on catchment ecology

Anthropogenic disturbance can have a significant impact on the sustainable functioning of a catchment system. For example, (i) point source and diffuse pollution has been reported to have a deleterious influence on lake water quality and ecosystem resilience; and (ii) disturbance to catchment hydrological process (e.g. water drainage and abstraction) can have a potentially long-term effect on lake abiotic and biotic conditions. In addition, the anthropogenic disturbance has an influence on the catchment-scale hydrological regime. For example, sediment erosion may change the shape of the stream bed, and consequently influence the discharge of water flow. Dams and other barriers, built for flood control and energy generation, also change the natural hydrological regime and disrupt the sediment and nutrient supply to the downstream.

1.2.3 Research objectives

The controls on macrophyte species diversity are complex and recent research (Jacquemyn et al., 2007) has shown that lake-scale environmental filters can be constrained and shaped by catchment- and/or landscape-scale factors such as land use and lake connectivity. Until now, few studies (e.g. Soininen et al., 2007) have focussed on the impact of lake connectivity on macrophyte species composition at the *topographic catchment* scale. The research presented here was designed to identify lake macrophyte species composition response to hydrological and landscape factors acting at two specific spatial scales (*local catchment* scale and *topographic catchment* scale). This research can inform management at the catchment scale to protect lake biodiversity.

1.3 Study sites

This work focuses on lakes located in mainland Britain, although the approaches developed have generic value. A total of 30 large, independent catchments were selected, and all of the study catchments contained two or more sub-catchments (Figure 1.1). The catchments were selected to include variability in latitude, altitude, geology, land cover and the intensity of human disturbance.

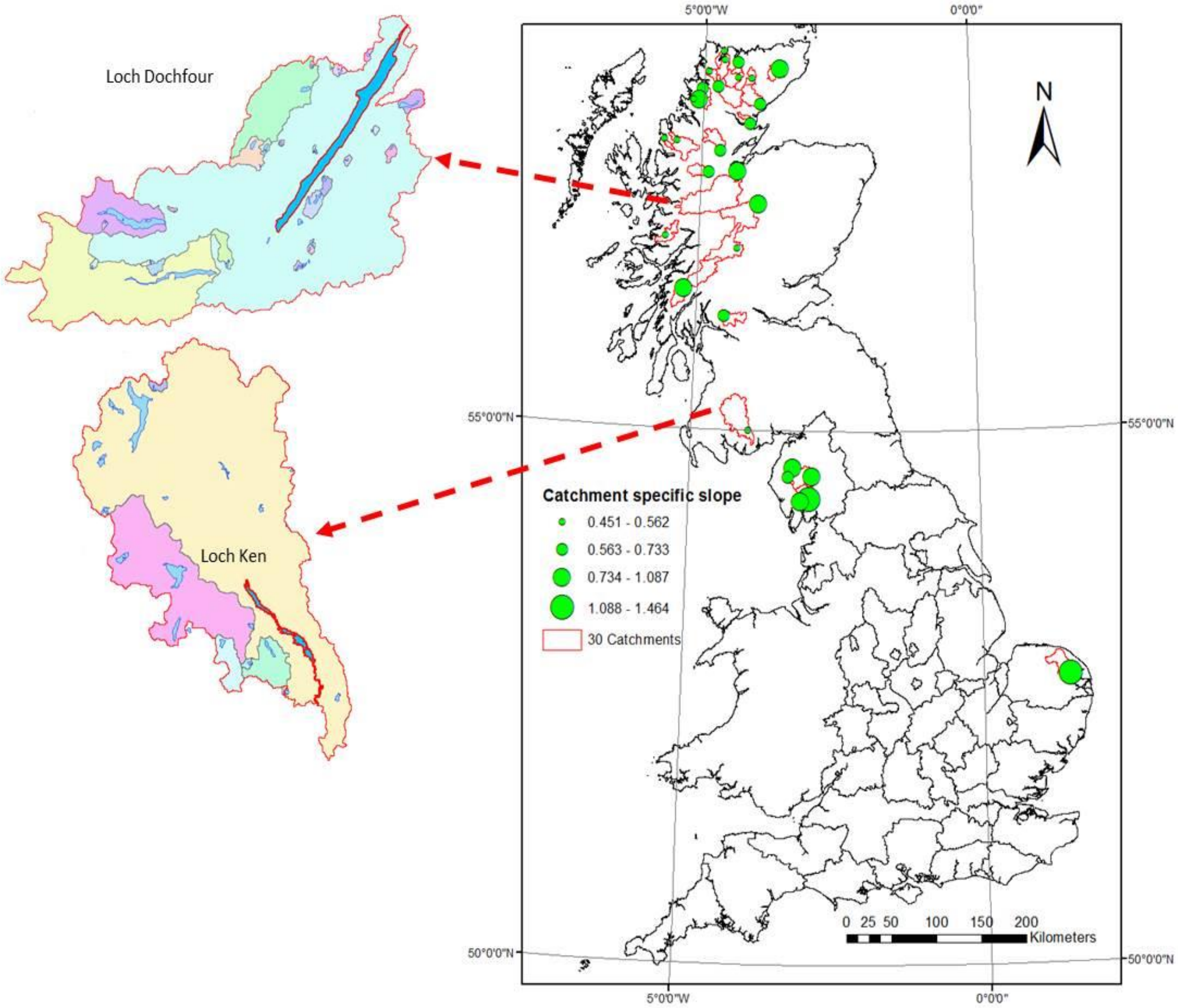


Fig. 1.1 Location of study catchments as well as sub-catchments (showing Loch Ness and Loch Ken as examples)

1.4 Research results introduction

The research presented in this thesis is organised into four chapters, consisting of a literature review on scale-dependency and multi-scale interaction of lake aquatic vegetation (Chapter 2), followed by three primary research manuscripts. Chapter 3 documents the impact of hydrology and landscape features on macrophyte species richness in lakes with the application of GIS-based buffer analysis. The study selected 90 upland British lakes as research objects and compared the role of drivers at catchment and landscape scale in explaining the lake macrophyte richness. Chapter 4 aimed to determine what drivers explain patterns of macrophyte species turnover between lakes. The degree of hydrological and geographical connectivity between lake pairs was measured and the relative importance of each assessed in determining species turnover. Chapter 5 evaluated the influence of lake- and catchment-scale variables, and their interaction, on the beta-diversity of lake macrophytes using an approach based on cross-scale analysis.

Chapter 2 – Scale-dependency and multi-scale interaction of lake aquatic vegetation: A review

2.1 Abstract

This chapter reviews current literature on multi-scale environmental pressures and their interaction in structuring aquatic plant (or macrophyte) communities in lakes and wetlands. It has been reported that lake-scale environmental filters and broad-scale processes control the distribution of macrophyte communities within freshwater ecosystems. This chapter identifies current research gaps in our understanding of the interaction between these scale-dependent processes and the potential implications for the conservation and management of freshwater ecosystems.

Lakes and streams are not ecosystems in isolation since they connect with the wider hydrological network across the landscape. The main factors and processes which control macrophyte species composition in lakes are lake physico-chemistry variables, landscape factors (e.g., lake connectivity) that operate over different spatial scales (from the catchment- to the continental-scale) and the degree of habitat connectivity as this directly influences the dispersal ability of plants. Whilst the composition of lake macrophyte communities can be considered to be a result of the interaction between lake-scale environmental factors and catchment- and/or landscape-scale factors, it is the lake environmental factors that often exert the greatest influence on macrophyte species composition (the so-called "environmental filter" effect).

Despite the apparent importance of the lake environment in shaping the distribution of macrophyte communities in lakes, relatively little is understood about the landscape factors in constraining this relationship. In particular, there has been a lack of quantitative analysis of the importance of different environmental drivers of macrophyte composition at different spatial scales, partly due to the difficulty in obtaining large datasets. Consequently, most studies have focused on the drivers of macrophyte composition at the lake scale with far fewer examining the important of regional scale factors. This is further complicated by the possible existence of interaction between lake- and regional scale factors in determining the composition of macrophyte species in lakes. There is a need for an improved understanding of these interactions to inform regional management strategies to restore and maintain good ecological status in lakes and other freshwater systems.

2.2 Introduction

Lakes represent important aquatic gene pools in the landscape as well as an important link between various elements of the wider freshwater meta-ecosystem and key regulators of change occurring within the catchment (Mitsch & Gossilink, 2000). Nutrient enrichment from point and non-point sources has, however, disturbed the delicate stoichiometric balance of freshwater ecosystems during rapid phases of urbanization and agricultural intensification during the 20th and early 21st centuries (Rasmussen & Anderson, 2005). The resulting processes of eutrophication and the degradation and loss of diverse macrophyte communities has reduced the ecological integrity, resilience and function of lake ecosystems in the UK and globally (Makkay et al., 2008).

Macrophytes play an irreplaceable role in maintaining the ecological balance of lakes contributing significantly to aquatic primary production and the regulation of nutrient cycling (Thomaz & Cunha, 2010). The latter is particularly important for controlling the availability of nutrients and suppression of algal blooms. At the lake scale, the relative importance of top-down control of phytoplankton by zooplankton (Carvalho, 1994) and bottom-up control (Jeppesen et al., 1997) by nutrients in maintaining high plant abundance is recognised (Center et al., 2014). As a result, the use of macrophyte in the restoration of freshwater bodies has become a well-established approach (Baart et al., 2010).

The purpose of this chapter is to review the literature on the scale-dependency and multi-scale interaction of environmental factors that influence lake biodiversity, especially in relation to aquatic vegetation. While there are a multitude of studies on a range of environmental factors that control the richness and diversity of freshwater aquatic species, many of these studies considered the issue at a single scale and from a site-specific standpoint.

2.3 Background review

There is a mutual interaction and control between the macrophyte community and the freshwater environment, whereby a change in one can precipitate significant change in the other (Lacoul & Freedman, 2006; Oťaheľova et al., 2007). The growth environment for macrophytes can be viewed as a three dimensional space (e.g. a vertical and lateral gradient) and extends through time (i.e. annual cycles of solar radiation). There have been studies of strong vertical environmental gradients, such as climate (Peltier & Welch, 1970; Verschuren et al., 2000), light (Barko et al., 1982; Schwarz et al., 2000; Herb & Stefan, 2003) and temperature (Dale & Gillespie, 1977; Dale, 1986; Olesen & Madsen, 2000), and their influence on the growth of macrophyte. For example, light is a key limiting factor for macrophyte growth, and such impact leads to an improvement in the quality of lake water. Reductions in nutrient loads improve the light climate through reduced algae biomass. The theory of alternative stable states is based on this relationship: hypothesing that a shallow lake can have clear water dominated by macrophytes or turbid water dominated by phytoplankton within a certain range of nutrient concentration (Scheffer et al., 1993; Janssen et al., 2014).

There is, also, the existence of similar but lateral environmental gradients. It is difficult to define precisely what controls the dispersal of macrophytes within a given hydrological system, but it is often a combination of factors including: water chemistry (e.g. phosphorus and nitrogen) (Smolders et al., 2002; Jampeetong & Brix, 2009); flow of chemistry and energy (Mulholland & Hill, 1997); and upstream pollution (Lougheed et al., 2001). Disturbance is also an important factor determining macrophyte community composition in lakes. Undisturbed freshwater systems facilitate continuity in environmental conditions and promote the establishment and persistence of macrophytes and their ability to disperse to new environments.

Research on macrophyte communities originally tended to divide the lake environment into two parts: the physical and the biological environment (Karus & Feldmann, 2013). However, this is artificial and ignores some indirect effects of other environmental organisms. Lake environments are dynamic, changing over time (cyclically or cumulatively) and influenced by changes in water flow and energy. Thus lakes are complex environments comprised of many interrelated components that interact internally but also with the external catchment- and/or landscape-scale variables. It is important to view lakes as integral components of a wider meta-ecosystem.

The vast majority of studies on the diversity of macrophytes in lakes have focused mainly on community responses to and impact on nutrient availability and cycling. In contrast, the effect of the hydrological regime on lake macrophyte communities has been comparatively neglected. Studies on lake systems have typically emphasised the influence from human disturbance. However, the evidence in the literature indicates that, whilst factors operating from local to broader scales individually impact on the composition of freshwater macrophyte species, there have been few studies assessing the interaction between processes operating at different scales and their collective role in determining the distribution of freshwater macrophytes.

2.4 Factors controlling macrophytes in lakes at multi-scale

For a long time, the main environment determinants of macrophyte communities have been considered to be lake scale biotic and abiotic variables; this is supported by the niche theory (Zillio & Condit, 2007). Environmental factors, such as altitude (Chappuis et al., 2011), lake depth (Vincent et al., 2006), slope (Rolon et al., 2012), eutrophication (Vestergaard & Sand-Jensen, 2000a; Feldmann & Noges, 2007), lake morphometry (Rooney & Kalff, 2000; Weithoff et al., 2010) and sediment composition (Chappuis et al., 2014) have all been shown to have a significant effect on the distribution and composition of macrophyte species. Lake environmental factors are likely to be the primary controls on macrophyte communities along with catchment-scale factors, such as land-use and hydrological connectivity, acting to determine the lake-scale variability in macrophyte species abundance and composition. In addition to these direct influences, it seems likely that catchment- and/or landscape-scale processes (hereafter collectively referred to as broad-scale processes) play an indirect role in shaping the macrophyte community, for example, through their impact on nutrient availability. For example, lake hydrological connectivtiy may influence total phosphorus concentration of lakes, which may influence the macrophyte occurrence.

Lake environment factors and landscape factors have been used to explain the richness and diversity of macrophyte species in freshwaters (Vincent et al., 2006; Capers et al., 2010; Akasaka & Takamura, 2011). Several approaches, such as the principal coordinates of neighbour matrices (O'Hare et al., 2012), homogeneity of multivariate dispersion (Alahuhta & Heino, 2013), non-metric multidimensional scaling ordination (NMDS) (Alexander et al., 2008), have been used to understand how macrophyte communities respond to different pressures. These include land use (Cheruvelil & Soranno, 2008; Hicks & Frost, 2011), isolation (Rolon et al., 2012), flooding (Sousa et al., 2011), habitat diversity and connectivity (Dos Santos & Thomaz, 2007; O'Hare et al., 2012) and the landscape structure (Mumby, 2001). Most of these studies have found that the lake environmental filter is more important than the landscape characteristics for explaining macrophyte species diversity (Alahuhta & Heino, 2013).

The niche-based theory of community assembly has dominated community ecology for a long time; yet, recent studies have indicated that lake environmental filter and broad-scale processes collectively shape the distribution of macrophytes (Li et al., 2011; Sharma et al., 2011). One review paper, relevant to meta-community ecology, highlighted the relative importance of the spatial structure of the landscape in structuring community composition (Leibold et al., 2004); this is a result of a series of ecological processes working simultaneously.

Two types of spatial structure can be identified: (i) spatial dependency and (ii) spatial autocorrelation (Sharma et al., 2011). Spatial dependency is produced due to the spatial structure of environmental variables acting on the biotic community through species-environment relationship. Spatial autocorrelation is generated by the biotic processes such as dispersal limitation; indeed, dispersal limitation is believed to be a particularly strong factor that can lead to spatial autocorrelation (Legendre et al., 2009).

The dispersal ability of a meta-community organization affects the relative importance of environmental filter and broad-scale processes (Capers et al., 2010; Heino, 2013). For example, island biogeography studies indicate that less mobile species are often absent from fragmented habitats and, where this leads to isolation, a reduction in species richness can be expected (Prugh et al., 2008; Ockinger et al., 2009). The impact of isolation can be observed at the landscape scale as well. Distance decay theory predicts that ecological communities will show increasing dissimilarity as the physical distance between them increases, due to dispersal limitation (Poulin et al., 1999; Poulin, 2003; Soininen et al., 2007).

The dispersal rate of aquatic species is considered to be a function of habitat connectivity; this is dependent on the geographic distance and the occurrence of dispersal corridors or barriers (Ricketts, 2001). In freshwater ecosystems, the dispersal ability of species can be highly constrained by habitat connectivity. Habitat connectivity in freshwater systems can be measured as the hydrological or geographical connectivity (Ganio et al., 2005). Hydrological connectivity depends on the continuous watercourse providing an important pathway for aquatic species dispersal across freshwater bodies. However, this connectivity can be lost by the construction of dams and other structures (Miyazono et al., 2010) or by the changes in river flow during periods of low rainfall . Geographical connectivity, which can be viewed as the Euclidian distance between geographically separated habitats, provides a measure of the overland connectivity between habitat patches and is arguably a more relevant measure for those species that disperse via external vectors, such as wind or animals (Hartvigsen & Kennedy, 1993). A large number of studies, mainly focused on aquatic insects and fish, have shown that river corridors are important in maintaining aquatic biodiversity in freshwater (Beier & Noss, 1998; Olden et al., 2001; Bouvier et al., 2009; Ishiyama et al., 2014). However, few studies have investigated the relative importance of habitat connectivity to the dispersal of macrophyte species among freshwater bodies, which may in part be due to the difficulty in obtaining the quantitative measurement of the hydrological connectivity between freshwater habitats.

It is important to recognise the most significant spatial extent for each aquatic species is due to its different dispersal ability (Alahuhta & Aroviita, 2016). For example, fish can disperse only through river channels connecting water bodies (Hitt & Angermeier, 2008). While for macrophytes, their seeds can be transported across the *topographic catchment* via river channels or can be dispersed within and between *topographic catchments* by wind or aquatic organisms (Soons, 2006; Gronroos et al., 2013). Moreover, the impact of the broad-scale processes may weaken as the increase of spatial extent due to the dispersal limitation (Heino, 2011; O'Hare et al., 2012; Meynard et al., 2013).The structure and function of the freshwater ecosystem is influenced by the spatial heterogeneity of multiple habitat scales, expanding from lake to catchment and global scales (Ogdahl et al., 2010; Heffernan et al., 2014). Modern technology such as geographical information systems (GIS) allows large-scale environmental data to be recorded, manipulated and modelled. Previous studies have indicated that, over the regional scale, dispersal limitation plays an important role in shaping the structure of macrophyte communities (Thomaz & Cunha, 2010). However, on a continental and global scale, the variation of macrophyte communities in freshwater ecosystems is determined by landscape factors and regionally-structured environmental variables (Viana et al., 2016). Most of the studies focus on the impact of catchment-scale controls in determining freshwater macrophyte community composition.

The study of catchments as meta-ecosystems and their impacts on macrophytes has also focused on the interaction of abiotic and biotic variables. It has been found, for example, that catchment area (Cheruvelil & Soranno, 2008), soil characteristics (Beck et al., 2013), land use (Rasmussen & Anderson, 2005; Sass et al., 2010; Hicks & Frost, 2011; Rosso & Cirelli, 2013), lake hydrological position (Makela et al., 2004) and hydrological regime (Sinkeviciene, 2007; Thomaz et al., 2007) in catchments had clear and strong effects on macrophyte species diversity, especially on emergent plants (Alahuhta et al., 2011). Some ecological hypotheses, tested at the regional scale, include the landscape filter concept, the species-area relationship and the meta-community concept (Stendera et al., 2012).

In these studies, the "catchment" as the spatial unit for the analysis has been variously (and often rather subjectively) defined as: *local catchment* (area of land in close proximity to the lake shore, smaller than the *topographic catchment*); *topographic catchment* (a basin-shaped area of land that drains surface and sub-surface water to a receiving body of water); and *freshwater ecoregion* (defined as an area encompassing homogeneous freshwater systems)

(Table 2.1). A brief overview of some findings across each of these defined catchment types are provided below.

2.4.1 *Local catchment* (Aquatic-terrestrial ecotones)

Local catchment, also referred to as lake riparian buffer zones or lake marginal zones, have been advocated as environment tools to reduce the impact of anthropogenic activity on lake water quality and aquatic vegetation (Parkyn, 2004). They are diverse freshwater habitats with heterogeneous vegetation and, thus, they are typically highly productive and support high diversity and biomass of aquatic organisms (Mitsch & Gossilink, 2000). Emergent macrophytes usually dominate this ecotone and thus it plays an important role in filtering diffuse sources of contamination, stabilizing stream banks and regulating water temperature, with resulting water quality benefits for downstream water bodies (Lacoul & Freedman, 2006; Alahuhta et al., 2011). The role of aquatic-terrestrial ecotones could be assessed through buffers, which refer to the zones around the lake shore. Many previous studies have shown the significant influence of land use (Pedersen et al., 2006; Alahuhta et al., 2012) and soil characteristics (Alahuhta et al., 2016) in *local catchment* on the macrophyte composition in lakes. Different macrophyte growth forms can be affected differently by land use characteristics at different spatial scales. In a study by Akasaka et al. (2010), it was found that the spatial scale over which land use was found to influence macrophyte species diversity varied from 100 m for submersed species, to 500 m for floating-leaved species and 1000 m for emergent species. Hydrological pathways are considered to determine the effectiveness of buffer strips constructed to protect freshwater ecosystems from adverse land use practices. Thus, the importance of taking catchment-wide perspectives to riparian management has been emphasised.

2.4.2 *Topographic catchment*

The *topographic catchment* of a lake is defined as a basin-shaped area of land that drains surface and sub-surface water, sediment and other materials to a receiving body of water. A large number of studies have focused on the impact of the catchment-scale processes on lakes, particularly through the use of watershed models such as SWAT (Soil and water assessment tool) (Arnold et al., 1998), AnnAGNPS (Annualized Agricultural Non-Point Source Pollution) (Li et al., 2015) and WEPP (Water Erosion Prediction Project) (Brooks et al., 2016). These models have been used to evaluate the impact of various natural and human disturbances at the *topographic catchment* scale on the water quality and freshwater biodiversity in outlet lakes. Natural processes occurring within the catchment, such as rainfall runoff, groundwater discharge and river flow, provide beneficial dispersal services for transporting macrophytes between water bodies and wetlands. Thus, hydrological connectivity contributes to the dispersal of macrophytes to downstream water bodies (Freeman et al., 2007; Obolewski et al., 2014). The topography within a catchment controls the drainage of water and related hydrological processes (Hwang et al., 2012). Lateral hydrologic connectivity is influenced by flooding (Van Geest et al., 2005) and human disturbances such as water extraction and the construction of drainage ditches (Ecke, 2009) or dams (Oťaheľova et al., 2007). As these factors directly affect the water level of lakes and the connectivity within the catchment, they can exert a significant influence on the composition and abundance of macrophytes. Previous studies have examined the influence of catchment-scale properties on the abundance and diversity of macrophytes (Cheruvelil & Soranno, 2008; Beck et al., 2013). Aquatic algae were evaluated in relation to land use (Norton et al., 2012; Couture et al., 2014), climate change (Moorhouse et al., 2014) and hydrological regime within the *topographic catchment*.

2.4.3 *Freshwater ecoregion*

The freshwater ecoregion (Omernik, 1987) is an ecological unit including homogenous freshwater systems and the surrounding terrestrial system (Yu et al., 2015). The concept is taken from landscape limnology and argues that hydrological processes are impacted by ecological disturbance at the broad scale (Soranno et al., 2010).

Studies undertaken at the *freshwater ecoregion* scale have examined the conservation of aquatic biodiversity (Abell et al., 2008), habitat diversity (Munne & Prat, 2004) and water quality (Wang et al., 2015) in regions such as the U.S.A. (Omernik, 1987), Australia (Davies et al., 2000), China (Yu et al., 2015), Hungary (Lukacs et al., 2015) and South Africa (Kennedy et al., 2016). The intensity of anthropogenic stress and its impact on macrophyte communities in *freshwater ecoregions* has been proved to be shaped by interactions with geo-climate drivers (Pearson & Boyero, 2009; Heino, 2011; Feld et al., 2016), habitat diversity (Oberdorff et al., 2011) and geographical history (Alahuhta, 2015). However, not all studies have observed significant relationships between ecoregion-scale variables and distribution patterns of freshwater communities (Kong et al., 2013), such as the distribution of macrophytes (Wright et al., 1998). The reason is probably because it is inaccurate to base analyses on the mean value of environmental variable (such as physico-chemistry) rather than the variability of environmental attributes in the entire ecoregion (Allan & Johnson, 1997; Palmer et al., 1997; McDonald et al., 2005).

Based on the hierarchical macrosystems in which components interact with each other at a lake-, catchment- and ecoregion-scale, there are four major types of interaction (Peters et al., 2007) related to different catchment scales:

i. Teleconnection addresses interaction among distant climatic systems at the ecoregion scale;
ii. Catchment-scale feedback indicates the interaction of components at the catchment scale;
iii. Cross-scale interaction relates to how catchment drivers influence the relationships with lake-scale drivers;
iv. Cross-scale emergence emphasises that lake-scale drivers can impact on the processes at the catchment scale.

However, it introduces errors in analyses on the impact of the catchment drivers in explaining species distributions because of the simple scaling that ignores the catchment-scale processes that influence the lake environment (Heffernan et al., 2014).

Multi-scale effects of properties such as spatial complexity (Dibble & Thomaz, 2006), hydrological regime (Kennard et al., 2007; Morandeira & Kandus, 2015), habitat heterogeneity (Poizat & Pont, 1996) and geographical factors (Brind'Amour et al., 2005) on water quality and macrophyte species composition, have been examined in previous studies. The multi-scale concept has been used to indicate the presence of more than one scale in the analysis without implying any interaction between drivers across different spatial scales. The term cross-scale interaction has been used to define situations where predictor variables and response variables operate at different scales and interact linearly or nonlinearly (Cash et al., 2006; Peters et al., 2007). Previous studies have focused on the interaction among multi-scale dependent factors and how these regulate abiotic and biotic properties of lakes (Soranno et al., 2014). This includes research on the impact of land use or hydrology at the catchment scale on determining lake TP or chlorophyll-a concentrations (Fergus et al., 2011). However, no previous studies have considered the interaction of multi-scale drivers on lake macrophyte communities.

Table 2.1 Relevant studies on lake macrophyte richness and diversity across different catchment scales

Spatial scale	People and time	Definition of catchment	Derived from	Study lakes	Explainary datasets	conclusions
Local catchment of lake	Pedersen et al., (2006)	**Lake buffer zone** (buffer size = 50/100/200/400/800/1600/3200 m)	Arc GIS / Buffer Tool based on lake boundary	100 Danish lakes	Land use	**<3000 m** lake buffer were most strongly associated with the occurrence of *Littorella uniflora.*
	Cheruvelil & Soranno (2008)	***Local catchments*** (immediate drainage area surrounding lake) (buffer size = 500 m)	Digitizing topographic boundaries using Digital Raster Graphic topographic maps	54 north temperate lakes located in Michigan, U.S.A	landscape features including hydrologic, catchment morphometric and land use	Land use in riparian can be considered as predictor of macrophyte cover metrics.
	Akasaka et al., (2010)	**Lake buffer zone** (Buffer extent = 5/10/25/50/75/100/250/500/750/1000 m)	Arc GIS/ Buffer Tool	55 irrigation ponds in south-western Hyogo, Japan	Land use	The most significant buffer scales differ according to growth forms: **100 m** for submersed, **500 m** for floating-leaved and **1000 m** for emergent.
	Alahuhta et al., (2012)	**Lake Marginal Zone** (LMZs= 100 / 300 / 500 m)	Arc GIS/ Buffer Tool	110 lakes in Finland	Land use	Land use adjacent to the lake shoreline (**LMZs of 300 m and 500 m**) had a more effect on the metrics.
	Alahuhta et al., (2016)	**Aquatic-terrestrial ecotones** (Buffer scale = 50 / 100 / 300 / 500 m)	Arc GIS/ Buffer Tool	408 boreal lakes in Finland	Environment gradients including lake, climate and land cover	The importance of the agriculture land and soil variables increased towards the wider buffer scale (**from 50 m to 500 m**).
Topographic catchment of lake	Pedersen et al., (2006)	***Topographic catchment***	The districts in Denmark	100 Danish lakes	Land use	The *topographic catchment* area of lake was an irrelevant unit to study effects of soil type and land use
	Cheruvelil & Soranno (2008)	**Cumulative catchments** (the *local catchment* in addition to all upstream drainage from connected lakes and streams) for each lake	Digitizing topographic boundaries using Digital Raster Graphic topographic maps	54 study lakes located in Michigan, U.S.A	Catchment morphometric and land use	Catchment morphometry and land use proportion have effects on macrophyte metrics.
	Ecke (2009)	***Topographic catchment* of each lake**	provided by Swedish Meteorological and Hydrological Institute	17 shallow humic Swedish soft-bottomed lakes in Sweden.	Land use /drainage ditches.	Impact of drainage ditching on lake water and macrophyte composition is greater than land cover
	Gorman et al., (2014)	***Topographic catchment* of each lake**	Farm Service Agency (FSA) color digital orthophoto quadrangles from 2003 / GIS hydro tools – Hydrologically corrected digital elevation models	70 shallow lakes in western Minnesota (USA)	Phosphorus/ fish biomass/ land use	High impact of fish communities and phosphorus levels on lake algal abundance.
Freshwater ecoregions of lake	Sass et al., (2010)	***Freshwater ecoregion***: Areas within which there is spatial coincidence in characteristics of geographical phenomena associated with differences in the quality, health, and integrity of ecosystems. (Omernik, 2004)	Ecoregions of Wisconsin (Omernik et al., 2000)	53 lakes in Two ecoregions: The northern lakes and South-eastern plain ecoregions, Wisconsin, U.S.A.	Catchment development level (Urban + Agriculture)	Catchment development has an effect on macrophyte communities.
	Alahuhta et al., (2011)	The second division size category in Finnish **hydrological regime**	Finnish CORINE land use classification /Landsat ETM Satellite images (from 1999-2002)	848 catchments across Finland	Land use, geomorphology and climate	Drainage ditch intensity importantly contributed to emergent macrophytes at national level.
	Kissoon et al., (2013)	Two **Ecological provinces** of Minnesota: Laurentian Mixed Forest Province (LMP) and Prairie Parkland Province (PP)	Ecological Province map from the United States Forest Service (USFS), displays the ecological subregions for the conterminous United States.	38 shallow lakes in Minnesota, U.S.A.	Catchment-scale variables such as sediment characteristics and land use	Lake macrophyte communities are driven by site- and catchment- scale factors in shallow lakes.

2.5 Discussion

2.5.1 Contribution of environmental filtering and broad-scale processes to structuring of macrophyte assemblages

Community ecology is concerned with the distribution and abundance of species communities and takes the view that the species distribution patterns vary with the observing scale. Further, it argues that the factors that determine the distribution of species are likely to vary depending on the spatial scale (Levin, 1992; Chase & Leibold, 2002; Leibold et al., 2004). Understanding the relative importance of environmental filter and broad-scale processes in determining the species variation within meta-communities is one of the key questions that concerns ecologists. Most studies assume that environmental filters and broad-scale processes often operate together to explain meta-community structuring at broad spatial scales (Mykra et al., 2007; Bennett et al., 2010). However, this view has been challenged by some authors who argue it is necessary to also consider the role of dispersal and dispersal pathways to understand the structure of macrophyte communities (Beisner et al., 2006; Sharma et al., 2011).

There are two opposite views on the impact of spatial factors in structuring lake macrophyte communities. One view argues that spatial factors will predominant over lake environmental drivers in determining the distribution of macrophyte species over large spatial scales (i.e. *freshwater ecoregion*) (Cottenie, 2005; Heino et al., 2007, 2010; Heino, 2011). Other studies, have found that the effect of catchment- and/or landscape- scale processes on macrophyte species distribution is unrelated to the spatial scale (Alahuhta & Heino, 2013).

Moreover, the relationship can be further complicated because responses vary between different macrophyte growth forms. For submersed and floating-leaved plants, the landscape variables were found to account for a similar proportion of the variation to the lake physico-chemistry variables (Capers et al., 2010). The relative importance of landscape variables increased slightly for emergent and free-floating macrophytes (Alahuhta & Heino, 2013). While numerous studies have assessed the relative importance and interaction between various environmental variables in explaining macrophyte composition, these studies have generally only focused on lake scale environmental filters and comparatively few studies have considered the interaction between drivers at different spatial scales.

2.5.2 Multi-scale dynamics in freshwater ecosystem

As the pressure on freshwater resources increases, it is increasingly important to understand the likely responses of macrophyte communities to a range of different pressures. Studies on the relative role of multi-scale drivers and their interaction in determining the variation in macrophyte composition is necessary to provide the efficient conservation and management implications across different spatial scales.

At the lake scale, the main environmental factors involved in determining the status of macrophyte species in lakes and wetlands include the following: light, temperature, competition and nutrient status. The effects of these factors have been reviewed in previous studies (e.g. Franklin et al., 2008; Bornette & Puijalon, 2011). The broad-scale processes that structure macrophyte communities in freshwaters include anthropogenic disturbance such as urbanization (Hicks & Frost, 2011) and agriculture (Egertson et al., 2004) at the *local catchment*, *topographic catchment* and *freshwater ecoregion*.

Despite the apparent importance of the hydrological regime in regulating macrophyte communities in lakes, the nature of the processes controlling their dynamics is not well understood. Moreover, there is a lack of broad-scale analyses that focus on the impact of landscape and hydrological variables on lake macrophyte communities. This probably reflects an obvious division between ecologists interested in the effects of hydrological connectivity and flood events on macrophyte communities in freshwaters, while hydrologists and engineers concentrate on the water dynamics and velocity in relation to macrophyte species in separate catchments or ecoregions. Improvement in the understanding of broad-scale processes on macrophyte community composition requires better knowledge of the mechanisms through which landscape or hydrological variables are manifested especially at the lake scale.

Until now, little attention has been given to the scale-dependency of the habitat heterogeneity, land use and hydrological regimes at the broad scale (> 3000 m). The current lack of understanding of the scale-dependent interaction of different factors in determining macrophyte community composition in lakes and wetland could lead to potential significant economic and environmental costs in some freshwater systems. There is, therefore, a need to improve understanding of which is the most influential scale in influencing macrophyte communities in lakes. In the past, some studies were limited by the available capability to measure and model broad-scale ecological processes and constrains. However, nowadays, advances in technologies, such as GIS, remote sensing and fluid dynamics models, allow for research to be undertaken readily at the catchment scale and beyond.

Current studies on the interaction between lake-scale environmental filters and catchment- and/or landscape-scale processes and their relationship with macrophyte community composition show significant differences between habitat types and macrophyte growth forms both spatially and temporally. Many studies have studied the variation partitioning among different datasets (e.g. lake environmental filters and landscape variables) to explain the macrophyte species composition (Hajek et al., 2011; Sharma et al., 2011; Alahuhta & Aroviita, 2016; Viana et al., 2016). However, the quantitative understanding of the interactions across different spatial scales is relatively limited due to the difficulty of modelling these interaction relationships (Stephan & Gutknecht, 2002). Carpenter & Turner, (2000) amongst others, have recently developed the theory of cross-scale interaction as a framework for understanding the complex interactions between the factors and processes over different spatial scales within freshwater ecosystems (Cash et al., 2006; Soranno et al., 2014). However, there appears to be very little consideration of these interactions in the current literature. Progress now needs to be made in improving the quantification of the interactions between different spatial scales: lake, *local catchment*, *topographic catchment*, *freshwater ecoregion* and continental scales with respect to the macrophyte community in freshwater ecosystems. In particular, there is a need for further research on the classification of spatial scales and the mechanisms of cross-scale interaction in determining macrophyte species distribution.

The current research gaps identified from this review are summarized in Figure 2.1. Previous studies have examined the influence of the catchment- and/or landscape-scale variables on lake macrophyte communities. They highlighted that the strongest effects are often in close proximity to the lake shore (e.g., within 3 km). Chapter 3 thus presents a study on the scale-dependency of the relationship between species richness and hydrology and land use variables for a population of 90 British lakes over spatial extents ranging from 0.25 km to 10 km.

Most of the studies on macrophytes at the *topographic catchment* scale have tended to focus on individual catchments and often only consider pressures that occur at a single scale, perhaps due to the challenges of acquiring the data. However, the influence of factors that operate at the lake scale may be moderated by interactions with catchment-scale drivers. Chapter 5 therefore presents a study on how cross-scale interactions at the catchment scale directly and indirectly determine macrophyte composition in 450 British lakes across 30 *topographic catchments*.

Within an ecoregion, dispersal limitation plays an important role in structuring the distribution patterns of macrophytes. Geographical and hydrological connectivity are important in determining the biogeographical distribution of macrophyte species by controlling dispersal between water bodies. However, few studies have considered the hydrological connectivity of lakes at the regional scale. Thus, in Chapter 4 we selected 272 hydrologically-connected lakes using GIS and explored the relative importance of different dispersal pathways in explaining the variability in species turnover.

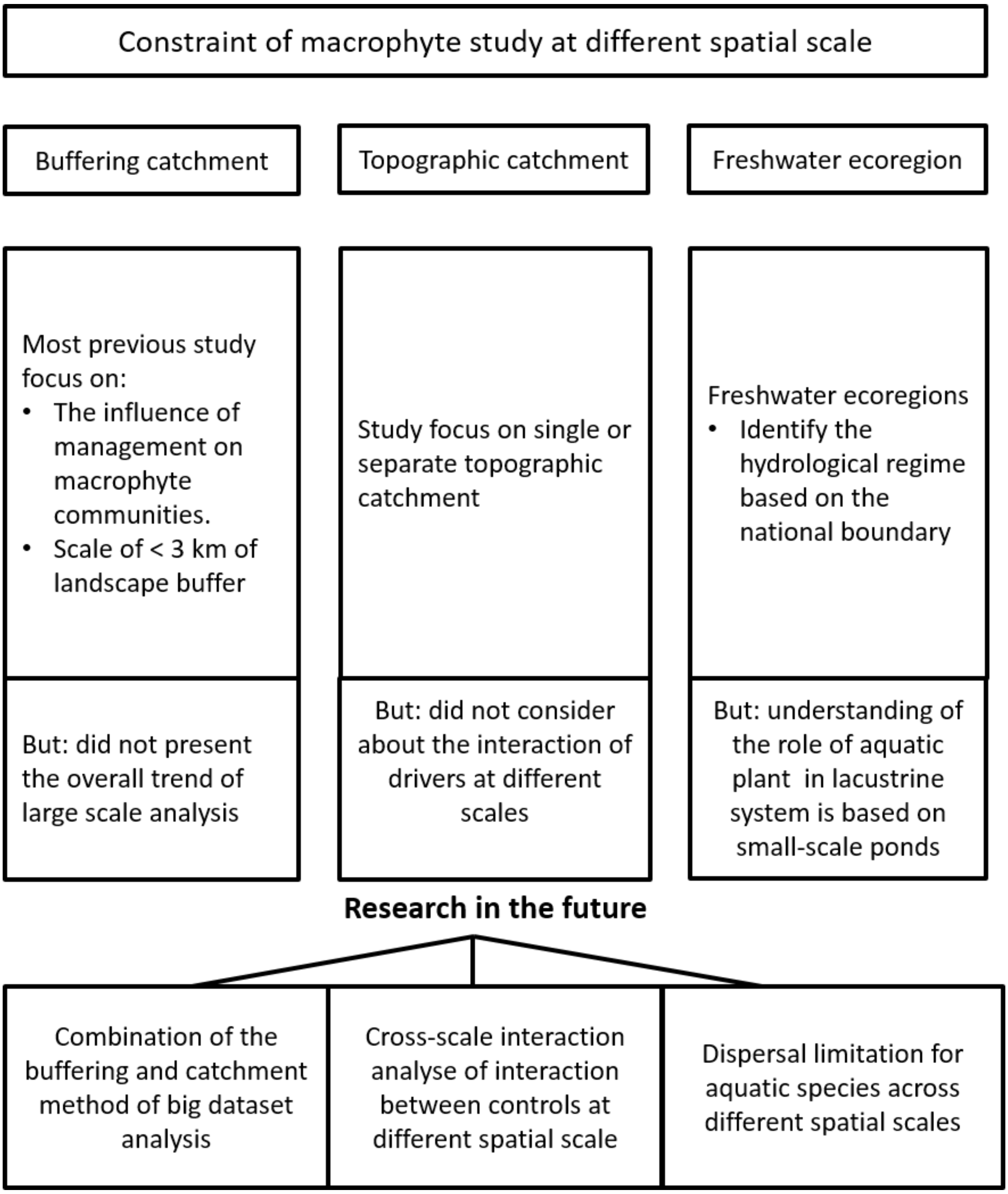


Fig. 2.1 Research gaps in the structuring of macrophyte communities

Chapter 3 – A buffer analysis of hydrology and land use influences on macrophyte richness in lakes – the role of catchment versus landscape

3.1 Abstract

In biogeography it is well established that environmental variables often have scale-dependent effects on abundance and distribution of species. This chapter presents results from a study on scale-dependency of aquatic plant (macrophyte) richness to hydrology and land use indicators. Hydrological connectivity and land use within the landscape surrounding 90 UK lakes, at nine spatial extents varying from 0.25 km to 10 km from the shoreline, with (*catchment buffer*) and without (*landscape buffer*) adherence to the catchment boundary, were constructed using GIS. These variables were used to explain variation in macrophyte richness derived from field surveys. The results revealed strong scale-dependency. The effects of land use were most apparent at small spatial scales and grossly outweighed the importance of hydrology at all spatial scales. The total richness of macrophyte was most strongly determined by land use and hydrology within 1 km of *landscape buffers* and 500 m of *catchment buffers*. The nature of the scale-dependent effect also varied with macrophyte growth habit. In terms of growth form composition, the effects of hydrological connectivity were stronger than those of land use, being greatest at an intermediate distance (~ 5 km) from the lake. Our results indicate the importance of maintaining some lakes with natural catchment vegetation, at least within 1 km of the lake shore, while also minimising alterations to catchment hydrology (e.g. through drainage and diversions) over distances extending at least 5 km from the lake shore.

3.2 Introduction

Freshwater macrophytes are a fundamental component of aquatic food webs and their species richness is implicitly linked to ecosystem structure and function (Engelhardt & Ritchie, 2001; Bouchard et al., 2007). The degradation of aquatic vegetation is often associated with the loss of native species and invasion by non-native species (Di Nino et al., 2005; Hussner & Lösch, 2005; Willby, 2007). The impact of eutrophication can also lead to a shift from submersed aquatic plants towards predominantly floating and emergent species (Egertson et al., 2004), followed by a collapse in the whole aquatic vegetation (Rasmussen & Anderson, 2005). Studies characterising the anthropogenic controls on lake water quality and macrophyte abundance have typically been undertaken at two different scales: the landscape scale (Pedersen et al., 2006) and the (topographic) catchment scale.

Lake riparian buffer zones or lake marginal zones are usually advocated as the target area for tools designed to reduce impacts of anthropogenic activity on lake water quality and aquatic vegetation at landscape scale. The effect of land use on macrophyte species richness, and the extent to which this relationship is scale-dependent, has been explored in a number of previous studies. Pedersen et al., (2006), for example, used spatial buffers constructed in Geographic information system (GIS) at varying distances from the lake shore to examine the effect of land use on the occurrence of specific macrophyte species in a series of Danish lakes. The results showed that land use within the < 3 km buffer zone exerted a stronger effect on the occurrence of *Littorella uniflora* than that observed at larger spatial scales. Similarly, others have also shown that landscape diversity and the proportion of managed land within the immediate vicinity of the lake exerts a significantly greater influence on macrophyte richness than at the broader catchment scale (Steffan-Dewenter et al., 2002). There is also evidence that the scale-dependent effect of land use on macrophyte richness varies depending on macrophyte growth form (Akasaka et al., 2010) and that the size of the effect is proportional to the area of the lake (Alahuhta et al., 2012). Hydrological pathways are considered to determine the effectiveness of buffer strips and, thus, a catchment-wide perspective of lake riparian management was suggested (Wissmar & Beschta, 1998).

The *topographic catchment* of a lake is defined as the basin of land that drains surface and sub-surface water with sediments and other materials into the receiving water body. The topography within a catchment is a major determinant of surface hydrology (Hwang et al., 2012) including the extent of connectivity between discrete habitats. The stream and river network connecting water bodies is one of the dominant mechanisms controlling the flow of materials including nutrients, seeds and vegetative propagules between lakes and thus it exerts a major influence on the occurrence of macrophytes (Bornette et al., 1998; Jencso et al., 2009; Oťaheľova et al., 2011). Water flow is the pathway by which pressures are transferred from the catchment to receiving water bodies and simultaneously provides the network via which many aquatic organisms disperse (Andersson et al., 2000). When connectivity is disrupted by, for example, dam construction in streams, the dispersal of macrophytes is impacted (Oťaheľova et al., 2007). The landscape connectivity between limnology networks is considered to be a key variable in shaping the macrophyte communities of lowland rivers (Demars & Harper, 2005). Flooding, water velocity and the resulting impacts on lake water level regime has also been shown to be closely correlated with macrophyte species distribution and abundance (Barendregt & Bio, 2003; Thomaz et al., 2007; Baattrup-Pedersen et al., 2008; Baart et al., 2010; Steffen et al., 2014).

Different land use types and patterns within the catchment also influence nutrient availability and thus can impact on downstream lake water quality and primary production through overland flow and runoff (Lee et al., 2009; Gorman et al., 2014). Downstream water quality and macrophyte abundance is linked with (i) the proportion of urban or industrial land within the upstream catchment (Tong & Chen, 2002; White & Greer, 2006; Sass et al., 2010); (ii) the proportion of agricultural land, which influences nutrient loading and thus primary production (Knoll et al., 2003; Gorman et al., 2014); and (iii) the type of agricultural land, for example, arable crops have a higher N:P stoichiometry compared with pasture (Arbuckle & Downing, 2001). Whilst it is generally understood that nutrient loading from land has an important impact on the trophic status of lakes and the abundance and structure of the phytoplankton (Downing & McCauley, 1992; Smith & Bennet, 1999), areas of localised nutrient enrichment can also serve to promote or reduce macrophyte growth (Lacoul & Freedman, 2006).

Despite the apparent importance of the runoff regime in regulating macrophyte communities in lakes, the nature of the processes and the constraints on their dynamics are not well documented. With the exception of Ecke (2009) who examined the relationship between the density of drainage ditching within a Swedish catchment and lake macrophyte community abundance, few studies have focused on the effect of stream density and lake spatial structure on macrophyte richness and composition. This is probably because of the difficulty in measuring some hydrological features at regional scales. For the present work, stream density and lake density at different buffer spatial scales were derived to explore the initial relationship between the hydrological features and macrophyte species richness. In particular, the landscape pattern method (O'Neill et al., 1988) was introduced in the analysis to assess the influence of lake physical structure and landscape connectivity on macrophyte species richness in lakes over multiple scales rather than at a single scale.

Previous studies of the impact of anthropogenic disturbance on lake macrophytes were mostly conducted on a small scale of < 3 km in *landscape buffers* (Pedersen et al., 2006; Akasaka et al., 2010; Alahuhta et al., 2012). Our study used a maximum size of 10 km as the buffer spatial scale because many of the study lakes had large catchments. This allows for the overall trend in the impact of hydrology and land use in *landscape buffers* and *catchment buffers* on lake macrophyte richness to be compared across a wide range of spatial scales.

This work firstly proposes the concept of *catchment buffer* to allow scale-dependent influence of hydrology and land use on the lake macrophyte richness to be compared between two buffer types. Previous studies have concluded that the impact of land use on macrophyte communities at the landscape scale is more important than that from the whole *topographic catchment* (Pedersen et al., 2006; Sass et al., 2010). Our work examines the effect of land use and hydrological connectivity on macrophyte species richness and to what extent this effect is scale-dependent within the *topographic catchment* and the wider landscape. Two hypotheses are explored:

(i) Hydrology and land use within the *topographic catchment* have a less important effect on lake macrophyte richness than at the landscape scale at comparable distances;

(ii) Land use and hydrological connectivity in the immediate vicinity of a lake exerts a stronger influence on macrophyte species richness than at larger distances but the strength of this effect also varies with macrophyte growth form.

The study thus sheds new light on connectivity and macrophyte dispersal and identifies the optimal spatial scale of the buffer zone for conserving macrophyte biodiversity in lakes.

3.3 Methods

3.3.1 Study sites

This study focuses on 90 lakes within mainland Britain, selected from a larger database of physicochemical and macrophyte data for 2558 lakes surveyed between 1985 and 2000 from historical survey data held by the Joint Nature Conservation Committee (JNCC) and the UK environmental agencies. The lakes selected met two requirements: (i) the shoreline was at least 10 km from the sea such that the *landscape buffers* were entirely terrestrial in nature; (ii) the minimum distance from the lake shoreline to the catchment boundary was also at least 10 km to enable a complete set of *catchment buffers* to be constructed (Figure 3.1).

Figure 3.2 shows the latitudinal gradient of the study lakes, ranging from northern Scotland to the midlands of England and Wales. The distribution of the study sites reflects the fact that the majority of lakes in Great Britain are located in Scotland. The population of study lakes varied considerably in terms of their morphology, chemistry and landscape location. The characteristics of the selected study sites are summarised in Appendix 3.1.

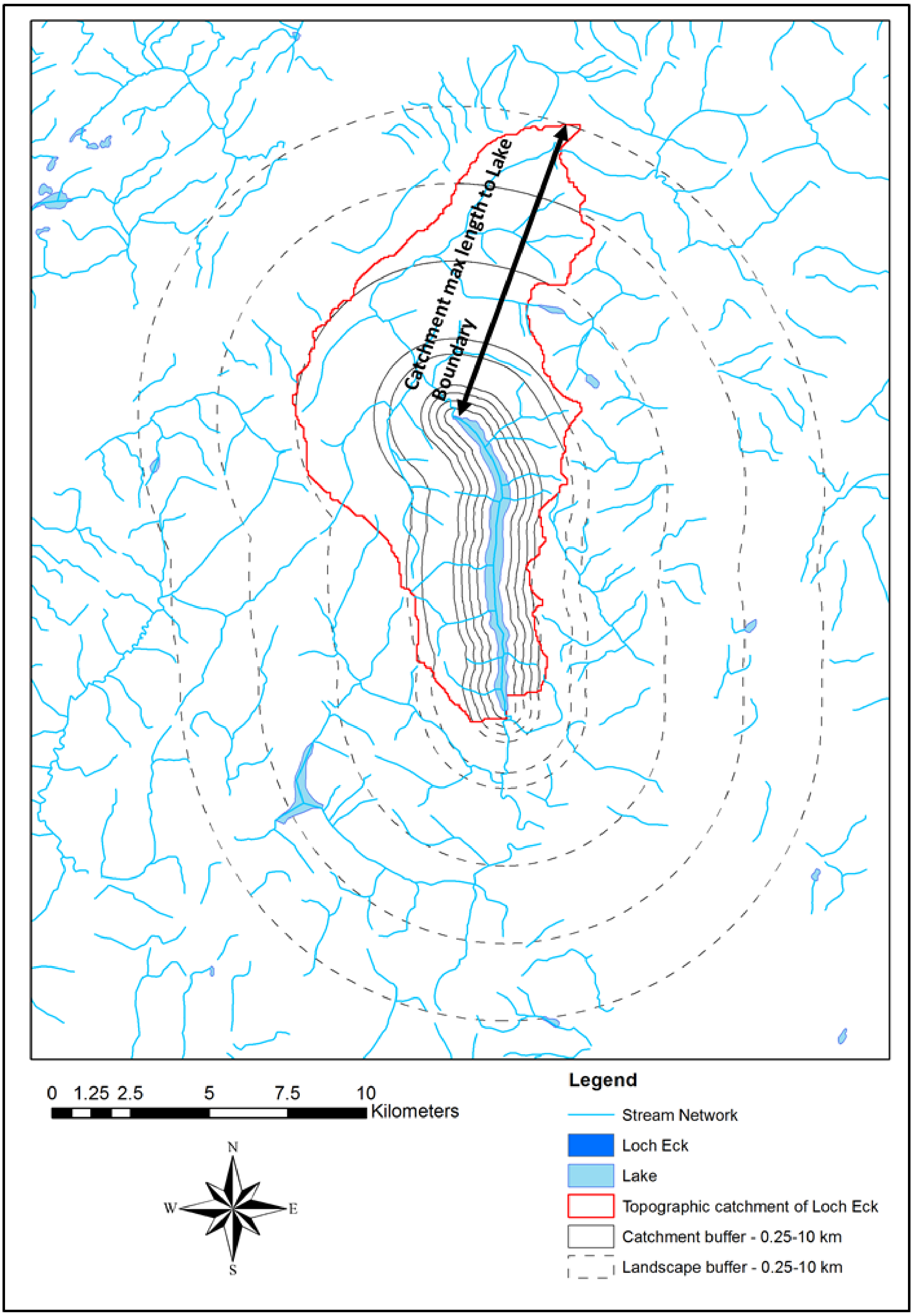


Fig. 3.1 Explanation of two buffer types. Example shown is for Loch Eck (WBID: 24996, Catchment area: 103.24 km^2)

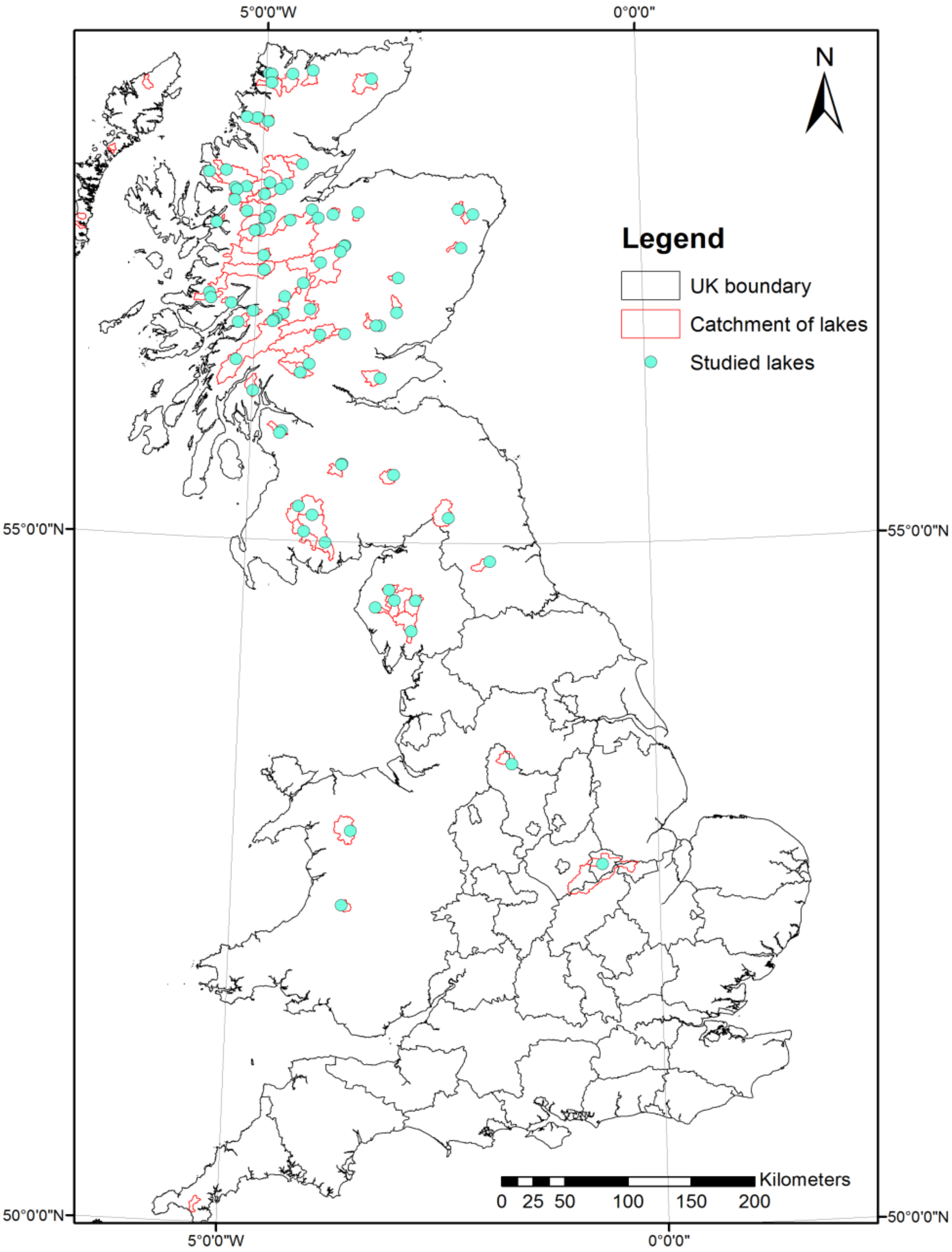


Fig. 3.2 Geographical positions of the study lakes and their catchments

3.3.2 Lake and macrophyte sampling

Macrophytes were surveyed by traversing each water body in a boat along multiple transects and by wading within the shallower parts of the littoral zone (Gunn et al., 2010). A rake was usually used to collect samples but in shallow water a bathyscope was also used to identify plants in situ. Surveys were conducted between July and September. The recorded species were assigned to different growth form categories: emergent, free-floating, floating-leaved and submersed. The emergent category included only those emergent plants encounted in the water column and did not reflect the full complement of emergent and marginal plants in a lake. Total macrophyte richness was calculated as the sum of the species in different growth form categories.

For each lake, water samples were taken near the outflow in summer and winter. Variables such as conductivity and alkalinity showed little variation on a decadal scale (Willby et al., 2012), whilst variables such as total phosphorus, total nitrogen and pH sometimes exhibited marked differences. Alkalinity was considered the key variable to represent water quality (Vestergaard & Sand-Jensen, 2000b) and has been widely found to be a major driver of macrophyte composition in lakes (Vestergaard & Sand-Jensen, 2000a), probably due to its influence on inorganic carbon supply and co-variation with major nutrient concentrations (Kolada et al., 2014). A significant positive relationship ($R^2 = 0.531$; $p < 0.001$) between total phosphorus and alkalinity for lakes within the database (349 of the 2584 lakes have available TP and alkalinity data) supported this assumption. Lake area, a major determinant of macrophyte richness (Rorslett, 1991), was determined subsequently using GIS.

3.3.3 GIS analysis

(1) Catchment definition

The *topographic catchments* of 90 study lakes were generated using Arc Hydro Tools in ArcGIS (v 10.2; ESRI, U.S.A) with application of the vectorised lake boundaries and Digital terrain model (DTM) at a 50 m grid resolution using data from the UK Ordnance Survey (MERIDIAN^{TM} 2 and OS Terrain 50). Concentric buffers at spatial distances of 0.25, 0.5, 0.75, 1, 2, 2.5, 5, 7.5 and 10 km from the lake shoreline were subsequently calculated using Buffer Tool in ArcGIS. These are hereafter termed *landscape buffers* as they take no account of the boundary of the *topographic catchment*. The *landscape buffers* were subsequently intersected with the polygon layer representing the *topographic catchment* for each lake to derive the *catchment buffers* (Figure 3.1) at each aforementioned buffer distance.

(2) Hydrological and land use indicator

Hydrological indices were generated from two-dimensional vector maps of the lakes and rivers network of the UK supplied by the Ordnance Survey (MERIDIAN^{TM} 2) in order to construct the framework for estimating the effect of lake hydrological connectivity on macrophyte richness. From this, stream density, lake density and lake coverage were calculated in each of the incremental spatial scales for the two separate buffer types.

A 1:25000 UK land cover map (LCM2007: http://www.ceh.ac.uk/services/land-cover-map-2007) was used to estimate the influence of anthropogenic disturbance on lake macrophyte richness. The percentage cover of the most impacted land use types was quantified within the *landscape buffers* and *catchment buffers* for each spatial scale of each lake. The two broad categories of land use considered were: (i) agriculture, consisting of improved grassland, arable cereals, arable horticulture and arable non-rotational; and (ii) urban, defined by suburban/rural developed land in addition to designated urban areas.

Indices of landscape pattern were calculated using land cover map (LCM2007) in Fragstat 4.1 to characterise the physical structure and arrangement of water and land use patches within the different buffer types of each lake. The effect on biota of either the structure of the habitats surrounding lakes, or the landscape diversity, will vary with the scale of *landscape* and *catchment buffers* (Steffan-Dewenter et al., 2002). Since different landscape diversity indices are inter-correlated only those variables listed in Appendix 3.2 were used in this study. Table 3.1 shows the mean and range of the hydrological and land use indicators across *landscape buffers* and *catchment buffers*. With the exception of the variables Euclidean nearest-neighbour distance, Landscape division index and Agriculture coverage, all mean values decrease with increasing buffer zone distance as a result of scale effects.

Table 3.1 Mean value of hydrological and land use indicators of the study lakes within *landscape buffers* and *catchment buffers* across continuous buffer distance from 0.25 km to 10 km (The table summarises the minimum and maximum value of the selected variables across two buffer types)

Explanatory variables		***Landscape buffers***		***Catchment buffers***	
	Unit	Minimum value (Buffer distance / km)	Maximum value (Buffer distance / km)	Minimum value (Buffer distance / km)	Maximum value (Buffer distance / km)
Hydrological features					
Stream density	km/km^2	0.69(B10)	1.46(B0.25)	0.77(B10)	1.48(B0.25)
Water body coverage	%	2.78(B10)	33.7(B0.25)	4.93(B10)	34.0(B0.25)
Lake density	n/km^2	0.15(B10)	1.15(B0.25)	0.21(B10)	1.27(B0.25)
Lake fractal index	-	1.07(B10)	1.09(B0.25)	1.08(B10)	1.09(B0.25)
Core area percentage of landscape	%	1.34(B10)	17.2(B0.25)	2.51(B10)	17.3(B0.25)
Disjunct core area density	n/km^2	0.044(B10)	0.50(B0.25)	0.08(B10)	2.08(B0.5)
Euclidean nearest-neighbour distance	m	85.4(B0.25)	845.9(B10)	78.6(B0.25)	895.2(B7.5)
Proximity index	%	17.3(B10)	22.2(B1)	15.9(B10)	21.1(B1)
Interspersion juxtaposition index	%	64.1(B7.5)	68.4(B0.25)	62.7(B2)	68.3(B0.25)

Cohesion index	%	96.1(B10)	96.3(B0.25)	94.9(B0.5)	95.9(B0.25)
Landscape division index	%	0.86(B0.25)	1.0(B10)	0.86(B0.25)	0.99(B10)
Land use indicators					
Urban coverage	%	0.72(B5)	0.98(B0.25)	0.47(B10)	1.03(B0.25)
Agriculture coverage	%	8.22(B0.25)	12.7(B2.5)	8.09(B0.25)	12.28(B1)
Urban patch density	n/km^2	0.23(B10)	1.10(B0.25)	0.28(B10)	1.09(B0.25)
Agriculture patch density	n/km^2	0.96(B10)	3.80(B0.25)	1.16(B10)	3.94(B0.25)

3.3.4 Statistical analyses

The distribution of all hydrological and land use indicators (Table 1) was normalised by $\log_{10}$ transformation and values were then standardised to zero mean and unit standard deviation. Principal components analysis (PCA) was performed to prioritise the non-correlated variables from the sets of hydrological and land use indicators for each buffer type (catchment and landscape) and for each buffer distance (from 0.25 km to 10 km). Three components, "PCA1-lake spatial dispersal", "PCA2-land use" and "PCA3-lake shape and connectivity", were extracted and explained over 70% of the total variation for each buffer spatial scale (Table 4). The bivariate correlations between the derived PCA components were calculated for each buffer spatial scale. If the correlation value r was >0.6, we filtered the most highly correlated variables, such as alkalinity, conductivity and pH, then repeated the initial PCA analyses before the non-correlated PCA components were extracted.

Univariate regression was used to identify the key hydrological and land use predictors of lake macrophyte richness for each growth form. Due to low group membership of two growth forms, free-floating and floating-leaved were aggregated into a single group for this analysis. In order to identify the lake environmental filters best explaining the richness of each growth form, generalized linear model (GLLM) with a Poisson log link function were initially used since the response variable was count data. However, due to over-dispersion a negative binomial generalized linear model (GLLM-NB) was later used in preference.

Based on the optimal model for each growth form, separate models were fitted along with each hydrological / land use predictor and PCA gradients for each buffer type (catchment and landscape) and for each buffer distance (from 0.25 km to 10 km) with the Akaike information criterion (AIC) being used to compare the goodness of fit for each model. Finally, ΔAIC of each model was calculated to identify the optimal buffer spatial scale for explaining macrophyte richness for each macrophyte growth form by each hydrological / land use indicator and PCA gradients separately.

Partial Redundancy Analysis (Partial RDA) was used to identify the catchment and landscape scale that can best explain growth form composition, based on the relative number of species in the major growth forms. First, using the corvif function from 'AED' package in R (Zuur, et al., 2009), the variance inflation factor (threshold of 3) of all variables was determined within the separate environmental (Appendix 3.1), hydrological and land use variables data sets to reduce colinearity among model predictors. As a result, the variables stream density, lake proximity index, water body coverage, lake density, Euclidean nearest-neighbour distance and lake fractal index were retained within the hydrological dataset. Similarly, agricultural coverage, urban coverage and agricultural patch density were retained within the land use dataset. An automated, forward stepwise selection of variables within the Partial RDA was then used to identify the environmental variables that best explain macrophyte growth form composition. The adjusted R^2 of the Partial RDA models based on the selected hydrological and land use indicators were then compared between *catchment buffers* and *landscape buffers* respectively.

All of the statistical analyses were conducted in R. The GLM-NB model was fitted using the "mass" package (Venables & Ripley, 2002). PCA analysis was conducted in "ade4" package (Dray & Dufour, 2007) and Partial RDA was performed in the "vegan" package (Oksanen et al., 2007).

3.4 Results

3.4.1 Response of macrophyte richness to hydrological and land use indicators

All of the environmental variables defined for the 90 study lakes in Appendix 3.1 were considered as explanatory variables to predict the macrophyte richness. The results for the GLM-NB models showed that the drivers of macrophyte richness differed with macrophyte growth form (Table 3.2). In particular, the key factors explaining emergent macrophyte richness are lake area and alkalinity, while the richness of floating macrophytes was best explained by lake conductivity alone. Overall, lake area, conductivity and pH were the most significant variables explaining total macrophyte richness within the 90 study lakes.

Table 3.2 The best performing GLM-NB models using environment variables to predict the richness for each macrophyte growth form based on AIC. The significance of each predictor in GLM models was tested through the analysis of variance (ANOVA) Chi-square test (*p<0.1; **p<0.01).

Predictor	**Model selected**	**Step forward results for GLM model**	**Residual deviation on d.f.**	**AIC**
Total plant richness	GLM-NB	Lake Area* + lake Conductivity + lake pH	95.63, 88	579.63

Submersed plants	GLM-NB	Lake Area** + lake Alkalinity* + lake Conductivity*	97.85, 88	501.56
Emergent plants	GLM with Poisson	Lake Area + lake Alkalinity*	77, 90	327.51
Floating plants	GLM with Poisson	Lake Conductivity	91.55, 90	325.34

Table 3.3 ΔAIC values of GLM models for explaining macrophyte richness by key hydrological and land use predictors based on the most significant factors for each growth form. The (+ or -) indicates the sign of coefficient for the factor. AIC values that indicate an improvement from the basic environmental model are shown in bold.

Predictor		Total richness		Submersed richness		Emergent richness		Floating richness	
Buffer type		Landscape	Catchment	Landscape	Catchment	Landscape	Catchment	Landscape	Catchment
Original AIC		579.63		501.56		327.51		325.34	
Stream density	B0.25	1.75	2	1.72	1.99	1.78	1.76	**-0.27(+)**	1.28
	B0.5	0.13	1.84	0.4	1.86	1.78	1.98	**-2.31(+)**	0.79
	B0.75	**-0.68(+)**	1.85	**-0.48(+)**	1.83	1.46	1.95	**-3.33(+)**	0.77
	B1	**-1.96(+)**	1.59	**-1.18(+)**	1.7	1.22	1.93	**-5.80(+)**	**-0.3**
	B2	1.17	1.93	1.91	1.62	1.48	1.92	**-3.55(+)**	0.1
	B2.5	1.1	1.94	1.62	1.73	1.56	1.95	**-1.36(+)**	0.43
	B5	0.21	2	0.48	1.99	1.12	1.99	**-0.12(+)**	1.14
	B7.5	**-0.40(+)**	1.92	**-0.18(+)**	1.79	1.13	1.96	0.01	1.64
	B10	**-1.17(+)**	1.97	**-0.88(+)**	1.99	0.88	1.92	**-0.18(+)**	1.05
Lake density	B0.25	2	1.51	1.99	1.7	1.68	1.48	1.05	1.99
	B0.5	1.9	1.78	1.99	1.76	1.99	1.87	0.48	1.91
	B0.75	1.99	1.9	1.93	1.75	1.71	1.96	1.7	1.93
	B1	1.98	1.99	1.98	1.96	1.6	1.92	1.57	1.83
	B2	1.88	1.99	1.99	1.89	0.55	1.31	0.85	1.36
	B2.5	1.89	2	1.99	1.71	**-0.10(+)**	0.88	0.67	1.15
	B5	1.98	1.99	1.8	1.56	0.44	1.03	0.88	1.25
	B7.5	1.96	2	1.93	1.78	0.05	0.92	1.25	1.17
	B10	1.92	2	1.99	1.63	0.04	0.89	1.3	1.19
Lake coverage	B0.25	1.45	1.44	**-0.39(-)**	**-0.27(-)**	1.08	1.04	1.09	1.25
	B0.5	1.75	1.83	0.7	0.93	1.09	1.03	0.99	0.84
	B0.75	1.94	1.98	1.53	1.62	0.97	0.83	0.85	0.56
	B1	2	1.99	1.92	1.96	0.76	0.5	0.54	0.11
	B2	1.25	1.39	1.39	1	0.64	**-0.32(+)**	**-0.46(+)**	**-0.57(+)**
	B2.5	1.38	1.31	1.14	**-0.19(-)**	0.02	**-1.50(+)**	0.49	0.1
	B5	1.82	0.66	1.62	**-2.83(-)**	**-0.02(+)**	**-1.03(+)**	1.74	0.92
	B7.5	2	1.25	1.99	**-1.22(-)**	**-0.33(+)**	**-1(+)**	2	1.68
	B10	0.56	1.53	0.22	**-0.60(-)**	**-1.80(+)**	**-1.32(+)**	1.18	1.91
Lake fractal index	B0.25	1.42	1.62	1.41	1.38	1.31	1.78	1.39	1.67
	B0.5	1.01	1.49	1.61	1.45	1.72	2	1.07	1.44
	B0.75	1.65	1.44	1.69	1.33	1.94	1.88	1.92	1.75
	B1	1.72	1.44	1.65	1.16	1.95	1.85	1.93	1.77
	B2	2	0.55	1.98	**-0.20(-)**	1.95	1.6	1.54	1.75
	B2.5	0.71	**-2.88(-)**	1.57	**-2.88(-)**	**-0.76(-)**	**-0.20(-)**	2	0.31
	B5	1.7	**-2.75(-)**	1.69	**-5.35(-)**	1.83	1.5	1.08	1.35
	B7.5	1.07	0.38	0.98	**-0.66(-)**	1.99	1.8	0.57	1.86
	B10	0.37	0.11	**-0.05(-)**	**-1.03(-)**	1.99	1.34	**-2.05(+)**	1.95
Land use/ Agriculture	B0.25	**-200(+)**	**-200(+)**	**-173(+)**	**-173(+)**	**-109(-)**	**-109(-)**	**-111(+)**	**-111(+)**
	B0.5	**-189(+)**	**-194(+)**	**-165(+)**	**-169(+)**	**-103(-)**	**-106(-)**	**-102(+)**	**-107(+)**
	B0.75	**-160(+)**	**-188(+)**	**-140(+)**	**-164(+)**	**-86(-)**	**-103(-)**	**-86(+)**	**-104(+)**
	B1	**-160(+)**	**-176(+)**	**-140(+)**	**-154(+)**	**-86(-)**	**-95(-)**	**-85(+)**	**-96(+)**
	B2	**-114(+)**	**-160(+)**	**-99(+)**	**-140(+)**	**-59(-)**	**-86(-)**	**-60(+)**	**-88(+)**
	B2.5	**-92(+)**	**-148(+)**	**-81(+)**	**-131(+)**	**-47(-)**	**-80(-)**	**-46(+)**	**-81(+)**
	B5	**-36(+)**	**-133(+)**	**-32(+)**	**-116(+)**	**-16(-)**	**-72(-)**	**-17(+)**	**-74(+)**
	B7.5	**-15(+)**	**-133(+)**	**-13(+)**	**-115(+)**	**-7(-)**	**-72(-)**	**-7(+)**	**-74(+)**
	B10	**-3.4(+)**	**-132(+)**	**-2.5(+)**	**-115(+)**	**-1(-)**	**-72(-)**	**-1(+)**	**-74(+)**
Land use/ Urban	B0.25	**-382(+)**	**-382(+)**	**-327(+)**	**-327(+)**	**-217(-)**	**-217(-)**	**-214(+)**	**-214(+)**
	B0.5	**-358(+)**	**-363(+)**	**-307(+)**	**-311(+)**	**-205(-)**	**-207(-)**	**-200(+)**	**-204(+)**
	B0.75	**-352(+)**	**-352(+)**	**-302(+)**	**-302(+)**	**-201(-)**	**-201(-)**	**-196(+)**	**-196(+)**
	B1	**-329(+)**	**-335(+)**	**-283(+)**	**-288(+)**	**-187(-)**	**-191(-)**	**-185(+)**	**-188(+)**
	B2	**-297(+)**	**-329(+)**	**-256(+)**	**-282(+)**	**-168(-)**	**-188(-)**	**-167(+)**	**-183(+)**
	B2.5	**-254(+)**	**-316(+)**	**-217(+)**	**-271(+)**	**-140(-)**	**-180(-)**	**-143(+)**	**-177(+)**
	B5	**-174(+)**	**-302(+)**	**-148(+)**	**-261(+)**	**-97(-)**	**-171(-)**	**-94(+)**	**-167(+)**
	B7.5	**-133(+)**	**-290(+)**	**-114(+)**	**-251(+)**	**-69(-)**	**-164(-)**	**-71(+)**	**-161(+)**
	B10	**-92(+)**	**-290(+)**	**-77(+)**	**-251(+)**	**-48(-)**	**-164(-)**	**-49(+)**	**-161(+)**

The ΔAIC value of the GLLM model (Table 3.3) for *landscape buffers* and *catchment buffers* indicated that the majority of the different hydrological and land use indicators can be used to explain macrophyte richness separately when the different growth forms are considered. Land use explained far greater variation in macrophyte richness than hydrological features. Among the different land use types, urban land cover explained a greater proportion of macrophyte species richness than agriculture regardless of buffer type or spatial scale. For hydrological features, the best three variables for predicting macrophyte species richness were stream density, lake coverage and lake fractal index. In addition, the optimum hydrological feature(s) changed with macrophyte growth form. For example, stream density (*landscape buffer*) was related more closely with floating plant richness, whilst the lake fractal index (*catchment buffer*) was shown to have a closer relationship with submersed plants. For each variable, the coefficient of determination changed across the buffer spatial scales, demonstrating a scale dependency in the model predictions. The estimates of all coefficients including their confidence were provided in the supplementary information.

Furthermore, the comparison of buffer types demonstrated that for land use indicators and some hydrological variables (i.e. lake coverage and lake fractal index), the ΔAIC value showed that *catchment buffers* explained more of the variation in lake macrophyte richness (lower ΔAIC value) than *landscape buffers*. By contrast, for hydrological features (e.g. stream density), *landscape scale* is generally better to predict macrophyte richness than *catchment scale.*

3.4.2 Optimal spatial distances in explaining total species richness

The first three PCA axes explained over 70% of the variation in all selected variables for *landscape buffers* and *catchment buffers*, with almost equal amounts being explained by PCA axes 1 and 2 (Table 3.4). Variables in each PC axis were very similar for *landscape* and *catchment buffer*. Specifically, PC axis 1 was positively associated with variables related to lake area (e.g. water body coverage, largest lake index and lake cohesion index) and negatively correlated with lake structural variables (e.g. lake density, stream density and lake division index). The second axis was positively associated with land use characteristics such as extent of agriculture. PC axis 3, explained 9.5% to 11.6% of the variation and, was positively related to lake shape index and lake proximity index.

Table 3.4 Summary of correlation coefficients for three PC axes explained scores based on the hydrological and land use indicators. Ranges show the differences in a buffer type across scales from 0.25 to 10 km.

Landscape Buffer			
PCA components	PC axis1 Lake spatial dispersal	PC axis2 Land use	PC axis3 Lake shape and connectivity
Explained range (lowest to highest/Buffer distance (km))	23.9%(B5) to 31.3%(B0.25)	24.9%(B5) to 30.9%(B1)	9.5%(B10) to 11.6(B5)
Variables (correlation coefficients with PC axis)	Stream density (-0.593 to -0.397)	Agriculture coverage (0.747 to 0.938)	Proximity index (0.493 to 0.782)
	Water body coverage (0.834 to 0.978)	Agriculture patch density (0.779 to 0.926)	Lake fractal index (0.518 to 0. 826)
	Lake density (- 0.815 to -0.560)	Urban coverage (0.382 to 0.846)	
	Largest patch index (0.953 to 0.985)	Urban patch density (0.674 to 0.921)	
	Cohesion (0.637 to 0.762)		
	Division (- 0.951 to -0.893)		
Catchment Buffer			
PCA component	PC axis1 Lake spatial dispersal	PC axis2 Land use	PC axis3 Lake shape and connectivity
Explained range (lowest to highest/Buffer distance (km))	24.6%(B2.5) to 31.04%(B0.25)	24.5%(B2) to 27.5%(B7.5)	9.01%(B10) to 11.4(B0.75)
Variables (correlation coefficients with PC axis)	Stream density (-0.593 to -0.329)	Agriculture coverage (0.838 to 0.955)	Proximity index (0.437 to 0.782)
	Water body coverage (0.924 to 0.980)	Agriculture patch density (0.871 to 0.935)	Lake fractal index (0.542 to 0. 806)
	Lake density (- 0.846 to -0.532)	Urban coverage (0.646 to 0.880)	
	Largest patch index (0.945 to 0.984)	Urban patch density (0.652 to 0.938)	
	Cohesion (0.551 to 0.744)		
	Division (- 0.952 to -0.921)		

The GLLM-NB model of total macrophyte richness, after taking account of lake area, conductivity and pH (Table 3.2), included at least one significant PCA component at each buffer spatial scale, indicating that total richness of macrophytes can be explained partially by the hydrological and land use indicators. The total richness of macrophyte species was best explained by PCA components at the finer spatial scale – specifically at the 1 km scale for the *landscape buffers* and the 0.5 km scale for the *catchment buffers* (Figure 3.3).

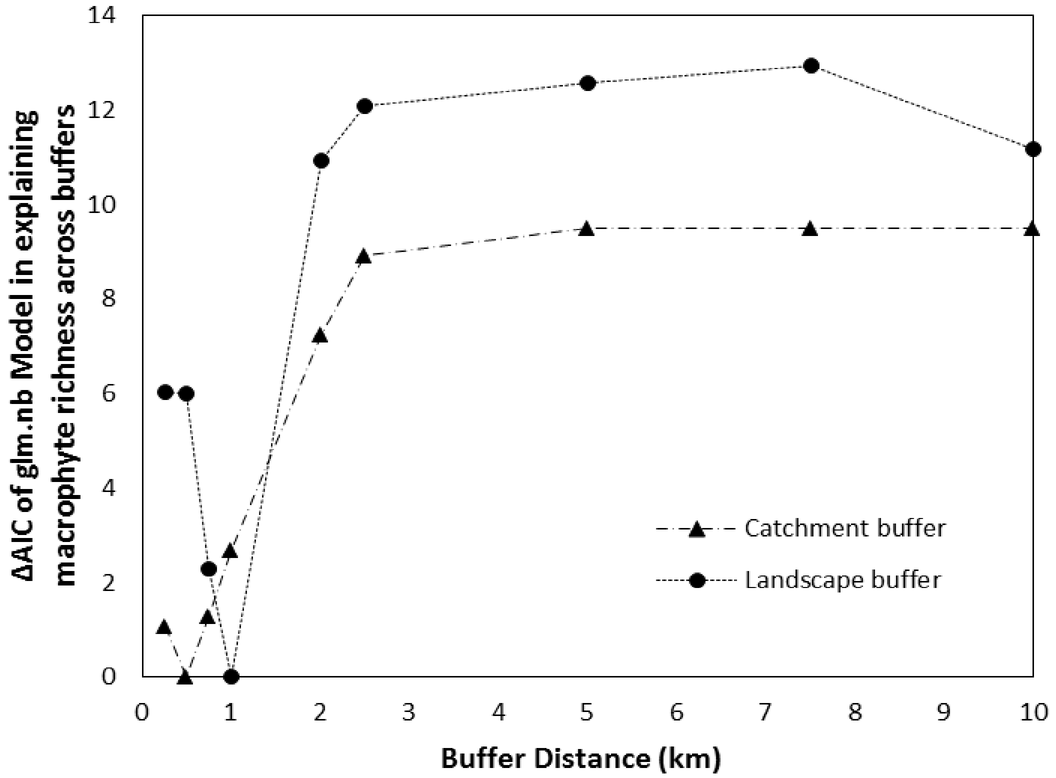


Fig. 3.3 Comparison of the transition of the fitted GLM-NB models that applying hydrology and land use in different buffer types and spatial scales for explaining macrophyte richness

The independent variable is the residual from the model based on lake area and chemistry, and explanatory variables are PCA components (three PCA axes described in Table 3.4) according to *landscape buffers* and *catchment buffers*. ΔAIC shows the variation among AIC values of the model at each buffer scale (from 0.25 to 10 km), the best model being indicated by the lowest ΔAIC.

3.4.3 Effect of hydrology and land use on macrophyte growth form composition at the optimal buffer spatial scale

Adjusted R^2 values from the Partial RDA models for the multiple spatial scales (Figure 3.4) showed different trends in terms of explaining macrophyte growth form composition using hydrological and land use datasets separately. For land use indicators (Figure 3.4A), the total variance explained for both *landscape buffers* and *catchment buffers* increases before peaking at **1** km, followed by a drop with increasing buffer distance. For the hydrological dataset (Figure 3.4B), a similar trend is shown for the *landscape buffer*, with **1**-**2** km being the most significant spatial scales in terms of explaining growth form composition. However, using *catchment buffers* variation in growth form composition was best explained at a spatial scale of **5** km (13%), with models using hydrology in *catchment buffers* proving non-significant at the finest spatial scales (<1 km). Moreover, there is a turning point at the scale of about 1.5 km which marks a shift in importance from *landscape buffer* to *catchment buffer* in explaining macrophyte growth form composition across multiple spatial scales.

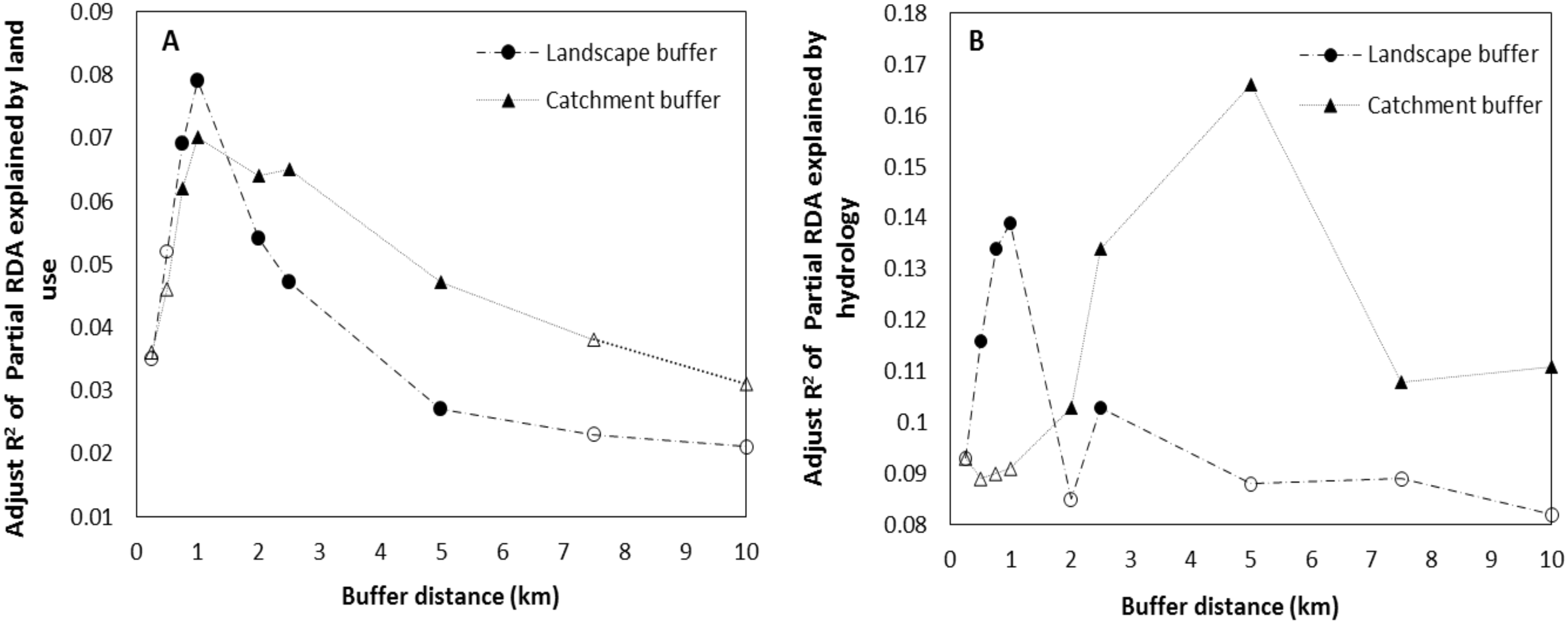


Fig. 3.4 Spatial dependency of Partial Redundancy models in explaining macrophyte growth form composition using hydrological and land use predictors within a *landscape buffer* or *catchment buffer*. The solid points represent significant ($P < 0.05$) Partial RDA models, whilst the hollow points represent non-significant models.

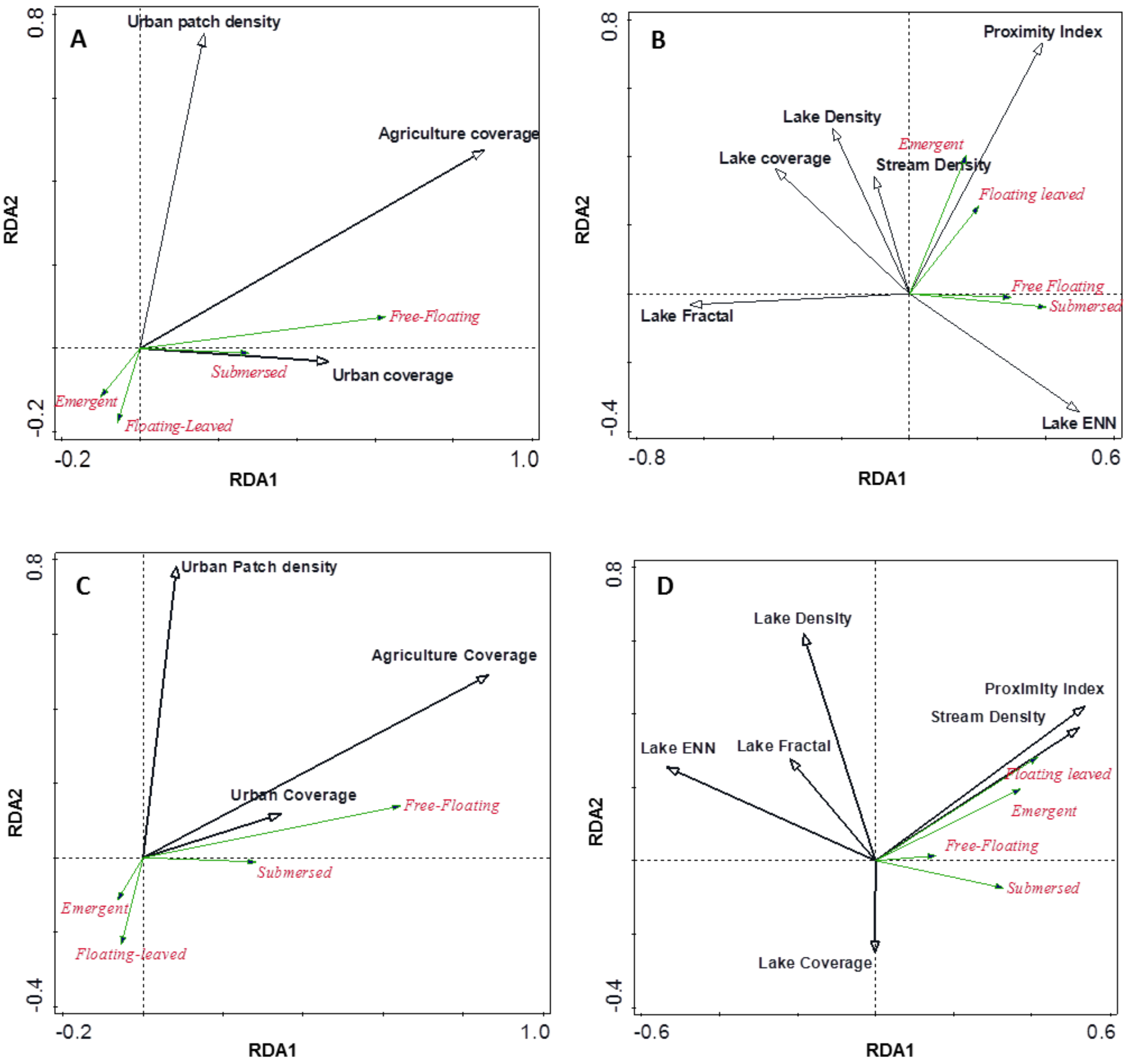


Fig. 3.5 Partial Redundancy Analyses of macrophyte growth form composition related to the key hydrological and land use indicators at the optimal spatial scale of *landscape buffer* and *catchment buffer*. Fig. 3.5A - Scale of 1 km in *catchment buffer* explained by land use; Fig. 3.5B - Scale of 5 km in *catchment buffer* explained by hydrological features; Fig. 3.5C - Scale of 1 km in *landscape buffer* explained by land use; Fig. 3.5D - Scale of 1 km in *landscape buffer* explained by hydrological features.

Figure 3.5 illustrates how the partial RDA of macrophyte richness in different growth forms corresponded to the key hydrological and land use indicators at the spatial distance where the relationship between the explanatory variables and composition was strongest in *landscape buffers* and *catchment buffers*. For hydrological features (see Figure 3.5B, Figure 3.5D), lake fractal index was found to be a key variable as defined by a forward selection model to explain richness for all growth forms. It was negatively correlated to richness of submersed macrophytes and free-floating macrophytes. Lake proximity index was positively correlated with the richness of emergent macrophytes and floating-leaved macrophytes at the optimal scale of *landscape buffer* and *catchment buffer*. For land use indicators (see Figure 3.5A, Figure

3.5C), urban coverage was closely correlated with the richness of free-floating macrophytes and submersed macrophytes, whilst agriculture was strongly negatively related to the richness of floating-leaved and emergent macrophytes at a scale of 1 km in *landscape buffer*.

3.5 Discussion

3.5.1 Effect of buffer-scale drivers on macrophyte richness

The landscape-scale variables are important in determining the biogeographical distribution of the aquatic plants that disperse through the biological vectors (e.g. birds or mammals) or wind-aided transport, while the catchment-scale variables will be related to the dispersal process of macrophyte species that are dependent on hydrochory.

The impact of hydrological and land use variables on macrophyte species richness was clearly different depending on the macrophyte growth forms (Table 3.3). The richness of floating macrophytes was more strongly associated with stream density within *landscape buffers* (Table 3.3). This might be explained by floating macrophytes being more reliant on the hydrological network, and flood events in particular, for dispersal between water bodies (Thomaz et al., 2007). Interestingly, however, the relationship between stream density and floating plant richness was significant at the landscape scale rather than the catchment scale, especially at smaller buffer sizes, implying that floating plants can disperse by means other than direct hydrochory. The seeds of some floating plants are buoyant (e.g., due to pulpy arils in *Nymphaea*, hydrophobic structures in *Nymphoides*) facilitating upstream transfer by wind or animals (Santamaria, 2002). It could be that floating plants transfer readily to other lakes at a small spatial scale (probably < 1 km) via wind or animals rather than the hydrological networks. The seeds of most floating plants are buoyant, such as pulpy arils in *Nymphaea*, hydrophobic structures in *Nymphoides*. The physical attributes of macrophyte seeds could facilitate transfer to the upstream or nearby lakes by wind and birds at larger buffer sizes (Santamaria, 2002).

Numerous studies have shown that lake chemistry is strongly impacted by inputs and processing from the stream network and surrounding environment (Lottig et al., 2011), whereas the diversity of drainage network increases the contribution of processing in determining the lake water quality. Systems with a complex drainage network are expected to have more similar water chemistry in lakes and streams. Thus one might expect agricultural inputs to lakes will be accelerated in catchments with a higher density stream network leading to greater fertility of lake water (Downing et al., 2008). Such conditions generally favour free-floating macrophytes over other growth forms (Vestergaard & Sand-Jensen, 2000a; Heegaard et al., 2001; Meerhoff et al., 2003).

The richness of emergent macrophytes was generally related to extent of standing open water in both *landscape buffers* and *catchment buffers*. Our results support previous observations of a positive relationship between lake-surface area and richness of emergent plants in ponds (Alahuhta et al., 2011; Moller et al., 2016). PCA analyses show that lake coverage is negatively correlated with lake density in the two buffer types (Table 3.4), thus lake buffer zones with high lake coverage and low lake density are characterised by a few large surface-area lakes. Regions with a high extent of shallow open water are likely to be beneficial to emergent macrophyte species simply through the increased provision of habitat (Friday, 1987; Rorslett, 1991).

The positive relationship between land use and macrophyte species richness that was found in this study is unsurprising since many lakes in the north of Britain are naturally nutrient poor and thus moderate nutrient subsidies from low intensity agriculture are likely to stimulate macrophyte diversity (Heino & Toivonen, 2008). The emergent growth form was the only one where richness was negatively influenced by managed land coverage. This may be explained by increased dominance of typical competitive emergent species (e.g. *Typha latifolia* or *Phragmites australis*) that benefit from eutrophication (Maemets & Freiberg, 2004; Partanen et al., 2009). Alternative causes may include loss of shallow water habitat associated with physical impacts of land use, or deterioration of habitat quality, e.g. through increased fine sediment inputs (Jones et al., 2003).

3.5.2 Effect of buffer-scale drivers on macrophyte growth form composition

The main determinants of macrophyte species richness in previous studies include geographical distribution (e.g. latitude), lake water quality (e.g. alkalinity and major nutrient concentrations), climate (e.g. mean annual temperature) and land use (e.g. human disturbance) (Alahuhta et al., 2012; Chappuis et al., 2012; Alahuhta, 2015). More recently, factors such as habitat heterogeneity have also been related to macrophyte species richness and composition (Kreft & Jetz, 2007; Rolon et al., 2008; Shi et al., 2010). Our results indicate that both hydrological and land use variables had an influence on macrophyte species richness at the catchment and landscape scale once the effects of the lake environment were excluded. More specifically, partial RDA analyses showed the impact of hydrological variables (adjusted R^2 varying from 0.08 to 0.17, Figure 3.4B) on macrophyte growth form composition was stronger than that of land use (adjusted R^2 varying from 0.02 to 0.09, Figure 3.4A). This implies that catchment and landscape hydrology is one of the principle drivers of aquatic vegetation structure in the study catchments. This finding differs from previous studies indicating that macrophytes of inland lakes are distributed mainly according to a gradient of land use intensity (i.e. agriculture and urban) within the catchment (Lougheed et al., 2001), although our results confirm that this is the major determinant of richness of the overall flora and individual growth forms. Our results can be explained by the fact that the majority of the catchments considered in our study have good water quality or, where historical impacts have occurred, water quality has been restored through management actions (Marsden & Mackay, 2001). Regulatory control over anthropogenic disturbance, especially diffuse pollution, means that runoff from agriculture plays a less important role in determining macrophyte species richness in lakes in northern Britain. Moreover, these areas have a highly developed river channel network (Scotland alone has over 6000 rivers with a total length in excess of 100000 km (Gilvear et al., 2002) plus a high density of lakes (>21000 water bodies >0.25 ha in area)). These hydrological features (e.g. stream density, lake density) are evidently important factors controlling the distribution of different macrophyte growth forms between lakes via the stream network. Physical connectivity of such rivers and current flow regulation practices are therefore likely to influence plant dispersal, with adverse consequences for distribution of some species (Johansson et al., 1996).

3.5.3 Comparisons between the effects of two buffer types and Management Implications

The most appropriate spatial extent over which to target nutrient reduction as part of lake restoration strategies has been found to vary, probably reflecting differences in climate, lake size, connectivity, water depth and macrophyte composition. Previous studies have reported the strongest effects on macrophyte richness at spatial scales ranging from 3000 m (Pedersen et al., 2006) to 1000 m (Akasaka et al., 2010) and 500 m (Alahuhta et al., 2012). However, these studies only considered relationships within *landscape buffers*. In our study, 1 km was regarded as the most relevant *landscape buffer* for determining effect of land use on lake macrophyte richness in different growth forms, while a 5 km *catchment buffer* showed the strongest relationship between macrophyte growth form composition and hydrological features.

Buffer zones are widely used to improve water quality by reducing nutrient inputs and soil erosion (Correll, 2005) and their use to protect aquatic vegetation is well supported (Akasaka et al., 2010; Alahuhta et al., 2012). Guidelines for lake protection often suggest controlling land use within close proximity of the shore, based on the finding that the terrain adjacent to a lake's shoreline has more direct contact with the lakes, and thus ability to influence the status of macrophytes, compared with the whole *topographic catchment* (Pedersen et al., 2006; Akasaka et al., 2010; Sass et al., 2010). Our results are consistent with previous findings that the strongest relationships with land use and hydrological variables occur when considered at the landscape scale rather than the more restricted catchment scale, with the strength of the effect being broadly inversely proportional to the distance from the lake. However, we suggest that such restrictions would be more effective if they transcend catchment boundaries due specifically to the higher significance of *landscape buffer* in explaining species richness (Figure 3.4). Moreover, we observed the impact of drivers in *catchment buffers* was stronger than those in *landscape buffers* when the buffer distance was greater than 1.5 km. This is possibly because land use can only affect lake condition at larger distances (e.g. > 1.5 km in this study) if there is an adequate connection through the hydrological network (i.e. in *catchment buffers*), while at short distance (e.g. < 1.5 km in this study), this effect can occur independently of hydrological connectivity (i.e. in *landscape buffers*). The results further suggest that scale-dependency of the land use effects may be associated with direct anthropogenic effects from the riparian zone and indirect hydrological connectivity impacts originating in headwater streams and lakes (Alahuhta et al., 2012).

Our results highlight the potentially important role of buffer strips at both catchment- (through runoff processes) and landscape-scale (through direct influence, such as groundwater exchange process) in the conservation of freshwater biodiversity. We recommend, wherever possible, limiting management activity and drainage works within a short distance (~1km) of a lake's shoreline. This approach will be most effective if not restricted to the catchment boundary (i.e. a *landscape buffer* is utilised). However, at larger distance, catchment plays a much more important role in governing lake macrophyte diversity, probably through the impact of runoff processes. Alleviating barriers to connectivity between freshwater at the catchment scale may serve to naturalise plant growth form composition. However, such actions may also serve to dispserse invasive species or redistribute stressors linked to artificial land use which, as our analyses show, is a primary determinant of plant species richness in lakes.

Due to the limitation of the statistical methods, we are not able to directly evaluate the uncertainty of the explanatory power of models in this study. This error could strongly affect our interpretation of the results although the trends presented are in line with most published findings. The application of our results to management and future studies should therefore be considered with caution.

3.6 Conclusions

Our study aimed to determine the impact of hydrological features (lake spatial pattern and lake connectivity) and land use on lake macrophyte richness across *landscape buffers* and *catchment buffers* and whether these relationships are scale sensitive. Through the comparison of *catchment buffers* and *landscape buffers*, the results indicate that a larger spatial extent (5 km) of *catchment buffers* dominated by hydrological features has the greatest influence on lake macrophyte growth form composition. This research sheds new light on the connectivity between limnology and macrophyte dispersal and identifies the scales over which human disturbance exerts most influence on the vegetation of lakes. The study demonstrates that characteristics of *landscape buffers* within **1.5** km drive growth form composition of lake macrophytes, while the impact of *catchment buffers* was strongest at coarser scales. Moreover, the most significant hydrological and land use indicators to explain macrophyte richness differed between growth forms. For example, floating macrophytes were found to be most affected by stream density within *landscape buffers,* suggesting that floating plants were more reliant on the biological vectors (e.g. birds or mammals) or wind-aided transport at small spatial scale and more dependent on water-borne dispersal (hydrochory) at larger buffer sizes. While emergent macrophytes were found more correlated with the variable of lake coverage in catchment buffers. Potentially the seeds of emergent plants were easy to disperse through wind or biological vectors and benefit from the increased availability of edge habitat associated with water body extent (Rorslett, 1991).

Our study also highlights the key spatial extent of *landscape* or *catchment buffers* for restricting adverse effects of human activities, such as drainage, stream engineering and farming, on lake ecosystems, especially those with protected status. **1 km** of *landscape buffer* from the lake shoreline is regarded as the most relevant area influenced by agriculture and urbanization, while we suggest controlling drainage activities within **5 km** of the lake upper area (within *catchment buffer*) to reduce impacts on macrophyte species richness in lakes.

Chapter 4 – Response of macrophyte species turnover to habitat connectivity at the catchment scale in northern UK lakes

4.1 Abstract

Previous studies have shown that spatial turnover of macrophyte species in lakes is driven by niche filtering. However, only a few studies have also assessed the influence of lake connectivity on species turnover. Here, we investigate the spatial turnover of macrophyte species in lakes as a function of hydrological connectivity (i.e. watercourse dispersal) or geographical connectivity (i.e. overland dispersal) at the *topographic catchment* scale. Data were compiled on the presence/absence of macrophyte species in 222 lakes within 12 study catchments located in northern England and Scotland. The species turnover rates were calculated to determine the level of dissimilarity between lake macrophyte assemblages at the catchment scale. Subsequently, these were regressed against a range of landscape variables for each catchment. Lake pairs that feature a clear upstream/downstream relation by location were selected from the study catchments. The environmental and connectivity variables (i.e. hydrological connectivity and geographical connectivity) were used to explain the variance of macrophyte species turnover (Jaccard index) between lake pairs.

The *Topographic catchment*s controls surface water flow and was considered to be a vital element in determining the dispersal of macrophyte species among lakes. At the catchment level, a combination of environmental filters (abiotic and biotic variables) was most influential in structuring the lake macrophyte assemblage. The results indicated that geographical connectivity explained more of the variability in species turnover than hydrological connectivity. Moreover, this study showed that species turnover was determined by the environmental and connectivity variables which were very sensitive to the degree of human disturbance. In catchments with a higher degree of human disturbance, species turnover was less strongly related to the degree of environmental dissimilarity or spatial connectivity, suggesting that anthropogenic effects can override these intrinsic patterns.

4.2 Introduction

Macrophytes have a restricted distribution in lake networks, which is potentially dependent upon lake-scale factors such as environmental filtering or presence of competitors (Heino et al., 2007; Peres-Neto et al., 2012; Alahuhta & Heino, 2013), coupled with processes that govern dispersal at the catchment scale such as hydrological isolation or flooding (Shmida &

Wilson, 1985; Bouvier et al., 2009). Intensive studies on the bio-geographical distribution of macrophytes have often considered the impact of lake-scale abiotic variables (Jackson et al., 2001) and latitude (Virola et al., 2001). Besides lake scale variables, different dispersal processes of aquatic species are important to maintaining regional biodiversity (Naiman et al., 1993; Akasaka & Takamura, 2011). Wind, water flow and waterbirds are the most important dispersal agents for lake plants (Morris, 2012), although each of these vectors differ in the distance, time and direction of the species they transport.

Many submersed and floating plants have propagules with good flotation capability and have been identified as largely dependent on carriage by water flow (Dahlgren & Ehrlen, 2005) and subsequently, in some cases, by waterbirds (Chen et al., 2007) to move to distant sites. Emergent plants are able to release their seeds into the air and thus have the potential to initially disperse by wind (Dahlgren & Ehrlen, 2005) and subsequently by water birds or water flow. Emergent plants having seeds with terminal velocities below 2 ms^{-1} (Soons, 2006), such as emergent plants of the genera *Typha*, *Phragmites* and *Isolepis*, have a particular potential for long-distance dispersal by wind. Wind dispersal will be enhanced when the source habitat has high seed abundance (Hovenden et al., 2008) or experiences strong storm force winds parallel to the prevailing wind direction (Davies & Sheley, 2007). Water disperses lake plant species through streams and the floodplain network, and is important in structuring aquatic plant populations (Boedeltje et al., 2004; Merritt & Wohl, 2006; Chen et al., 2007). This unidirectional dispersal is often used to explain why higher biodiversity appears in downstream habitats (Gornall et al., 1998; Liu et al., 2006). The dispersal distance of plants in water is promoted by increasing river discharge such as floods (Nilsson et al., 1991) and the duration of seed buoyancy (Middleton, 1999; Boedeltje et al., 2004). Spreading via water flow may therefore be constrained in lakes that lack hydrological connection to other lakes. Water-dwelling animals are particularly important in transporting aquatic plants to some hydrologically isolated lakes not colonised through wind dispersal (Green et al., 2008). Seeds and other propagules can be dispersed to new sites by waterbirds, either through attachment to their feet or plumage or via ingestion, which produces different patterns of connectivity between lakes contingent on the bird species present, their density, feeding habits and migratory behaviour (Viana et al., 2016).

The dispersal abilities of different macrophyte species contribute to the variation in vegetation composition observed in lakes and wetlands. Assessment of potential lake connectivity can help understand the effective modes of dispersal and colonization of macrophytes among lakes (Guimaraes et al., 2014). Attempts to assess lake connectivity have so far utilised distance metrics and spatial pattern metrics such as different landscape indices (Morris, 2012). In the present work, the connectivity of lakes within the landscape can either be measured as the degree of (i) geographical connectivity or (ii) hydrological connectivity. Geographical connectivity between lakes was applied to estimate the potential impact of wind or waterbirds in determining the mobility of aquatic plants in the landscape (Hartvigsen & Kennedy, 1993; Ganio et al., 2005; Miyazono et al., 2010). Hydrological connectivity is the distance between two lakes measured as continuous water-course length and is a major pathway for water-mediated dispersal of plants across the landscape (Johansson et al., 1996; Ward et al., 2002). Fluvial corridors not only input a large number of plant seeds via drainage from floodplains, but also provide food and habitat for waterbirds which increases the probability of seed carriage (Beier & Noss, 1998; Ishiyama et al., 2014). Flood events disperse plant propagules to floodplain lakes and influence the species sorting process (Middleton, 2000; Thomaz et al., 2007). The loss of hydrological connectivity caused, for example, by damming, thus disrupts the movement of propagules to downstream lakes by altering the hydrological regime (Jansson et al., 2000; Merritt & Wohl, 2006).

The distance-decay relationship, i.e., the decay of community similarity with geographic distance induced by species turnover in space, was first proposed by Whittaker (1960) in a study of plant communities in the Siskiyou Mountains in the USA, and further developed by Nekola & White (1999) who compared the rate of similarity decay in several species groups across spruce-fir forests in North America. A large number of studies have confirmed the existence of distance-decay patterns in aquatic taxa (including both macro- and microorganisms) such as parasite and fish (Poulin et al., 1999; Poulin, 2003) across different geographic and environmental gradients (Novotny et al., 2007; Qian & Ricklefs, 2007; Martiny et al., 2011); yet such patterns remain poorly understood for freshwater plants. The few available studies indicate that similarity of aquatic plants (Heegaard, 2004), phytoplankton and zooplankton (Soininen et al., 2007) decay with distance among freshwater habitats, although one study found that phytoplankton and zooplankton composition was unrelated to geographic distance but positively correlated with environmental heterogeneity (Mazaris et al., 2010). These findings suggest that both dispersal processes and niche filtering will contribute to the structuring of aquatic plant communties (Hubbell, 2001; Chase & Leibold, 2002).

The meta-analyses of distance-decay relationships indicate the pattern of distance-decay is strongly impacted by other elements, such as spatial gradients and human disturbance. For example, Soininen et al., (2007) observed a faster decay of β diversity in high latitude habitats than low latitude ones. Different trophic conditions were found to influence the relative importance of environmental filter and catchment- and/or landscape-scale process in structuring diatom communities (Vilar et al., 2014).

The majority of studies examining the relative role of dispersal processes in structuring lake macrophyte assemblages have used the overland geographical distance as the indicator of lake connectivity, perhaps because it is easier to measure than hydrological connectivity. Consequently, few studies have directly compared the importance of hydrological and geographical connectivity as determinants of species turnover at the catchment scale. The one exception to this considered the role of small ponds in maintaining habitat connectivity and concluded that both geographical connectivity and the hydrological connectivity were important in maintaining the aquatic animal biodiversity (Ishiyama et al., 2014). In addition, most existing studies have investigated the role of lake connectivity (Ishiyama et al., 2014) and environmental dissimilarity (Heegaard, 2004) as drivers of patterns in macrophyte species turnover within a single river system; few studies address how these relationships differ across multiple drainage basins (Heino, 2011) and it is therefore unclear to what extent the dispersal of macrophytes is limited by the confines of *topographic catchments*. Therefore, the following hypotheses are proposed:

- Hydrologically-connected lakes that are located closer together will have more species in common than lakes that are further apart;
- Hydrological connectivity plays a more important role in explaining the turnover in macrophyte species between lakes compared to geographical connectivity;
- The decay in species similarity with distance and environmental dissimilarity is sensitive to the intensity of human disturbance.

This study therefore focuses on the relative importance of different processes (e.g. environmental filtering and dispersal) in shaping variation in macrophyte communities. For example, one could expect that hydrological connectivity is a key determinant in explaining species turnover between pairwise lakes with hydrologic connections. However, if two lakes are geographically close but connected via a long reach of river channel, hydrological distance may prove subordinate to geographical distance in determining species turnover. It is also predicted that the relative role of dispersal ability and environmental filtering will change with different intensities of human disturbance. Confirmation of such an effect would inform the understanding of lake recovery processes in disturbed landscapes.

4.3 Method

4.3.1 Study sites

This study sites considered were located in Scotland and the north of England. These regions were specifically chosen for this study because of their high density drainage network (Scotland, for instance, has over 6000 rivers with the total stream length in excess of 100,000 km) and a high density of lakes (Gilvear et al., 2002). Further, the low intensity of agriculture in most of these regions (compared to the south of Britain), and improved regulatory control over anthropogenic activities, especially diffuse pollution, means that currently most rivers, lakes and estuaries in the north of Britain are considered to have high ecological quality (Marsden & Mackay, 2001). This therefore allows the importance of landscape connectivity in a well-developed hydrological network to be examined in the absence of significant anthropogenic stress.

A total of 12 hydrologically-independent catchments were included in the study (Figure 4.1). The catchments were chosen because they satisfied several requirements: (i) no overlap between catchments; (ii) catchment area in excess of 200 km^2; (iii) the number of upstream lakes was greater than 10; (iv) the lake order, as defined by Riera et al., (2000), at the outlet point was greater than 4; and (v) there were a large number (≥ 14 pairs) of hydrologically-connected lakes in each catchment. The *topographic catchments* used in the study were calculated from digitised lake shorelines (MERIDIAN^{TM} 2) and a digital terrain model (DTM; Terrain 50) obtained from the Ordnance Survey at a 50 m grid resolution using the Arc Hydro extension in ArcGIS (v10.3).

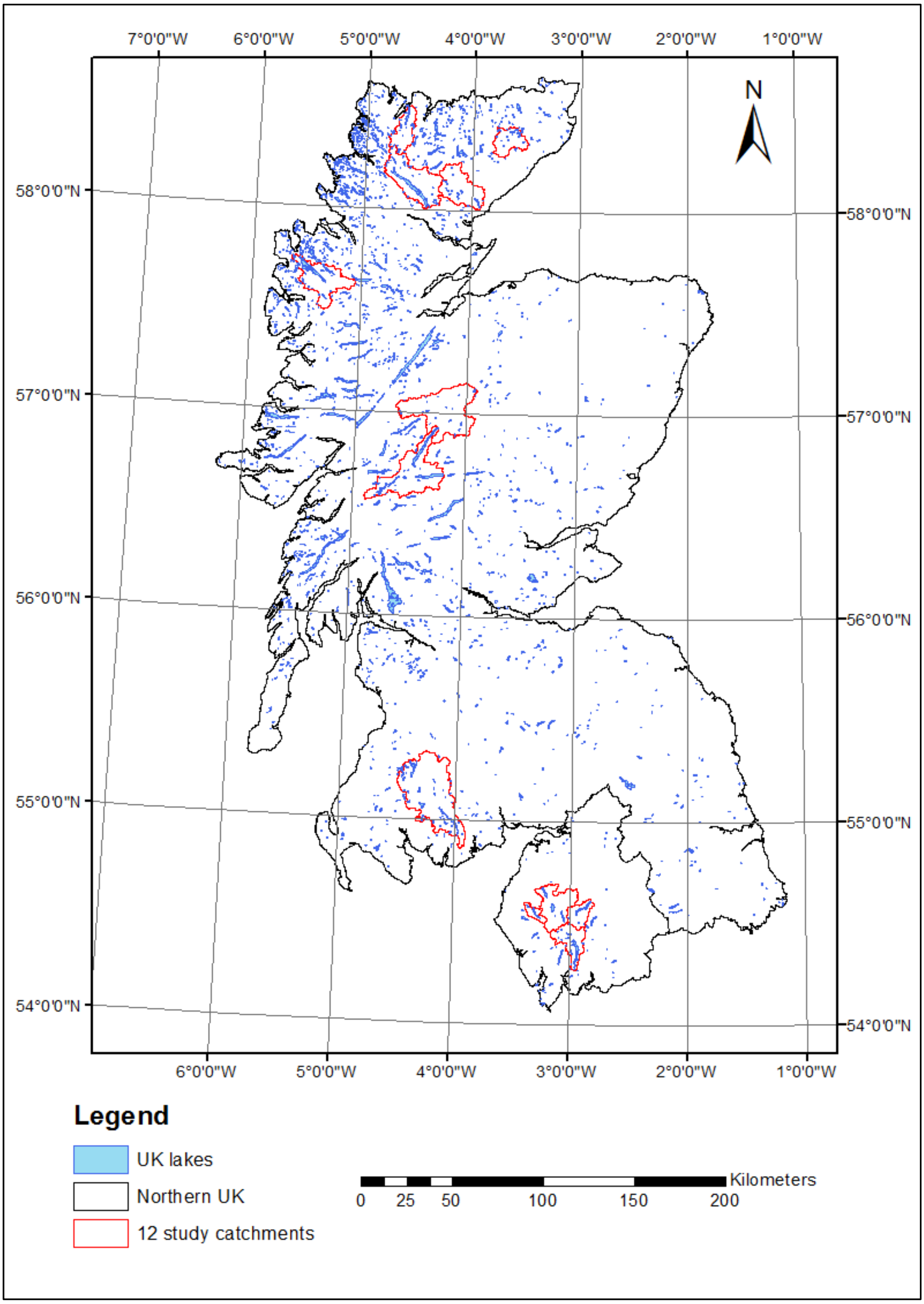


Fig. 4.1 Location of the study catchments in Scotland and northern England

4.3.2 Macrophyte sampling

The macrophyte data were obtained from survey organised by the Joint Nature Conservation Committee (JNCC) and the UK environment agencies between 1980 and 2003. This historical dataset includes records on the occurrence of aquatic plants and associated water chemistry variables for 2558 UK lakes and ponds. Where repeat surveys were carried out the most recently available data was used, although testing of within lake changes in vegetation during this time period indicated that any differences were consistently small compared to between lake differences. In total, 222 lakes extracted from the survey dataset were located in the catchments considered in this study.

The field surveys were conducted between July and September. Macrophytes were sampled along multiple transects in the shallow parts of the littoral zone. The observed species were classified according to their growth habit (i.e. free-floating, floating-leaved, submersed or partly emergent) with free-floating and floating-leaved subsequently being aggregated into a single group due to low membership. Water samples were collected at the same time and analysed for total alkalinity, pH and conductivity. Data on lake attributes including area, depth and shoreline complexity for subsequently derived from a GIS analysis or via information retrieved from the UK lakes portal (https://eip.ceh.ac.uk/apps/lakes/about.html).

Approximately 90 macrophyte species were recorded across the 222 study lakes. The total species richness was subsequently calculated for each catchment (Figure 4.2). Submersed plants dominated in all catchments except in Ullswater and Windermere in the north of England where partially emergent plants were more abundant. Generally, fewer emergent and floating plants were recorded in catchments at higher latitudes.

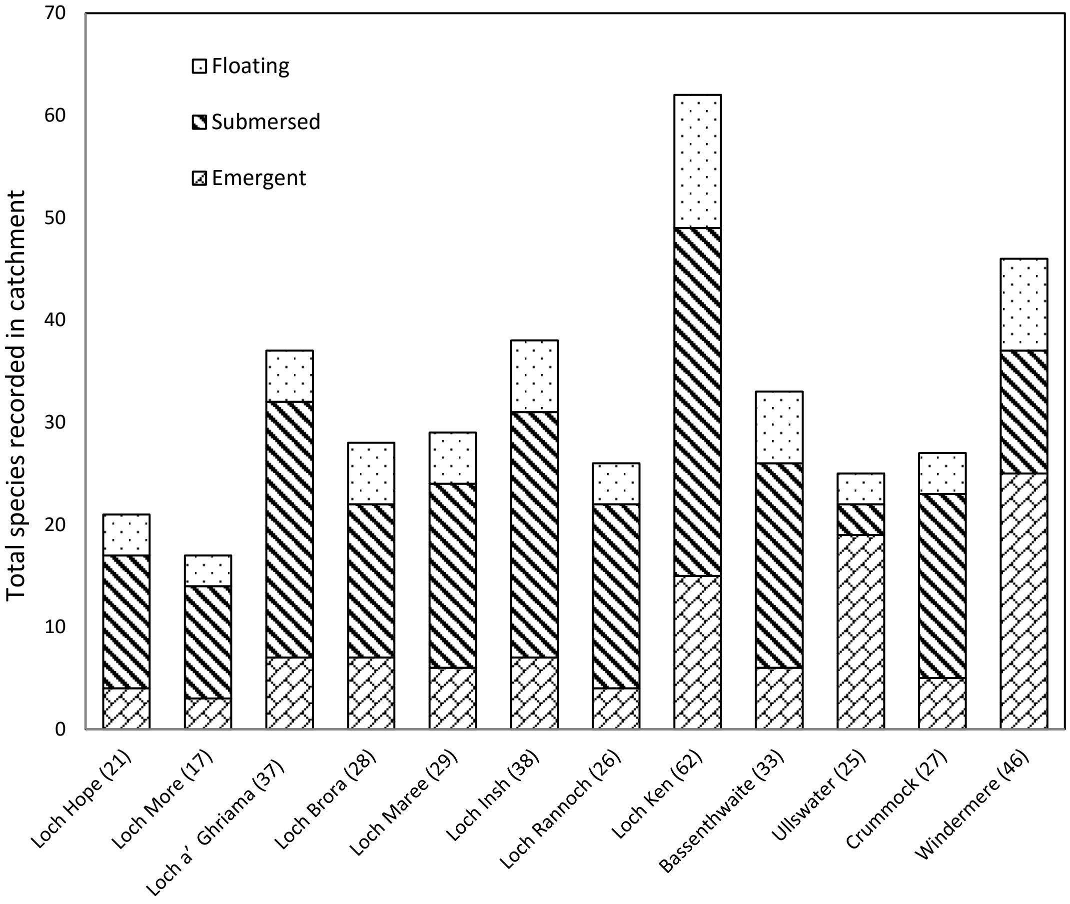


Fig. 4.2 Total species richness of macrophytes in 12 study catchments grouped according to their potential growth habit. (The catchments were ranked from north to south across UK.)

4.3.3 GIS analysis

(1) Lake connectivity

In this study, two measures of landscape connectivity were considered: (i) geographical connectivity and (ii) hydrological connectivity. Geographical connectivity was assessed by measuring the Euclidean distance between the centroids of any two paired lakes in ArcGIS (v10.3). Hydrologic connectivity was determined by calculating the river length between lake pairs using a two-dimensional vector map of the UK stream network (MERIDIAN^{TM} 2). The digitised stream network can be considered as being representative of the hydrological connectivity under normal flow conditions; this study did not consider changes in the degree of hydrological connectivity that might occur under during flood or drought events.

In total, 162 of the 222 lakes were considered to maintain a permanent hydrological connection with the river network. The remaining lakes were isolated and not considered to maintain a permanent above-ground hydrological connection with other lakes in the catchment. From this, 272 hydrologically-connected lake pairs (Table 4.1) distributed over the 12 study catchments were identified where both the pairwise geographical and hydrological connectivity between the lakes could be calculated (Figure 4.3).

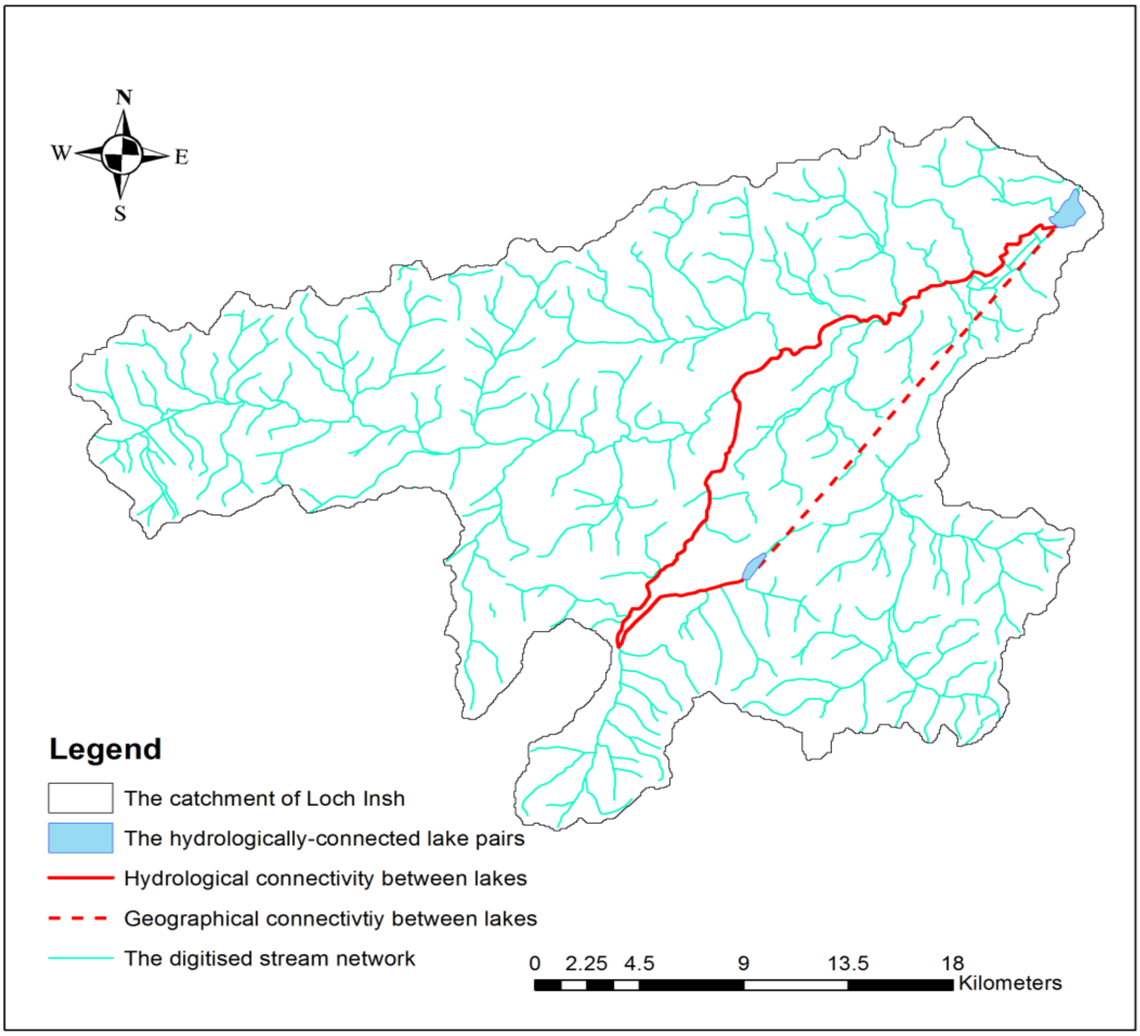


Fig. 4.3 Illustration of two measures of lake connectivity considered in this study using Loch Insh as an example catchment (WBID 20860, Catchment area: 768 km^2)

(2) Hydrological and land use variables

The digitised catchment boundaries were used to calculate a range of hydrological variables in ArcGIS (v10.3) including catchment area, mean catchment slope, upstream lake numbers, stream density and proximity index (Gustafson & Parker, 1994). The proximity index was calculated as the ratio between lake size and the hydrological distance to the closest neighbouring lakes within a defined radius. The variables of stream density and Proximity index were used to characterize the level of hydrological connectivity and spatial connectivity respectively on a catchment scale.

The UK land cover map (LCM2007: http://www.ceh.ac.uk/services/land-cover-map-2007) was used to determine the extent of urban (i.e. suburban and continuous urban) and agricultural (including improved grassland, arable cereals, arable horticulture and arable non-rotational) land in each catchment as an indicator of anthropogenic disturbance. Data was extracted using FRAGSTATS (v4.1). The extent of urban land cover was very low in the catchments considered in this study (< 7%) so, for simplicity, agriculture and urban types were aggregated to provide a single variable representing the extent of "managed land" (Table 4.1). Subsequently, the study catchments were categorised into "low intensity" (managed land < 0.1%), "medium intensity" (managed land between 0.1% and 1%) and "high intensity" (managed land > 1%) to enable the impact of human disturbance on the relationship between landscape connectivity and the spatial turnover of aquatic plant species to be considered.

Table 4.1 Hydrological and land use indicators calculated for the study catchments

Catchment name	Catchment area	Managed land	Human disturbance	Distance to sea from Downstream lake	Upstream lakes	Stream density	Mean slope	Non-isolated lake number	Hydrological connected lake pairs
	km^2	%	-	km	-	km/km^2	-	-	-
Loch Hope	216	0.23	Medium	3.4	33	1106	9.79	18	39
Loch More	205	0.02	Low	22.9	24	924	2.51	11	13
Loch a' Ghriama	534	0.06	Low	11.7	27	845	5.54	27	31
Loch Brora	380	0.02	Low	6.5	16	887	5.66	15	20
Loch Maree	427	0.22	Medium	11.8	22	610	12.5	14	15
Loch Insh	768	0.58	Medium	43.4	19	988	9.79	14	38
Loch Rannoch	639	0.5	Medium	40.6	25	833	7.89	7	15
Loch Ken	1001	0.66	Medium	13.4	38	726	6.83	22	30
Bassenthwaite Lake	354	4.11	High	18.3	15	615	13.8	13	28
Ullswater	147	2.03	High	35	7	639	16.7	7	8
Crummock Water	62.8	1.8	High	19.1	8	654	18.1	8	9
Lake Windermere	62.8	6.53	High	10.6	39	545	12.3	16	26

4.3.4 Statistical analyses

(1) ***Species turnover at catchment scale***

To test the homogeneity of macrophyte beta diversity among study catchments (Figure 4.4), the betadisper models were constructed using the functions 'adonis' and 'betadisper' in the package ‘vegan’ (Anderson et al., 2006). The site mean value for lakes in a given catchment represents the centroid for that catchment, and the dispersion of distances between each site and the centroid represents within-catchment species diversity. The significance of the models was analysed using permutation test ($p<0.001$), indicating that species turnover at the catchment scale was significantly different among study catchments.

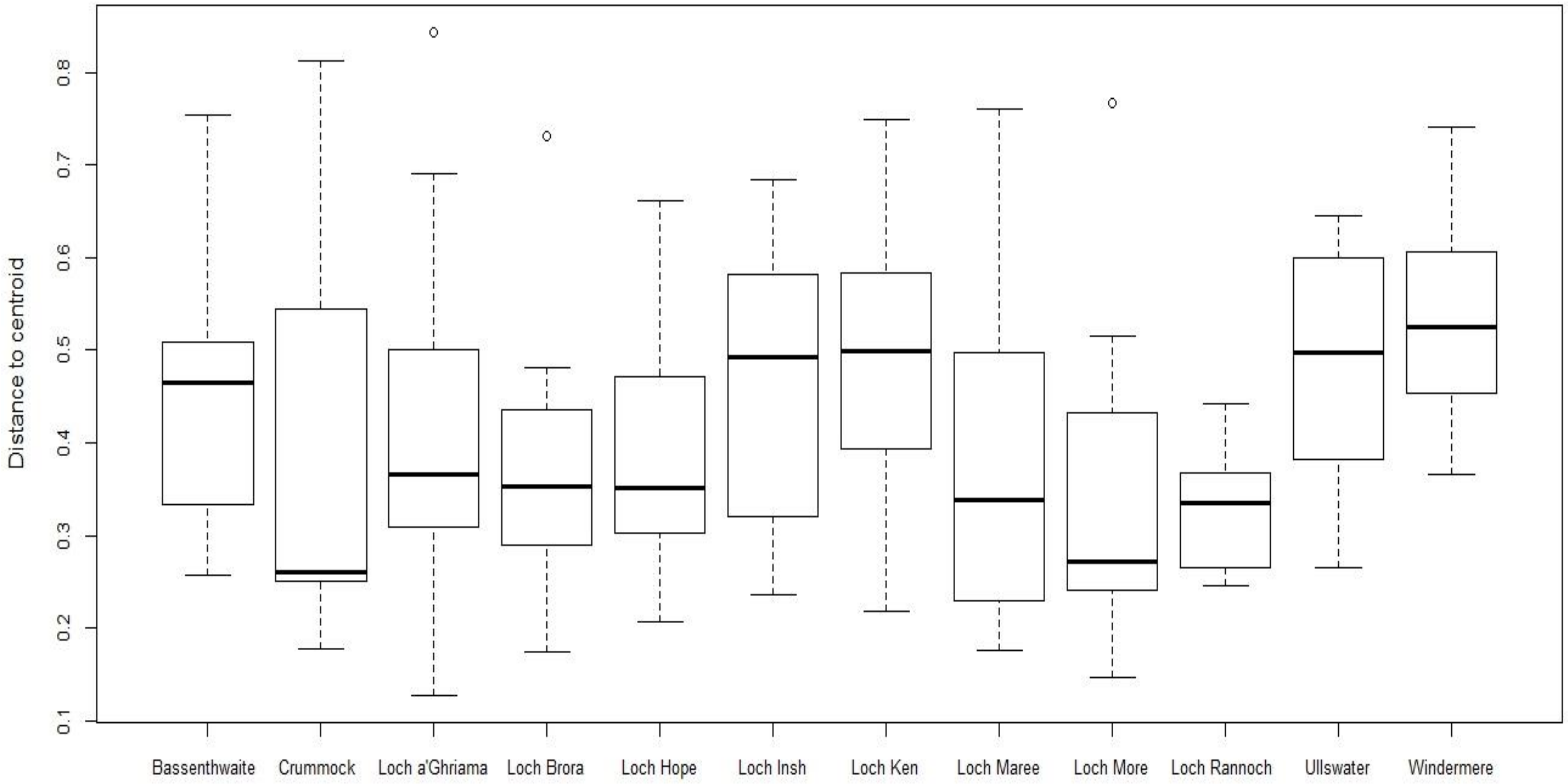


Fig. 4.4 Boxplot displaying catchment scale variation in the turnover of macrophytes in lakes. The boxes show the median and interquartile range for the distance between the catchment centroid and the site score of its component lakes. The analyses were based on betadisper model.

Non-metric multidimensional scaling (NMDS) was applied to estimate the species turnover at the catchment scale using macrophyte data from the 222 study lakes. Stress tests were used to assess the goodness of the fitted NMDS models. The biplots of the macrophyte composition (species scores) and lakes (site scores) were obtained from the two-dimensional NMDS in the 'vegan' package (Oksanen, 2012) in R (v2.15.3). The area of the bounding polygon encompassing the lakes located in each catchment was then determined using the function 'ordihull' in the 'vegan' package (Figure 4.5). Calculating the area of the bounding polygon provides an estimate of species beta-diversity that is arguably less sensitive to sampling biases than other methods based on average distance to centroid. Species turnover was then calculated as the residual variation from a regression (Figure 4.5) between the area of the bounding polygons from the NMDS bi-plots and species richness in each catchment (Heegaard, 2004). The catchment species richness was defined as the total numbers of macrophyte species recorded in the lakes surveyed within that catchment. The calculated species turnover was then regressed against the catchment-scale hydrological and landscape variables using Ordinary least squares (OLS) in R (v2.15.3).

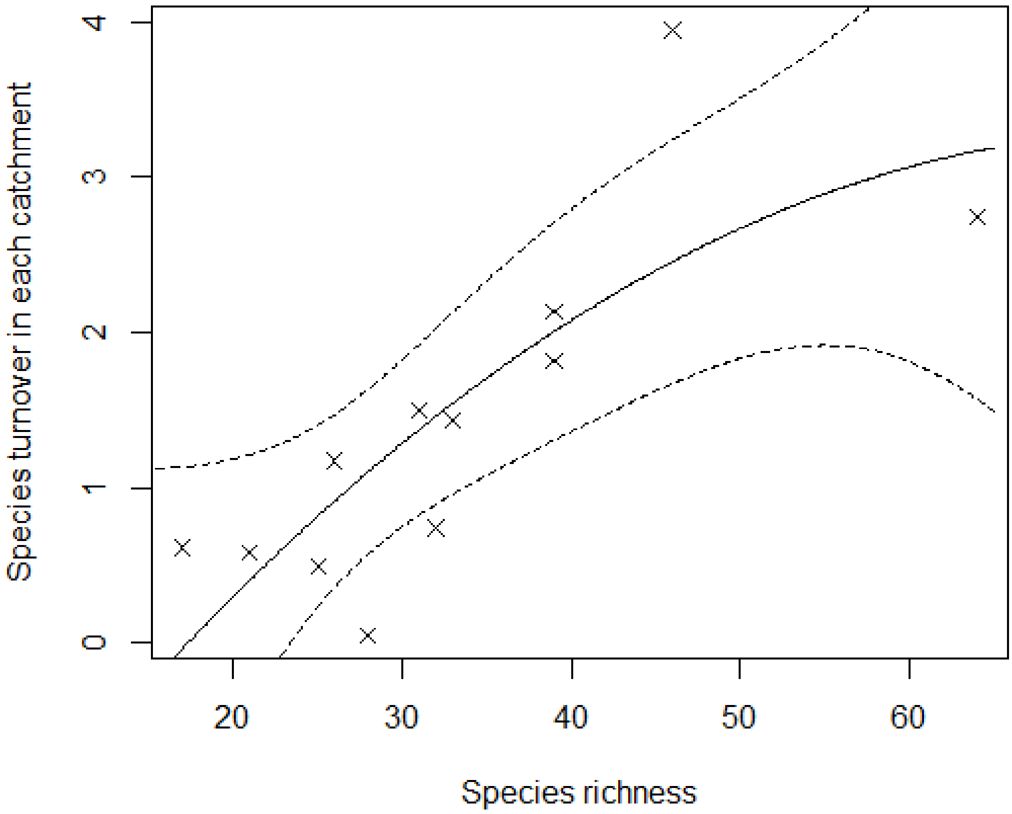


Fig. 4.5 Relationship between the area of the bounding polygons from the NMDS bi-plots and species richness on a catchment scale (r^2=0.89; p<0.001).

(2) *Species turnover at lake scale*

To assess the species turnover in relation to lake landscape connectivity, we selected 272 hydrologically-connected lake pairs and calculated the species turnover using Jaccard’s index. The use of Jaccard’s index over other indices was based largely on its simplicity and intuitiveness (Magurran, 2004). Jaccard’s coefficients of dissimilarity (Cj) are defined as: Cj = 1 – *a* / *(b+c-a)*, where *a* represents the number of shared species in both lakes, and *b* and *c* represent the number of species unique to the two lakes. Higher Cj values indicate fewer shared species and therefore higher turnover (I.e. greater dissimilarity) between the lake pair.

NMDS was used to assess the degree of dissimilarity in lake morphometry and physicochemical variables including lake area, altitude, mean depth, conductivity, pH, alkalinity and shoreline development index for lakes in each catchment separately (stress <0.3 for each catchment). The distance between sites (i.e. lake pairs) in the ordination biplot was used as a measure of the heterogeneity in the abiotic environment within a catchment.

Beta diversity (i.e. the Jaccard’s index between each lake pair in a catchment) was related to the dissimilarity in the abiotic environment and the landscape connectivity (i.e. hydrological and geographical distance) between all pairs of lakes by fitting generalized additive models (GAMs) (Hastie & Tibshirani, 1990). GAMs are used for non-linear regression to predict the system response for the specified conditions through application of smoothing techniques such as spline functions. In this study, The GAMs were fitted using Jaccard’s index as the response and the various indices measuring dissimilarity in environmental conditions or connectivity were used as explanatory variables. Catchment identity was used as a factor in all models. Model selection was performed by comparison against a null model containing only the catchment identity factor.

Lake environmental dissimilarity is largely reflected by the difference in lake area, altitude, mean depth, conductivity, pH and alkalinity, which were logged and analysed independently or as part of the multiple regression to identify their individual or combined influence on species turnover. Model selection was based on the Bayesian Information Criteria (BIC) and the Akaike’s information Criteria (AIC) (Hastie et al., 2009). The proportion of deviance explained by a single predictor was calculated using the ‘sp’ function in the ‘mgcv’ package (Wood & Augustin, 2002) in R (v2.15.3) to determine the difference in the deviance explained after dropping terms sequentially compared to the full model.

Lake pairs were then partitioned according to the intensity of managed land use (low, medium or high) within their catchments. In each group, the relative role of environmental dissimilarity and landscape connectivity in determining the species turnover was then tested using GAMs.

Considering the possible bias introduced by pseudoreplication, we removed the repeated lakes from the reference lake pairs (272 lake pairs) so that each lake pair was unique (i.e. no lakes were shared between lake pairs). The same GAM models were fitted without the duplication of lakes. All the coefficients of models from 111 non-repeated lake pairs were compared with that of the original models to test whether the statistical inference is affected. The possible effect of pseudoreplication and its implication for the findings is considered in the discussion.

4.4 Results

4.4.1 Catchment scale species turnover

The 90 aquatic plant species (Figure 4.6a) and 222 study lakes (Figure 4.6b) were well separated in 2-dimensional NMDS ordination space (NMDS stress = 0.22). For the purpose of this study, it is assumed that lakes located closely together on the ordination bi-plot will have greater similarity in aquatic plant composition than those lakes located further apart. The species turnover for each catchment is thus proportional to the area of the polygon enclosing all the lakes that are located within that catchment (Figure 4.6b). The species turnover between lakes will be higher in the catchment with a large polygon area (Figure 4.6b), and there is a greater probability of potential lake habitats being occupied by different species. The species turnover within a catchment was then regressed against catchment-scale variables (e.g. hydrology, land use).

Managed land use (r^2 = 22.2%) and lake density (r^2 = 53.3%), were positively related to the species turnover standardized by the catchment level richness. This indicates that spatial variation in aquatic plant composition was greater in catchments with high lake density and a greater proportion of agricultural land (Figure 4.7 a&b). Stream density and the proximity index had no significant effect on species turnover (Figure 4.7 c&d).

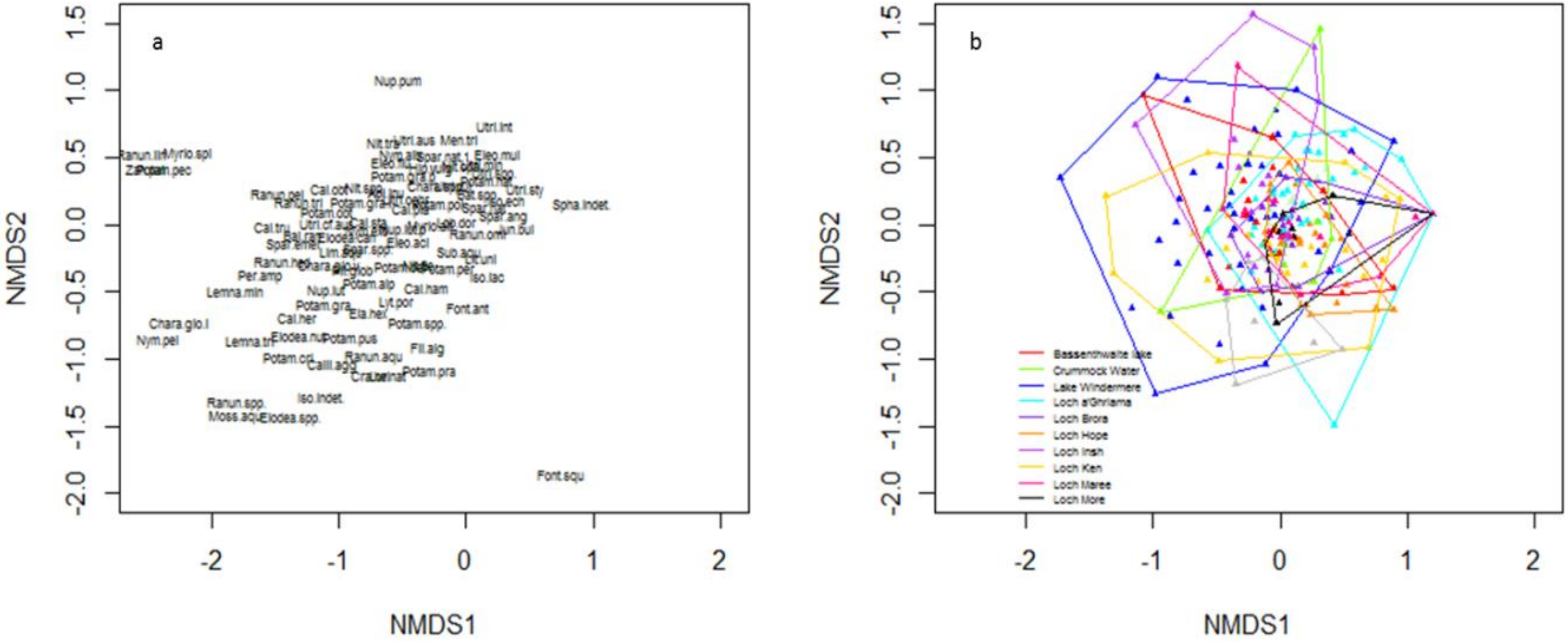


Fig. 4.6 Two-dimensional NMDS ordination of the macrophyte assemblages for the 222 study lakes identified by each catchment (2 Dimensions, Stress = 0.22, r^2=0.949). Codes for the different species names are shown in the appendices.

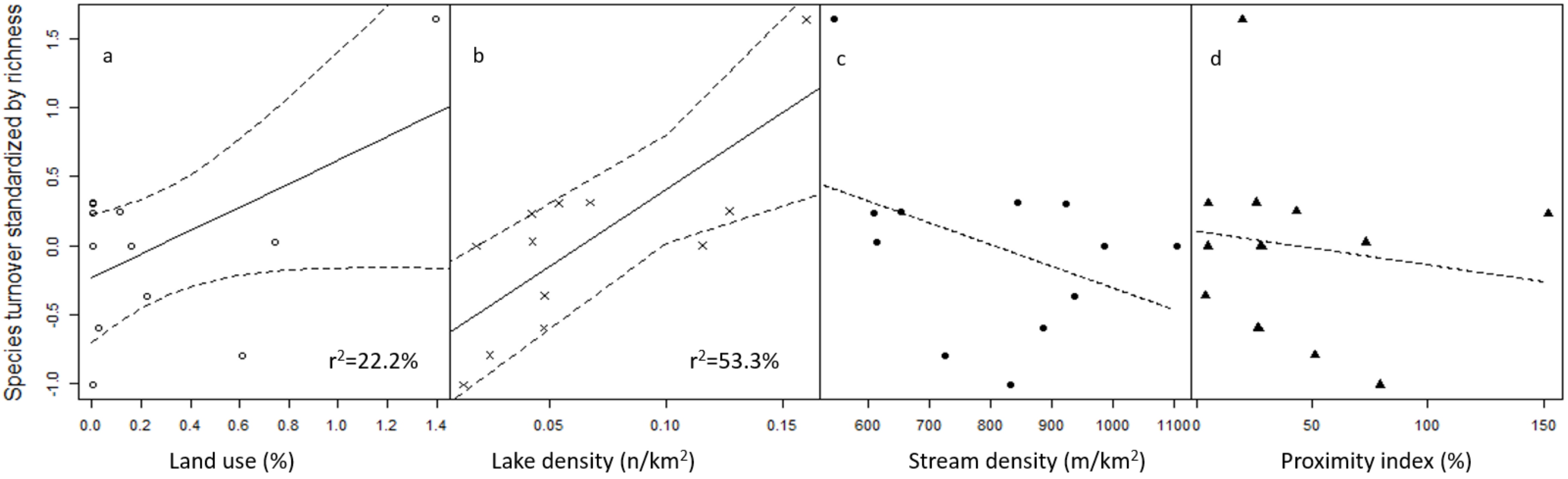


Fig. 4.7 Species turnover related to catchment-scale hydrological and land use variables (The regions between dotted lines are 95% credible intervals for the significant regression models; Models considering stream density and proximity index as predictors are non-significant (p>0.1)). Each data point represents a dicrete catchment.

4.4.2 Lake scale species turnover

(1) Environmental and connectivity predictor

Jaccard's index was used to summarize the dissimilarity in macrophyte species composition between lake pairs. The lake pairs with a low Jaccard's index value indicate high similarity among macrophyte communities in two hydrologically-connected lakes. Figure 4.8 illustrates the Pearson correlation coefficients between the paired explanatory variables used in the GAMs. A statistical summary of the relationships between species turnover and the difference in the lake morphological and physicochemical variables (lake altitude, conductivity, pH, alkalinity, area and mean depth) is provided in Table 4.2. As the most significant factor, catchment identity can explain 26.39% of the variation in species turnover on its own, probably because it is a geographical indicator that is related to lake environmental dissimilarity or potentially, anthropogenic disturbance. The difference in lake depth explained the greatest amount of variation in species turnover (5.57%) among the various environmental indicators. The best subset of variables, which explained 51.7% of the variation in lake species turnover, included catchment identity alongside difference in altitude, conductivity, area and depth between the lake pairs. A comparison of the relative importance of hydrological and geographical connectivity indicated that geographical connectivity (5.77%) explained a greater amount of the variability in species turnover between the lake pairs than hydrological connectivity (3.39%) (Table 4.2, Figure 4.10 e&i). However, neither of these terms appeared in the top model.

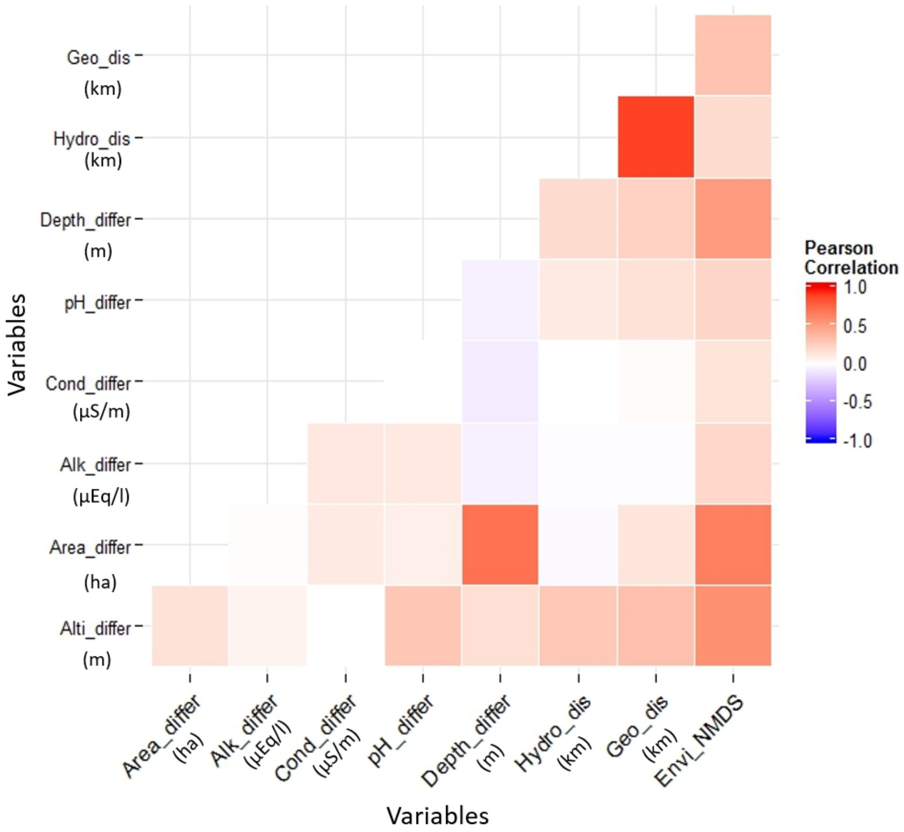


Fig. 4.8 Pearson correlation between explanatory variables in GAMs

Table 4.2 Association between dissimilarity of lake macrophytes based on Jaccard's index and the difference in lake environment for hydrologically-connected lake pairs. Each parameter tested for its influence on species turnover in the reference lake pairs was supplemented with the catchment identity. s represents the smoothing function. The GAM model with lowest AIC value was fitted using a step forward procedure for variable selection.

Variables (log(x))	Terms with s	ResDf	Dev	AIC	BIC	Deviance explained (%) with catchment	Unique contribution
NULL	1	271	10.04	-121.54	-114.33	0.000	-
Catchment	1 + factor(catchment)	260	5.77	-250.11	-203.23	0.425	26.39%
Altitude difference (x1)	s(x1,1)	258.99	5.29	-271.65	-221.17	0.473	4.78%
Conductivity different (x2)	s(x2,3)	258.99	5.35	-268.44	-217.96	0.467	4.18%
pH difference (x3)	s(x3,3.25)	257.12	5.35	-264.03	-205.73	0.466	4.18%
Alkalinity difference (x4)	s(x4,3.31)	258.34	5.56	-256.16	-201.91	0.446	2.09%
Area difference (x5)	s(x5,1.95)	258.99	5.51	-260.57	-210.09	0.451	2.58%
Depth difference(x6)	s(x6,5.54)	256.64	5.21	-269.67	-208.43	0.480	5.57%
Geographical distance(x7)	s(x7,4.21)	255.78	5.19	-268.46	-203.23	0.482	5.77%
Hydrological distance(x8)	s(x8,2.44)	257.56	5.43	-260.6	-202.67	0.459	3.39%
Multiple regression	x1+x2+x5+x6+factor(catchment)	254.52	4.85	-285.22	-216.42	0.517	-

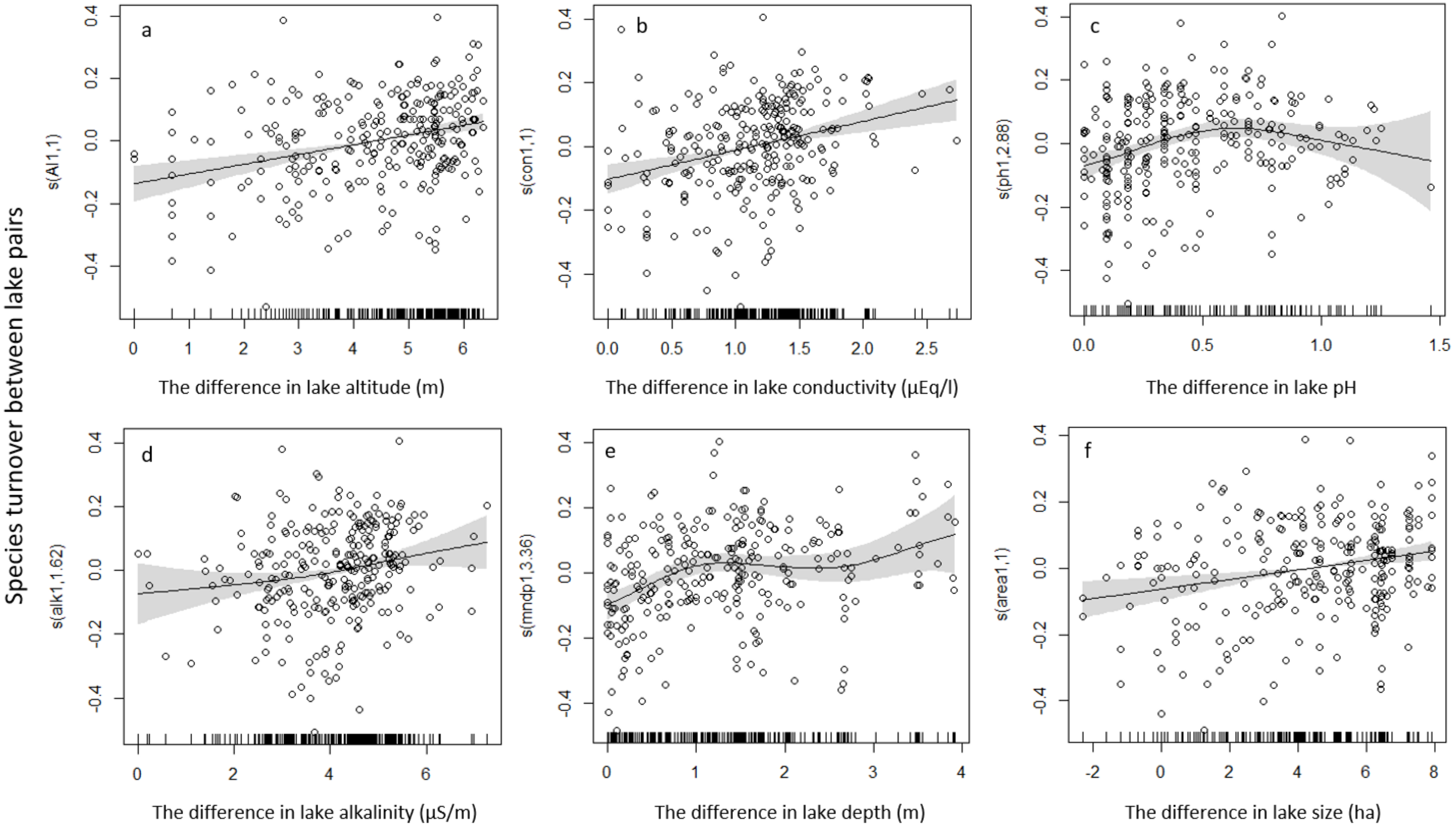


Fig. 4.9 Trends in species turnover in relation to the difference in lake altitude (a), lake conductivity (b), lake pH (c), lake alkalinity (d), lake depth (e), lake size (f) between the hydrologically-connected lake pairs within each catchment. The 95% individual confidence interval is represented by a grey zone.

There was a weak relationship between the species turnover and the difference in lake size and alkalinity among the lake pairs (Figure 4.9 f&d). In contrast, the difference in lake depth and altitude had strong positive effects on species turnover (Figure 4.9 e&a). Compared with other variables, the relationship between lake pH difference and species turnover showed a slight increase up to pH difference of 0.5, but a decrease in dissimilarity thereafter (Figure 4.9 c).

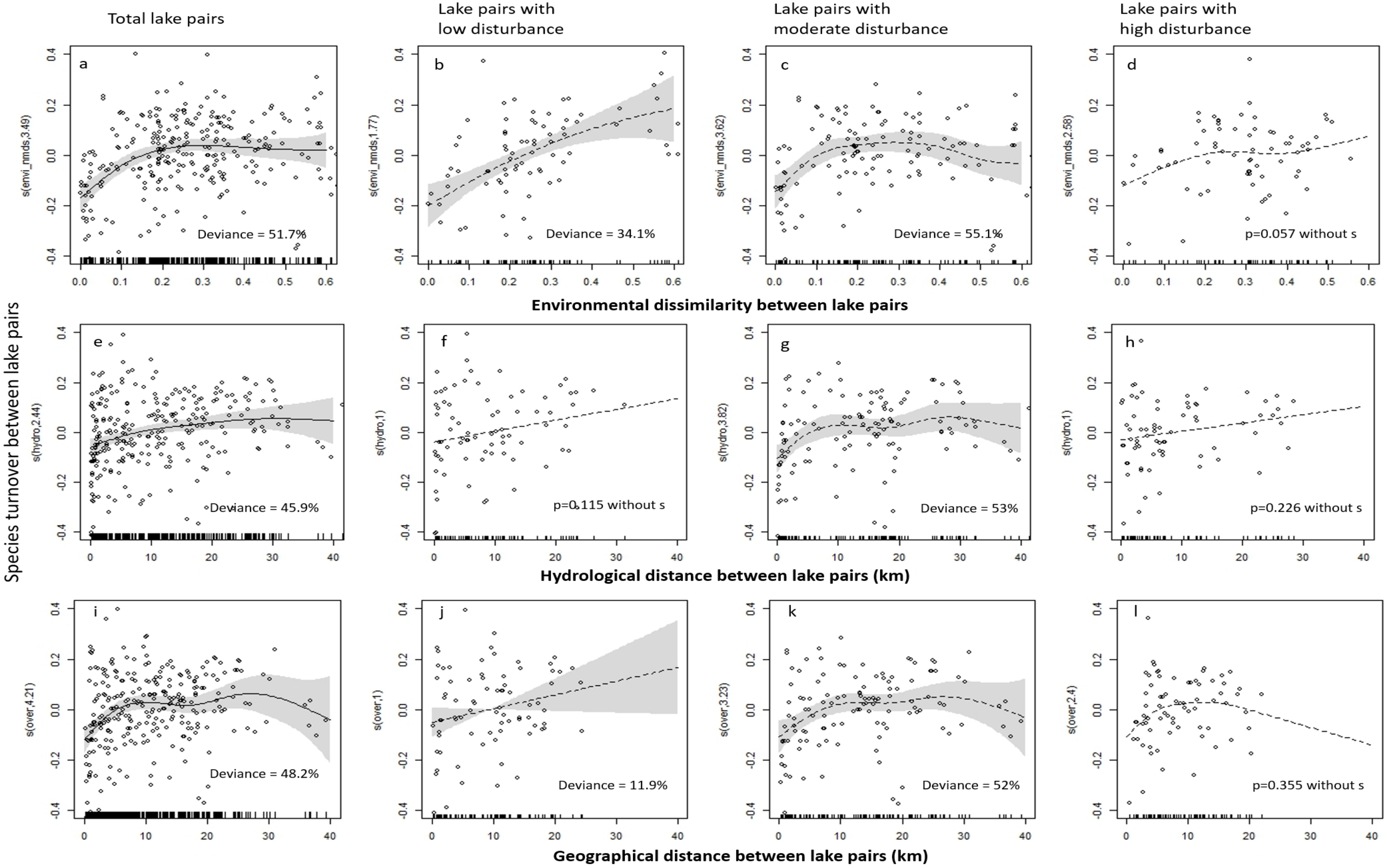
There is a possible bias introduced by pseudoreplication in the 272 reference lake pairs because the same lake may be shared by several lake pairs. To avoid this we fit the same model but avoided this duplication by focussing on the unique lake pairs only. The results of the statistical inference (Appendix 5.5) for the new model indicates that the pseudoreplication in lake pairs has little influence on coefficients or estimates of model fit.

The non-repeated lake pairs indicated that geographical distance (5.4%) could better explain the species turnover compared with the hydrological distance (2.1%), which is consistent with the results from the original model containing all 272 lake pairs. However, the model using the revised dataset showed a slight difference in the explanatory value of the different environmental variables. In the original model, the difference in depth (5.5%) was the most important environmental variable to explain the species turnover of hydrologically-connected lake pairs. While the new model indicated that the difference in lake area (7.5%) could explain the most variation in species turnover, followed by the depth difference between lake pairs (6.2%).

(2) Disturbance effects

Considering all lake pairs, there was a strong increase in species turnover with the initial increase in environmental dissimilarity followed by a flattened response (Figure 4.10 a). This suggests that close similarity in aquatic plant communities between lakes was mainly the result of close similarity in abiotic conditions, but that reducing similarity in abiotic conditions beyond a possible threshold will not yield an increased biological difference. Indeed, it is worth noting that some lakes pairs with quite different lake environment have a high degree of species similarity. A similar trend could also be observed in the relationship between species turnover and hydrological (Figure 4.10 e) and geographical connectivity (Figure 4.10 i). Generally speaking, for lakes up to distances of ~20 km, the further the lakes were apart, the greater the difference in their macrophyte composition. However, some lakes located very close to each other were biologically quite different and some of the most distant pairs of lakes only had average biological dissimilarity.

The lake pairs were then partitioned into three groups with low, moderate and high intensity of human disturbance, and the relationship between species turnover and the environmental co-variates was assessed separately for each group. The relationship between the degree of environmental dissimilarity and aquatic plant species turnover clearly varied depending on the intensity of human disturbance (Figure 4.10 b-d). The geographical connectivity (Deviance= 11.9%, Figure 4.10 j) provided a slightly better explanation of the species turnover than the hydrological connectivity ($p=0.115$, Figure 4.10 f) for lakes overall and also for those located in low-disturbance catchments. There was a simple linear response of turnover to environmental dissimilarity in the least disturbed catchments (Figure 4.10 b). The importance of environmental dissimilarity and landscape connectivity in explaining the species turnover peaked (Deviance > 50%) in the lake pairs situated in catchments with moderate intensity of human disturbance. However, none of these variables could explain species turnover in lake pairs from catchments with a high intensity of human disturbance (Figure 4.10 d, h and l).



Total lake pairs
Lake pairs with low disturbance
Lake pairs with moderate disturbance
Lake pairs with high disturbance
Species turnover between lake pairs
a
s(envi_nmds,3.49)
Deviance = 51.7%
b
s(envi_nmds,1.77)
Deviance = 34.1%
c
s(envi_nmds,3.62)
Deviance = 55.1%
d
s(envi_nmds,2.58)
p=0.057 without s
0.4
0.2
0.0
-0.2
-0.4
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Environmental dissimilarity between lake pairs
e
s(hydro,2.44)
Deviance = 45.9%
f
s(hydro,1)
p=0.115 without s
g
s(hydro,3.82)
Deviance = 53%
h
s(hydro,1)
p=0.226 without s
0
10
20
30
40
Hydrological distance between lake pairs (km)
i
s(over,4.21)
Deviance = 48.2%
j
s(over,1)
Deviance = 11.9%
k
s(over,3.23)
Deviance = 52%
l
s(over,2.4)
p=0.355 without s
Geographical distance between lake pairs (km)

Fig. 4.10 Response shapes of predictor variables (i.e. environmental dissimilarity, hydrological connectivity and geographical connectivity) in the generalized addictive model (GAM) used for modelling macrophyte species turnover. The y-axis indicates the effect of the respective variables (on the scale of the additive predictor). Confidence intervals (95%) for the response are indicated with a grey zone for the significant variables and with the value of deviance change (%). The non-significant models are represented with a dashed line. s represents the fit of the smoothing spline for the variables in each GAM.

4.5 Discussion

4.5.1 Role of Niche theory in explaining macrophyte species turnover

This study indicates that environmental homogeneity increases species similarity among a series of lakes connected through surface water flow (Figure 4.10a). This result is consistent with niche theory which suggests that dissimilarity in the species assemblages between habitats is positively correlated with their environmental difference (Jacquemyn et al., 2007). This study has shown that the difference in lake depth (Unique contribution of 5.57% with catchment identity) and altitude (Unique contribution of 4.78% with catchment identity) were the most important drivers influencing the species turnover between pairs of lakes (Table 4.2). Shallow lakes, with little wave action and organic bottom sediments can support the growth of rooted aquatic plants from the shore to the lake centre, while in deep lakes the steep littoral slope and more intense wave action around the shoreline can prevent plant colonisation and growth. For example, UK lakes in which most of the basins are deeper than 10-15 m are likely to contain only limited submersed vegetation. In addition, shallow lakes may suffer periodic isolation within a drainage system during low flows, while a high density of aquatic plants may not be conductive to dispersal if it impedes flow. Altitude is a vital control which may cause a decrease of macrophyte richness in lakes (Jones et al., 2003). In low-altitude lakes, aquatic plants tend to colonize deeper and reach greatest abundance in deeper water compared with high-altitude lakes, which was attributed to the warmer conditions and longer growing period at lower altitude (Jones et al., 2003).

Numerous studies have shown that larger areas provide a greater variety of niches and thus promote species turnover (e.g. Jones et al., 2003). However, the results indicated a relatively weak relationship between difference in lake size and species turnover (Figure 4.9 f), although similar results have been reported for other UK lakes (Heegaard, 2004). The impact of water chemistry on macrophyte species turnover has long been known and studied, with alkalinity often being considered a fundamental driver of species richness and composition (Toivonen &

Huttunen, 1995; Vestergaard & Sand-Jensen, 2000b; Heegaard et al., 2001). However, the present results show that differences in lake chemistry specifically only explained a limited amount of the variation in species turnover between lakes (Table 4.2, Figure 4.9). This is probably due to the fact that many of the study lakes were low alkalinity and naturally oligotrophic and as such could be expected to support very similar plant communities.

Interestingly, the species-environment relationship was not monotonic and the strength of the relationship between environmental dissimilarity and species dissimilarity diminished as the degree of dissimilarity increased (Figure 4.10 a). Indeed, some lakes with very different physicochemical conditions were biologically quite similar. This is probably in part because many common macrophytes have broad environmental tolerances enabling them to occur in lakes with different environmental conditions. The wide tolerance range indicated that most species have a high potential for dispersal and can survive in a new environment, particularly in well-connected systems.

4.5.2 Spatial connectivity in explaining macrophyte species turnover

The distribution of aquatic plant species in freshwater lakes is not only influenced by the difference in physico-chemical conditions between lakes but also the ability of species to disperse and colonise new sites (Heino, 2013). According to neutral theory, communities decay with geographical distance because they become increasingly dispersal-limited, even if the environment is homogenous (Hubbell, 2001). The distance-decay concept can also be used to argue that environmental differences between lakes increase with increasing geographic separation, which then leads to greater biological differences (Soininen et al., 2007). The geographical distance between the water bodies is no doubt a key determinant of whether exchanges of aquatic organisms (e.g. fish, zooplankton, bacteria and phytoplankton) can occur between them (Poulin et al., 1999; Foster et al., 2003; Heegaard, 2004; Miyazono et al., 2010).

Hydrological distance has previously been shown to be important in determining species turnover between lakes, especially for fish (Ishiyama et al., 2014). Water dispersal plays a role in the distribution of aquatic plants, and river corridors are good for maintaining the freshwater biodiversity (Johansson et al., 1996). Ecological processes, such as transport of plant fragments and other propagules downstream, can promote the appearance of similar plant communities in lakes with different environmental conditions (Riis & Sand-Jensen, 2006; Tremp, 2007) or the exchange of genes between populations (Fer & Hroudova, 2009). Consequently, hydrologically connected lake pairs are expected to show low turnover rates of macrophytes. Although hydrological distance between lake pairs showed a strong correlation with geographical distance (Figure 4.8), it could only weakly explain turnover compared with geographical distance (see Table 4.2). There are two interpretations here; (i) the measure of hydrological connectivity is too crude because it takes no account of artificial barriers to dispersal via water courses (dams, weirs) or the effect of variation in discharge on effective connectivity, (ii) despite being widely accepted as the dominant means of dispersal by water plants vectors other than water flow (wind, birds, humans) are of significant importance.

4.5.3 Determinants of lake macrophyte species turnover at different spatial scales

The study selected the hydrologically-connected lake pairs at the catchment scale. The results indicated catchment identity is significantly more important than all other variables in explaining the macrophyte species turnover. That is probably because catchment identity captures the combination of characteristics (such as topography, climate, soil type and land use) which is not reflected in the explantory sets of lake environmental dissimilarity and connectivity variables considered in the study.

In relative terms, the environmental differences between lakes within a catchment were more important than hydrological or geographical connectivity in explaining species turnover (see Table 4.2). The result is consistent with previous studies that report environmental filtering could better explain the regional patterns of lake macrophytes rather than the spatial processes (Alahuhta, 2015). Mazaris et al. (2010), for example, found that phytoplankton and zooplankton communities were positively correlated with the environmental difference while being uncorrelated with the geographical connectivity between freshwater systems.

One study relevant to macrophyte communities suggested that the relative contribution of environmental controls and spatial processes varies unpredictably with the spatial extent (Alahuhta & Heino, 2013). The present results based on catchment scale analyses do not support this conclusion. At a broad scale (>10 km), the deviance explained by the environmental dissimilarity dropped sharply to 0.9% compared to 12.5% at a small scale (<10 km) (Table 4.3). In addition, geographical connectivity was observed to become more important in explaining species turnover with increasing spatial scale (from 0.14 at a small scale to 0.25 at a large scale).

Table 4.3 The unique contribution (Deviance explained %) of environmental dissimilarity, geographical distance and hydrological distance in explaining species turnover for hydrologically-connected lake pairs at two different scales. (ENVI - environmental dissimilarity; Hydro - hydrological connectivity; Geo - geographical connectivity)

Two spatial scales	Small scale (n=136) geographical distance <10 km				Large scale (n=138) geographical distance >10 km			
Factors in GAM model	Catchment variables (%)	Environmental dissimilarity (%)	Hydrological connectivity (%)	Geographical connectivity (%)	Catchment variables (%)	Environmental dissimilarity (%)	Hydrological connectivity (%)	Geographical connectivity (%)
Catchment+ ENVI+Hydro	36.4%	12.5%	0.05%		47.3%	0.9%	0.002%	
Catchment+ ENVI+Geo	36.4%	8.3%		0.14%	53.5%	0.8%		0.25%

Within a *topographic catchment*, based on the community assembly theory, the dispersal of aquatic plants between lakes should be largely controlled by the connectivity between systems, whereas their ability to colonise and persist in new environments is determined by the lake environmental conditions (the so-called "environmental filter") (Figure 4.11). This study indicated that the species turnover between lakes was related to geographical distance more than to hydrological distance (Table 4.2). This could be illustrated, for example, by a situation where lakes, although geographically close to each other, are separated by a long hydrological distance meaning that non-hydrological vectors (e.g. wind, humans or water birds) are the most probable means of transfer of propagules between lakes.

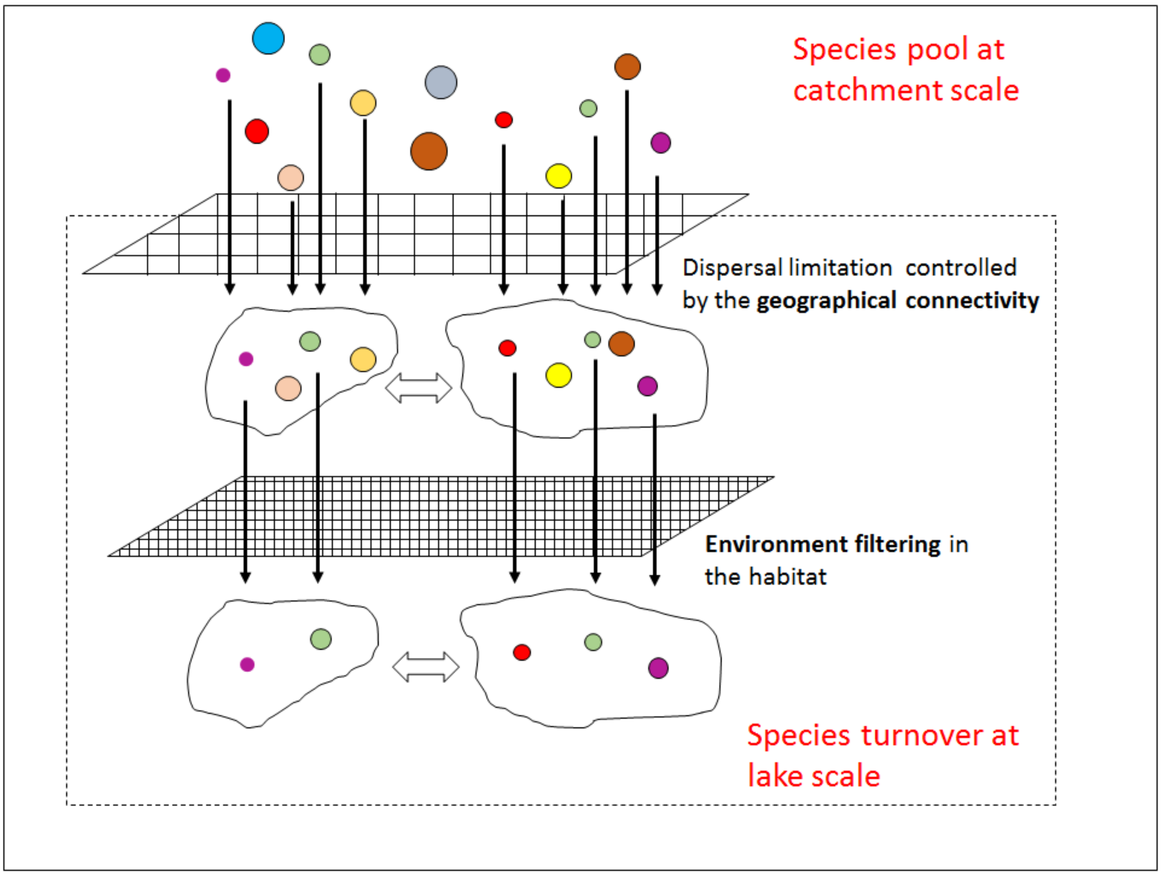


Fig. 4.11 The controls on macrophyte species turnover in lakes

4.5.4 Distance-decay relationship influenced by human disturbance

It has been argued that the distance-decay relationship is governed by three mechanisms, namely, niche-based processes, neutral theory and spatial configuration (Cottenie, 2005). However, the effect of distance-decay processes on aquatic plant diversity in this study also proved sensitive to the degree of human disturbance at the catchment scale, expressed in terms of extent of managed land use. There are only a few studies of distance-decay relationships focussing on freshwater assemblages, such as macroinvertebrates and fish, at the basin scale (Maloney & Munguia, 2011; Rouquette et al., 2013).

The study indicated that each ecological process (environmental dissimilarity and landscape connectivity) constrained the aquatic species turnover according to the different intensity of human disturbance. Figure 4.12 illustrates conceptually the key drivers of macrophyte species turnover according to the spatial scale and the intensity of human disturbance. In low-disturbance catchments, turnover can be seen to be positively related to the environmental dissimilarity of the lakes. However, the relationship between environmental dissimilarity and species turnover was noticeably weaker at intermediate levels of disturbance and absent in the most intensively disturbed catchments. Evidently, human impacts (e.g. increased nutrient or fine sediment loading), even at a modest scale as in this study, can override the template set by underlying environmental heterogeneity.

This finding is consistent with several previous studies. For example, Vilar et al., (2014) found that lake eutrophication can influence distance-decay relationships through reducing the turnover rates of microorganisms. Human disturbance through processes such as urban development, agriculture and silviculture have often been overlooked in analysing their direct impact on macrophyte species richness and composition in lakes (Hicks & Frost, 2011), or their influence on the environmental and landscape factors that determine aquatic species turnover. For example, diatom communities respond strongly to lake environmental conditions in eutrophic environments and are negatively related to broad-scale processes under low fertility (Vilar et al., 2014).

No evidence was found to support the idea that the environment and spatial connectivity could explain turnover between lake pairs when under a high degree of human disturbance; however, it should be noted that although increased disturbance apparently dampened the fine scale response to lake environmental variation it did not lead to homogenisation of the flora – indeed some of the more disturbed catchments actually showed greater overall turnover between their lakes (Figure 4.7 a) implying that a longer gradient of impact within a catchment can promote turnover and may compensate for the dampened response to natural abiotic variation. Also, in reality, the most disturbed catchments were only comparatively lightly impacted and under heavier disturbance a shortening of the disturbance gradient would be expected to greatly constrain turnover.

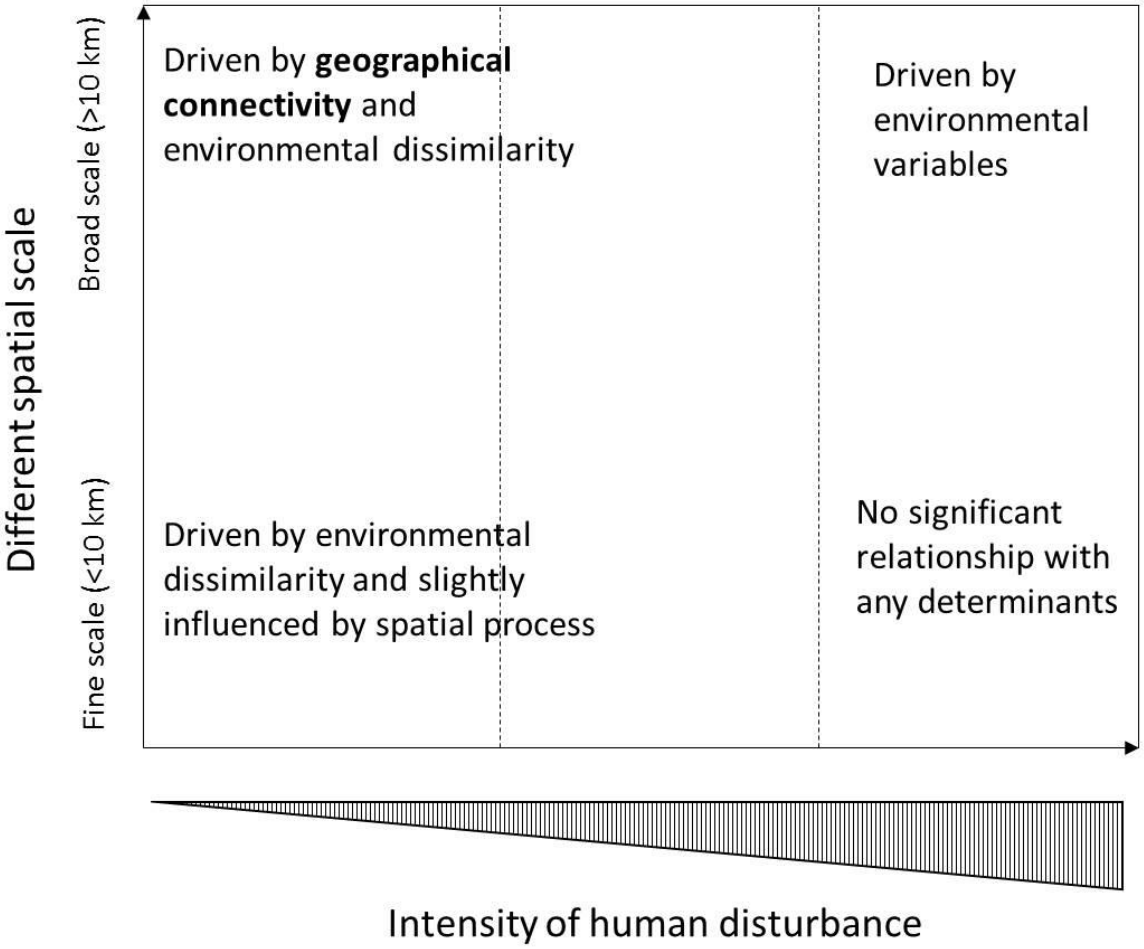


Fig. 4.12 The relative contribution of environmental dissimilarity and connectivity variables in explaining turnover of lake pairs across different spatial scales (y-axis) and under different intensity of human disturbance (x-axis)

4.6 Conclusions

Species turnover among lakes could not be explained by only one particular theory but rather seems to be jointly driven by multiple ecological, geographical and physical effects (Korhonen et al., 2010).

Catchments, to some extent, can be considered as either closed ecosystems (hydrology) or open ecosystems (energy flow). This study demonstrated that the *topographic catchment*, as a hydrological boundary for lake ecosystems, is an important driver of species turnover of lake macrophytes. Distance-decay relationships were clearly evident in lake macrophytes but these relationships were sensitive to the intensity of human disturbance.

For landscape factors, geographical distance was much more closely correlated to species turnover than the hydrological distance, suggesting that a range of vectors besides water are at least as important in the dispersal of macrophytes between water bodies.

Chapter 5 – Cross-scale interaction of lake- and catchment-scale determinants of macrophyte species composition in UK lakes

5.1 Abstract

Macrophytes are one of the key biotic elements of lakes and play important roles in maintaining the structure and function of freshwater ecosystems. However, increasing human modification of lakes and catchments has led to marked changes in macrophyte composition and an overall decline in species richness in many regions globally. The controls on macrophyte composition are complex and recent research has shown that the effect of environmental factors at the lake-scale can be constrained and shaped by catchment-scale factors such as the coverage, density and connectivity of waterbodies and land use.

The aim of the study was to investigate the interaction between the determinants of macrophyte composition at the lake- and catchment-scale. We used data from macrophyte surveys and physicochemical monitoring of UK lakes and investigated the interactions between alkalinity, the dominant lake-scale driver of macrophyte composition, and a suite of landscape-scale variables (e.g. lake and stream density, fragmentation indices, land cover), expressed at the catchment scale, using mixed effects models.

The results showed that the effect of alkalinity on macrophyte composition at the lake-scale is affected by landscape factors at the catchment level. More specifically, (1) turnover in macrophyte composition with lake alkalinity is stronger in catchments of low lake and stream density, and weaker in catchments with a well-developed hydrological network; (2) abiotic factors such as alkalinity and its correlates have more influence on macrophyte composition in lowland catchments with higher urban and agricultural land cover and greater landscape fragmentation (suggestive of niche filtering), but spatial factors such as lake and stream density are more influential in less disturbed upland catchments (suggestive of dispersal limitation).

5.2 Introduction

Freshwater ecosystems are complex and hierarchically structured by a variety of diverse components, scale multiplicity and spatial heterogeneity (Wu & David, 2002). Macrophytes (aquatic plants) are an integral component of lake littoral zones, playing a critical role in maintaining ecosystem structure and function, especially in shallow lakes. Macrophytes not only sustain ecosystem services, such as sediment stabilisation and nutrient sequestration, but may dominate primary production and control the flow of energy to higher trophic levels (Vadeboncoeur et al., 2002). Macrophytes are important bio-indicators of lake condition and are used as one of the biological quality elements for the assessment of lake ecological status under the European Water Framework Directive (2000/60/EC). However, over recent decades, the increase in human disturbance and pressure on lakes and their catchments has resulted in a widespread decline in macrophyte species abundance and richness (Egertson et al., 2004) with significant implications for ecosystem integrity, resilience and service provision.

Macrophytes species composition in freshwater lakes is determined by factors operating and interacting at scales that range from the lake to the catchment and potentially up to continental scales. The effects of lake-scale factors on macrophyte composition and distribution have been widely studied and are generally considered to be the primary determinants of the biogeographical distribution of macrophytes (Jones et al., 2003). They include physical factors, such as sediment type, shoreline morphology and altitude (Recknagel et al., 2006; Vincent et al., 2006; Feldmann & Noges, 2007; Hunter et al., 2008; Weithoff et al., 2010), as well as chemical parameters, including nutrient availability, alkalinity and water transparency (Capers et al., 2010; Akasaka & Takamura, 2011; O'Hare et al., 2012; Kolada et al., 2014).

In addition to lake-scale factors catchment-scale processes can influence macrophyte composition. A large body of research demonstrates that land use change, particularly the intensification of agriculture and urbanisation (Alexander et al., 2008; Sass et al., 2010; Hicks & Frost, 2011; Alahuhta et al., 2012; Rosso & Cirelli, 2013), can have pronounced effects on lake macrophytes, typically driving the loss of submersed species and a shift to floating and emergent plant dominance (Egertson et al., 2004). In extreme cases, entire collapse of the macrophyte community has been observed (Rasmussen & Anderson, 2005).

Furthermore, because lakes and streams are not closed or isolated systems, their connectivity across the landscape and with the wider hydrological network can also influence the distribution of macrophytes at the catchment-scale. However, recent evidence suggests that regional scale processes influencing dispersal are strongly correlated with lake environmental filters in regulating lake macrophyte composition (Alahuhta & Heino, 2013; Chappuis et al., 2014). Here we distinguish two indicators of connectivity: landscape connectivity, which represents the physical proximity of lakes over the land surface, and hydrological connectivity, which reflects connectivity of lakes via the drainage network (Freeman et al., 2007; Bracken et al., 2013). The connectivity of lakes, over the landscape or via the hydrological network, influences macrophyte composition indirectly through its impact on the exchange of water or other materials (e.g. pollutants) and directly by its effect on ease of dispersal. Landscape connectivity is important in determining the biogeographical distribution of those species that disperse through biological vectors (e.g. birds, mammals) or via wind-aided transport of seeds, whereas species dependent on water-borne dispersal (hydrochory) should be more sensitive to hydrological connectivity (Johansson et al., 1996; Makela et al., 2004).

Hydrological variables such as catchment area, catchment slope, precipitation and runoff are commonly reported to influence lake macrophyte composition or richness (Cheruvelil & Soranno, 2008; Jeppesen et al., 2009; Kissoon et al., 2013), yet few studies have considered the influence of lake and stream density at the catchment scale. Studies in floodplain systems confirm that catchment-scale processes can moderate the influence of lake environmental fiters such as water chemistry (Van Geest et al., 2005; Dos Santos & Thomaz, 2007). Lakes with stronger connectivity are more likely to have similar biogeochemical conditions and thus greater similarity in vegetation (Thomaz et al., 2007), the most pronounced dissimilarities occurring at low water level, when connectivity between lakes is lowest. In addition, hydrological connectivity and species dispersal is also strongly influenced by the frequency and magnitude of flood events (Van Geest et al., 2003).

More recently, consideration has been given to the interaction between lake- and catchment-scale factors that regulate abiotic and biotic properties and processes in lakes. Lakes are influenced by drivers that operate over multiple spatial scales. The influence of factors that operate at the lake-scale (e.g. water chemistry) may be moderated by interactions with catchment-scale processes. These so-called cross-scale interactions arise when driver and response variables operate at different spatial scales, often resulting in nonlinear behaviour (Carpenter & Turner, 2000; Cash et al., 2006; Peters et al., 2007; Soranno et al., 2014), but such interactions are poorly understood and are often difficult to observe in empirical studies due to data constraints. Fergus et al., (2011), in one of the few studies to explicitly consider effects of cross-scale interactions on lake ecosystems, investigated interactions between human land use at the catchment scale and relationships between lake cover, lake phosphorus and water colour and found a strong effect of regional setting. Similarly, Soranno et al., (2014) showed that the cross-scale influence on lake phosphorus concentrations (lake-scale) in the northeast US depends on extent of agricultural land at the wider catchment scale.

Research on catchment-scale drivers of lake ecosystem condition, and their interaction with lake scale factors, is limited by the challenges of acquiring suitable data at a regional scale.

Moreover, existing studies on drivers of lake macrophyte composition tend to focus on a single scale. Water alkalinity is widely regarded as one of the most important determinants of lake macrophyte composition (Vestergaard & Sand-Jensen, 2000b; O'Hare et al., 2012) because it can buffer against rapid pH changes while also regulating inorganic carbon availability in the form of bicarbonate. However, the effect of alkalinity on macrophyte composition is likely to vary between catchments due to the added influence of catchment-scale variables such as landscape and hydrological connectivity. In this study, we use data from a large population of lakes in 30 discrete catchments in Britain to investigate how the relationship between lake alkalinity and macrophyte composition is affected by landscape setting. More specifically, we evaluate how cross-scale interaction at the catchment scale determine macrophyte composition and assess the relative importance of a suite of hydrological and landscape variables. Ultimately, improved understanding of the relationship between lake-scale and catchment-scale drivers of macrophyte composition will aid in predicting the immediate and longer term impacts of land use change on lake ecology at the catchment level.

5.3 Materials and Methods

5.3.1 Data description

Macrophyte species occurrence and physicochemical monitoring data were compiled for 2558 British lakes from historical survey data held by the Joint Nature Conservation Committee (JNCC) and the UK environmental agencies. The original survey data were collected mainly between 1985 and 1998 according to standard methodologies. The asynchronicity of the survey data was not considered to be a significant limitation to our analysis because species occurrence is far more stable over time than species abundance (Sinkeviciene, 2007), while resurveys of a subsample of these lakes mostly demonstrated only very minor changes on a decadal scale. The physicochemical data were contemporaneous to the macrophyte survey data for all lakes. Surface water samples were taken at the position of maximum water depth in summer and winter for each lake and then taken into laboratory to investigate the alkalinity, conductivity, pH concentration. Digitised boundaries for the lakes were obtained from the Ordnance Survey along with a digitised stream network for the UK (MERIDIAN^{TM} 2). Digital terrain model (DTM) data at a 50 m grid resolution were also obtained from the Ordnance Survey for the UK (OS Terrain 50).

5.3.2 Determinants of macrophyte species composition

(1) Input datasets

Three sets of explanatory variables were constructed as potential drivers of macrophyte composition: (i) lake environment; (ii) catchment hydrology; and (iii) landscape. The lake environment set covered lake physicochemistry and morphometry and was linked to the biological data via a set of unique water body identifiers (Bennion et al., 2005). The hydrology (presumably related to connectivity) and landscape sets (involving spatial structure and land use) were derived according to the *topographic catchment* of each lake. The catchment boundaries for the largest 961 of the 2558 lakes were digitized using Arc Hydro Tools in ArcGIS (v10.2) using the vectorised lake boundaries and DTM from Ordnance Survey. The resulting catchment boundaries were used to calculate a range of hydrological variables in ArcGIS including catchment area, mean catchment slope, lake density and stream density. The remaining 1439 lakes were too small for their catchment areas to be determined reliably. The 961 lakes for which catchment boundaries could be derived (40% of the total number of lakes originally surveyed) encompassed 101 of the 170 macrophytes species (68%) recorded in the complete dataset from 2558 lakes. The macrophyte species recorded in the 961 lakes are listed in Appendix 5.1 according to their growth form.

Lake order was calculated using Arc Hydro Tools (following Martin & Soranno, 2006) and measures of lake density and spatial structure at the catchment level were derived through the analysis of a UK land cover map (LCM2007: http://www.ceh.ac.uk/services/land-cover-map-2007) using FRAGSTATS (v4.1). The landscape datasets included various metrics describing land use and its spatial structure. For simplicity we aggregated agricultural and urban land cover into one class termed 'managed land'. The landscape variables were derived from LCM2007 data in FRAGSTATS (v4.1). The complete list of explanatory variables, their definition and source is provided in Table 5.1.

Table 5.1 Environmental characteristics involved in three datasets of mean, standard deviation (St.Dev) and range (minimum and maximum value) of 960 lakes; ID is the abbreviation used in the results.

Datasets	ID	Variable	Unit	Definition	Source	Mean ± St.Dev	Range
Environment Dataset	L_area	Lake area	km^2	Area of water body	UK agencies	0.69 ± 2.40	0.011 – 38.1
	L_elev	Altitude	m	Lake elevation	UK agencies	158 ± 138	0.2 - 927
	l_Alk	Alkalinity	mEq/L (log)	Alkalinity concentration of lake water	UK agencies	2.43 ± 0.48	1.09 - 3.81
	L_conduc	Conductivity	μS/cm	Conductivity concentration of lake water	UK agencies	171 ± 384	12-8150
	L_pH	pH	-	pH value of lake water	UK agencies	6.70 ± 0.91	3.74 – 10.09
	L_SDI	Shoreline Development Index	-	Ratio of lake perimeter to area	UK agencies	1.74 ± 0.66	1.05 – 6.63
	L_MNDP	Mean Depth	m	mean depth of lake basin	UK agencies	6.00 ± 5.86	0.31 – 69.8
Hydrological Dataset	L_order	Lake order	-	Lake order in the outlet point	Ordnance survey	-	0-4
	C_area	Catchment area	km^2	Area of lake catchment	Ordnance survey	24.7±92.4	0.12-1764
	C_SDI	Catchment shoreline development index	-	Shoreline development index of catchment	Ordnance survey	1.64±0.24	1.23-2.87
	C_drain_des	Catchment drainage density	km/km^2	Total stream length/ catchment area(km/km^2)	Ordnance survey	1.49±3.01	0.026-62.8
	C_Slope	Catchment slope	Degree	Slope of catchment	Ordnance survey	7.64±5.34	0.19-29.94
	C_PLAND	Total lake area in catchment	%	Total lake area / catchment area (%)	FRAGSTATS	7.93±6.30	0.08-44.91
	C_PD	Catchment Lake density	n/ km^2	number of lakes per 1 km^2 in catchment	FRAGSTATS	0.89±1.02	0.02-7.80
	C_FRAC	Lake Fractal Dimension index	-	Average degree of complexity of lakes based on a perimeter/ area ratio in catchment	FRAGSTATS	1.07±0.02	1.02-1.20
	C_AI	Aggregation index	%	The number of like adjacencies patches between lakes in catchment	FRAGSTATS	102±270	57.14-8462
Landscape dataset	D_to_sea	Distance to sea	km	Distance to sea (m)	Ordnance survey	12.4 ± 13.1	0.10-85.4
	M_PD	Patch density	n/ km^2	Total patch numbers/Catchment area	FRAGSTATS	10.33±7.86	0.23-66.51
	M_LSI	Landscape shape Index	-	provides a standardized measure of total edge or edge density that adjusts for the size of the landscape	FRAGSTATS	6.49±6.20	1.48-57.1
	M_CONTIG	Contiguity Index	-	The mean contiguity value for the cell in a patch minus 1, divided by the sum of the template values minus 1.	FRAGSTATS	0.65±0.08	0.34-0.93
	M_CIRCLE	CIRCLE Index	-	Area (m^2) of each patch/1km^2 around patch.	FRAGSTATS	0.57±0.05	0.28-0.69
	M_DIVISION	Landscape Division Index	Proportion	Measure of the fragmentation of the landscape	FRAGSTATS	0.69±0.22	0.03-0.99
	M_PLAND	Land use coverage	%	Managed land area (agriculture + urban)/ Catchment area	FRAGSTATS	0.75±3.46	0.0001-52.26

5.3.3 Cross-scale interactions

(1) Description of study catchments

In order to explore the existence and significance of cross-scale interactions between the factors potentially influencing macrophyte composition at the lake and the catchment scale, we selected a subset of 450 lakes from the original dataset of 2558 located in 30 independent catchments that were considered to be broadly representative of the diversity of conditions found in Britain (Figure 5.1). This allowed the effect of environmental variables on macrophyte composition to be considered not only between lakes but also between catchments with differing characteristics (e.g. geology, altitude, land use). Lakes and catchments were selected to satisfy the following requirements: (1) catchments showed no overlap; (2) each lake was unique to one catchment; (3) each catchment exceeded 50 km^2; (4) there were >4 surveyed lakes with complete physico-chemistry and hydrological data per catchment. Table 5.2 and Figure 5.2 summarise the physical and hydrological characteristics of the 30 catchments selected. All catchments had a well-developed stream network and contained lakes with a high lake order, as defined by Riera et al., (2000). They also demonstrated significant contrasts in land use, with intensive land cover generally increasing southwards. Figure 5.1 illustrates the different subsets of data used in this paper.

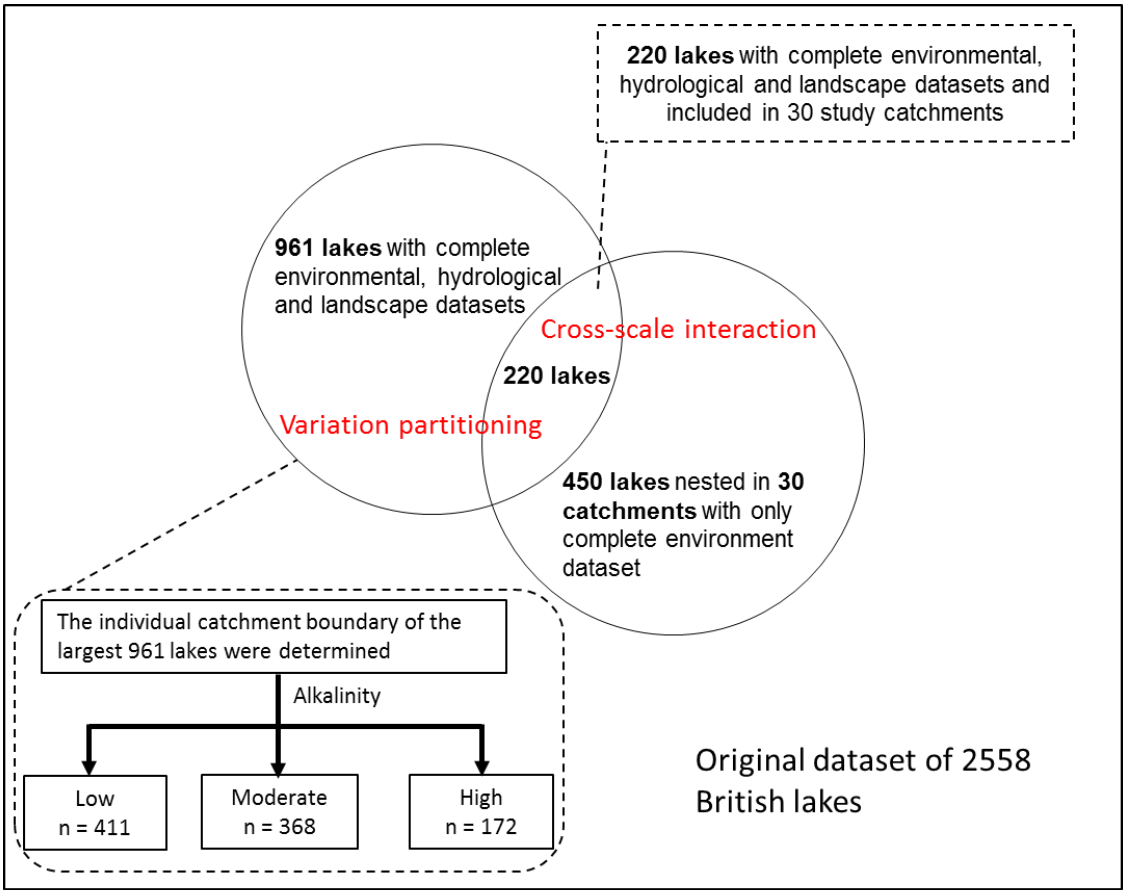


Fig. 5.1 Explanation of data subsets used for to investigate the determinants of macrophyte composition in UK lakes.

The 30 catchments were then further divided at the sub-catchment scale (Figure 5.3) whereby each individual lake and its sub-catchment were only encompassed by one of the 30 large catchments thus enabling them to be treated as independent observations in later statistical analysis. In total the dataset contained the sub-catchment boundaries for 220 lakes within the 30 catchments, as previously mentioned the remaining lakes were too small to enable the sub-catchment boundaries to be reliably defined (Figure 5.1). These lakes also had complete lake environment data. Figure 5.1 summarises the different subsets of data used in the paper and Figure 5.3 summarises the different scale of analysis considered in the study.

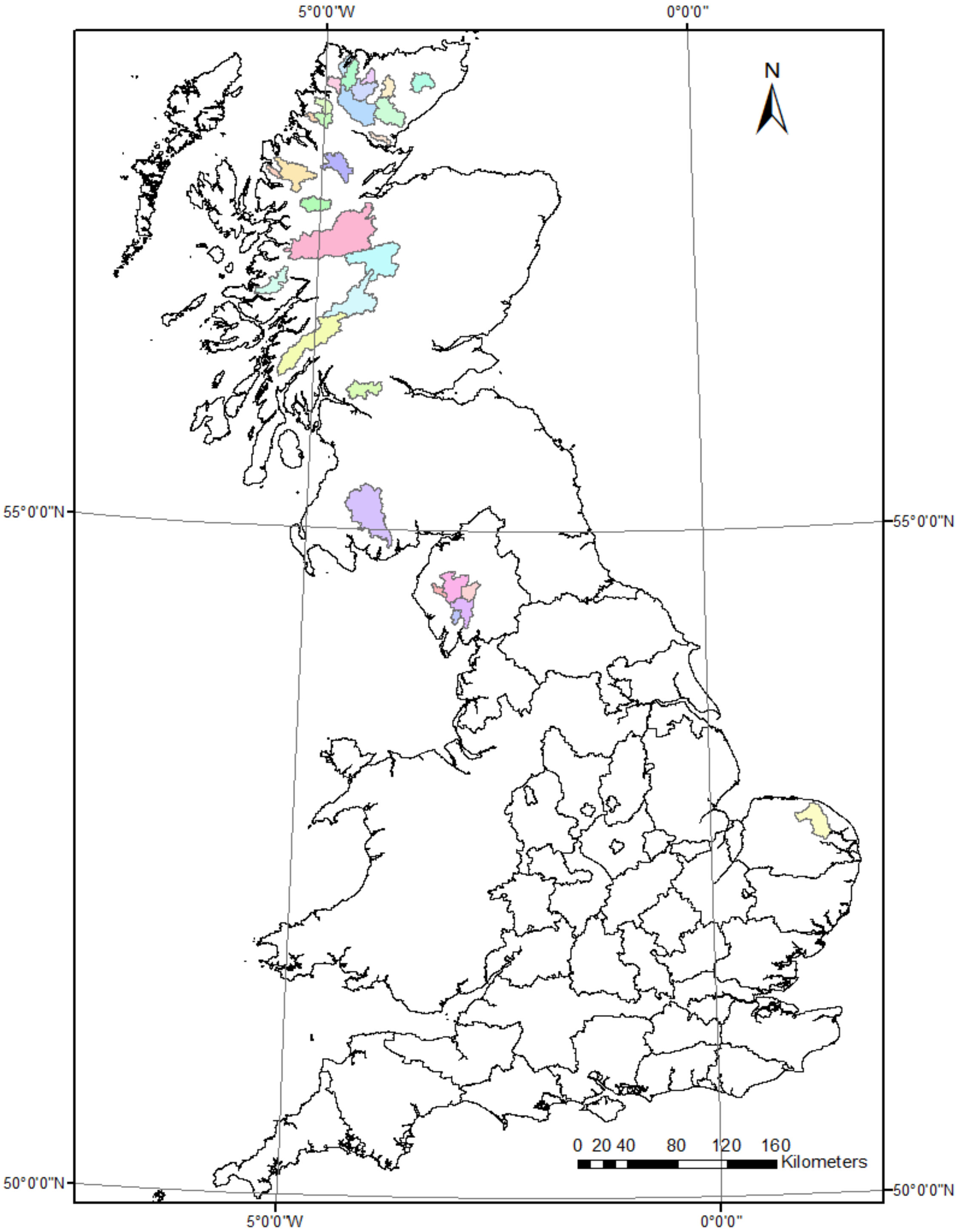


Fig. 5.2 Location of the study catchments presented in term of different colour.

Table 5.2 Physical characteristics of the studied catchments (D_lake order = Downstream lake order; C_area = Catchment area; U_lake = Upstream lakes; C_stream density = Catchment stream density; C_slope = Mean catchment slope; D_Lake area = Downstream lake surface area).

Downstream lake	Land-use (%)	Distance to sea (km)	D_lake order	C_area (km^2)	U_ lake numbers	C_stream density (km/km^2)	C_slope	D_Lake area (ha)
Loch Uamh Dhadhaidh	0	0.20	3	106	9	0.695	9.08	2.70
Loch Hope	0.23	3.40	4	216	33	1.106	9.79	638
Loch Craggie	2.38	5.30	4	88.7	16	0.979	6.03	118
Loch More	0.02	22.9	4	205	24	0.924	2.51	196
Loch Stack	0.05	7.20	4	103	15	1.102	13.6	252
Loch nan Clar or 'Loch Rimsdale'	0.61	25.5	4	138	8	0.913	4.09	923
Loch Naver	0.41	17.4	3	238	16	0.923	5.92	559
Loch a' Ghriama	0.06	11.7	4	534	27	0.845	5.54	109
Loch Assynt	0.23	7.20	2	119	11	0.942	10.8	800
Loch Veyatie or 'Loch a' Mhadail'	0.10	10.9	4	118	9	0.898	7.65	257
Loch Sionascaig	0.10	4.70	4	42.9	7	0.907	11.5	558
lLoch Brora	0.02	6.50	5	380	16	0.887	5.66	66.5
Loch Evelix	1.03	0.40	2	69.9	8	0.934	5.63	17.7
Loch Maree	0.22	11.8	4	427	22	0.610	12.5	2798
Loch Bad a' Chròtha	0.09	0.90	3	56.5	11	0.825	8.39	18.2
Loch Garve	0.16	13.6	4	297	18	0.762	11.3	145
Loch Dochfour	1.27	6.80	5	1764	88	0.824	9.97	48.9
Loch a' Mhuillidh	0.18	25.1	4	229	10	0.728	15.4	42.0
Loch Insh	0.58	43.4	4	768	19	0.988	9.79	131
Loch Shiel	0.8	8.50	4	249	5	0.721	17.1	1993
Loch Awe	0.36	12.3	4	815	37	1.012	11.4	3804
unnamed	14.7	11.2	3	269	6	0.845	5.77	12.8
Loch Rannoch	0.50	40.6	4	639	25	0.833	7.89	1881
Loch Ken or River Dee	0.66	13.4	4	1001	38	0.726	6.83	698
Bassenthwaite Lake	4.11	18.3	4	354	5	0.615	13.8	524
Ullswater	2.03	35.0	3	147	6	0.639	16.7	868
Crummock Water	1.80	19.1	2	62.8	4	0.654	18.0	250
Windermere	6.53	10.6	4	243	14	0.545	12.3	1436
Coniston Water	5.08	8.80	2	62.7	4	0.702	11.6	471
Wroxham Broad	29.2	20.7	3	422	9	0.389	1.04	31.8

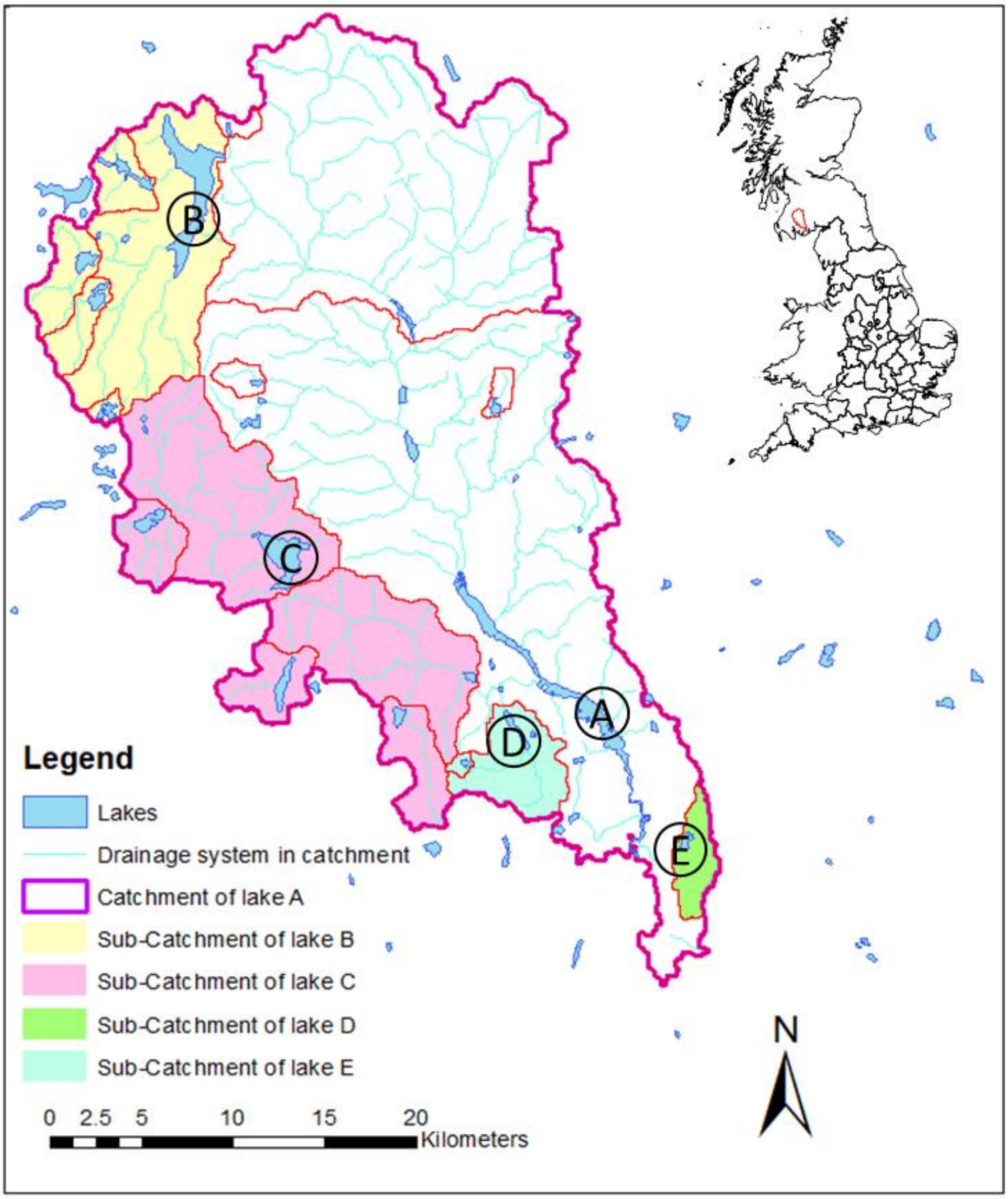


Fig. 5.3 Different catchment scale Introduction - Loch Ken example. It can be clearly seen that there are three different levels within the catchment: Local lake of lake A, B, C, D and E; Sub-catchments showed different colour in plot are catchments of lake B, C, D and E; All sub-catchments are involved in one big catchment of lake A, which showed by the pink boundary.

(2) Theoretical approach

Our primary focus was the relationship between macrophyte composition and the environmental covariates that interact across the contrasting scales of lake and catchment. We hypothesized that catchment scale drivers, such as land use and hydrology, influence physicochemical parameters (e.g. alkalinity) and thereby macrophyte species composition of lakes at the catchment scale. Meanwhile, the alkalinity of lakes affects macrophyte growth directly at the lake scale. We were interested in examining how the effect of these variables changes over catchment scales. In addition, we also considered the interaction between variables at the sub-catchment and lake scale. This was because the intermediate sub-catchment scale links responses at the lake- and catchment-scale and as such can help to explain how factors such as spatial heterogeneity and transport processes interact over fine- and broad-scales.

The cross-scale interaction model (Figure 5.4) presents how the different factors determining lake macrophyte species composition may interact over different scales of analysis. The response variable is lake macrophyte composition (derived from ordination analysis as described below); the explanatory variables are hydrological and landscape factors at the three different scales of analysis: lake, sub-catchment and catchment. In our study, the drivers from lake scale (e.g. alkalinity) and sub-catchment scale (e.g., hydrological and landscape variables) were used as covariates to explain variability in lake macrophyte composition. The slope of the relationships observed at the lake or sub-catchment scale were then regressed against catchment-scale variables to explore possible cross-scale effects.

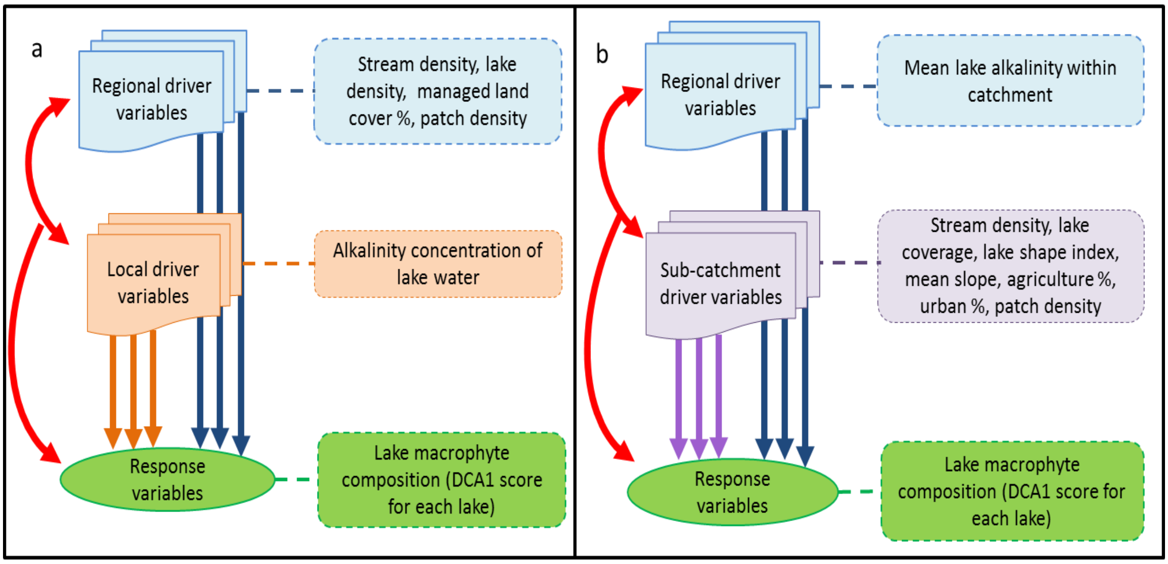


Fig. 5.4 The conceptual model of cross-scaled interaction between lake and catchment scale factors determining macrophyte composition in lakes. a) lake-catchment scale interaction; b) sub-catchment – catchment scale interaction)

(3) Statistical analyses

(i) Variation partitioning analyses

Variation partitioning (Peres-Neto et al., 2006; De Bie et al., 2012) was performed with a spatial redundancy analysis (spatial RDA) and up to four subsets of environment, hydrology, landscape and spatial variables to quantify the unique and combined fraction of macrophyte variation explained by each data set. The lakes were then partitioned into low alkalinity (<10 mg $CaCO_3$ L^{-1}, n=411), moderate alkalinity (10-50 mg $CaCO_3$ L^{-1}, n=368) and high alkalinity (>50 mg $CaCO_3$ L^{-1}, n=172) types to enable the effect of the four sets of explanatory variables to be compared between different major lake types. These lake alkalinity boundaries were established by UK Technical Advisory Group for defining lakes typologies under the European Water Framework Directive.

The latitude-longitude data for each lake were transformed into Cartesian coordinates using the function 'geoxy' from package 'soda' in R. Macrophyte species presence-absence data were Hellinger transformed. The spatial RDA model was completed to act on the spatial eigenvectors obtained from Moran's Eigenvector Maps (MEM, Dray et al., 2006), which is referred to as principal coordinates of neighbour matrices (PCNM, Borcard et al., 2004) in previous studies. These resulting orthogonal spatial eigenvectors modelling the positive spatial correlation of lakes were considered as the explanatory matrix in the variation partitioning analysis to clarify the effect of environment, hydrology and landscape. A total of 11 MEMs, 26 MEMs and 19 MEMs were derived to form a spatial dataset for each of the three alkalinity-based lake groups (low, moderate and high).

We independently ran a forward selection (Blanchet et al., 2008) for the environment, hydrology, landscape and spatial dataset using function 'ordir2step' in package 'vegan' firstly. Lake order, as a factor variable in hydrological dataset, cannot be handled by function 'varpart' and was recoded as a dummy binary variable. Variation partitioning with four explanatory matrices is uncommon but can be found in one previous study (Viana et al., 2016). In this case the partitioning generates 16 fractions: 4 pure effects of environment, hydrology, landscape and spatial dataset, 12 joint effects of the two or three separate sets and 1 unexplained variation. Each pure fraction was tested for significance with the Monte Carlo permutation test (Number of permutations: 999).

(ii) Cross-scale interaction analyses

Information on the macrophyte community in each lake was summarised using Detrended Correspondence Analysis (DCA). DCA provides a quantitative analysis of vegetation heterogeneity but without considering the spatial distribution of sites or underlying environmental gradients (Kissoon et al., 2013). DCA is particularly appropriate in this study with the respect of the aims to identify the primary patterns of macrophyte species and survey lakes along the dominant axis. It is suitable for situations presenting the unimodal distribution of species data over the ‘long’ gradient (Leps & Smilauer, 2003; Schmidtlein & Sassin, 2004). Detrending standardizes the biotic dissimilarity between lakes along the ordination axes and preserves among-axis independence (Hill & Gauch, 1980; ter Braak & Smilauer, 2015). DCA was applied to the lake macrophyte data for the sample of lakes (n=450) considered for the catchment scale analyses. We used DCA axis 1 (DCA1) because it symbolized the “longest” gradient in macrophyte species composition. DCA axis 2 (DCA2) represented the ‘longest’ gradient in the macrophyte variation not accounted for by DCA1; however, the mixed effect model including DCA2 did not run successfully and did not reveal any additional insights. DCA analyses were undertaken in the R (v3.1.3) package ‘vegan’ (Oksanen, 2012).

The interaction between catchment scale variables (e.g. hydrology, land use) and the effect of lake alkalinity on macrophyte composition was performed using the linear mixed-effect (LME) models with the ‘lme’ function in package ‘nlme’ (Pinheiro et al., 2007). Firstly, we fitted the mixed effect model considering all the lake environmental variables (all variables were tested for multicollinearity using the function “corvif”, VIF<2) as the fixed effects and the catchment as the random effect to model DCA1. The most significant three predictors produced by the comparison among reduced LME models by the function “anova” in the AED package were lake alkalinity, lake area and lake altitude. The model was then fitted using DCA1 scores as the response variable and lake alkalinity, lake area and altitude as the fixed effects and catchment identity as the random effects. As the DCA1 scores represent a continuous non-normal response variable, the assumption of normality for LME models was checked by plotting the residual of the model and performing the Kolmogorov–Smirnov test on the residual. To explore the catchment level variation, we performed the random intercept and slope model to allow the slope and intercept of lake alkalinity to vary by different catchments and explained the exclusion of random slopes for lake area and altitude. To test the effect of the spatial correlation structure of lakes, we ran the same LME model with the spatial correlation form structured as ‘correlation = corGaus (1, form=~latitude + longitude)’. The result indicated that without the spatial structure, alkalinity is a statistically significant driver of macrophyte composition and that after controlling for lake location and the known underlying correlation structure, this relationship is still significant. This analysis provided a slope, measuring the strength of the relationship between alkalinity and macrophyte turnover, for each catchment (hereafter termed catchment-specific model slope). These slopes were then regressed against individual catchment-scale hydrological and land use variables (see Table 5.1) in the general linear model (GLM) with normal errors and identity link. The catchment-specific model slopes were Box-Cox transformed to improve normality. A Chi-square test was used to assess the difference in deviance between models. Afterwards, the hydrological and landscape variables were combined into two separate models; the backward stepwise regression procedure and Akaike information criterion (AIC) were employed to identify the variables with the greatest explanatory power in each dataset. To make it easier to interpret the results, OLS models were used to plot the correlation between the slope and the selected catchment-scale variables. We used the residual statistics (Cook’s distance) to examine outliers. The specific slope of catchments （Windermere, Coniston Water and Wroxham Broad, all located in England） were found to have a high Cook’s distance (close to 1) (See Appendix 5.3 a), which indicates a possible influence of these outlier on the regression model outcomes. The catchments with a high Cook’s distance were deleted to test the significance of each model and the results indicated that the significance and the trend differed very little from the original model (See Appendix 5.3 b). The Box-Cox transformation was undertaken in the package ‘forecast’ in R, while the GLM was fitted using the ‘mass’ package in R (Venables & Ripley, 2002).

As previously stated, 220 sub-catchments within 30 larger catchments were chosen in order to examine how the mean alkalinity of lakes within the catchment influences the effect of land-use and hydrology on macrophyte composition in lakes. The explanatory hydrological and land-use variables factors were standardized to ensure the derived catchment- specific slopes were comparable. Subsequently, mixed effects models were fitted using the hydrological and land-use variables as fixed effects and the catchment as a random effect. Again, this produced a catchment-specific slope for each explanatory variable. Finally, the effect of mean lake alkalinity within the catchment on the catchment-specific slope for each explanatory variable was examined using a linear model.

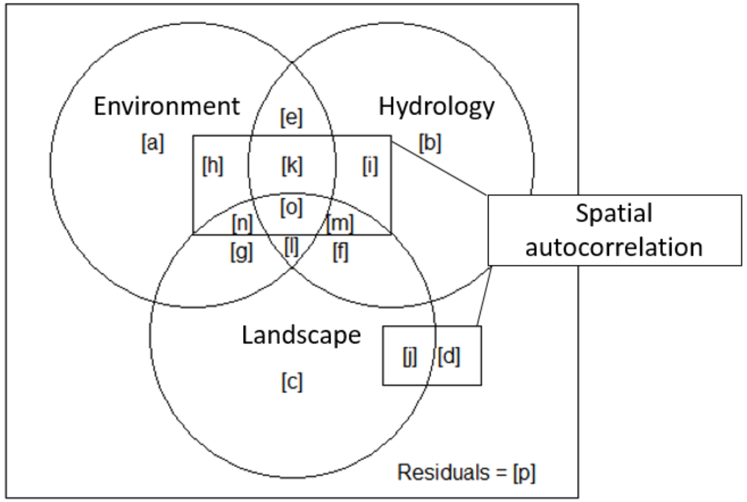
5.4 Results

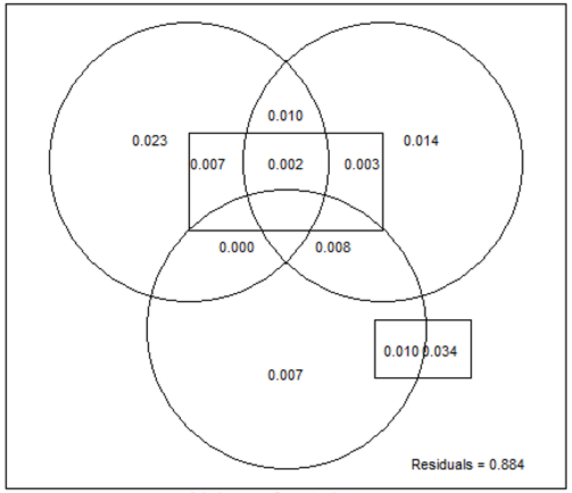
5.4.1 Variation partitioning

The whole set of environment, hydrology, landscape and spatial variables collectively explained 11.6%, 18% and 23.9% of the total variation in macrophyte communities in the low-, moderate-, and high-alkalinity lakes respectively (Figure 5.5). The results indicated that the fraction of the total variation (FTVE) explained independently or jointly by each dataset varies with alkalinity.

For each of the three groups, most of the explained community variation could be contributed to the pure effect of the spatial patterns (fraction [d] in Figure 5.5; 3.4%, 6.2% and 11% for low-, moderate-, and high-alkalinity lakes respectively). Except spatial set, the other three sources of variation have significant unique contributions: the environment alone (fraction [a] in Figure 5.5; 2.1%-2.3%), the hydrology alone (fraction [b] in Figure 5.5; 0.3%-1.4%) and the landscape alone (fraction [c] in Figure 5.5; 0.7%). All of the pure component fractions are significant in Monte Carlo permutation tests ($p<0.001$) except the landscape fraction in high alkalinity lakes ($R^2_{adj}=-0.004$; $p=0.43$). The low R^2 adjustment of the FTVE for the landscape variables could be explained by the high shared fraction among the landscape and spatial components (fraction [j] in Figure 5.5; 1%-2.5%), indicating that a large amount of the variation explained by the landscape variables was spatially structured.

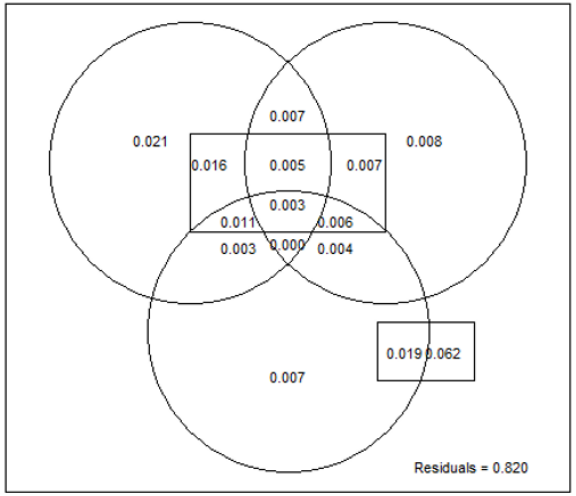
The joint contribution of the four explanatory datasets was consistently small ($R^2_{adj} < 1.0\%$) across the different alkalinity types. The amount of variance shared by combinations of explanatory datasets revealed greater dependency on lake alkalinity. Thus the FTVE explained commonly by the environment, hydrology and spatial explanatory datasets increased from 0.2% to 1.9% (fraction [k] in Figure 5.5), while the shared contribution of both landscape and hydrological variables decreased from 0.8% to <0 (fraction [f] in Figure 5.5) moving from low to high alkalinity.



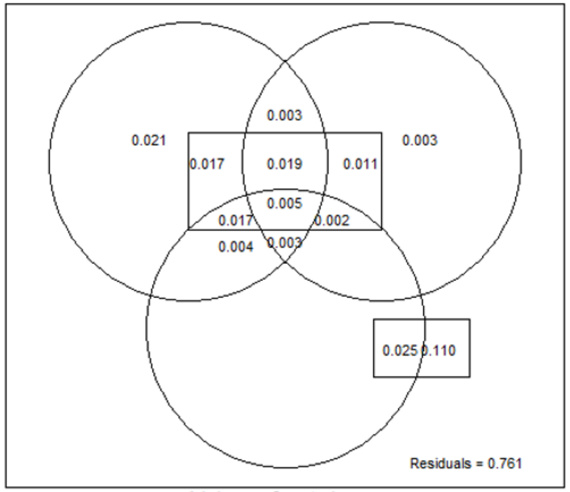


Values <0 not shown

Low alkalinity
(<10 mg $CaCO_3$ L^{-1}, n=411)



Moderate alkalinity
(10-50 mg $CaCO_3$ L^{-1}, n=368)



Values <0 not shown

High alkalinity
(>50 mg $CaCO_3$ L^{-1}, n=172)

Fig. 5.5 Variation partitioning of the Hellinger-transformed macrophyte data into an environmental component (upper left-hand circle), a hydrological component (upper right-hand circle), a landscape component (lower circle) and a spatial component (disjoined rectangles). Negative R^2 adj value for the fraction was not shown in the plot which explains less of the variation than would be expected by chance.

5.4.2 Cross-scale interaction analyses

(1) Lake-catchment scale interactions

DCA was used to analyse the variability in macrophyte species composition between the study lakes. The biplot in Figure 5.6 shows that lakes with a high DCA1 score were characterised by large surface area, high alkalinity and high pH with a flora dominated by floating plants and algae (e.g., nymphaeids, *Lemna* spp and filamentous algae). Lakes with low DCA1 scores were mostly smaller upland lakes with good water quality, and a flora dominated by small submersed and emergent plants such as isoetids. The distribution of species in ordination space was thus consistent with their known environmental preferences. There was limited variation on DCA2, with the greatest range of scores coinciding with the upper end of DCA1, suggesting that DCA2 differentiates species assemblages according to levels of nutrient enrichment in base-rich environments.

The DCA analysis suggested that alkalinity explained more of the variation in macrophyte composition compared with other environmental variables and thus we carried this variable forward into the mixed effect models. We could not consider the effect of total phosphorus because such data were not available for the majority of our study lakes. However, the importance of alkalinity as the main driver of macrophyte composition in UK lakes is strongly supported by previous studies, especially for many of the high latitude UK lakes considered in this study (Vestergaard & Sand-Jensen, 2000b).

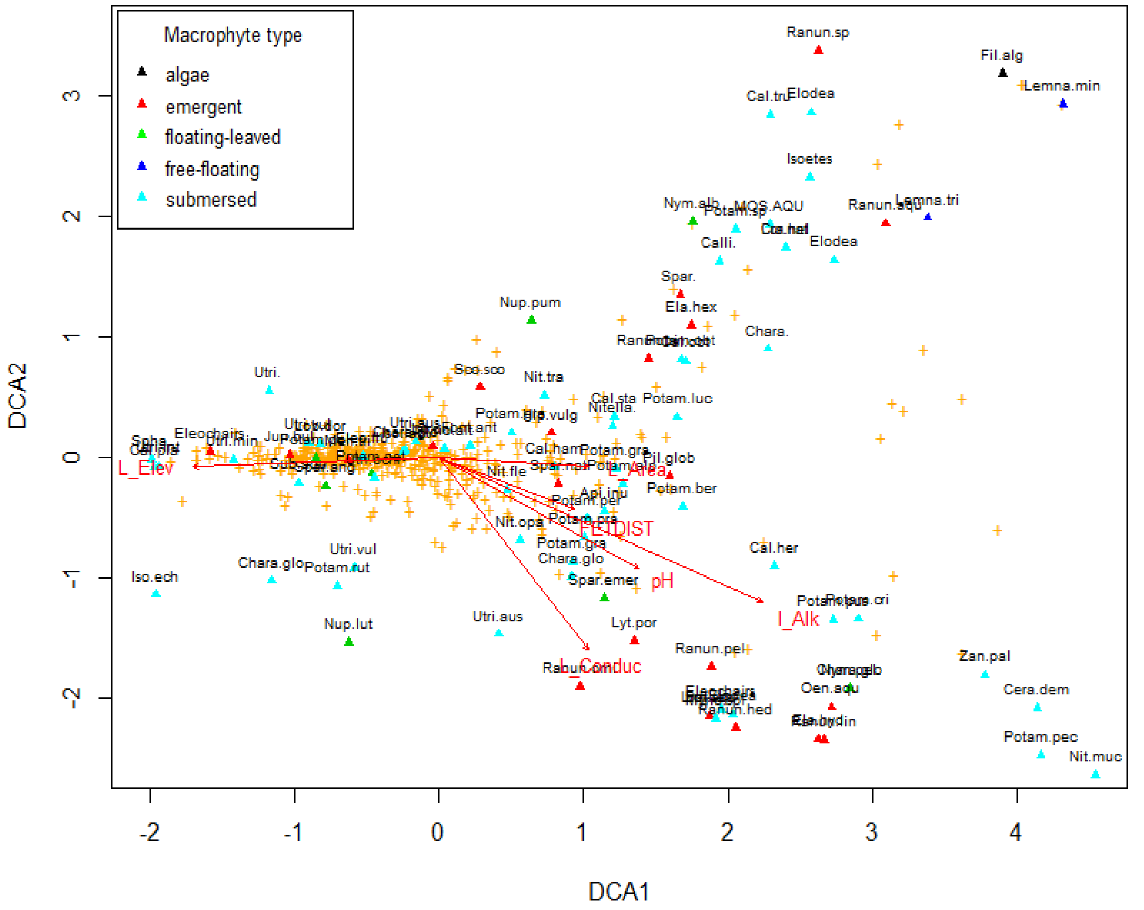


Fig. 5.6 The correlation between DCA score of species and lake as well as the lake environmental factors. Orange points represent different lakes, and triangles indicate different macrophyte species. Macrophyte species based on DCA score can be divided into three geo-environment types, which can be clearly seen from the figure (left, upper right, lower right). Variable abbreviations are as follows: L_Elev - lake Elevation; L_area - lake Area; FETDIST - lake Fetch index; L_Alk - lake Alkalinity; L_Conduc - lake Conductivity; pH - lake pH. Species abbreviations can be found in Appendix 5.1.

Figure 5.7a shows the catchment-specific effect of alkalinity on macrophyte species composition (represented by the site scores on DCA1) obtained from the mixed effect model. In Figure 5.7a, each line represents a single catchment. The slope of the lines, ranging from 0.45 to 1.46, reflects the amount of turnover in macrophyte composition in relation to lake alkalinity across the surveyed lakes within each catchment. For catchments with model slopes close to zero, we can infer that macrophyte composition varies little over the gradient in lake alkalinity present within the catchment while high model slopes imply that species composition changes strongly with variation in lake alkalinity. The majority of catchments with a model slope close to zero occurred in the north and west of Scotland (Figure 5.7b).

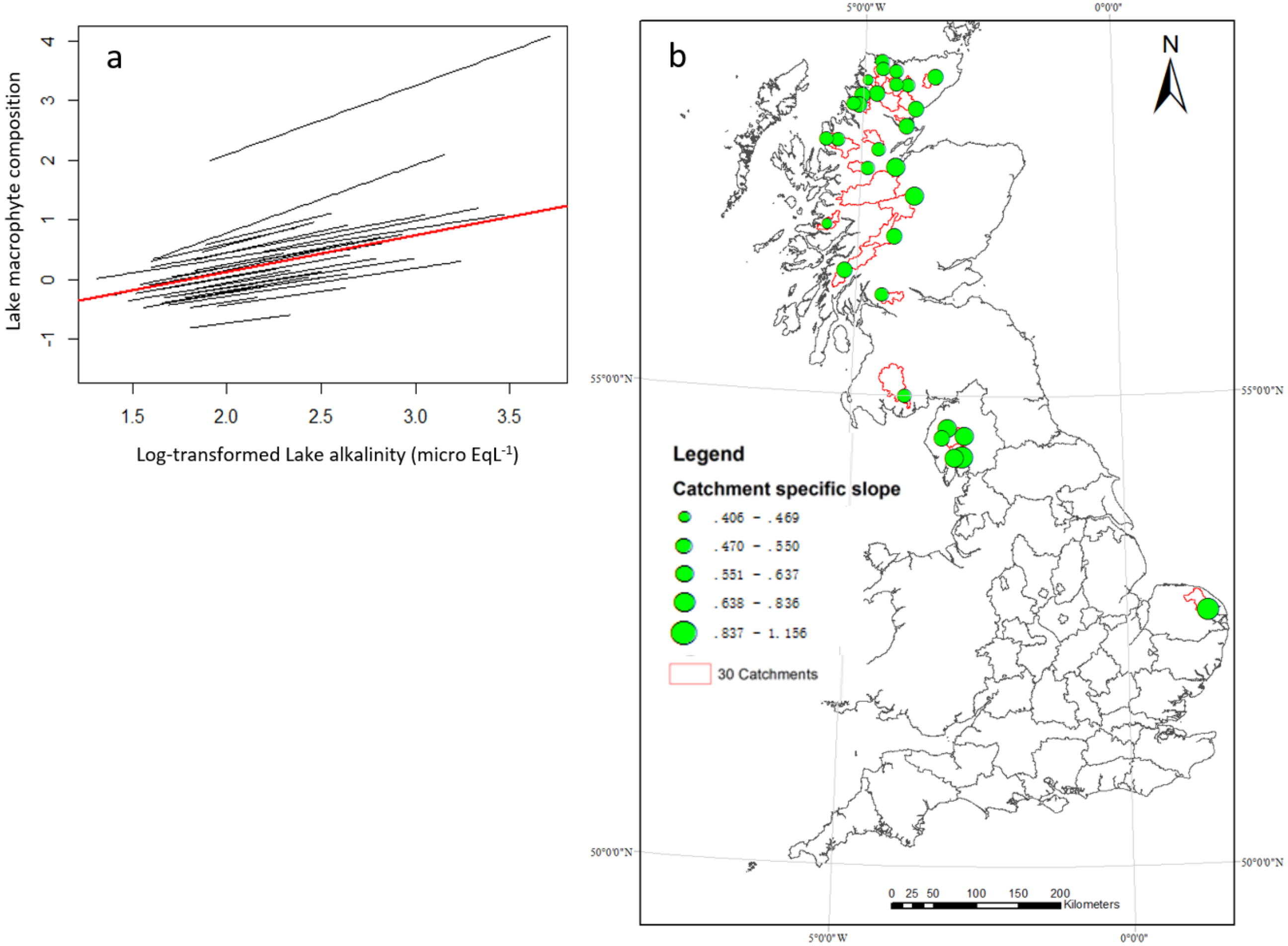


Fig. 5.7 Introduction of catchment specific model slope. (a) Catchment specific slope of the relationship between lake alkalinity and macrophyte composition (DCA1), modelled for each catchment. The thick red line is the random slope for the "average catchment". (b) The relationship between catchment specific slope and the latitude for the catchment (based on latitude of the most downstream lake per catchment) (Projected coordinate system: British-National-Grid).

We subsequently examined the extent to which the slope of the relationship between alkalinity and macrophyte composition was influenced by individual catchment-scale landscape and hydrological variables (Table 5.3). The backward stepwise regression procedure was employed for hydrological and landscape datasets separately to identify the variables with the greatest explanatory power in each dataset (Table 5.4). Lake density, mean catchment slope, percentage managed land and landscape patch density were selected to be the most important measures of lake-landscape interaction (Alexander et al., 2008; Cheruvelil & Soranno, 2008; Vaughn & Davis, 2015). Figure 5.8 shows the pairwise relationships between the catchment-specific model slopes from the mixed effect models and the hydrological and landscape variables. The effect of alkalinity on macrophyte composition was strongest in catchments with a low density of water bodies (lakes and streams), high mean topographic slopes, a high percentage of managed land, and highly fragmented landscapes dominated by small individual patches. Overall, patch density, percentage managed land and water body density were the main factors accounting for variation in the relationship between alkalinity and macrophyte species composition.

Table 5.3 General linear model (GLM) relating the catchment-specific slope to individual catchment-scale hydrological and landscape variables

Explanatory dataset	ID	Explanatory variables	Slope	AIC	Chis-q
Hydrological Dataset	C_area	Catchment area	5.324e-05	17.189	0.561
	C_SDI	Catchment shoreline development index	-0.075	17.058	0.492
	C_drain_des	Catchment drainage density	-0.597*	6.045	0.0002*
	C_Slope	Catchment slope	0.0274***	0.59	P<0.001***
	C_PLAND	Total lake area in catchment	-0.011	16.219	0.258
	C_PD	Catchment Lake density	-0.633*	13.611	0.047*
	C_FRAC	Lake Fractal Dimension index	1.109	17.345	0.654
	C_AI	Aggregation index	-0.008	16.928	0.441
Landscape dataset	D_to_sea	Distance to sea	0.007*	11.479	0.0121*
	M_PD	Patch density	0.025***	0.351	P<0.001***
	M_LSI	Landscape shape Index	0.0058**	9.872	0.0042**
	M_CONTIG	Contiguity Index	-1.226**	8.478	0.0016**
	M_CIRCLE	CIRCLE Index	-1.446	17.123	0.528
	M_DIVISION	Landscape Division Index	0.502	14.954	0.111
	M_PLAND	Land use coverage	0.02***	0	P<0.001***

Table 5.4 Stepwise Logistic Regression with GLM relating the catchment-specific slope to catchment-scale hydrological and landscape dataset

Variables included in the Full model	The remained variables after stepwise	AIC
Hydrological dataset	C_PD (**) + C_Slope (***)	-34.91
Landscape dataset	M_PD (***) + M_PLAND (***)	-39.88
Hydrological + Landscape dataset	C_area + C_SDI (*) + C_Slope (***) + M_PD (**) + M_PLAND (**)	-44.92

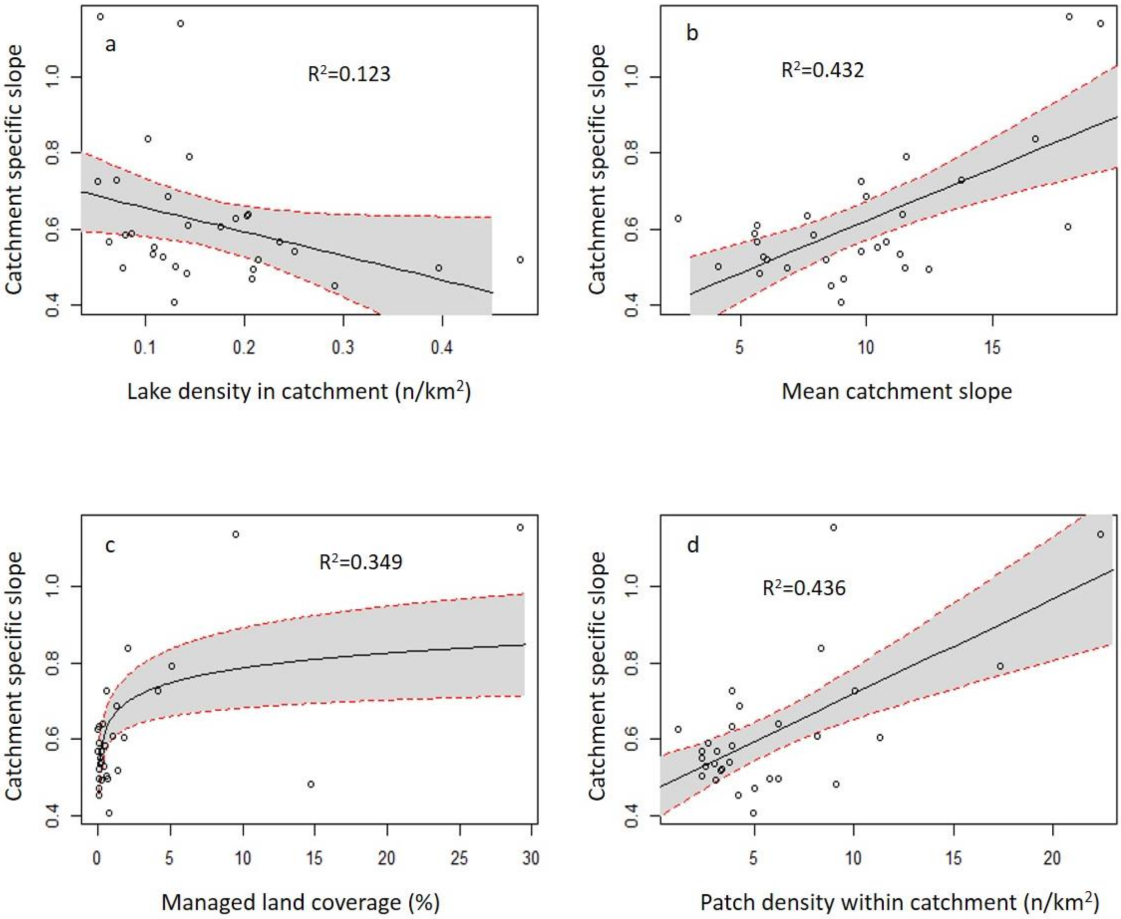


Fig. 5.8 Lake alkalinity effects on macrophyte species composition related to catchment-scale hydrological and landscape variables. Hollow circles are catchment-specific model slope estimates (see Fig 5.7a), shown with the multilevel regression line with the relevant hydrological variables including lake density in catchment, mean slope, managed land coverage and patch density of catchment. Light-grey shaded regions are 95% credible intervals for each model.

Lake density was negatively correlated with the catchment specific model slope (Figure 5.8 a). Turnover is therefore likely to be higher for a given alkalinity in catchments with a higher distance between lakes. The mean catchment slope (Figure 5.8 b) was positively related to the catchment specific model slope, indicating that macrophyte composition varies more strongly with alkalinity in steeper catchments, perhaps because of enhanced variation in other influential factors such as altitude or depth. For landscape variables (Figure 5.8 c&d), positive trends were observed between managed land use and patch density and the catchment specific model slope. In catchments with high intensity of land use or a high level of fragmentation, there is therefore increased turnover in macrophyte composition per unit alkalinity.

(2) Lake sub-catchment scale interactions

Figure 5.9 shows the effect of hydrological and landscape variables measured at the sub-catchment scale on the relationship between lake macrophyte composition and the mean alkalinity of each catchment. The hydrological variables (Figure 5.9 a) at the sub-catchment scale were found to have little effect on lake macrophyte composition in low alkalinity catchments, as indicated by the near zero catchment-specific slopes. The catchment-specific slope of lake coverage showed a positive relationship with mean catchment alkalinity, while conversely stream density showed a declining trend. The latter relationship agreed with the results observed at the catchment scale. Conversely, the percentage of managed land within the catchment (Figure 5.9 b), especially urban, was found to have a strong effect on lake macrophyte composition in low alkalinity catchments. The percentage of agricultural land was not found to have a significant effect. Most low alkalinity catchments considered in this study were located in northwest Scotland. In these catchments, macrophyte composition would seem to be more strongly controlled by landscape factors rather than lake-scale physicochemical variables.

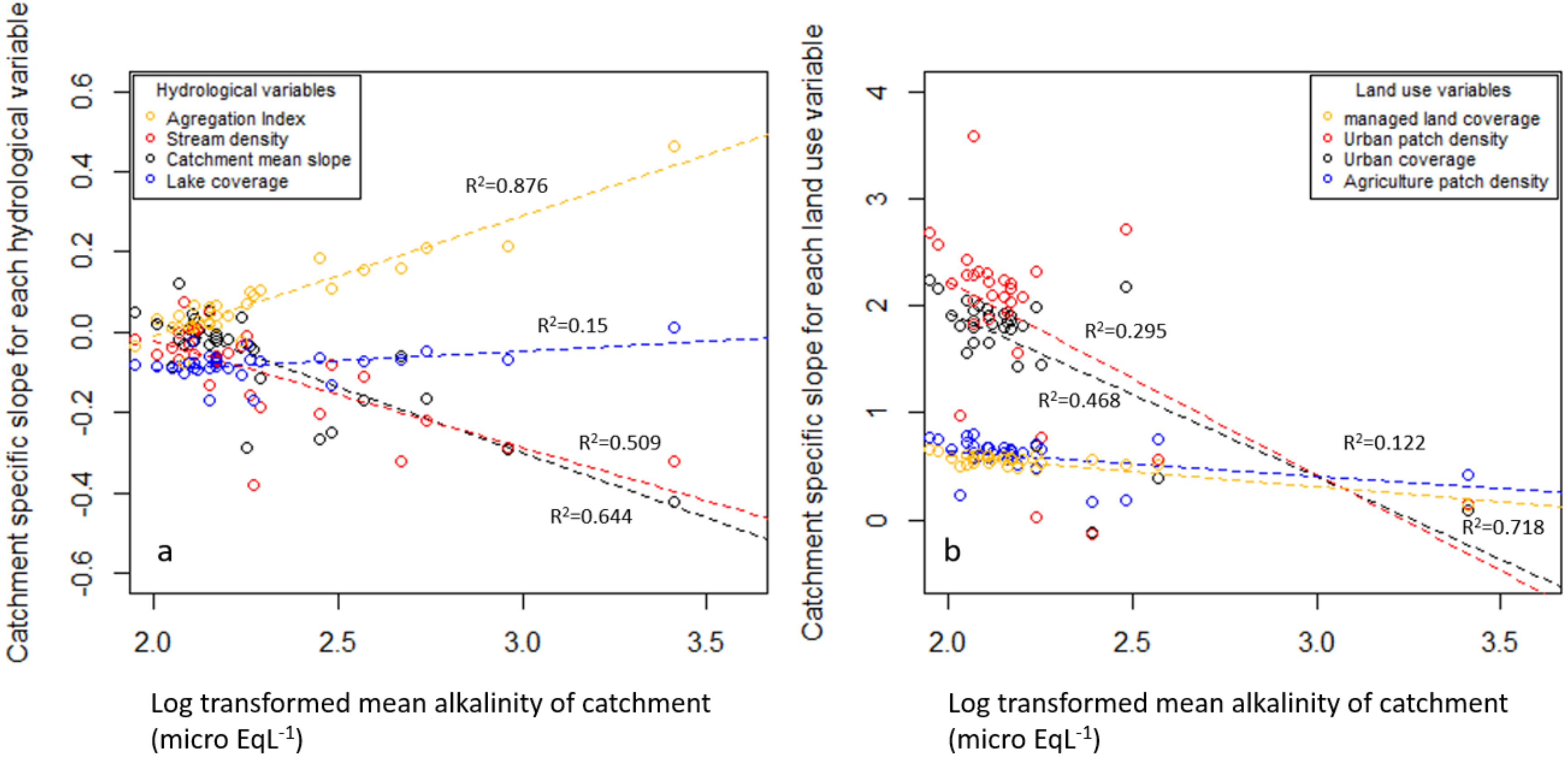


Fig. 5.9 The relationship between the catchment-specific slope of hydrological (Fig. 5.9a) and landscape variables (Fig. 5.9b) calculated at sub-catchment scale and the mean lake alkalinity of each catchment. The hydrological variables involved stream density, catchment mean slope, lake coverage and lake aggregation index. The variables of urban coverage, urban patch density, agriculture patch density, managed land coverage were selected as the land use variables.

5.5 Discussion

5.5.1 Determinants of macrophyte composition in British lakes

The importance of interactions between lake and catchment scale variables as determinants of lake ecological condition and biodiversity is widely acknowledged (Morandeira & Kandus, 2015). The effect on macrophyte composition of environmental conditions such as alkalinity, nutrients, light availability, water depth and physical disturbance, is well documented (Scheffer et al., 1993, Smolders et al., 2002). However, equivalent studies on the effect of catchment-scale variables are comparatively scarce. In this study we examined the interaction between lake-scale factors and a suite of catchment-scale variables such as stream density, lake density and mean slope, which have had limited previous consideration (Sousa et al., 2011; O'Hare et al., 2012; Rolon et al., 2012), partly because of the restricted availability of suitable large scale datasets.

Our study indicates that spatial autocorrelation is more important than the lake- and catchment-scale variables in explaining the variation of lake macrophyte communities at a broad extent (national scale). While at a fine extent (catchment scale), the spatial autocorrelation was observed to not significantly influence the distribution of macrophyte species. The results are consistent with some previous studies that spatial structure increases with the increasing extent and accounts for more variation of macrophyte communities at a broader extent (Cottenie, 2005; Heino, 2011; Alahuhta & Heino, 2013). Besides, the variation partitioning shows the effect of the spatial structure was found to become progressively more important as the alkalinity of the system increased, which follows our expectations. This is because the substantial groundwater contact and close hydrological connectivity in high alkalinity lakes increases the proximity of these lakes to each other when compared to low alkalinity lakes.

However, for this study, we are more interested in the impact of lake- and catchment-scale determinants on macrophyte composition after controlling for spatial autocorrelation. Macrophyte composition in inland waters is diverse and heterogeneous, and influenced by physico-chemical conditions at the lake scale as well as catchment-scale hydrological, climatic and landscape characteristics. The lakes considered in this study displayed marked differences in macrophyte composition that typify the transition from nutrient limitation to light limitation which occurs across productivity and alkalinity gradients (e.g. dominance of low-alkalinity lakes by small submersed species shifting to floating-leaved plants and filamentous algae in high alkalinity lakes). The results of variation partitioning reveal that macrophyte composition was strongly determined by the lake environment in different alkalinity types, whereas catchment-scale variables related to hydrology and landscape diversity were proportionally more influential in low-alkalinity lakes. Typically, the low alkalinity lakes were located in catchments with a high density of water bodies and a low percentage cover of managed land and thus less human disturbance. The importance of lake chemistry as a determinant of macrophyte composition is widely acknowledged (Kolada et al., 2014) and thus it is not unexpected that in those lakes with high alkalinity, and in regions of intensive land use and higher levels of nutrient enrichment, the effect of catchment-scale hydrological and landscape variables was comparatively weak. A negative value for the pure landscape fraction in high alkalinity lakes in the variation partitioning analysis reflects strong multicollinearity between the landscape dataset and spatial control. However, historically, prior to the advent of major human impacts, such catchment-scale variables may have exerted a stronger influence on community assembly in high alkalinity lakes.

The relative importance of catchment-scale variables on macrophyte composition in low alkalinity lakes, can be explained, in part, because these systems are generally located in upland areas where macrophyte composition is more likely to be shaped by dispersal limitation (due to low density of suitable vectors) than in lowland lakes where factors such as poor water quality are likely to control recruitment and persistence, while vectors such as water birds and humans are abundant. This is especially true for the submersed species since effective dispersal as vegetative propagules will occur primarily via transport through the hydrological network (Glime, 2007) due to the risk of desiccation associated with aerial dispersal over all but very short distances (Keddy, 1976). Conversely, emergent plants that are relatively more important in high alkalinity, lowland lakes readily reproduce from seeds that are dispersed by water, wind or animals (Soons, 2006). The ability of such species to colonise other water bodies is thus more dependent on environmental filtering as well as broad-scale processes (i.e. ability to dispersal by wind).

5.5.2 Interactions between lake- and catchment-scale factors

The results of this study show that lake and catchment scale factors independently influence macrophyte composition in lakes but further that these assemblages are also shaped by interactions between these different variables. For this study, we assumed that alkalinity would explain most variation in macrophyte composition in British lakes in line with other studies (Vestergaard & Sand-Jensen, 2000a; Kolada et al., 2014). We could not consider the separate effect of total phosphorus (TP) because such data were unavailable for most of our study lakes. Moreover, alkalinity and TP have been proved strongly correlated using available lake datasets (r^2=0.531; $p<0.001$), firstly because alkalinity is indicative of the background supply of phosphorus by rock weathering, and secondly because nutrient loading from intensive agriculture and human effluent is most likely in lowland, base-rich catchments (Kolada et al., 2014). Specifically, we show that while lake alkalinity is the most important determinant of macrophyte composition the strength of this effect is significantly affected by catchment scale variables, including lake density, catchment topography, the proportion of managed land and the degree of landscape fragmentation. These variables are collectively measures of lake landscape position, connectivity and disturbance and, as such, our findings are both consistent with observations from comparable studies in the recent literature (e.g. Rolon et al., 2012) and in line with general ecological theory (e.g. niche theory and neutral theory, Zillio & Condit, 2007).

Landscape position has previously been shown to be an important factor determining water quality in lakes (e.g., Martin & Soranno, 2006), and thus community composition, because it effectively dictates the nature and intensity of land use within the catchment, and particularly within the near-shore region where the lake-landscape interaction is strongest. The importance of habitat connectivity to the structure or function of lake ecosystems has been widely documented (e.g., Beier & Noss, 1998; Forbes & Chase, 2002; Cloern, 2007; O'Hare et al., 2012). Connectivity between lakes, whether overland or through the hydrological network, is critical to the flow and exchange of water, energy and other materials, including macrophyte seeds and propagules. The level of connectivity between ecosystems is thus fundamental to the maintenance of biodiversity, with well-connected systems being likely to share similar environmental conditions and thus ecological niches, as well as recruiting from a common species pool (Bornette et al., 1998; Wiens & Donoghue, 2004).

In this study, we demonstrate that macrophyte composition is less strongly associated with alkalinity in catchments with high lake connectivity, with the importance of alkalinity (or correlated factors) increasing with lake isolation. High hydrological connectivity favours the dispersion of propagules between lakes within catchments via the stream network, which could be summarized by the positive correlation between stream density and catchment-specific slope (see Table 5.3). In the absence of such connectivity, material exchange can still occur via other vectors, especially where lakes are located in close geographical proximity. Thus, in well-connected systems, we might expect few strong differences in macrophyte species composition between lakes. These findings echo those of Sousa et al., (2011), Makela et al., (2004) and others who have found that inter-lake variability in environmental conditions, for example spatial turnover in alkalinity, is strongly related to degree of connectivity and this consequently drives spatial patterns of macrophyte composition. Isolation was previously found to reduce macrophyte species richness and similarity in freshwater systems due to the constraints it imposes on dispersion (Rolon et al., 2012). We also show that in catchments with a stronger coastal influence macrophyte composition was less influenced by lake alkalinity. The conclusion is supported by Table 5.3 indicating a positive relationship between distance to sea and catchment-specific slope. This might be the result of increasing maritime influence on local meteorology and climate, or a reflection of the change in catchment topography and land use in lowland catchments (May et al., 2001; Moss et al., 2005).

Our results also indicate that chemistry is more important as a determinant of macrophyte biodiversity in catchments impacted by intensive land use while connectivity was less important in such catchments. The most readily observed symptom of intensive land use within catchments is the increased nutrient input to waterbodies through agricultural activities or wastewater discharge. There is an extensive literature on negative effect of intensive land use practices on aquatic biodiversity (Schelske et al., 2005). However, our findings refine this by showing explicitly that human disturbance also fundamentally alters the underlying processes that structure biodiversity in lakes, such as habitat connectivity. Whether this reflects a shift towards environmental filtering due to multiplying type and intensity of stressors, or a shift away from dispersal limitation due to the greater abundance of potential dispersal vectors in more productive landscapes with typically larger-sized water bodies is presently unclear.

Our study applied the cross-scaled interaction approach to the analysis of lake macrophyte data also to help inform water policy and management strategies. This study could promote the identification of individual catchments that are most vulnerable to human disturbance at the catchment scale. We anticipate that management and policy will benefit from considering the interaction of local-scale and catchment-scale variables on macrophyte at the broader spatial scales than at a single scale. The results indicate that management strategies for protecting lake biodiversity should also consider the constraints operating at a catchment scale. Moreover, we suggest a flexible catchment-specific management approach for different regions that take an account of the response of catchment-scale variation to human disturbance.

This study highlights that the response of macrophyte communities to water quality pressures is complex and likely to be moderated by catchment-scale factors, such as lake landscape position and connectivity, whose influence are often overlooked. The findings of this study suggest that the equilibrium state in species composition exposed to common pressures, such as those driven by intensive land use, is likely to vary between catchments. In catchments with strong physical connectivity between lakes, maintaining high macrophyte diversity should be assisted by weak environmental gradients and greater potential for species dispersion and colonisation. However, we concede that the conclusions from the cross-scale interaction analyses based on 30 studied catchments may not be suitable to apply to other lakes or catchments with contrasting characteristics which may behave in different ways.

5.6 Conclusions

The factors that determine macrophyte diversity are complex and operate over different scales. This study deepens our understanding of the mechanisms that shape macrophyte communities and the wider biodiversity of lake ecosystems in a cross-scale system. The results of this study reveal that while lake scale factors such as alkalinity are predominant determinants of macrophyte species diversity, the strength of their effect is moderated by interactions with catchment-scale properties such as lake position, connectivity and catchment disturbance and fragmentation. Understanding the complexity of these interactions is necessary to predict the influence of human disturbance at the catchment scale on macrophyte species response at the lake-scale and to inform and improve catchment management actions designed to restore and conserve freshwater biodiversity.

Chapter 6 – General discussion and conclusion

6.1 General discussion

This research has explored the response of macrophyte communities in British lakes to hydrological connectedness and anthropogenic disturbance at both the lake- and catchment scale. We did not take sampling or surveyor biases into consideration since we assumed that these are small when surveyors are experienced, well trained and work in pairs using agreed methods. Also, in most cases all lakes within a catchment were surveyed by the same or a very small number of teams. We concede that the lack of the error measurement among different sampling biases may affect the accuracy of the models based on the observed macrophyte distributions. However, it is of the utmost importance to recognize the problems to be addressed and the aims of study. This research has sought to investigate the scale-dependent mechanisms influencing the distribution patterns of lake macrophytes and incorporates theories centred on cross-scale interaction and intermediate disturbance. Land-use and connectivity variables were explored to assess their impacts on macrophyte species turnover at two specific catchment scales i.e. *local catchment* scale and *topographic catchment* scale. The findings from this work have implications for catchment-scale conservation and management strategies, which are discussed further here.

The literature review presented in Chapter 2 identified that whilst much work has been undertaken on assessing the role of multiple catchment scale drivers and their controls on macrophyte communities, little research has examined combined effects or their spatial context. The "catchment" as the spatial unit for the analysis has been variously (and often rather subjectively) defined as: *local catchment* (Figure 3.1); *topographic catchment* (Figure 3.1); and *freshwater ecoregion*. The *local catchment* is defined as the *landscape buffer* zones immediately surrounding the lake shoreline (Pedersen et al., 2006; Alahuhta et al., 2012), and management of this zone is advocated to reduce the negative impact of anthropogenic contaminants on lake water quality and aquatic vegetation. The *topographic catchment* is a natural hydrological boundary that controls the dispersal of organisms (and waterborne stressors) among ponds through the runoff process. The *freshwater province* is the ecological unit shared by the homogenous freshwater system and the geographical topography. The literature demonstrates that land-use and hydrological variables in the *local catchment* have a strong impact on species richness, and that the strength of this relationship decreases with increasing distance from the shoreline.

The role and relative importance of the *local catchment* (riparian buffer zones) is assessed in Chapter 3. This incorporates an assessment of the role of *local catchment* alone (the so-called *landscape buffers*) (see Figure 3.1) as well as combined area, which consists of the intersection of *local catchment* area and *topographic catchment* boundary (the so-called *catchment buffers*) to explain the species richness.

To assess the role of hydrological connectivity, species dissimilarity between pairs of lakes within the catchment was evaluated. Hydrological connectivity (i.e. through continuous water-course) and geographical connectivity (i.e. Euclidean distance) between lake pairs were measured to estimate the relative role of potential dispersal modes (e.g. wind, water-course or water-bird) in explaining the observed lake macrophyte composition (Chapter 4).

A hierarchical structure was observed in our dataset that suggests that lakes are nested within *topographic catchments*. The mixed effect model was applied to estimate the cross-scale interaction of both lake- and catchment- scale drivers in determining macrophyte species composition (Chapter 5). An improved understanding of this interaction can aid in predicting the immediate and longer term impact of anthropogenic disturbance on freshwater ecosystem health and thus inform effective management strategies at the catchment scale.

6.1.1 Understanding species richness of lake macrophytes

Numerous studies have revealed the controls on macrophyte species richness (Bornette & Puijalon, 2011). Much of the evidence demonstrates the important role of environmental filtering (Jeppesen et al., 2000; Vestergaard & Sand-Jensen, 2000a; Rolon et al., 2008) and broad-scale processes (Rorslett, 1991; Van Geest et al., 2005; Houlahan et al., 2006). More specifically, species richness has been linked with lake size (Scheffer et al., 2006; Rolon et al., 2008); trophic state (Hoyer & Canfield, 1994; Jeppesen et al., 2000); lake alkalinity (Vestergaard & Sand-Jensen, 2000b); altitude (Rorslett, 1991; Jones et al., 2003); land use intensity (Crosbie & Chow-Fraser, 1999; Houlahan et al., 2006) and flood events (Riis & Hawes, 2003; Van Geest et al., 2005) at varying temporal and spatial scales.

A number of publications have shown scale-dependent effects of land use and hydrological variables on species richness. For example, in Denmark & USA, land use and hydrological connectivity in the immediate vicinity of a lake proved to have a stronger influence on macrophyte species richness than at a broader scale (Pedersen et al., 2006; Cheruvelil & Soranno, 2008; Alahuhta et al., 2012; Alahuhta & Aroviita, 2016). The results presented in chapter 3 revealed a strong scale-dependency between the drivers at the *local catchment* scale and species richness. Macrophyte species richness was strongly influenced by the land use and hydrology within the 1 km of *landscape buffers* zones and within the 500 m *catchment buffers* zones. The scale-dependency effect varied with macrophyte growth form. For example, the richness of floating macrophytes was more strongly associated with stream density within *landscape buffers* rather than *catchment buffers*. This implies that floating plants perhaps disperse disproportionately through watercourses (or via other vectors that are positively correlated with water course length). The species richness of emergent macrophytes was significantly related to open water coverage in both *landscape buffers* and *catchment buffers* which may regulate attractiveness of dispersal vectors such as water birds. Previous studies have indicated that the strongest impact of land-use and hydrological variables occurs at the landscape scale within a short distance of the lake shoreline. Similarly, this study has shown that the impact of land use and hydrological variables in *catchment buffers* became more important than those for *landscape buffers* when the distance was greater than 1.5 km.

6.1.2 Characterising macrophyte species turnover in lakes

Environmental or niche filtering has long been considered a key determinant of the variation in macrophyte species turnover (e.g. Niche theory; Cottenie, 2005; Heino et al., 2007, 2010), while some studies also emphasized the importance of spatial drivers within the catchment (e.g. Neutral theory; Alahuhta & Heino, 2013). Chapter 4 demonstrates the application of NMDS to estimate macrophyte species turnover within each catchment. The NMDS values within each catchment were then regressed against the catchment-scale variables. Both overland and hydrological connectivity between lakes, are shown to be important for the maintenance of lake biodiversity but strongly subordinate to environmental filtering. Geographical connectivity is important in determining the distribution of macrophytes dispersed via wind or water-birds, while hydrological connectivity controls propagule dispersal through watercourses. The results indicate that geographical connectivity could explain more variability in species turnover than hydrological connectivity. The degree of human disturbance was shown to regulate the biological response (species turnover) to environmental dissimilarity, and hydrological and geographical connectivity. The findings were consistent with previous study that found lake eutrophication can influence distance decay relationships by reducing the turnover rates of microorganisms (Vilar et al., 2014).

6.2 Wider implications and future research

6.2.1 The conservation of macrophytes from aspect of catchment ecology

Macrophytes are one of the bio-indicators to assess freshwater ecosystem health under the European Water Framework Directive (2000/60/EC). Previous studies (Pedersen et al., 2006; Akasaka et al., 2010; Alahuhta et al., 2012) have identified some of the key environmental gradients from lake and regional scales that explain macrophyte composition in lakes (Cheruvelil & Soranno, 2008). This research has developed an understanding of how individual catchments respond to anthropogenic disturbance and enables those catchments with a high intensity of disturbance and requiring more careful management to be identified. Equally, effective management requires an understanding of how lake macrophyte diversity responds to the anthropogenic disturbance within both the *landscape buffer* and the *catchment buffer* scale. The results highlight the importance of the spatial extent of the landscape and *catchment buffers* for minimising adverse effects of human disturbance on lake ecosystems. The 1 km *landscape buffer* zone for each lake is identified as being the most influential zone in terms of agriculture and urbanization. For the hydrological influence, the drainage network within the 5 km *catchment buffer* is identified as being most critical for maintaining lake macrophyte diversity. Furthermore, our study applied cross-scaled interaction analyses in the lake macrophyte study to help inform policy and management strategies. The study could promote the identification of individual catchments that are most vulnerable to human disturbance at the catchment scale. The results indicate that management strategies for the protection of lake biodiversity should consider the constraints at a catchment scale as well. Moreover, we suggest flexible catchment-specific management decisions for different regions based on the response of catchment-scale variation to human disturbance.

However, we concede that some high impact sites in this study are only moderately impacted in a European context. This study was conducted mainly based on a dataset of British lakes, most of which are small and little-disturbed. Thus, the conclusion from this study is suitable for small lakes and ponds in regions of ow disturbance; whether it could be applied in other European countries lakes with more severe human impacts requires testing in the future. Further studies could be focused on the differences in response to the various eutrophication levels.

6.2.2 Future research on lake macrophytes

This research provides an important step towards understanding the impact of lake connectivity on the pattern of macrophyte species distribution in lakes. Further studies would greatly add to this knowledge by investigating how other water bodies, especially small ponds, act as habitat corridors for protecting biodiversity in freshwater ecosystems. Small lakes are hydrologically unstable, but more dynamic due to their intensive biological activity compared with larger deeper waterbodies (Downing, 2010). Thus, they are considered to be a key landscape corridor for macrophyte species to disperse through the landscape. The comparative lack of publications about small ponds indicates that future studies should focus on the role of ponds within the landscape (such as their landscape position, size and distribution) in influencing and structuring the occurrence and composition of macrophyte communities.

As described earlier, within the *topographic catchment* research, we assumed that the *topographic catchment* is more important for predicting hydrological impacts rather than the *freshwater ecoregion* (Omernik, 2004). Future research could focus on cross-scale interactions at different spatial scales (i.e. buffer-, catchment- and ecoregion scale) to compare the relative strength of key drivers at each spatial scale in explaining macrophyte richness and diversity. Moreover, as the spatial scale increases, the relative importance of continent-wide gradients (such as climate or geography; Chambers et al., 2008; Kosten et al., 2011) may also need to be taken into account when explaining the response of aquatic macrophytes to environmental factors.

Previous studies have confirmed the potential impact of groundwater on the distribution of lake macrophytes especially in groundwater-dependent freshwater ecosystems, including some small ponds. Groundwater flux was reported to strongly influence lake water level fluctuation and thus the distribution of lake macrophyte communities in lakes (Van Geest et al., 2005; Lubis et al., 2008). The chemistry (Maassen et al., 2015), velocity (Lodge et al., 1989), and flow patterns (Hagerthey & Kerfoot, 1998, 2005) of groundwater have been shown to affect the biomass and composition of lake macrophytes. In addition, groundwater inputs interacting with lake sediment distribution have been shown to determine the occurrence of different macrophyte growth forms (Lillie & Barko, 1990). Future research needs to address the interaction of surface runoff and groundwater in explaining lake water quality and macrophyte community-level patterns. While groundwater flows may not themselves influence dispersal of plants between water bodies they may influence transmission of stressors through the landscape, and thus, indirectly, the ability of certain species to survive locally. For greater accuracy, 3D river catchment models could also be constructed to allow the effects of water dynamics and flooding events to be considered in terms of their influence on the connectedness of otherwise isolated water bodies.

Spatial autocorrelation is an important factor to take into account when characterising the distribution pattern of macrophytes in lakes. Future studies that include spatial autocorrelation analyses at the lake- and catchment scale would be extremely advantageous. This work considered spatial autocorrelation to be a significant explanatory variable in explaining the distribution of lake macrophytes among lakes. However, spatial-autocorrelation between discrete catchments was not taken into consideration in the analyses due to the low numbers of discrete catchments considered in this study (n=30). It would be helpful to establish a complete hydrological network with nested hierarchical levels of basin, catchment, sub-catchment and lakes. This would permit the impact of spatial autocorrelation to be assessed at both the fine scale (within-catchment scale) and broad scale (among-catchment scale).

This research focuses on the response of lake macrophyte communities to environmental variables at different spatial scales. However, the temporal variability of macrophyte occurrence and abundance related to climate change, or shorter term fluctuations (e.g. in water levels) was not taken into consideration due to the limitations of acquiring a suitable long-term dataset on lake macrophytes at a sufficiently broad geographical scale. Specific studies that address the long-term variation of macrophyte species turnover are needed to determine what can be attributed to short term environmental perturbation or climate change.

6.3 Conclusions

This thesis explores the broad-scale ecological patterns of lake macrophyte communities based on a combination of lake environmental filters and catchment- and landscape- scale processes. Chapter 2 in its review of the literature identified the need for research that took into account cross scale interactions of multiscale drivers to determine lake macrophyte composition, which has rarely figured in previous research. The three experimental chapters analysed gradients of species richness (Chapter 3), structure of species turnover (Chapter 4) and patterns of species composition (Chapter 5) of lake macrophyte communities across a broad spatial scale. These three chapters also demonstrated the direct and indirect effect of catchment landscape and hydrological variables to constrain the geographical distribution of lake macrophytes.

The drivers of macrophyte richness were scale-dependent and the effects of land use were apparent at small spatial scales and greatly outweighed the importance of hydrology at all spatial scales. Macrophyte richness was strongly determined by land use and hydrology within the 1 km of *landscape buffer* zones and 0.5 km of *catchment buffer* zones. The impact of hydrological features was stronger than those of land use in terms of macrophyte growth form composition, being greatest at an intermediate distance (~5 km) from the lake shore. It is therefore recommended that the natural catchment vegetation is maintained, as far as possible, within at least the 1 km zone around the lake shore and the manipulation of the drainage network is avoided within at least 5 km of the lake shoreline.

The *topographic catchment* controls the surface water flow and significantly affects macrophyte species turnover in lakes (Chapter 4). Environmental filtering, specifically via lake physical and chemical properties, was the strongest influence on lake macrophyte assemblages. Broad-scale processes, such as hydrological and geographical connectivity, also explained some of the variation in macrophyte species turnover as well. The results illustrated that the relative roles of geographical and hydrological connectivity were sensitive to the degree of human disturbance. In those catchments with a moderate degree of human disturbance (managed land between 0.1% and 1%), species turnover was strongly correlated to the degree of environmental dissimilarity and spatial connectivity. However, we concede that the definition of the intensity degree of human disturbance needs to be carefully analysed in the future as it represents only intermediate stress in the context of Europe as a whole. This study was conducted mainly based on the dataset of British lakes, most of which are rather small and comparatively undisturbed water bodies. Thus, the conclusions from this study require further testing before application to more disturbed catchments elsewhere Europe.

Many previous studies have shown that the impact of lake environmental filters can be constrained by catchment variables such as lake connectivity and land use. In Chapter 5, long-term macrophyte and physico-chemical data drawn from a large number of British lakes was used to investigate how the effect of lake alkalinity on macrophyte composition is strongly mediated by landscape variables at the catchment scale. The results indicated that the relationship between macrophyte composition and lake alkalinity is stronger in catchments with low lake and stream density and weaker in catchments with a well-developed hydrological network. Lake abiotic variables also have more influence on macrophyte composition in lowland catchments that experience a higher intensity of human disturbance. Moreover, the catchment-scale factors that promote the establishment of distinct communities are likely to vary between catchments depending on lake type, environmental heterogeneity and hydrological connectivity.

Finally, it should be conceded that these conclusions, based on British lakes and their catchments, may have limited generic applicability, at least outside north west Europe. Further research should consider the role of small-sized lakes and ponds within catchments, which may behave differently under different intensities of disturbance and are likely to be more isolated hydrologically. Moreover, applicability of the findings presented here should be considered both within more complex hydrological and more impacted landscape systems in the UK and in contrasting bioclimatic regions globally.

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Appendices

Appendix 3.1

Characteristics of physical and chemistry variables of study lakes

	Unit	Minimum	Maximum	Mean	Std. Deviation
Local environmental Variables					
Local Area	ha	3.8	3804.3	343.7	666
Elevation	m	2.0	438.0	129.8	106.2
Lake Perimeter	km	0.9	107.7	13.2	19.1
Alkalinity	mg $CaCO_3$ L^{-1}	1.7	3.6	2.3	0.37
Conductivity	μS/m	20.5	1650.0	112.8	191.5
pH	-	4.9	10.1	6.7	0.77
Shoreline Development Index	-	1.1	5.8	2.25	1.1
Lake Fetch	m	265.1	17486	3350.4	3823.7
Mean Depth	m	0.8	69.8	11.8	12.9
Max Depth	m	1.5	161.8	31.2	32.8
Catchment variables					
Catchment Area	km^2	16.5	1764.2	158.9	248.6
Catchment Perimeter	km	21.9	374.6	78.4	62.5
Lake Order	-	2	5	3	0.9
Upstream Lake Numbers	-	1	88	8	11.2
Average Slope	Degree	1.76	27.3	10.7	5.01
Distance to Sea	m	10.6	50.6	19.8	12.9

Appendix 3.2

Introduction of the key landscape pattern index

Measure	ID	Variables	Definition	Range	Explanation	Unit	Dataset Applied
Area/Density/Edge	PLAND	Percentage of total class area to landscape	Total area of lakes or land use patches / each buffer area	(0,100]	Approaches 0 - Almost no lake or land use patches in the study buffer. 100 - The entire buffer consists of the same lake or land use patches.	%	Hydrology/Landscape
	PD	Patch density	Total number of lakes or land use patches per 1 km^2 in buffers	> 0	Approaches 0 - Almost no lake in the study buffer. >0 - The increasing lake density within the study buffer.	n/km^2	Hydrology/Landscape
Shape	FRAC	Perimeter Area Fractal Dimension	Average degree of complexity of lakes based on a perimeter/ area ratio in buffers	[1,2]	1 – The shape of the lake shoreline turns to be round. 2 – The lake shape turns to be more complex.	-	Hydrology
Core area	CPLAND	Core area Percentage of Landscape	The core area of lakes (km^2) /each buffer area (km^2)	[0,100)	0 - The entire buffer consists of increasing smaller lakes. Approaches 100 - The entire buffer consists of lakes (the single patch type).	%	Hydrology
	DCAD	Disjunct Core Area Density	Total number of disjunct core areas / each buffer area (km^2)	≥ 0	0 - There are no core areas in the buffer. >0 - There are increasing number of disjunct core areas in the buffer.	n/km^2	Hydrology
Isolation/Proximity	PROMIX	Proximity Index	The focal lake area (km^2) / (The distance between the focal lake and other lakes within the study buffer (km))^2.	≥ 0	0 - The focal lake has no neighbour lakes within the study buffer. >0 - The focal lake has increasing neighbour lakes which distributed much closer within the study buffer.	%	Hydrology
	ENN	Euclidean Nearest Neighbour Index	The shortest straight-line distance from the focal lake to the nearest neighbouring lakes with the study buffer (m).	≥ 0	0 - The focal lake is very close to the neighbour lake. >0 - indicates the increasing distance from the focal lake to the nearest neighbour lake.	m	Hydrology
Contagion/ Interspersion	IJI	Interspersion Juxtaposition Index	Describes the distribution of adjacencies among the lakes and other patch types in the study buffer.	(0,100]	Approaches 0 - The lake is adjacent to only 1 other patch type (such as grass or agriculture) in the study buffer. 100 - The lake is adjacent to all of other patch types in the study buffer.	%	Hydrology
	DIVISION	Landscape Division Index	Measures the fragmentation of the corresponding lakes in the study buffer	[0,1)	0 - The entire buffer consists of lakes (single patch). Approaches 1 - The entire buffer comprises a small proportion of lakes.	%	Hydrology

Connectivity	COHESION	Patch Cohesion Index	Measures the physical connectedness of the corresponding lakes in the study buffer.	[0,100)	0 - The study buffer consists of increasing subdivided and less physically-connected lakes. Approaches 100 – The study buffer comprises of more physically-connected lakes.	%	Hydrology

Appendix 5.1

Macrophyte abbreviations in the study

species	***ID***	***Commonest growth habit***
Apium inundatum	*Api.inu*	*submersed*
Aponogeton distachyos	*Apo.dis*	*floating leaved*
Baldellia ranunculoides	*Bal.ran*	*submersed*
Batrachospermum spp.	*Bat.spp*	*submersed*
Callitriche agg	*Calli.agg*	*submersed*
Callitriche hamulata	*Cal.ham*	*submersed*
Callitriche hermaphroditica	*Cal.her*	*submersed*
Callitriche obtusangula	*Cal.obt*	*submersed*
Callitriche platycarpa	*Cal.pla*	*submersed*
Callitriche stagnalis	*Cal.sta*	*submersed*
Callitriche truncata	*Cal.tru*	*submersed*
Ceratophyllum demersum	*Cera.dem*	*submersed*
Chara spp.	*Chara.spp*	*submersed*
Chara globularis sens.lat	*Chara.glo.l*	*submersed*
Chara globularis var.annulata	*Chara.glo.a*	*submersed*
Chara globularis var.globularis	*Chara.glo.g*	*submersed*
Chara globularis var.virgata	*Chara.glo.v*	*submersed*
Crassula helmsii	*Cra.hel*	*submersed*
Elatine hexandra	*Ela.hex*	*emergent*
Elatine hydropiper	*Ela.hyd*	*emergent*
Eleocharis acicularis	*Eleo.aci*	*submersed*
Eleocharis multicaulis	*Eleo.mul*	*emergent*
Eleogiton fluitans	*Eleo.flu*	*submersed*
Elodea canadensis	*Elodea.can.*	*submersed*
Elodea nuttallii	*Elodea.nut.*	*submersed*
Elodea spp.	*Elodea.spp.*	*submersed*
Filamentous algae	*Fil.alg*	*algae*
Fontinalis antipyretica	*Font.ant*	*submersed*
Fontinalis squamosa	*Font.squ*	*submersed*
Hippuris vulgaris	*Hip.vulg*	*emergent*
Isoetes indet.	*Iso. Indet.*	*submersed*
Isoetes echinospora	*Iso.ech*	*submersed*
Isoetes lacustris	*Iso.lac*	*submersed*
Juncus bulbosus	*Jun.bul*	*submersed*
Lemna minor	*Lemna.min*	*free floating*
Lemna trisulca	*Lemna.tri*	*free floating*
Limosella aquatica	*Lim.aqu*	*emergent*
Littorella uniflora	*Lit.uni*	*submersed*
Lobelia dortmanna	*Lob.dor*	*submersed*
Luronium natans	*Lur.nat*	*submersed*
Lythrum portula	*Lyt.por*	*emergent*
Menyanthes trifoliata	*Men.tri*	*emergent*
Myriophyllum alterniflorum	*Myrio.alt*	*submersed*
Myriophyllum spicatum	*Myrio.spi*	*submersed*
Nitella spp.	*Nit.spp.*	*submersed*
Nitella flexilis agg.	*Nit.fle*	*submersed*
Nitella mucronata	*Nit.muc*	*submersed*
Nitella opaca	*Nit.opa*	*submersed*
Nitella translucens	*Nit.tra*	*submersed*

Nuphar lutea	*Nup.lut*	*floating leaved*
Nuphar lutea x pumila (N. x spenneriana)	*Nup.lut.p*	*floating leaved*
Nuphar pumila	*Nup.pum*	*floating leaved*
Nymphaea (exotic cultivars)	*Nym.exo*	*floating leaved*
Nymphaea alba	*Nym.alb*	*floating leaved*
Nymphoides peltata	*Nym.pel*	*floating leaved*
Persicaria amphibia	*Per.amp*	*emergent*
Pilularia globulifera	*Pil.glob*	*emergent*
Potamogeton alpinus	*Potam.alp*	*submersed*
Potamogeton berchtoldii	*Potam.ber*	*submersed*
Potamogeton crispus	*Potam.cri*	*submersed*
Potamogeton gramineus	*Potam.gra*	*submersed*
Potamogeton gramineus x lucens (P. x zizii)	*Potam.gra.l*	*submersed*
Potamogeton gramineus x perfoliatus (P. x nitens)	*Potam.gra.p*	*submersed*
Potamogeton lucens	*Potam.luc*	*submersed*
Potamogeton natans	*Potam.nat*	*floating leaved*
Potamogeton obtusifolius	*Potam.obt*	*submersed*
Potamogeton pectinatus	*Potam.pec*	*submersed*
Potamogeton perfoliatus	*Potam.per*	*submersed*
Potamogeton polygonifolius	*Potam.pol*	*floating leaved*
Potamogeton praelongus	*Potam.pra*	*submersed*
Potamogeton pusillus	*Potam.pus*	*submersed*
Potamogeton rutilus	*Potam.rut*	*submersed*
Potamogeton spp.	*Potam.spp*	*submersed*
Ranunculus indet.	*Ranun.indet*	*emergent*
Ranunculus aquatilis agg.	*Ranun.aqu*	*emergent*
Ranunculus hederaceus	*Ranun.hed*	*emergent*
Ranunculus lingua	*Ranun.lin*	*emergent*
Ranunculus omiophyllus	*Ranun.omi*	*emergent*
Ranunculus peltatus	*Ranun.pel*	*emergent*
Ranunculus spp.	*Ranun.spp*	*emergent*
Ranunculus trichophyllus	*Ranun.tri*	*emergent*
Scorpidium scorpioides	*Sco.sco*	*emergent*
Sparganium spp.	*Spar.spp*	*emergent*
Sparganium angustifolium	*Spar.ang*	*floating leaved*
Sparganium angustifolium natans	*Spar.nat*	*floating leaved*
Sparganium emersum	*Spar.emer*	*floating leaved*
Sparganium natans	*Spar.nat*	*emergent*
Sphagnum indet.	*Spha.indet*	*submersed*
Subularia aquatica	*Sub.aqu*	*submersed*
Utricularia spp.	*Utri.spp*	*submersed*
Utricularia australis	*Utri.aus*	*submersed*
Utricularia cf. australis	*Utri.cf.aus*	*submersed*
Utricularia intermedia sens. lat.	*Utri.int*	*submersed*
Utricularia minor	*Utri.min*	*submersed*
Utricularia ochroleuca	*Utri.ochr*	*submersed*
Utricularia stygia	*Utri.sty*	*submersed*
Utricularia vulgaris sens. lat.	*Utri.vul.l*	*submersed*
Utricularia vulgaris sens. str.	*Utri.vul.s*	*submersed*
Zannichellia palustris	*Zan.pal*	*submersed*

Appendix 5.2

Detailded information of the study lakes

WBID of the study lakes	*WBID of catchment*	***X***	***Y***	*NAME*
2270	*2270*	***245414***	***964246***	*Loch Uamh Dhadhaidh*
2395	*2270*	***245996***	***961346***	*Loch na Càthrach Duibhe*
2409	*2270*	***246616***	***961214***	*Loch a' Choire*
2438	*2270*	***245792***	***960719***	*Loch Ach'an Lochaidh*
2479	*2270*	***245970***	***960260***	*Loch Cragaidh*
2490	*2490*	***246306***	***954896***	*Loch Hope*
2584	*2490*	***246121***	***958973***	*unnamed*
2739	*2490*	***245599***	***957301***	*Loch a' Choin-bhoirinn*
2772	*2270*	***244666***	***957089***	*unnamed*
2828	*2270*	***244406***	***956672***	*Loch na Creige Duibhe*
3164	*2270*	***242779***	***954647***	*unnamed*
3183	*2490*	***243283***	***954500***	*unnamed*
3199	*2490*	***243674***	***954396***	*unnamed*
3205	*2270*	***239483***	***954410***	*'Lochan Havurn'*
3216	*2270*	***238953***	***954232***	*unnamed*
3243	*2490*	***242447***	***953936***	*Loch Bealach na Sgeulachd*
3260	*2490*	***242898***	***953953***	*unnamed*
3300	*2490*	***243207***	***953720***	*unnamed*
3316	*2490*	***242840***	***953678***	*unnamed*
3369	*2490*	***242203***	***953438***	*'Loch Lean Charn'*
3458	*3458*	***261573***	***952046***	*Loch Craggie*
3694	*2490*	***246022***	***951991***	*Loch Bacach*
3713	*3458*	***262846***	***951842***	*Loch na Mòine*
3773	*2490*	***249404***	***951006***	*Loch na Seilg*
3904	*3458*	***262120***	***947511***	*Loch Loyal*
3927	*2490*	***246828***	***950610***	*Dubh-loch na Beinne*
3937	*2490*	***248499***	***950528***	*unnamed*
3981	*2490*	***245114***	***950265***	*Lochan na Feàrna*
3986	*2490*	***250621***	***950042***	*Dubh-loch na Creige Riabhaich*
4003	*2490*	***249737***	***949673***	*Loch a' Ghobha-Dhuibh*
4089	*2490*	***245541***	***949378***	*unnamed*
4113	*2490*	***245717***	***949291***	*unnamed*
4155	*3458*	***258425***	***949183***	*Loch na Creige Riabhaich*
4199	*4672*	***302581***	***948577***	*Caol Loch*
4307	*4672*	***296649***	***948138***	*Lochan Ealach Mór*
4329	*4672*	***307063***	***947580***	*Loch Eileanach*
4340	*4672*	***306026***	***947859***	*Lochan Dubh nan Geodh*
4457	*4672*	***297536***	***947419***	*Loch na Cloiche*
4513	*4672*	***305057***	***946934***	*Loch Gaineimh*
4672	*4672*	***307723***	***945380***	*Loch More*
4942	*5350*	***228673***	***945313***	*Loch Airigh a' Bhàird*
5001	*4672*	***305719***	***944964***	*Lochan Chairn Léith*
5016	*5350*	***229192***	***944615***	*Loch an Nighe Leathaid*
5060	*2490*	***236884***	***944610***	*Loch na Seilge*
5073	*5350*	***228330***	***944581***	*Loch a' Cham Alltain*
5218	*5350*	***228419***	***944041***	*Caol Lochan*
5222	*6405*	***250205***	***941036***	*Loch Meadie*
5307	*3458*	***258078***	***943551***	*Loch Coulside or 'Loch Cuil na Sithe'*
5350	*5350*	***228892***	***942410***	*Loch Stack*
5412	*5350*	***228084***	***943333***	*Loch Grosvenor*
5749	*5350*	***230028***	***941738***	*unnamed*
5784	*4672*	***309707***	***940960***	*Loch Sand*
5791	*4672*	***310599***	***941269***	*Lochan Thulachan*
5839	*3458*	***256851***	***940960***	*Loch a' Mhoid*
5849	*6297*	***270933***	***941061***	*Palm Loch*

5901	*6405*	***257933***	***940603***	*Loch Staing*
5914	*6405*	***259280***	***940317***	*Loch Eileanach*
6004	*3458*	***255847***	***940229***	*Loch Dionach-caraidh*
6019	*6297*	***271564***	***940108***	*Loch Rosail*
6140	*5350*	***232548***	***937408***	*Loch More*
6297	*6297*	***275701***	***935158***	*Loch nan Clar or 'Loch Rimsdale'*
6405	*6405*	***261452***	***936428***	*Loch Naver*
6517	*8455*	***237899***	***937662***	*Loch Ulbhach Coire*
6545	*2490*	***241417***	***937653***	*Lochan na Creige Riabhaich*
6599	*2490*	***241061***	***937316***	*unnamed*
6604	*4672*	***299206***	***937372***	*Glutt Loch*
6644	*2490*	***242271***	***936742***	*Loch an Aslaird*
6737	*2490*	***241632***	***936104***	*Loch an t-Seilg*
6759	*6405*	***244851***	***936093***	*Loch Coire na Saidhe Duibhe*
6885	*2490*	***240875***	***935541***	*Loch an Tuim Bhuidhe*
6964	*8455*	***237175***	***934977***	*Loch Eas na Maoile*
7092	*6297*	***274978***	***933592***	*Loch an Alltan Fheàrna*
7171	*6405*	***252050***	***933117***	*Loch Ben Harrald*
7183	*6297*	***271174***	***932795***	*Loch Truderscaig*
7222	*8455*	***238940***	***931393***	*Loch Merkland*
7234	*6297*	***271971***	***932926***	*Lochan Dubh*
7273	*6297*	***272276***	***932687***	*unnamed*
7439	*6405*	***249694***	***931223***	*An Glas-loch*
7527	*6405*	***256797***	***931185***	*Loch an Tairbh*
7593	*6405*	***255917***	***930535***	*Loch na Glas-choille*
7669	*6297*	***276694***	***930416***	*Loch na Gaineimh*
7730	*8455*	***244789***	***929320***	*Loch Fiag*
7774	*6405*	***255661***	***930197***	*unnamed*
7902	*6405*	***256651***	***929232***	*Loch nan Uan*
7944	*6405*	***255319***	***929389***	*unnamed*
8200	*8455*	***246197***	***928316***	*Loch Poll a' Phac*
8305	*6405*	***247376***	***927963***	*Loch Camasach*
8353	*6405*	***248301***	***927755***	*Loch Eileanach*
8360	*8455*	***241202***	***927922***	*Sùil a' Ghriama*
8455	*8455*	***239079***	***926500***	*Loch a' Ghriama*
8496	*11611*	***270665***	***927174***	*Gorm-loch Beag*
8651	*8455*	***242315***	***926880***	*Loch Strath Duchally*
8676	*8455*	***247916***	***926769***	*Loch an Alaskie*
8682	*11611*	***271373***	***926846***	*unnamed*
8751	*8751*	***221081***	***924581***	*Loch Assynt*
8777	*8751*	***216251***	***926224***	*Loch na h-Innse Fraoich*
8890	*8455*	***251000***	***925974***	*Loch an Fheòir*
8898	*8751*	***216374***	***925851***	*Loch Tòrr an Lochain*
8912	*8751*	***221820***	***925957***	*unnamed*
8975	*8751*	***226445***	***925587***	*Loch Bealach na h-Uidhe or 'Loch Bealach a*
9006	*8751*	***221912***	***925523***	*Lochan an Duibhe*
9063	*8455*	***246122***	***925196***	*unnamed*
9070	*8751*	***222885***	***925178***	*Lochan Feòir*
9145	*8751*	***227450***	***924760***	*Loch Fleodach Coire*
9164	*8455*	***251557***	***924770***	*unnamed*
9221	*8455*	***250470***	***924361***	*unnamed*
9250	*8455*	***251078***	***924188***	*unnamed*
9260	*8751*	***219964***	***924183***	*Loch a' Mhuilinn*
9266	*8751*	***226975***	***924098***	*unnamed*
9290	*8455*	***250479***	***924059***	*unnamed*
9299	*8751*	***229138***	***923894***	*Loch nan Cuaran*
9303	*8751*	***226454***	***924020***	*unnamed*
9316	*8455*	***249441***	***923871***	*Loch an Fheòir*
9326	*8455*	***250729***	***923880***	*unnamed*
9356	*8455*	***252849***	***923651***	*Loch Dubh Cùl na Capulich*
9358	*11611*	***271209***	***923312***	*Gorm-loch Mór*

9362	8455	**255616**	**923653**	Loch a' Ghiubhais
9419	8751	**229023**	**923401**	Loch nan Caorach
9467	8455	**249212**	**922853**	Loch an Ulbhaidh
9479	8751	**229027**	**922996**	Loch Meall nan Caorach
9601	8455	**252453**	**922375**	Loch na Capulich
9942	8455	**266030**	**920107**	Glas-loch Beag
9975	8455	**267142**	**919611**	Glas-loch Mór
10065	8751	**227668**	**919437**	Loch Mhaolach-coire
10221	8455	**252347**	**918785**	Loch an Staing
10230	8455	**241508**	**918827**	unnamed
10245	11611	**265115**	**918760**	Loch nam Breac Beaga
10307	11611	**268161**	**918312**	Lochan Dubh Cadhafuaraich
10485	11611	**265993**	**917192**	Loch a' Mheallain Leith
10607	8455	**263600**	**916507**	Loch Coire na Bruaiche
10624	8455	**260328**	**916297**	Loch na Fuaralachd
10713	11611	**267666**	**915881**	Loch an t-Slugaite
10714	8751	**224195**	**915864**	Loch na Gruagaich
10719	10719	**217878**	**913750**	Loch Veyatie or 'Loch a' Mhadail'
10737	8751	**224567**	**915300**	Loch Awe
10767	10719	**221951**	**915548**	Loch a' Chroisg
10781	8455	**260938**	**915590**	Loch Beag na Fuaralachd
10786	10786	**211497**	**913946**	Loch Sionascaig
10799	11611	**267079**	**915493**	Lochan Sgeireach
10802	8751	**226912**	**915398**	unnamed
10858	11611	**267104**	**915125**	'Lochan Sgeireach'
10892	11611	**268484**	**914613**	Loch Beannach
10897	10786	**209198**	**914553**	Loch Call an Uidhean
10914	10786	**208811**	**914738**	unnamed
10934	10719	**221337**	**913488**	Cam Loch
10958	11611	**275887**	**914331**	Lochan Dubh Cùl na h-Amaite
11025	11611	**276553**	**913822**	Loch Bad na h-Earba
11055	10786	**209734**	**913590**	'Polly Lochs'
11074	10786	**208437**	**913532**	Loch na Dàil
11097	10719	**227041**	**913530**	Feur Loch
11099	8455	**259988**	**913472**	unnamed
11109	8455	**246229**	**913386**	Lochan a' Choire
11115	11611	**275970**	**913264**	Loch na Glaic
11151	10786	**208899**	**913226**	unnamed
11187	8455	**259928**	**912612**	Loch Beannach
11252	11611	**274557**	**912273**	Lochan Dubh
11328	11611	**273967**	**911227**	Loch Beannach
11353	8455	**246749**	**911154**	Loch Sgeireach
11355	10719	**226273**	**910805**	Loch Borralan
11385	10719	**224397**	**909919**	Loch Urigill
11424	10719	**219052**	**910265**	Lochan Fhionnlaidh
11427	11611	**274413**	**910143**	Loch Grùdaidh
11484	8455	**261654**	**909288**	Loch Tigh na Creige
11526	10786	**217537**	**908925**	Loch nan Ealachan
11539	11611	**287601**	**908934**	Loch an Tubairnaich
11611	11611	**285247**	**907880**	Loch Brora
11625	8455	**260686**	**908070**	Loch Dola
11642	8455	**262458**	**907487**	Loch Craggie
11755	8455	**257935**	**906608**	'Loch Shin outflow'
12300	13470	**260843**	**899391**	Loch Laro
12546	13470	**273125**	**895939**	Loch Laoigh
12578	13470	**265825**	**895590**	Loch an Lagain
12697	13470	**273713**	**894522**	Loch Lànnsaidh
13832	16206	**233250**	**882564**	unnamed
13833	16206	**233043**	**882532**	unnamed
13974	16206	**226974**	**880616**	Loch a' Choire Ghrànda
14038	16206	**233187**	**879834**	Gorm Loch

14057	14057	193061	871605	Loch Maree
14234	16206	228135	876073	Loch a' Gharbhrain
14374	14057	187137	874072	Loch Doire na h-Airighe
14432	14057	186201	873233	unnamed
14443	14057	202610	871094	Lochan Fada
14462	14462	178648	872812	Loch Bad a' Chròtha
14512	14057	191730	872436	unnamed
14555	14462	177252	871816	Loch Clàir
14573	14057	192343	872051	'Lochan on Eilean Subhainn'
14598	14057	192125	871915	unnamed
14621	14462	176728	871660	unnamed
14701	14462	179849	870950	Lochan Fuar
14717	14462	181048	870797	Lochan Sgeireach
14729	14462	179759	870365	Loch Bràigh Horrisdale
14783	14462	180962	870238	unnamed
15400	16206	238028	866501	Lochan nam Breac
15698	14057	197487	864566	Loch Bhanamhóir
15801	14057	199114	863417	unnamed
15807	14057	198939	863329	Loch Allt an Daraich
16206	16206	241018	859715	Loch Garve
16257	14057	204195	859850	unnamed
16273	14057	203869	859756	unnamed
16323	14057	204406	859177	Lochain Féith an Leothaid
16328	14057	204032	859236	unnamed
16367	14057	205393	858765	unnamed
16373	14057	205057	858668	unnamed
16443	14057	199904	857234	Loch Clair
16590	14057	201405	855355	Loch Coulin
18563	18563	260705	838876	Loch Dochfour
18594	18563	260942	839504	unnamed
18645	18714	205017	838868	Loch Calavie
18714	18714	227425	838038	Loch a' Mhuillidh
18715	18563	260117	838092	Abban Water
18717	18714	209300	837997	Loch an Tachdaich
18767	18563	250401	823954	Loch Ness
18789	18714	208202	837616	unnamed
18828	18714	208437	837191	Lochan Gobhlach
18839	18714	207240	837286	unnamed
18859	18714	207974	837007	unnamed
19024	18563	254652	835357	Loch Laide
19121	18563	245571	834307	unnamed
19135	18563	245711	834007	unnamed
19153	18563	244550	833671	Lochan an Tairt
19161	18563	245578	833557	unnamed
19166	18563	248156	833383	Loch Gorm
19179	18563	249278	833195	Loch nam Bàt
19180	18563	249840	833122	'Loch na ba Ruaidhe'
19223	18563	249377	832504	Loch nam Faoileag
19227	18563	239235	832572	unnamed
19229	18563	260576	832354	Lochan na Curra
19249	18563	248607	832172	Lochan an Torra Bhuidhe
19286	18563	248855	831649	unnamed
19381	18563	243485	830137	Loch Meiklie
19540	18563	261631	827781	Loch Ruthven
19769	18563	255233	824536	Loch a' Bhodaich
19800	18563	255487	823970	Loch an Ordain
19841	18563	254387	823577	Loch na Craoibhe-beithe
19865	18563	235235	823202	unnamed
19901	18563	235233	822906	unnamed
19952	18563	234194	821739	Loch ma Stac
19983	18563	239222	821802	Loch nam Brathain

20002	18563	**236434**	**821230**	Loch a' Chràthaich
20023	18563	**243285**	**821643**	Loch an t-Sionnaich
20050	18563	**258715**	**821267**	Loch Conagleann
20054	18563	**253070**	**821362**	Loch Ruairidh
20092	18563	**239718**	**820934**	Loch Liath
20116	18563	**244927**	**820686**	Loch a' Bhealaich
20117	18563	**245272**	**820671**	unnamed
20142	18563	**236120**	**820425**	unnamed
20155	18563	**239117**	**820143**	Loch an Dubhair
20158	18563	**239630**	**820193**	Loch na Feannaig
20162	18563	**238501**	**820069**	unnamed
20172	18563	**241550**	**819918**	Loch a' Mheig
20200	18563	**250827**	**819308**	Loch Bran
20251	18563	**235390**	**818482**	Bhlàraidh Reservoir
20328	18563	**246886**	**816412**	Loch Kemp
20465	18563	**245608**	**813596**	Loch Knockie
20495	18563	**244213**	**813044**	Loch nan Lann
20587	18563	**207417**	**811373**	Loch Cluanie
20588	18563	**220262**	**811597**	unnamed
20633	18563	**242500**	**809970**	Loch Tarff
20651	18563	**207900**	**809888**	Loch a' Mhaoil Dhìsnich
20751	18563	**240449**	**808024**	unnamed
20780	18563	**236946**	**807111**	Loch Uanagain
20800	18563	**244635**	**806927**	'Dubh Lochan'
20827	18563	**244682**	**806465**	Dubh Lochan
20845	18563	**244254**	**805832**	Lochan na Stairne
20860	20860	**283063**	**804450**	Loch Insh
20885	20860	**283676**	**804834**	unnamed
20917	18563	**244095**	**803953**	Loch Carn a' Chuilinn
20918	18563	**229596**	**803574**	Loch Lundie
20922	18563	**215887**	**803823**	Lochan Bad an Losguinn
20928	18563	**197389**	**803823**	Loch Coire nan Chàmh
20931	18563	**242128**	**803851**	unnamed
20937	18563	**243628**	**803696**	'Lochan Carn a' Chuilinn'
20946	18563	**198018**	**803622**	Loch a' Choire Bheithe
20954	20860	**281787**	**803485**	unnamed
20959	18563	**241977**	**803032**	Lochan Dearg Uillt
20960	18563	**243132**	**803426**	Lochan Carn a' Chuilinn
20961	18563	**243361**	**803262**	unnamed
20970	20860	**281528**	**803376**	unnamed
20974	18563	**242699**	**803206**	Lochan nam Faoileag
20976	18563	**205585**	**803128**	Loch Fearna
20984	20860	**281263**	**803180**	unnamed
21023	18563	**222491**	**801951**	Loch Garry
21034	20860	**274431**	**802258**	Loch Gynack
21053	20860	**279858**	**802217**	unnamed
21066	18563	**216709**	**801961**	Lochan Torr a' Gharbh-uillt
21107	20860	**279823**	**801338**	unnamed
21351	20860	**267847**	**795776**	unnamed
21357	20860	**267531**	**795615**	Lochain Uvie
21461	20860	**269081**	**793122**	Loch Etteridge
21554	20860	**262982**	**790875**	Loch Glas-choire
21828	20860	**274702**	**783132**	Loch Bhrodainn
21918	20860	**272251**	**779861**	Loch an Dùin
21925	21925	**179735**	**771795**	Loch Shiel
21937	21925	**190798**	**780220**	'Lochan Port na Creige'
21950	21925	**187374**	**779844**	Lochan nan Sleubhaich
22278	21925	**178654**	**768877**	unnamed
22308	21925	**180716**	**767704**	Loch Doilet
22358	21925	**183939**	**767012**	unnamed
22383	21925	**169100**	**766407**	unnamed

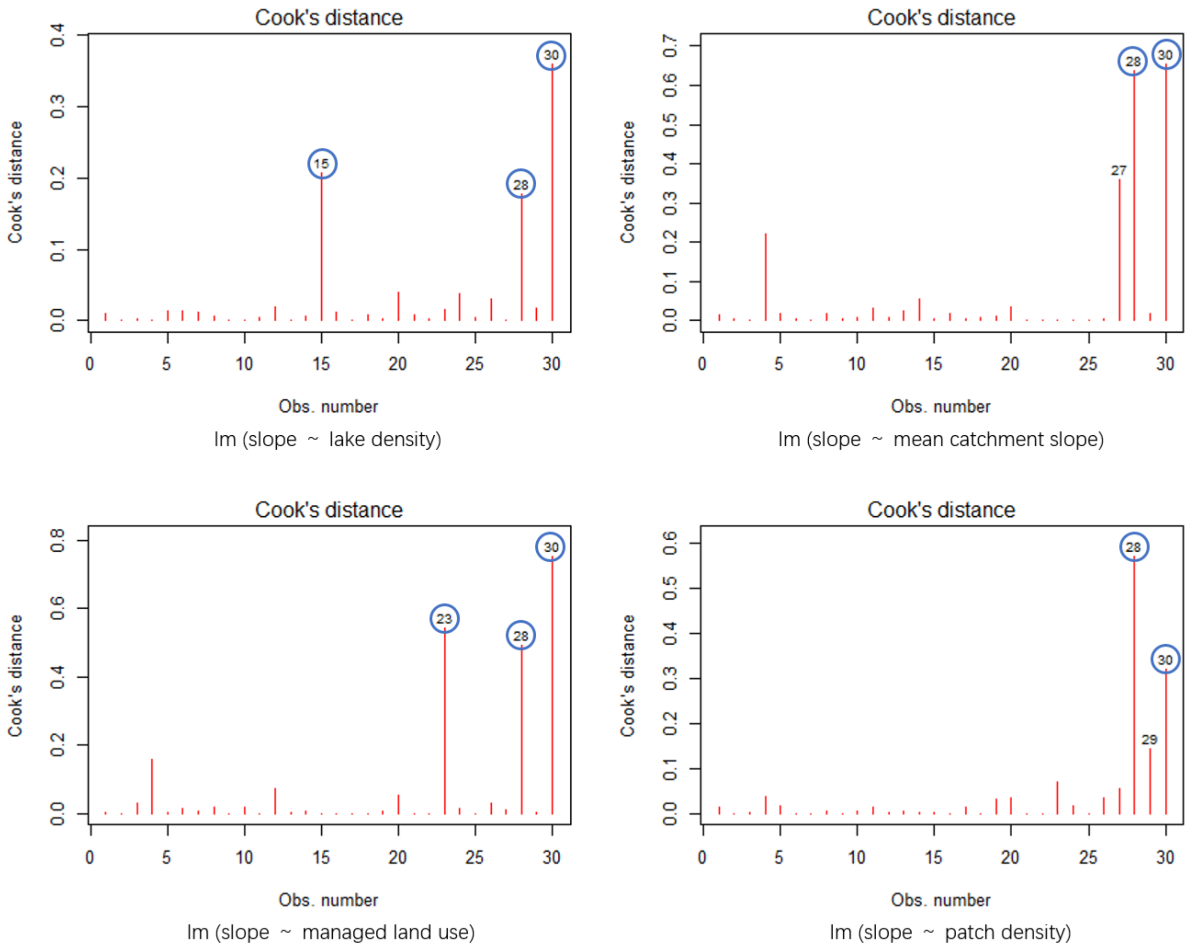
22782	27782	**259111**	**757829**	Loch Rannoch
22839	27782	**238153**	**754593**	Loch Laidon
23086	27782	**230255**	**753564**	Lochan Gaineamhach
23206	27782	**232407**	**750329**	Loch Bà
23229	27782	**231771**	**751192**	unnamed
23313	27782	**230217**	**749182**	Lochan na Stainge
23352	27782	**229709**	**748320**	Loch Buidhe
23361	27782	**231117**	**748028**	Lochan na h-Achlaise
23625	24025	**221313**	**741985**	Loch Dochard
23905	24025	**221949**	**731459**	Lochan Coire Thoraidh
23906	24025	**230884**	**731305**	Lochan na Bi
24025	24025	**200506**	**717494**	Loch Awe
24110	24025	**204319**	**725105**	Loch Tromlee
24464	24025	**193602**	**714500**	Loch Avich
24832	24025	**194475**	**703978**	unnamed
24837	24025	**194701**	**703728**	Loch nan Eilean
24839	24025	**193036**	**703452**	Fincharn Loch
24848	24025	**193732**	**703672**	Dubh Loch
24853	24025	**195046**	**703504**	Loch Geòidh
24870	24025	**186877**	**702620**	Loch Ederline
24897	24025	**191249**	**701854**	Dubh Loch
24898	24025	**186384**	**701877**	unnamed
24903	24025	**191441**	**701781**	unnamed
24911	24025	**191529**	**701534**	Loch Tunnaig
24914	24025	**191318**	**700828**	Loch Gaineanhach
24917	24025	**192653**	**701257**	'Loch a' Bhealaich'
24949	24025	**190492**	**698846**	Lochan Anama
24958	24025	**187445**	**698248**	Loch Leathan
25284	25284	**244419**	**687904**	unnamed
25355	25284	**266622**	**686639**	Loch Walton
25611	25284	**248608**	**679151**	Burncrooks Reservoir
25665	25284	**255015**	**678322**	Dumbrock Loch or 'Drumbrock Loch'
25680	25284	**247339**	**677942**	Lily Loch
27604	28003	**249779**	**597677**	Loch Doon
27610	28003	**251271**	**600824**	Loch Muck
27627	28003	**245915**	**598296**	Loch Finlas
27631	28003	**250931**	**598984**	unnamed
27675	28003	**243351**	**593465**	Loch Riecawr
27699	28003	**244016**	**591438**	Loch Macaterick
27705	28003	**260861**	**590469**	Kendoon Loch
27726	28003	**270079**	**590321**	Troston Loch
27730	28003	**269191**	**589704**	unnamed
27777	28003	**252783**	**586686**	Loch Harrow
27795	28003	**265850**	**585392**	Lochinvar
27808	28003	**244581**	**585124**	Loch Enoch
27827	28003	**252449**	**584471**	Loch Dungeon
27948	28003	**246902**	**579037**	Loch Dee
27961	28003	**270723**	**578660**	Lowes Lochs
27967	28003	**254237**	**577007**	Clatteringshaws Loch
28003	28003	**271182**	**568189**	Loch Ken or River Dee
28130	28003	**254210**	**569909**	Loch Grannoch
28144	28003	**264409**	**570403**	Stroan Loch
28200	28003	**267029**	**567448**	Woodhall Loch
28206	28003	**260541**	**568159**	Loch Skerrow
28271	28003	**264271**	**565599**	Lochenbreck Loch
28332	28003	**269269**	**561833**	Bargatton Loch
28336	28003	**276285**	**561271**	Carlingwark Loch
28847	28847	**321618**	**529390**	Bassenthwaite Lake
28905	28847	**332880**	**528151**	unnamed
28930	28847	**324460**	**525876**	Scales Tarn
28955	28955	**342534**	**520438**	Ullswater

28962	28847	330445	523562	Tewet Tarn
28965	28847	325978	520958	Derwent Water
28986	29000	312444	521715	Loweswater
29000	29000	315798	518895	Crummock Water
29008	29000	312442	519913	unnamed
29045	29000	312459	517038	Floutern Tarn
29052	29000	318258	515771	Buttermere
29060	28955	338370	516270	unnamed
29061	28847	327514	516128	Watendlath Tarn
29081	29000	316592	515439	Bleaberry Tarn
29083	28955	334808	515262	Red Tarn or 'Red Tarn, Helvellyn'
29086	28847	322962	515237	unnamed
29093	28955	341713	514346	Angle Tarn
29094	28847	327374	514368	Dock Tarn
29097	28847	329132	514093	Blea Tarn
29107	28847	331125	513626	Harrop Tarn
29116	28955	340275	512729	Brothers Water
29119	29000	319739	512938	unnamed
29121	29000	320188	512804	unnamed
29125	28955	343132	512183	Hayeswater or 'Hayes Water'
29126	28847	325844	512245	unnamed
29129	28955	334879	512052	Grisedale Tarn
29136	28847	330456	511488	unnamed
29142	29233	330753	511138	unnamed
29157	28847	322158	509853	Styhead Tarn
29163	28847	322788	509115	Sprinkling Tarn
29166	29233	330775	508764	Easedale Tarn
29167	29233	329670	508816	Codale Tarn
29176	29233	334904	507896	unnamed
29177	29233	328716	507684	Stickle Tarn
29179	28847	324419	507655	Angle Tarn
29184	29233	333850	506512	Grasmere
29191	29233	331949	506783	unnamed
29197	29233	335661	506139	Rydal Water
29210	29233	330164	505116	unnamed
29218	29233	329303	504412	Blea Tarn
29219	29233	334455	504360	Loughrigg Tarn
29222	29233	333379	504135	Elter Water or 'Elterwater'
29226	29233	326795	503714	unnamed
29231	29233	330917	503218	Little Langdale Tarn
29233	29233	339225	495840	Windermere or 'Lake Windemere'
29237	29233	335613	503052	unnamed
29249	29233	328482	502127	unnamed
29259	29233	339757	501149	unnamed
29262	29321	333125	501126	unnamed
29264	29233	335057	501063	'High Crag Tarn'
29268	29233	340831	500785	unnamed
29270	29233	336602	500487	Blelham Tarn
29271	29233	336302	500680	unnamed
29274	29321	332177	500462	Yew Tree Tarn
29275	29321	333051	500005	'Tarn Hows'
29303	29321	333115	498832	unnamed
29310	29321	327479	498271	Low Water
29311	29233	336772	498305	unnamed
29312	29233	336936	498220	unnamed
29318	29233	336866	498075	unnamed
29321	29321	330158	494042	Coniston Water
29322	29233	336869	497902	unnamed
29323	29233	335751	497848	Priest Pot
29326	29321	326599	497654	Goat's Water
29327	29233	337016	497575	Wise Een Tarn

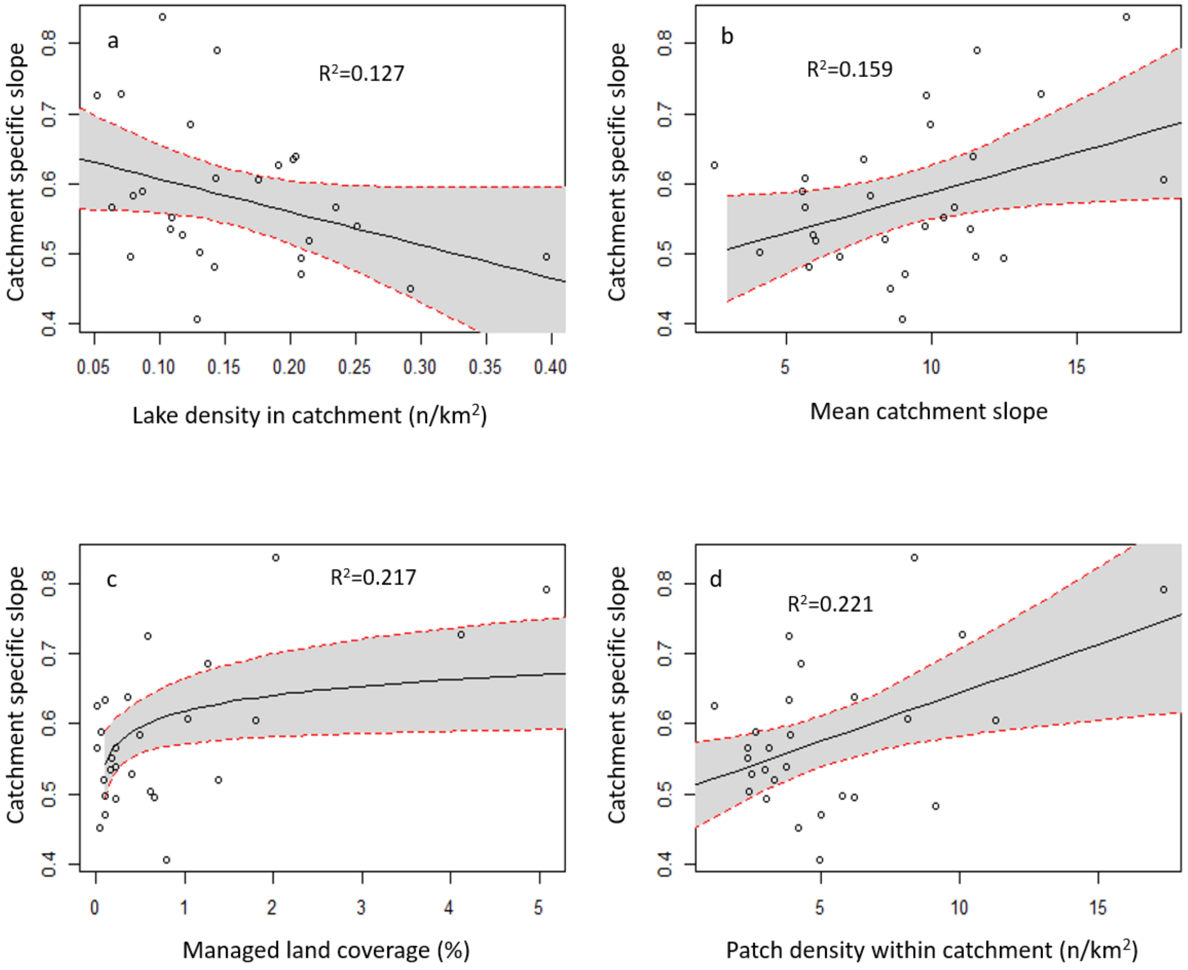
29328	*29233*	***336036***	***496423***	*Esthwaite Water or 'Claife, Wray Mires Tarn'*
29330	*29233*	***337280***	***497537***	*unnamed*
29334	*29233*	***337783***	***497365***	*Three Dubs Tarn*
29337	*29233*	***342804***	***497266***	*unnamed*
29348	*29233*	***315778***	***496966***	*Devoke Water*
29381	*29233*	***336597***	***494851***	*Out Dubs Tarn*
29415	*29233*	***339717***	***492738***	*unnamed*
29416	*29321*	***328051***	***492555***	*unnamed*
29419	*29233*	***339797***	***492274***	*'Ghyll Head Reservoir'*
29441	*29233*	***336241***	***490685***	*unnamed*
29450	*29233*	***336064***	***489856***	*'Great Green Hows Tarn'*
29466	*29233*	***336185***	***488759***	*High Dam*
34827	*35953*	***619016***	***338890***	*'Felbrigg Lake'*
34976	*35953*	***614908***	***335561***	*'Barningham Hall Lake'*
35004	*35953*	***619508***	***334904***	*unnamed*
35023	*35953*	***622179***	***334182***	*Great Water or 'Gunton Sawmill Pond' or*
35179	*35953*	***616317***	***331282***	*'Wolterton Hall Lake'*
35195	*35953*	***603150***	***330925***	*The Lake or 'Melton Hall Lake'*
35249	*35953*	***617699***	***329250***	*'Blickling Hall Lake'*
35397	*35953*	***627971***	***327104***	*'Captains Pond'*
35404	*35953*	***627321***	***327173***	*unnamed*
35529	*35953*	***626356***	***325825***	*'Scottow Pond'*
35761	*35953*	***621303***	***320182***	*'Stratton Strawless Lake'*
35952	*35953*	***629288***	***317211***	*Belaugh Broad*
35953	*35953*	***631039***	***316747***	*Wroxham Broad*
35974	*35953*	***629096***	***316878***	*unnamed*
36161	*35953*	***626955***	***314102***	*The Springs or 'Rackheath Springs Lake'*

Appendix 5.3

Appendix 5.3 a The Cook’s distance for each OLS model in Figure 5.8. Blue points were the outliers for the individual model that we took away from the next step analyses.



Appendix 5.3 b The new regression model after deleting the outliers with high Cook’s distance



Appendix 5.4

Supprting information of the estimates of coefficients for all of the models in the thesis

Appendix 5.4 a

The estimates of coefficients for GLM models in Table 3.2, including measures of confidence (2.5%-97.5%) in those coefficients

(1) the coefficients of the total richness

Landscape variables	Intercept	Lake area	Lake conductivity	Lake pH
Original Model	6.17156	1.00015	0.99951	1.11568
2.5%-97.5%	2.5560829-14.90096	1.0000141-1.000284	0.9989226-1.000098	0.9766124-1.274547

(2) the coefficients of the submersed species richness

Landscape variables	Intercept	Lake area	Lake alkalinity	Lakeconductivity
Original Model	2.26877	1.00019	1.69427	0.99905
2.5%-97.5%	0.9999448-5.1476196	1.0000506-1.0003356	1.1732235-2.4467241	0.9982031-0.9998952

(3) the coefficients of the emergent species richness

Landscape variables	Intercept	Lake area	Lake alkalinity
Original Model	5.51419	1.00009	0.72915
2.5%-97.5%	2.3978915-12.680451	0.9999159-1.000255	0.5110086-1.040403

(4) the coefficients of the floating species richness

Landscape variables	Intercept	Lake conductivity
Original Model	2.59201	0.99964
2.5%-97.5%	2.218796-3.028009	0.9988090-1.000476

Appendix 5.4 b

The estimates of coefficients for GLM models in Table 3.3, including measures of confidence (2.5%-97.5%) in those coefficients

(1) The coefficients of the total richness/ Landscape buffers

Landscape variables		Intercept	Lake area	Lake conductivity	Lake pH	Added variable
Original Model		6.17156	1.00015	0.99951	1.11568	
2.5%-97.5%		2.5560829-14.90096	1.0000141-1.000284	0.9989226-1.000098	0.9766124-1.274547	
Stream density	B0.25	5.65574	1.00016	0.99951	1.11711	1.05269
	2.5%-97.5%	2.1775132-14.68989	1.0000162-1.000304	0.9989228-1.000095	0.9778802-1.276157	0.8553901-1.295489
	B0.5	5.19426	1.00017	0.99954	1.10527	1.2138
	2.5%-97.5%	2.0919196-12.89739	1.0000347-1.000313	0.9989614-1.000128	0.9685552-1.261290	0.9192857-1.602665
	B0.75	4.97579	1.00017	0.99955	1.10441	1.31441
	2.5%-97.5%	2.0025142-12.36371	1.0000361-1.000309	0.9989703-1.000130	0.9686064-1.259263	0.9462686-1.825772
	B1	4.45961	1.00018	0.99955	1.11229	1.43659
	2.5%-97.5%	1.7707882-11.23121	1.0000411-1.000310	0.9989795-1.000128	0.9767901-1.266587	1.0031902-2.057224
	B2	5.02319	1.00016	0.99954	1.12327	1.21553
	2.5%-97.5%	1.8738731-13.46539	1.0000210-1.000293	0.9989550-1.000133	0.9829486-1.283620	0.8052130-1.834928
	B2.5	4.88496	1.00015	0.99956	1.12396	1.25909
	2.5%-97.5%	1.7921531-13.31515	1.0000196-1.000290	0.9989673-1.000153	0.9834842-1.284505	0.7917165-2.002352
	B5	4.13758	1.00015	0.9996	1.13258	1.49463
	2.5%-97.5%	1.4574349-11.74639	1.0000130-1.000279	0.9990068-1.000193	0.9910968-1.294263	0.8437325-2.647653
	B7.5	3.735	1.00014	0.99961	1.14137	1.61023
	2.5%-97.5%	1.2894026-10.81914	1.0000117-1.000277	0.9990226-1.000203	0.9981981-1.305069	0.9023052-2.873562

	B10	3.5143	1.00014	0.99965	1.14231	1.74164
	2.5%-97.5%	1.2337831-10.01011	1.0000090-1.000273	0.9990597-1.000249	1.0004459-1.304279	0.9662368-3.139291
Lake density	B0.25	6.14906	1.00015	0.9995	1.11606	1.00159
	2.5%-97.5%	2.4882553-15.19574	1.0000043-1.000296	0.9988051-1.000202	0.9756353-1.276701	0.9176954-1.093144
	B0.5	5.97664	1.00016	0.99943	1.11901	1.02514
	2.5%-97.5%	2.4262721-14.72226	1.0000128-1.000302	0.9986973-1.000169	0.9784725-1.279722	0.8831114-1.190015
	B0.75	6.12286	1.00015	0.9995	1.11651	1.00709
	2.5%-97.5%	2.4797404-15.11826	1.0000076-1.000294	0.9988147-1.000178	0.9761121-1.277106	0.8405208-1.206670
	B1	6.09925	1.00015	0.99948	1.11686	1.01467
	2.5%-97.5%	2.4848287-14.97121	1.0000106-1.000293	0.9987957-1.000173	0.9768037-1.277002	0.8224116-1.251863
	B2	6.07531	1.00016	0.99946	1.11605	1.0612
	2.5%-97.5%	2.5009760-14.75797	1.0000161-1.000293	0.9988128-1.000106	0.9768654-1.275071	0.7613695-1.479108
	B2.5	6.12634	1.00015	0.99947	1.11469	1.06778
	2.5%-97.5%	2.5317044-14.82479	1.0000160-1.000291	0.9988293-1.000103	0.9757179-1.273460	0.7293092-1.563348
	B5	6.14031	1.00015	0.9995	1.1156	1.03499
	2.5%-97.5%	2.5280038-14.91427	1.0000138-1.000287	0.9988772-1.000116	0.9764860-1.274535	0.6170516-1.736008
	B7.5	6.11273	1.00015	0.99949	1.11562	1.06874
	2.5%-97.5%	2.5137829-14.86424	1.0000149-1.000287	0.9988817-1.000101	0.9764713-1.274603	0.5901865-1.935315
	B10	6.09621	1.00015	0.99949	1.11537	1.10918
	2.5%-97.5%	2.5106848-14.80226	1.0000156-1.000287	0.9988813-1.000093	0.9762991-1.274257	0.5530439-2.224575
Lake coverage	B0.25	6.08426	1.00011	0.99956	1.10518	1.00252
	2.5%-97.5%	2.5245295-14.66343	0.9999359-1.000282	0.9989605-1.000164	0.9650174-1.265689	0.9959817-1.009106
	B0.5	6.15229	1.00012	0.99953	1.10865	1.00245
	2.5%-97.5%	2.5492550-14.84774	0.9999313-1.000302	0.9989385-1.000128	0.9680304-1.269707	0.9932086-1.011776
	B0.75	6.16539	1.00013	0.99952	1.11271	1.00146
	2.5%-97.5%	2.5529636-14.88937	0.9999410-1.000325	0.9989253-1.000107	0.9718512-1.273975	0.9895188-1.013536
	B1	6.17331	1.00015	0.99951	1.116	0.99978
	2.5%-97.5%	2.5569461-14.90442	0.9999552-1.000347	0.9989203-1.000100	0.9752417-1.277068	0.9850432-1.014736
	B2	6.32571	1.00021	0.99952	1.1221	0.98844

	2.5%-97.5%	2.6320627-15.20276	1.0000175-1.000404	0.9989287-1.000103	0.9824262-1.281640	0.9633220-1.014211
	B2.5	6.31813	1.0002	0.99951	1.12143	0.98783
	2.5%-97.5%	2.6251641-15.20617	1.0000152-1.000386	0.9989229-1.000098	0.9818598-1.280849	0.9588357-1.017703
	B5	6.37722	1.00016	0.99952	1.11457	0.99181
	2.5%-97.5%	2.6131070-15.56345	1.0000122-1.000316	0.9989338-1.000114	0.9758607-1.273003	0.9555771-1.029407
	B7.5	6.161	1.00015	0.99951	1.11578	1.00041
	2.5%-97.5%	2.5056242-15.14909	1.0000033-1.000294	0.9989218-1.000098	0.9764329-1.275008	0.9558971-1.047003
	B10	5.38647	1.00013	0.99949	1.12497	1.03201
	2.5%-97.5%	2.1924354-13.23369	0.9999912-1.000268	0.9989126-1.000071	0.9849753-1.284859	0.9812678-1.085371
Lake fractal index	B0.25	25.1016	1.00016	0.99949	1.10383	0.29605
	2.5%-97.5%	0.6819084-924.0099	1.0000219-1.000293	0.9988958-1.000078	0.9644519-1.263355	0.0142315-6.158524
	B0.5	46.3132	1.00016	0.9995	1.10245	0.16845
	2.5%-97.5%	0.8880326-2415.355	1.0000248-1.000295	0.9989134-1.000092	0.9643735-1.260302	0.0055628-5.100947
	B0.75	21.5207	1.00015	0.99951	1.10827	0.3301
	2.5%-97.5%	0.3165850-1462.926	1.0000189-1.000291	0.9989253-1.000102	0.9692311-1.267258	0.0083830-12.99852
	B1	21.09303	1.00015	0.99951	1.10807	0.33655
	2.5%-97.5%	0.2081152-2137.834	1.0000187-1.000291	0.9989218-1.000098	0.9681582-1.268193	0.0060364-18.76326
	B2	6.68875	1.00015	0.99951	1.11549	0.92916
	2.5%-97.5%	0.0307839-1453.332	1.0000133-1.000285	0.9989226-1.000098	0.9759672-1.274961	0.0073239-117.8781
	B2.5	174.707	1.00015	0.99953	1.11046	0.04655
	2.5%-97.5%	0.5821398-52431.89	1.0000192-1.000287	0.9989406-1.000114	0.9730943-1.267216	0.0002626-8.248275
	B5	0.85951	1.00015	0.99949	1.11781	6.17935
	2.5%-97.5%	0.0006887-1072.614	1.0000125-1.000282	0.9988935-1.000081	0.9780175-1.277573	0.0091786-4160.153
	B7.5	0.14489	1.00014	0.99948	1.11982	32.0917
	2.5%-97.5%	0.0000550-381.4814	1.0000080-1.000278	0.9988910-1.000068	0.9799210-1.279684	0.0235920-43652.62
	B10	0.02109	1.00014	0.9995	1.10212	212.772
	2.5%-97.5%	0.0000022-196.5600	1.0000030-1.000272	0.9989184-1.000084	0.9642428-1.259710	0.0038753-1168209
Agriculture	B0.25	6.61639	1.00016	0.99934	1.09329	1.00733
	2.5%-97.5%	2.0658695-21.19040	0.9999967-1.000323	0.9986160-1.000058	0.9239621-1.293660	0.9964391-1.018341

	B0.5	6.57476	1.00016	0.99938	1.08947	1.00669
	2.5%-97.5%	2.1123032-20.46461	1.0000064-1.000323	0.9986969-1.000058	0.9228634-1.286165	0.9979876-1.015474
	B0.75	7.51389	1.00016	0.9994	1.06929	1.00603
	2.5%-97.5%	2.5225925-22.38115	1.0000055-1.000306	0.9987517-1.000057	0.9090497-1.257779	0.9988302-1.013279
	B1	7.46947	1.00015	0.99942	1.07237	1.00517
	2.5%-97.5%	2.5278580-22.07127	1.0000021-1.000301	0.9987759-1.000067	0.9120643-1.260855	0.9985689-1.011814
	B2	6.31915	1.00016	0.99944	1.09749	1.0045
	2.5%-97.5%	2.2049536-18.11001	1.0000161-1.000304	0.9988142-1.000075	0.9373971-1.284916	0.9987585-1.010281
	B2.5	5.89281	1.00017	0.99944	1.10697	1.00442
	2.5%-97.5%	2.1110654-16.44916	1.0000246-1.000307	0.9988098-1.000065	0.9487936-1.291525	0.9989813-1.009893
	B5	5.65061	1.00016	0.99946	1.12165	1.00233
	2.5%-97.5%	2.1581868-14.79454	1.0000213-1.000298	0.9988456-1.000080	0.9690403-1.298286	0.9971408-1.007548
	B7.5	6.27292	1.00015	0.99949	1.10954	1.00143
	2.5%-97.5%	2.4651755-15.96216	1.0000106-1.000287	0.9988806-1.000103	0.9620651-1.279616	0.9961251-1.006755
	B10	6.42816	1.00015	0.9995	1.10763	1.00086
	2.5%-97.5%	2.5667774-16.09848	1.0000100-1.000283	0.9988929-1.000102	0.9622410-1.274980	0.9956045-1.006145
Urban	B0.25	9.30368	1.00017	0.99885	1.05546	1.00852
	2.5%-97.5%	1.6426070-52.69575	0.9999920-1.000355	0.9974600-1.000249	0.8258108-1.348968	0.9858371-1.031732
	B0.5	9.5611	1.00015	0.9988	1.0551	1.01461
	2.5%-97.5%	2.2600597-40.44790	0.9999836-1.000319	0.9975494-1.000058	0.8607614-1.293314	0.9783519-1.052220
	B0.75	11.0169	1.00016	0.99883	1.0274	1.02199
	2.5%-97.5%	2.5213594-48.13807	0.9999831-1.000328	0.9975457-1.000124	0.8346715-1.264625	0.9776517-1.068333
	B1	10.9982	1.00013	0.99891	1.03796	1.01409
	2.5%-97.5%	2.6391559-45.83323	0.9999571-1.000297	0.9976138-1.000209	0.8466318-1.272523	0.9649431-1.065742
	B2	6.86928	1.00016	0.99956	1.09348	1.0032
	2.5%-97.5%	1.6364622-28.83478	0.9999879-1.000338	0.9988878-1.000227	0.8902708-1.343084	0.9496337-1.059796
	B2.5	11.0928	1.00014	0.99961	1.02382	1.00481
	2.5%-97.5%	3.2250335-38.15494	0.9999787-1.000302	0.9989572-1.000254	0.8540815-1.227287	0.9488810-1.064025
	B5	9.55011	1.00015	0.99957	1.04151	1.02733

	2.5%-97.5%	3.0943302-29.47477	0.9999961-1.000304	0.9989330-1.000213	0.8807377-1.231630	0.9591499-1.100361
	B7.5	7.86855	1.00015	0.99958	1.07507	1.01488
	2.5%-97.5%	2.8239723-21.92444	1.0000117-1.000298	0.9989779-1.000189	0.9228135-1.252451	0.9502450-1.083901
	B10	7.48027	1.00016	0.9996	1.08213	1.01054
	2.5%-97.5%	2.7477530-20.36370	1.0000194-1.000299	0.9990056-1.000192	0.9312585-1.257444	0.9461994-1.079253

(2) The coefficients of the total richness/ Catchment buffers

Catchment variables		Intercept	Lake area	Lake conductivity	Lake pH	Added variable
Original Model		6.17156	1.00015	0.99951	1.11568	
2.5%-97.5%		2.5560829-14.90096	1.0000141-1.000284	0.9989226-1.000098	0.9766124-1.274547	
Stream density	B0.25	6.15771	1.00015	0.99951	1.11571	1.00135
	2.5%-97.5%	2.3904952-15.86174	1.0000052-1.000294	0.9989198-1.000100	0.9764903-1.274781	0.8231550-1.218107
	B0.5	5.92125	1.00016	0.99951	1.11269	1.0509
	2.5%-97.5%	2.3866540-14.69051	1.0000153-1.000296	0.9989222-1.000097	0.9736829-1.271553	0.8172191-1.351395
	B0.75	5.92968	1.00015	0.99951	1.11274	1.05678
	2.5%-97.5%	2.3876316-14.72636	1.0000153-1.000293	0.9989255-1.000101	0.9738007-1.271512	0.7912682-1.411384
	B1	5.68896	1.00016	0.99951	1.11308	1.10504
	2.5%-97.5%	2.2635954-14.29771	1.0000192-1.000297	0.9989219-1.000096	0.9747152-1.271081	0.8066011-1.513912
	B2	6.42379	1.00015	0.99951	1.11504	0.95836
	2.5%-97.5%	2.4891170-16.57821	1.0000083-1.000284	0.9989237-1.000098	0.9758105-1.274144	0.6823689-1.345973
	B2.5	6.42413	1.00015	0.99951	1.11503	0.95737
	2.5%-97.5%	2.4677326-16.72365	1.0000095-1.000284	0.9989237-1.000099	0.9757809-1.274155	0.6609979-1.386632
	B5	6.19471	1.00015	0.99951	1.11554	0.99625
	2.5%-97.5%	2.2096162-17.36700	1.0000128-1.000285	0.9989190-1.000103	0.9748491-1.276527	0.6002682-1.653437
	B7.5	6.70304	1.00015	0.99952	1.11203	0.92391
	2.5%-97.5%	2.2883624-19.63448	1.0000117-1.000284	0.9989283-1.000113	0.9707323-1.273902	0.5288608-1.614058
	B10	5.8796	1.00015	0.99951	1.11719	1.05289
	2.5%-97.5%	2.0367054-16.97335	1.0000138-1.000285	0.9989153-1.000096	0.9763511-1.278336	0.5879902-1.885351

Lake density	B0.25	6.56151	1.00013	0.99962	1.10964	0.97503
	2.5%-97.5%	2.6743542-16.09860	0.9999886-1.000275	0.9989617-1.000282	0.9706141-1.268569	0.9103344-1.044325
	B0.5	6.43337	1.00014	0.99961	1.11145	0.97152
	2.5%-97.5%	2.6212708-15.78939	0.9999942-1.000281	0.9989055-1.000312	0.9720960-1.270780	0.8661002-1.089782
	B0.75	6.32983	1.00014	0.99957	1.11331	0.97666
	2.5%-97.5%	2.5859292-15.49414	0.9999997-1.000284	0.9988908-1.000244	0.9739467-1.272616	0.8493345-1.123074
	B1	6.21896	1.00015	0.99953	1.11483	0.9925
	2.5%-97.5%	2.5369103-15.24511	1.0000065-1.000288	0.9988246-1.000234	0.9749185-1.274823	0.8469992-1.162999
	B2	6.1482	1.00015	0.9995	1.11593	1.00883
	2.5%-97.5%	2.5253913-14.96811	1.0000109-1.000290	0.9988425-1.000157	0.9765662-1.275172	0.7894069-1.289243
	B2.5	6.17461	1.00015	0.99951	1.11567	0.99818
	2.5%-97.5%	2.5459983-14.97479	1.0000103-1.000287	0.9988656-1.000159	0.9765694-1.274582	0.7589050-1.312892
	B5	6.19514	1.00015	0.99952	1.1156	0.98397
	2.5%-97.5%	2.5529397-15.03356	1.0000104-1.000285	0.9989094-1.000126	0.9765354-1.274469	0.6911128-1.400935
	B7.5	6.16824	1.00015	0.99951	1.11569	1.00249
	2.5%-97.5%	2.5409086-14.97386	1.0000122-1.000286	0.9989043-1.000115	0.9765793-1.274610	0.6809645-1.475821
	B10	6.18812	1.00015	0.99951	1.11559	0.98856
	2.5%-97.5%	2.5462097-15.03912	1.0000114-1.000285	0.9989072-1.000123	0.9764701-1.274531	0.6603377-1.479922
Lake coverage	B0.25	6.11159	1.00011	0.99956	1.1045	1.00247
	2.5%-97.5%	2.5367126-14.72436	0.9999389-1.000281	0.9989616-1.000168	0.9642331-1.265173	0.9960958-1.008881
	B0.5	6.18374	1.00012	0.99953	1.1093	1.00187
	2.5%-97.5%	2.5614750-14.92837	0.9999439-1.000305	0.9989345-1.000130	0.9681282-1.271056	0.9931591-1.010654
	B0.75	6.17994	1.00014	0.99951	1.11345	1.00086
	2.5%-97.5%	2.5581518-14.92938	0.9999552-1.000324	0.9989228-1.000106	0.9719381-1.275560	0.9899294-1.011901
	B1	6.16665	1.00016	0.99951	1.11719	0.99927
	2.5%-97.5%	2.5538848-14.89009	0.9999711-1.000341	0.9989194-1.000098	0.9755896-1.279332	0.9863047-1.012403
	B2	6.20053	1.00019	0.99951	1.1233	0.99297
	2.5%-97.5%	2.5806747-14.89788	1.0000198-1.000359	0.9989227-1.000096	0.9827617-1.283928	0.9755821-1.010669
	B2.5	6.22847	1.00018	0.99951	1.12248	0.99242

	2.5%-97.5%	2.5937459-14.95667	1.0000252-1.000343	0.9989261-1.000097	0.9825312-1.282362	0.9748076-1.010350
	B5	6.31946	1.00018	0.99951	1.12116	0.98909
	2.5%-97.5%	2.6395577-15.12964	1.0000346-1.000320	0.9989270-1.000092	0.9824837-1.279408	0.9709624-1.007556
	B7.5	6.27348	1.00017	0.9995	1.12057	0.99011
	2.5%-97.5%	2.6113462-15.07134	1.0000272-1.000313	0.9989180-1.000089	0.9813835-1.279489	0.9682969-1.012424
	B10	6.2738	1.00017	0.9995	1.11919	0.9913
	2.5%-97.5%	2.6049295-15.11001	1.0000225-1.000309	0.9989187-1.000091	0.9799908-1.278160	0.9670594-1.016140
Lake fractal index	B0.25	18.6327	1.00016	0.9995	1.10755	0.38025
	2.5%-97.5%	0.5555063-624.9783	1.0000207-1.000294	0.9989067-1.000088	0.9683396-1.266781	0.0192660-7.504839
	B0.5	24.9708	1.00016	0.9995	1.10643	0.29164
	2.5%-97.5%	0.5379404-1159.134	1.0000205-1.000292	0.9989145-1.000093	0.9676832-1.265066	0.0107089-7.942523
	B0.75	27.4209	1.00016	0.99951	1.10408	0.2708
	2.5%-97.5%	0.5589040-1345.326	1.0000201-1.000290	0.9989265-1.000104	0.9649712-1.263247	0.0096232-7.620544
	B1	29.5784	1.00016	0.99951	1.10278	0.25405
	2.5%-97.5%	0.5079030-1722.542	1.0000209-1.000292	0.9989202-1.000097	0.9631875-1.262613	0.0078111-8.262458
	B2	82.1782	1.00016	0.99951	1.10367	0.0979
	2.5%-97.5%	1.3863367-4871.299	1.0000230-1.000291	0.9989282-1.000101	0.9666817-1.260077	0.0027165-3.528186
	B2.5	1197.3	1.00016	0.99954	1.10902	0.00791
	2.5%-97.5%	12.749860-112442.3	1.0000310-1.000293	0.9989610-1.000114	0.9749065-1.261591	0.0001301-0.481096
	B5	1818.7	1.00016	0.99958	1.09648	0.00567
	2.5%-97.5%	12.139610-272494.3	1.0000240-1.000286	0.9990045-1.000159	0.9630493-1.248394	0.0006286-0.511560
	B7.5	250.915	1.00016	0.99956	1.10608	0.03363
	2.5%-97.5%	0.8848689-71150.45	1.0000222-1.000290	0.9989736-1.000147	0.9692306-1.262259	0.0002010-5.626672
	B10	408.998	1.00016	0.99957	1.1009	0.02192
	2.5%-97.5%	1.1090296-150834.3	1.0000247-1.000292	0.9989864-1.000161	0.9644187-1.256695	0.0001046-4.592946
Agriculture	B0.25	6.40657	1.00016	0.99932	1.09764	1.00791
	2.5%-97.5%	1.9975567-20.54714	0.9999991-1.000326	0.9985894-1.000044	0.9281377-1.298093	0.9968465-1.019094
	B0.5	6.69977	1.00016	0.99939	1.09059	1.00573
	2.5%-97.5%	2.1224642-21.14851	0.9999962-1.000318	0.9987039-1.000077	0.9235124-1.287904	0.9972102-1.014321

	B0.75	6.59825	1.00017	0.99943	1.0884	1.00568
	2.5%-97.5%	2.0825605-20.90546	1.0000058-1.000326	0.9987542-1.000098	0.9201692-1.287392	0.9984059-1.013014
	B1	7.52269	1.00015	0.99946	1.07195	1.00467
	2.5%-97.5%	2.4726386-22.88682	0.9999967-1.000307	0.9988041-1.000118	0.9098726-1.262889	0.9981879-1.011201
	B2	7.12733	1.00016	0.99946	1.07899	1.00458
	2.5%-97.5%	2.3577651-21.54532	1.0000062-1.000310	0.9988124-1.000106	0.9156213-1.271506	0.9986059-1.010596
	B2.5	6.57255	1.00016	0.99945	1.09021	1.00467
	2.5%-97.5%	2.1957790-19.67338	1.0000127-1.000315	0.9988017-1.000098	0.9260699-1.283449	0.9988368-1.010541
	B5	5.768	1.00016	0.99944	1.11826	1.00317
	2.5%-97.5%	2.0053912-16.59016	1.0000049-1.000309	0.9987849-1.000092	0.9551080-1.309288	0.9974271-1.008947
	B7.5	5.56842	1.00016	0.99944	1.1266	1.00241
	2.5%-97.5%	1.9264479-16.09557	1.0000033-1.000309	0.9987863-1.000099	0.9618329-1.319586	0.9964343-1.008421
	B10	5.38908	1.00016	0.99945	1.13388	1.00163
	2.5%-97.5%	1.8586827-15.62512	1.0000030-1.000310	0.9987949-1.000108	0.9677936-1.328461	0.9953694-1.007922
Urban	B0.25	9.38305	1.00017	0.99885	1.05437	1.00781
	2.5%-97.5%	1.6605366-53.01999	0.9999921-1.000354	0.9974591-1.000247	0.8250572-1.347407	0.9876113-1.028418
	B0.5	9.65939	1.00015	0.9988	1.0534	1.01367
	2.5%-97.5%	2.2350184-41.74628	0.9999807-1.000323	0.9974522-1.000157	0.8564899-1.295587	0.9814271-1.046967
	B0.75	11.598	1.00016	0.99888	1.0187	1.02325
	2.5%-97.5%	2.6684343-50.40931	0.9999845-1.000326	0.9976185-1.000140	0.8275018-1.254067	0.9838806-1.064199
	B1	11.663	1.00013	0.99893	1.02688	1.018
	2.5%-97.5%	2.7072336-50.24519	0.9999573-1.000302	0.9976433-1.000214	0.8329505-1.265969	0.9757615-1.062060
	B2	10.4716	1.00012	0.99957	1.0385	1.0027
	2.5%-97.5%	2.5082561-43.71762	0.9999496-1.000297	0.9989191-1.000218	0.8477560-1.272150	0.9541650-1.053697
	B2.5	12.5727	1.00011	0.99957	1.01756	0.99636
	2.5%-97.5%	3.2316401-48.91414	0.9999384-1.000272	0.9989283-1.000215	0.8377024-1.236039	0.9507524-1.044159
	B5	9.38362	1.00013	0.99956	1.05277	1.00132
	2.5%-97.5%	2.3068090-38.17060	0.9999577-1.000307	0.9988804-1.000240	0.8604762-1.288034	0.9456020-1.060313
	B7.5	9.63285	1.00013	0.99955	1.04923	1.004

	2.5%-97.5%	2.5219370-36.79387	0.9999658-1.000299	0.9988827-1.000224	0.8652971-1.272252	0.9348991-1.078208
	B10	9.61185	1.00013	0.99955	1.04937	1.00642
	2.5%-97.5%	2.5142513-36.74558	0.9999657-1.000299	0.9988738-1.000226	0.8654214-1.272422	0.9259626-1.093865

(3) The coefficients of the submersed species richness/ Landscape buffers

Landscape variables		Intercept	Lake area	Lake alkalinity	Lake conductivity	Added variable
Original Model		2.26877	1.00019	1.69427	0.99905	
2.5%-97.5%		0.9999448-5.1476196	1.0000506-1.0003356	1.1732235-2.4467241	0.9982031-0.9998952	
Stream density	B0.25	1.98918	1.00021	1.72251	0.99903	1.06376
	2.5%-97.5%	0.7619542-5.193005	1.0000541-1.000359	1.1869865-2.499634	0.9981846-0.9998757	0.8427775-1.342689
	B0.5	1.72225	1.00022	1.72155	0.99905	1.22027
	2.5%-97.5%	0.6858791-4.324593	1.0000731-1.000368	1.1949498-2.480222	0.9982097-0.9998860	0.8986645-1.656978
	B0.75	1.55864	1.00022	1.74997	0.99903	1.34269
	2.5%-97.5%	0.6099174-3.983090	1.0000768-1.000365	1.2148039-2.520892	0.9981984-0.9998663	0.9333028-1.931651
	B1	1.44048	1.00022	1.77705	0.99903	1.44283
	2.5%-97.5%	0.5566582-3.727549	1.0000790-1.000364	1.2337853-2.559517	0.9982018-0.9998583	0.9650868-2.157081
	B2	2.08587	1.0002	1.71497	0.99905	1.07212
	2.5%-97.5%	0.7650770-5.686810	1.0000517-1.000339	1.1758255-2.501325	0.9982039-0.9998958	0.6709015-1.713269
	B2.5	1.87552	1.0002	1.73739	0.99906	1.18324
	2.5%-97.5%	0.6763957-5.200480	1.0000541-1.000339	1.1925624-2.531138	0.9982168-0.9999081	0.6997565-2.000762
	B5	1.47772	1.00019	1.78627	0.9991	1.51695
	2.5%-97.5%	0.5125829-4.260110	1.0000487-1.000329	1.2291090-2.595994	0.9982611-0.9999407	0.7949980-2.894503
	B7.5	1.34455	1.00019	1.81194	0.99911	1.65941
	2.5%-97.5%	0.4651476-3.886544	1.0000466-1.000326	1.2476898-2.631365	0.9982772-0.9999501	0.8649837-3.183444
	B10	1.26173	1.00018	1.81504	0.99916	1.80575
	2.5%-97.5%	0.4435077-3.589467	1.0000439-1.000322	1.2548328-2.625337	0.9983176-0.9999941	0.9312037-3.501640

Lake density	B0.25	2.28551	1.00019	1.69044	0.99906	0.99733
	2.5%-97.5%	0.7619542-5.193005	1.0000541-1.000359	1.1869865-2.499634	0.9981846-0.9998757	0.8427775-1.342689
	B0.5	2.42277	1.00018	1.66079	0.99916	0.9784
	2.5%-97.5%	0.6858791-4.324593	1.0000731-1.000368	1.1949498-2.480222	0.9982097-0.9998860	0.8986645-1.656978
	B0.75	2.37014	1.00019	1.66987	0.99912	0.97283
	2.5%-97.5%	0.6099174-3.983090	1.0000768-1.000365	1.2148039-2.520892	0.9981984-0.9998663	0.9333028-1.931651
	B1	2.3173	1.00019	1.68199	0.99908	0.9847
	2.5%-97.5%	0.5566582-3.727549	1.0000790-1.000364	1.2337853-2.559517	0.9982018-0.9998583	0.9650868-2.157081
	B2	2.25998	1.00019	1.69647	0.99904	1.00458
	2.5%-97.5%	0.7650770-5.686810	1.0000517-1.000339	1.1758255-2.501325	0.9982039-0.9998958	0.6709015-1.713269
	B2.5	2.29805	1.00019	1.68722	0.99907	0.98184
	2.5%-97.5%	0.6763957-5.200480	1.0000541-1.000339	1.1925624-2.531138	0.9982168-0.9999081	0.6997565-2.000762
	B5	2.43017	1.00019	1.65921	0.99913	0.86672
	2.5%-97.5%	0.5125829-4.260110	1.0000487-1.000329	1.2291090-2.595994	0.9982611-0.9999407	0.7949980-2.894503
	B7.5	2.36623	1.00019	1.67277	0.99909	0.90962
	2.5%-97.5%	0.4651476-3.886544	1.0000466-1.000326	1.2476898-2.631365	0.9982772-0.9999501	0.8649837-3.183444
	B10	2.27663	1.00019	1.69249	0.99905	0.99155
	2.5%-97.5%	0.4435077-3.589467	1.0000439-1.000322	1.2548328-2.625337	0.9983176-0.9999941	0.9312037-3.501640
Lake coverage	B0.25	1.9677	1.00011	1.6695	0.99916	1.00569
	2.5%-97.5%	0.8594640-4.504968	0.9999266-1.000288	1.1612313-2.400247	0.9983212-0.9999916	0.9986313-1.012798
	B0.5	2.09992	1.00012	1.66868	0.9991	1.006
	2.5%-97.5%	0.9209568-4.788151	0.9999226-1.000311	1.1573609-2.405888	0.9982654-0.9999429	0.9960447-1.016052
	B0.75	2.18022	1.00014	1.67841	0.99907	1.00469
	2.5%-97.5%	0.9556962-4.973730	0.9999409-1.000345	1.1620815-2.424141	0.9982272-0.9999125	0.9918250-1.017730
	B1	2.23572	1.00017	1.68802	0.99905	1.00231
	2.5%-97.5%	0.9797397-5.101827	0.9999651-1.000379	1.1678231-2.439932	0.9982089-0.9999005	0.9863703-1.018499
	B2	2.39629	1.00025	1.69925	0.99906	0.98873
	2.5%-97.5%	1.0473187-5.482768	1.0000469-1.000457	1.1780108-2.451131	0.9982081-0.9999038	0.9613783-1.016865
	B2.5	2.44986	1.00026	1.69193	0.99906	0.98432

	2.5%-97.5%	1.0674818-5.622410	1.0000614-1.000456	1.1736297-2.439119	0.9982124-0.9999048	0.9526672-1.017027
	B5	2.50527	1.00022	1.65171	0.9991	0.98649
	2.5%-97.5%	1.0495948-5.979827	1.0000553-1.000381	1.1362078-2.401094	0.9982422-0.9999565	0.9456234-1.029116
	B7.5	2.3044	1.0002	1.68647	0.99906	0.99801
	2.5%-97.5%	0.9249524-5.741140	1.0000395-1.000351	1.1467581-2.480187	0.9981948-0.9999169	0.9464117-1.052413
	B10	1.63248	1.00017	1.8729	0.99892	1.04275
	2.5%-97.5%	0.6451309-4.130922	1.0000181-1.000312	1.2704053-2.761136	0.9980690-0.9997698	0.9828460-1.106302
Lake fractal index	B0.25	9.85663	1.0002	1.68091	0.99901	0.2659
	2.5%-97.5%	0.2413123-402.6036	1.0000601-1.000346	1.1649561-2.425374	0.9981474-0.9998644	0.0100728-7.019133
	B0.5	9.36723	1.0002	1.64959	0.99906	0.28685
	2.5%-97.5%	0.1119782-783.5902	1.0000574-1.000345	1.1339695-2.399665	0.9982101-0.9999079	0.0061623-13.35218
	B0.75	8.31385	1.0002	1.66653	0.99906	0.3134
	2.5%-97.5%	0.0855159-808.2725	1.0000560-1.000343	1.1517362-2.411419	0.9982102-0.9999055	0.0054910-17.88671
	B1	10.34768	1.0002	1.66654	0.99905	0.25621
	2.5%-97.5%	0.0733440-1459.893	1.0000570-1.000344	1.1517456-2.411417	0.9982030-0.9998985	0.0031606-20.76885
	B2	3.29604	1.00019	1.69041	0.99905	0.71105
	2.5%-97.5%	0.0093432-1162.754	1.0000506-1.000337	1.1691838-2.444009	0.9982039-0.9998975	0.0035017-144.3828
	B2.5	19.46952	1.0002	1.66783	0.99907	0.14116
	2.5%-97.5%	0.0340364-11136.97	1.0000537-1.000338	1.1530581-2.412420	0.9982242-0.9999214	0.0004552-43.77121
	B5	0.25881	1.00019	1.69169	0.99903	7.54718
	2.5%-97.5%	0.0001203-556.6164	1.0000491-1.000333	1.1719278-2.441962	0.9981805-0.9998791	0.0063047-9034.395
	B7.5	0.03256	1.00019	1.69027	0.99903	52.0989
	2.5%-97.5%	0.0000690-153.6104	1.0000440-1.000328	1.1730430-2.435545	0.9981882-0.9998692	0.0208026-130478.9
	B10	0.00203	1.00018	1.6588	0.99904	717.59
	2.5%-97.5%	0.0000096-42.70489	1.0000420-1.000323	1.1526760-2.387158	0.9982046-0.9998733	0.0657374-7833227
Agriculture	B0.25	3.79853	1.00018	1.33975	0.99913	1.00613
	2.5%-97.5%	1.2465400-11.57512	1.0000231-1.000337	0.8081967-2.220897	0.9982767-0.9999886	0.9930415-1.019394
	B0.5	4.41219	1.00019	1.23093	0.9992	1.00717
	2.5%-97.5%	1.4167659-13.74073	1.0000353-1.000338	0.7233283-2.094760	0.9983623-1.0000430	0.9958017-1.018661

	B0.75	5.55708	1.00019	1.09831	0.99929	1.00821
	2.5%-97.5%	1.8651414-16.55699	1.0000436-1.000333	0.6590975-1.830222	0.9984472-1.0001320	0.9989082-1.017593
	B1	5.4366	1.00019	1.11354	0.9993	1.00718
	2.5%-97.5%	1.8119384-16.31213	1.0000411-1.000330	0.6662406-1.861161	0.9984495-1.0001540	0.9986355-1.015806
	B2	3.48468	1.0002	1.35228	0.9992	1.00467
	2.5%-97.5%	1.1534512-10.52750	1.0000538-1.000343	0.8113937-2.253719	0.9983351-1.0000730	0.9969847-1.012407
	B2.5	3.10015	1.00021	1.41297	0.99917	1.00431
	2.5%-97.5%	1.0222819-9.401450	1.0000645-1.000353	0.8464346-2.358712	0.9982948-1.0000470	0.9968974-1.011781
	B5	1.95841	1.00021	1.77403	0.99903	1.00035
	2.5%-97.5%	0.6851034-5.598214	1.0000650-1.000355	1.0919254-2.882229	0.9981607-0.9998908	0.9933324-1.007413
	B7.5	1.90328	1.0002	1.83077	0.99902	0.99886
	2.5%-97.5%	0.6818368-5.312814	1.0000545-1.000345	1.1389144-2.942918	0.9981676-0.9998695	0.9917655-1.005995
	B10	1.97162	1.00019	1.81907	0.99902	0.99828
	2.5%-97.5%	0.7221815-5.382722	1.0000507-1.000338	1.1406641-2.900947	0.9981706-0.9998615	0.9912475-1.005366
Urban	B0.25	7.17315	1.00018	1.05266	0.99903	1.00833
	2.5%-97.5%	1.3918310-36.96864	1.0000055-1.000363	0.5053734-2.192612	0.9967956-1.0012610	0.9843743-1.032878
	B0.5	7.08509	1.00016	1.06944	0.99896	1.01398
	2.5%-97.5%	1.6207498-30.97237	0.9999986-1.000327	0.5478955-2.087462	0.9969429-1.0009840	0.9747342-1.054796
	B0.75	5.88107	1.00017	1.14747	0.99879	1.01792
	2.5%-97.5%	1.3641290-25.35464	1.0000070-1.000339	0.5839880-2.254629	0.9967720-1.0008110	0.9683130-1.070058
	B1	3.61846	1.00015	1.48788	0.99829	1.00143
	2.5%-97.5%	0.8545743-15.32140	0.9999785-1.000312	0.7647620-2.894721	0.9962906-1.0002990	0.9461383-1.059945
	B2	4.01048	1.00017	1.34058	0.99935	0.99001
	2.5%-97.5%	0.9929938-16.19743	0.9999999-1.000340	0.7197837-2.496785	0.9984050-1.0003010	0.9220813-1.062941
	B2.5	4.09528	1.00017	1.31717	0.99936	0.99443
	2.5%-97.5%	1.0831921-15.48325	1.0000050-1.000343	0.7262062-2.389057	0.9984260-1.0002980	0.9202600-1.074567
	B5	2.8721	1.00018	1.53174	0.9992	0.99591
	2.5%-97.5%	0.8596291-9.595937	1.0000194-1.000345	0.8867614-2.645848	0.9982868-1.0001120	0.9072042-1.093290
	B7.5	2.54867	1.00019	1.61914	0.99916	0.98528

	2.5%-97.5%	0.8182451-7.938615	1.0000401-1.000340	0.9673988-2.709972	0.9982824-1.0000480	0.9017023-1.076611
	B10	1.80332	1.0002	1.88802	0.99904	0.96614
	2.5%-97.5%	0.5993235-5.426079	1.0000508-1.000347	1.1447162-3.113986	0.9981727-0.9999055	0.8833521-1.056692

(4) The coefficients of the submersed species richness/ Catchment buffers

Catchment variables		**Intercept**	**Lake area**	**Lake alkalinity**	**Lake conductivity**	**Added variable**
Original Model		2.26877	1.00019	1.69427	0.99905	
2.5%-97.5%		0.9999448-5.1476196	1.0000506-1.0003356	1.1732235-2.4467241	0.9982031-0.9998952	
Stream density	B0.25	2.2197	1.0002	1.69894	0.99904	1.01039
	2.5%-97.5%	0.8655647-5.692303	1.0000426-1.000348	1.1712101-2.464469	0.9981889-0.999897	0.8114533-1.258099
	B0.5	2.11441	1.0002	1.70038	0.99904	1.0541
	2.5%-97.5%	0.8575473-5.213396	1.0000517-1.000349	1.1769786-2.456550	0.9981899-0.999886	0.7986811-1.391192
	B0.75	2.09037	1.0002	1.7056	0.99904	1.06716
	2.5%-97.5%	0.8334759-5.242686	1.0000527-1.000347	1.1789324-2.467552	0.9981862-0.999887	0.7743559-1.470687
	B1	2.01505	1.0002	1.71392	0.99903	1.1013
	2.5%-97.5%	0.7937960-5.115199	1.0000554-1.000349	1.1838197-2.481397	0.9981758-0.999879	0.7751887-1.564598
	B2	2.62119	1.00019	1.66192	0.99907	0.8869
	2.5%-97.5%	1.0144493-6.772758	1.0000401-1.000332	1.1441602-2.413977	0.9982281-0.999921	0.6040976-1.302081
	B2.5	1.87552	1.0002	1.73739	0.99906	1.18324
	2.5%-97.5%	0.9844901-6.753465	1.0000427-1.000332	1.1465093-2.421599	0.9982228-0.999919	0.5894372-1.361728
	B5	2.32551	1.00019	1.68817	0.99906	0.97855
	2.5%-97.5%	0.8029961-6.734760	1.0000493-1.000336	1.1521582-2.473554	0.9981919-0.999919	0.5498506-1.741484
	B7.5	2.64967	1.00019	1.66141	0.99908	0.8648
	2.5%-97.5%	0.9055523-7.753009	1.0000481-1.000335	1.1369533-2.427804	0.9982237-0.999941	0.4620661-1.618537
	B10	2.32805	1.00019	1.6892	0.99905	0.9753
	2.5%-97.5%	0.7880633-6.877411	1.0000497-1.000336	1.1567565-2.466730	0.9981963-0.999912	0.5050769-1.883286

Lake density	B0.25	2.42277	1.00018	1.66079	0.99916	0.9784
	2.5%-97.5%	0.8655647-5.692303	1.0000426-1.000348	1.1712101-2.464469	0.9981889-0.999897	0.8114533-1.258099
	B0.5	2.42969	1.00018	1.65669	0.99918	0.96698
	2.5%-97.5%	0.8575473-5.213396	1.0000517-1.000349	1.1769786-2.456550	0.9981899-0.999886	0.7986811-1.391192
	B0.75	2.43326	1.00018	1.65617	0.99917	0.95877
	2.5%-97.5%	0.8334759-5.242686	1.0000527-1.000347	1.1789324-2.467552	0.9981862-0.999887	0.7743559-1.470687
	B1	2.34259	1.00019	1.67508	0.99911	0.98053
	2.5%-97.5%	0.7937960-5.115199	1.0000554-1.000349	1.1838197-2.481397	0.9981758-0.999879	0.7751887-1.564598
	B2	2.37351	1.00019	1.66926	0.99912	0.95372
	2.5%-97.5%	1.0144493-6.772758	1.0000401-1.000332	1.1441602-2.413977	0.9982281-0.999921	0.6040976-1.302081
	B2.5	2.44479	1.00018	1.65354	0.99917	0.91392
	2.5%-97.5%	0.9844901-6.753465	1.0000427-1.000333	1.1465093-2.421599	0.9982228-0.999919	0.5894372-1.361728
	B5	2.45779	1.00018	1.65501	0.99914	0.86896
	2.5%-97.5%	0.8029961-6.734760	1.0000493-1.000336	1.1521582-2.473554	0.9981919-0.999919	0.5498506-1.741484
	B7.5	2.41441	1.00019	1.66274	0.99911	0.89664
	2.5%-97.5%	0.9055523-7.753009	1.0000481-1.000335	1.1369533-2.427804	0.9982237-0.999941	0.4620661-1.618536
	B10	2.46197	1.00019	1.65285	0.99914	0.86165
	2.5%-97.5%	0.7880633-6.877411	1.0000497-1.000336	1.1567565-2.466730	0.9981963-0.999912	0.5050769-1.883286
Lake coverage	B0.25	1.9763	1.00011	1.67157	0.99915	1.00537
	2.5%-97.5%	0.8630168-4.525730	0.9999342-1.000290	1.1627776-2.402987	0.9983199-0.999989	0.9985143-1.012283
	B0.5	2.1213	1.00013	1.67025	0.99911	1.00509
	2.5%-97.5%	0.9303747-4.836646	0.9999402-1.000317	1.1583381-2.408381	0.9982646-0.999946	0.9957382-1.014526
	B0.75	2.19311	1.00015	1.67968	0.99907	1.00379
	2.5%-97.5%	0.9615205-5.002218	0.9999596-1.000346	1.1630147-2.425873	0.9982250-0.999910	0.9920466-1.015668
	B1	2.24887	1.00018	1.68949	0.99905	1.00135
	2.5%-97.5%	0.9863235-5.127526	0.9999864-1.000375	1.1685584-2.442653	0.9982062-0.999898	0.9873578-1.015535
	B2	2.36017	1.00025	1.71813	0.99904	0.98999
	2.5%-97.5%	1.0428167-5.341708	1.0000705-1.000428	1.1912286-2.478102	0.9981989-0.999887	0.9710484-1.009296
	B2.5	2.36506	1.00026	1.73785	0.99904	0.98478

	2.5%-97.5%	1.0530007-5.311977	1.0000960-1.000430	1.2076777-2.500754	0.9982002-0.999874	0.9654675-1.004485
	B5	2.35951	1.00026	1.75608	0.99902	0.9763
	2.5%-97.5%	1.0648311-5.228320	1.0001071-1.000403	1.2279593-2.511324	0.9981972-0.999841	0.9559770-0.997058
	B7.5	2.42602	1.00024	1.72266	0.99903	0.97676
	2.5%-97.5%	1.0843066-5.427967	1.0000938-1.000392	1.2014083-2.470055	0.9981993-0.999859	0.9525232-1.001606
	B10	2.44993	1.00024	1.70949	0.99904	0.97684
	2.5%-97.5%	1.0893375-5.509936	1.0000880-1.000388	1.1909132-2.453874	0.9982056-0.999871	0.9500056-1.004435
Lake fractal index	B0.25	9.89003	1.00021	1.68315	0.99901	0.26373
	2.5%-97.5%	0.2556607-382.5880	1.0000614-1.000349	1.1667630-2.428085	0.9981571-0.999870	0.0103747-6.704004
	B0.5	11.1472	1.0002	1.66008	0.99904	0.24203
	2.5%-97.5%	0.1700030-730.9286	1.0000586-1.000345	1.1476337-2.401346	0.9981961-0.999894	0.0061772-9.482877
	B0.75	13.1381	1.0002	1.65687	0.99905	0.20872
	2.5%-97.5%	0.1995503-865.0022	1.0000589-1.000344	1.1457871-2.395917	0.9982055-0.999904	0.0052688-8.268409
	B1	17.3616	1.0002	1.6593	0.99904	0.16081
	2.5%-97.5%	0.2331276-1292.971	1.0000614-1.000347	1.1487399-2.396774	0.9981893-0.999888	0.0035456-7.293197
	B2	67.6344	1.00021	1.68558	0.99902	0.04408
	2.5%-97.5%	0.8580044-5331.468	1.0000649-1.000346	1.1725206-2.423146	0.9981697-0.999872	0.0008460-2.296678
	B2.5	699.604	1.00021	1.72247	0.99903	0.00481
	2.5%-97.5%	5.1133080-95720.18	1.0000710-1.000346	1.2055260-2.461088	0.9981955-0.999869	0.0000521-0.444212
	B5	4613.96	1.0002	1.67435	0.99911	0.00087
	2.5%-97.5%	21.346790-997276.1	1.0000690-1.000338	1.1790540-2.377721	0.9982925-0.999931	0.0000063-0.119550
	B7.5	378.615	1.0002	1.6925	0.9991	0.0086
	2.5%-97.5%	0.8913453-160824.2	1.0000644-1.000344	1.1801745-2.427227	0.9982609-0.999931	0.0000323-2.286076
	B10	655.851	1.00021	1.68516	0.99911	0.00519
	2.5%-97.5%	1.2066840-356465.9	1.0000690-1.000348	1.1765450-2.413647	0.9982742-0.999939	0.0000154-1.744296
Agriculture	B0.25	3.85597	1.00018	1.32762	0.99913	1.00678
	2.5%-97.5%	1.2725412-11.68412	1.0000248-1.000338	0.8033444-2.194058	0.9982687-0.999982	0.9935450-1.020197
	B0.5	4.29588	1.00018	1.25559	0.99919	1.00642
	2.5%-97.5%	1.4305409-12.90039	1.0000287-1.000335	0.7566488-2.083544	0.9983464-1.000037	0.9958375-1.017114

	B0.75	4.88773	1.00019	1.16043	0.99929	1.00745
	2.5%-97.5%	1.5687172-15.22893	1.0000406-1.000348	0.6866090-1.961241	0.9984254-1.000149	0.9981558-1.016821
	B1	4.99548	1.00019	1.15797	0.99931	1.00647
	2.5%-97.5%	1.6603465-15.02987	1.0000392-1.000337	0.6944567-1.930849	0.9984559-1.000163	0.9981682-1.014832
	B2	4.72919	1.00019	1.19037	0.99929	1.00571
	2.5%-97.5%	1.5710325-14.23601	1.0000425-1.000335	0.7173323-1.975336	0.9984258-1.000160	0.9981409-1.013337
	B2.5	4.67582	1.00019	1.19217	0.9993	1.00572
	2.5%-97.5%	1.5410092-14.18763	1.0000465-1.000336	0.7161312-1.984664	0.9984289-1.000165	0.9982894-1.013200
	B5	3.07921	1.00019	1.46676	0.99915	1.00241
	2.5%-97.5%	1.0365673-9.147032	1.0000351-1.000337	0.8937630-2.407098	0.9982787-1.000024	0.9951475-1.009734
	B7.5	2.69191	1.00019	1.56955	0.99911	1.00095
	2.5%-97.5%	0.9234381-7.847153	1.0000338-1.000337	0.9692276-2.541709	0.9982490-0.999979	0.9935777-1.008371
	B10	2.44884	1.00019	1.64459	0.9991	0.99972
	2.5%-97.5%	0.8543545-7.019128	1.0000341-1.000338	1.0262893-2.635405	0.9982393-0.999954	0.9921480-1.007351
Urban	B0.25	7.17367	1.00018	1.05331	0.99902	1.00759
	2.5%-97.5%	1.3936463-36.92586	1.0000056-1.000363	0.5063166-2.191251	0.9967944-1.001254	0.9862986-1.029346
	B0.5	7.36643	1.00016	1.04936	0.99908	1.01293
	2.5%-97.5%	1.6533816-32.82018	0.9999934-1.000328	0.5334221-2.064343	0.9969581-1.001203	0.9784266-1.048656
	B0.75	6.50949	1.00018	1.08777	0.99893	1.02251
	2.5%-97.5%	1.4945334-28.35227	1.0000116-1.000341	0.5501515-2.150771	0.9968856-1.000974	0.9782426-1.068787
	B1	4.06301	1.00015	1.39783	0.9984	1.01036
	2.5%-97.5%	0.9172024-17.99825	0.9999799-1.000320	0.7026519-2.780783	0.9963311-1.000474	0.9627010-1.060373
	B2	5.13667	1.00014	1.23724	0.99937	0.99502
	2.5%-97.5%	1.2714436-20.75229	0.9999697-1.000309	0.6623619-2.311064	0.9984192-1.000325	0.9318072-1.062515
	B2.5	5.15648	1.00013	1.25591	0.99934	0.98698
	2.5%-97.5%	1.3914146-19.10954	0.9999641-1.000293	0.7017768-2.247610	0.9984282-1.000256	0.9293579-1.048169
	B5	5.26448	1.00014	1.21812	0.99941	0.98994
	2.5%-97.5%	1.4493553-19.12212	0.9999777-1.000311	0.6924501-2.142849	0.9985069-1.000310	0.9251624-1.059259
	B7.5	5.40978	1.00015	1.20456	0.99941	0.99024

	2.5%-97.5%	1.5192893-19.26279	0.9999887-1.000303	0.6899616-2.102973	0.9985301-1.000292	0.9094282-1.078226
	B10	5.50971	1.00015	1.19377	0.99942	0.99167
	2.5%-97.5%	1.5400264-19.71194	0.9999886-1.000304	0.6828210-2.087058	0.9985390-1.000297	0.8978302-1.095319

(5) The coefficients of the emergent species richness/ Landscape buffers

Landscape variables		**Intercept**	**Lake area**	**Lake alkalinity**	**Added variable**
Original Model		5.51419	1.00009	0.72915	
2.5%-97.5%		2.3978915-12.680451	0.9999159-1.000255	0.5110086-1.040403	
Stream density	B0.25	5.72599	1.00008	0.72684	0.98046
	2.5%-97.5%	2.1241125-15.435610	0.9998989-1.000263	0.5079705-1.040002	0.7391914-1.300468
	B0.5	4.49189	1.00011	0.73744	1.16103
	2.5%-97.5%	1.6836671-11.984029	0.9999304-1.000283	0.5156290-1.054655	0.7997124-1.685585
	B0.75	4.16404	1.00011	0.74388	1.25722
	2.5%-97.5%	1.5307363-11.327400	0.9999346-1.000281	0.5193243-1.065533	0.8065033-1.959806
	B1	3.93809	1.00011	0.75082	1.33044
	2.5%-97.5%	1.4174482-10.941174	0.9999364-1.000281	0.5232584-1.077341	0.8128067-2.177726
	B2	4.06655	1.0001	0.76249	1.28153
	2.5%-97.5%	1.3801509-11.981911	0.9999273-1.000266	0.5265091-1.104234	0.7361847-2.230864
	B2.5	4.10083	1.00009	0.76197	1.28214
	2.5%-97.5%	1.3330259-12.615506	0.9999237-1.000261	0.5245300-1.106901	0.6842443-2.402497
	B5	3.66614	1.00008	0.77659	1.43714
	2.5%-97.5%	1.0931015-12.295844	0.9999154-1.000251	0.5305786-1.136668	0.6632958-3.113805
	B7.5	3.66347	1.00008	0.77891	1.43215
	2.5%-97.5%	1.0745520-12.489839	0.9999140-1.000250	0.5304990-1.143631	0.6527411-3.142224
	B10	3.48136	1.00008	0.78492	1.50824
	2.5%-97.5%	1.0170719-11.916439	0.9999115-1.000248	0.5345814-1.152480	0.6739908-3.375100

Lake density	B0.25	5.5064	1.00008	0.73524	0.98656
	2.5%-97.5%	2.3893726-12.689688	0.9998964-1.000259	0.5120248-1.055771	0.8883356-1.095649
	B0.5	5.59195	1.0001	0.71651	1.03247
	2.5%-97.5%	2.4305044-12.865603	0.9999186-1.000274	0.4967274-1.033525	0.8770299-1.215454
	B0.75	5.47254	1.00011	0.71342	1.09329
	2.5%-97.5%	2.3972314-12.493020	0.9999328-1.000285	0.4994240-1.019112	0.8963896-1.333437
	B1	5.52318	1.00011	0.71061	1.11454
	2.5%-97.5%	2.4218281-12.596047	0.9999328-1.000281	0.4971018-1.015821	0.8885075-1.398070
	B2	5.37627	1.00011	0.70715	1.33142
	2.5%-97.5%	2.3633028-12.230442	0.9999424-1.000286	0.4960360-1.008121	0.9143439-1.938758
	B2.5	5.36847	1.00011	0.70321	1.46007
	2.5%-97.5%	2.3587093-12.218736	0.9999442-1.000285	0.4931352-1.002772	0.9502692-2.243362
	B5	5.22759	1.0001	0.71553	1.57199
	2.5%-97.5%	2.2748790-12.012798	0.9999354-1.000274	0.5014535-1.020996	0.8558958-2.887194
	B7.5	5.0266	1.0001	0.7243	1.77133
	2.5%-97.5%	2.1737482-11.623584	0.9999336-1.000270	0.5079009-1.032909	0.8677602-3.615763
	B10	4.92879	1.0001	0.7294	1.94596
	2.5%-97.5%	2.1218583-11.448900	0.9999319-1.000267	0.5115830-1.039949	0.8436574-4.488521
Lake coverage	B0.25	5.11354	1.00005	0.7343	1.00206
	2.5%-97.5%	2.1004640-12.448814	0.9998383-1.000270	0.5139728-1.049072	0.9935647-1.010628
	B0.5	5.24653	1.00005	0.73031	1.00261
	2.5%-97.5%	2.2117173-12.445560	0.9998214-1.000283	0.5118669-1.041985	0.9905993-1.014757
	B0.75	5.26638	1.00004	0.72816	1.00388
	2.5%-97.5%	2.2459895-12.348547	0.9998045-1.000284	0.5104787-1.038669	0.9883363-1.019662
	B1	5.24078	1.00003	0.72621	1.00608
	2.5%-97.5%	2.2475476-12.220315	0.9997858-1.000276	0.5091056-1.035902	0.9869113-1.025613
	B2	5.20972	1.00002	0.72589	1.01189
	2.5%-97.5%	2.2376248-12.129472	0.9997823-1.000267	0.5090071-1.035188	0.9789619-1.045926
	B2.5	5.00925	1	0.72796	1.02044

	2.5%-97.5%	2.1436768-11.705374	0.9997714-1.000234	0.5106352-1.037768	0.9825151-1.059822
	B5	4.78178	1.00004	0.74372	1.02796
	2.5%-97.5%	2.0141623-11.352315	0.9998472-1.000226	0.5213851-1.060861	0.9798706-1.078404
	B7.5	4.38389	1.00004	0.76654	1.04005
	2.5%-97.5%	1.7818881-10.785467	0.9998580-1.000223	0.5341104-1.100122	0.9793034-1.104562
	B10	3.83435	1.00004	0.79376	1.06421
	2.5%-97.5%	1.5326340-9.5927970	0.9998682-1.000218	0.5517660-1.141891	0.9940716-1.139300
Lake fractal index	B0.25	52.8334	1.0001	0.7116	0.13295
	2.5%-97.5%	0.5020454-5560.0098	0.9999282-1.000266	0.4978741-1.017081	0.0022283-7.931623
	B0.5	33.9022	1.00009	0.70957	0.19928
	2.5%-97.5%	0.1729650-6645.0404	0.9999245-1.000265	0.4931396-1.020992	0.0019387-20.48487
	B0.75	16.751	1.00009	0.72299	0.36642
	2.5%-97.5%	0.0660199-4250.1742	0.9999202-1.000262	0.5055351-1.033987	0.0026054-51.53284
	B1	16.9106	1.00009	0.72222	0.36391
	2.5%-97.5%	0.0399149-7164.5165	0.9999195-1.000262	0.5043197-1.034277	0.0016358-80.95485
	B2	20.4536	1.00009	0.72626	0.29962
	2.5%-97.5%	0.0129693-32257.038	0.9999189-1.000260	0.5087258-1.036822	0.0003598-249.4760
	B2.5	5759.79	1.00009	0.70899	0.0017
	2.5%-97.5%	1.7308860-19166590	0.9999248-1.000262	0.4949326-1.015637	0.0000105-2.760690
	B5	53.2784	1.00009	0.73388	0.11989
	2.5%-97.5%	0.0029692-955994.20	0.9999177-1.000257	0.5137736-1.048272	0.0001308-1099.315
	B7.5	14.9398	1.00009	0.73031	0.39432
	2.5%-97.5%	0.0002598-85902.240	0.9999166-1.000258	0.5116599-1.042408	0.0001464-10620.62
	B10	7.98467	1.00009	0.73	0.70681
	2.5%-97.5%	0.0002467-25841790	0.9999153-1.000257	0.5104670-1.043943	0.0000496-100627.2
Agriculture	B0.25	8.12931	1.00009	0.6064	1.0038
	2.5%-97.5%	2.2558668-29.295060	0.9999032-1.000277	0.3376152-1.089165	0.9866846-1.021211
	B0.5	8.46081	1.00011	0.57956	1.00588
	2.5%-97.5%	2.3077941-31.018937	0.9999223-1.000292	0.3160017-1.062948	0.9909085-1.021085

	B0.75	8.01904	1.0001	0.5987	1.00464
	2.5%-97.5%	2.3648730-27.191717	0.9999205-1.000280	0.3406739-1.052142	0.9922676-1.017168
	B1	7.9184	1.00009	0.60713	1.00372
	2.5%-97.5%	2.3589147-26.580497	0.9999146-1.000273	0.3479785-1.059295	0.9923719-1.015206
	B2	6.25461	1.0001	0.67425	1.0026
	2.5%-97.5%	1.9599875-19.959366	0.9999205-1.000272	0.3990323-1.139285	0.9926960-1.012608
	B2.5	6.28672	1.0001	0.66883	1.00287
	2.5%-97.5%	1.9623998-20.140030	0.9999251-1.000275	0.3953463-1.131514	0.9933528-1.012478
	B5	5.57188	1.00009	0.72461	0.99996
	2.5%-97.5%	1.9093146-16.260226	0.9999166-1.000259	0.4464321-1.176127	0.9910785-1.008913
	B7.5	5.44669	1.00008	0.73589	0.99949
	2.5%-97.5%	1.9256747-15.405714	0.9999134-1.000255	0.4599669-1.177325	0.9905863-1.008468
	B10	5.00045	1.00009	0.76537	0.99856
	2.5%-97.5%	1.8086379-13.825048	0.9999184-1.000258	0.4827134-1.213548	0.9896857-1.007514
Urban	B0.25	19.0977	1.00009	0.42491	1.00668
	2.5%-97.5%	3.9589995-92.124830	0.9998837-1.000304	0.2203221-0.819483	0.9730865-1.041431
	B0.5	19.5575	1.00009	0.42112	1.01187
	2.5%-97.5%	4.4968186-85.059226	0.9998817-1.000290	0.2265574-0.782769	0.9544182-1.072779
	B0.75	15.51	1.0001	0.45904	1.01059
	2.5%-97.5%	4.4968186-85.059226	0.9998817-1.000290	0.2265574-0.782769	0.9544182-1.072779
	B1	9.80287	1.00008	0.58018	0.98763
	2.5%-97.5%	2.4342678-39.476441	0.9998752-1.000277	0.3171745-1.061266	0.9062670-1.076289
	B2	6.24867	1.0001	0.69377	0.97083
	2.5%-97.5%	1.6507484-23.653472	0.9999079-1.000299	0.3930290-1.224651	0.8833036-1.067032
	B2.5	8.74698	1.00009	0.61768	0.97616
	2.5%-97.5%	2.5229430-30.325556	0.9999006-1.000274	0.3599531-1.059926	0.8829617-1.079189
	B5	9.52155	1.0001	0.5789	1.00416
	2.5%-97.5%	2.9149684-31.101488	0.9999195-1.000282	0.3423392-0.978932	0.8906854-1.132102
	B7.5	6.30738	1.00008	0.71484	0.95761

	2.5%-97.5%	2.1050248-18.899089	0.9999051-1.000256	0.4415198-1.157354	0.8472790-1.082310
	B10	5.70642	1.00009	0.73566	0.96152
	2.5%-97.5%	1.9421637-16.766473	0.9999197-1.000268	0.4569264-1.184422	0.8510302-1.086354

(6) The coefficients of the emergent species richness/ Catchment buffers

Catchment variables		Intercept	Lake area	Lake alkalinity	Added variables
Original Model		5.51419	1.00009	0.72915	
2.5%-97.5%		2.3978915-12.680451	0.9999159-1.000255	0.5110086-1.040403	
Stream density	B0.25	5.7234	1.00008	0.72809	0.97852
	2.5%-97.5%	2.2199392-14.755930	0.9998986-1.000262	0.5100885-1.039261	0.7517865-1.273625
	B0.5	5.08645	1.0001	0.72903	1.06966
	2.5%-97.5%	2.0147540-12.841271	0.9999194-1.000272	0.5107082-1.040677	0.7650167-1.495627
	B0.75	4.94638	1.0001	0.73194	1.10002
	2.5%-97.5%	1.9246842-12.712034	0.9999220-1.000271	0.5124127-1.045530	0.7482771-1.617100
	B1	4.88947	1.0001	0.73289	1.11698
	2.5%-97.5%	1.8853582-12.680319	0.9999229-1.000272	0.5130084-1.047023	0.7325931-1.703042
	B2	5.62117	1.00008	0.72784	0.98268
	2.5%-97.5%	2.1245258-14.872774	0.9999108-1.000258	0.5085581-1.041684	0.6214178-1.553947
	B2.5	5.56656	1.00009	0.72854	0.99109
	2.5%-97.5%	2.0750781-14.932737	0.9999125-1.000258	0.5090569-1.042660	0.6002184-1.636506
	B5	5.40412	1.00009	0.73034	1.02099
	2.5%-97.5%	1.8695617-15.621036	0.9999156-1.000257	0.5098068-1.046261	0.5184396-2.010677
	B7.5	5.71243	1.00008	0.72723	0.9635
	2.5%-97.5%	1.9293806-16.913130	0.9999139-1.000255	0.5077742-1.041540	0.4626466-2.006585
	B10	4.79594	1.00009	0.7364	1.16103
	2.5%-97.5%	1.5939512-14.430217	0.9999193-1.000258	0.5140987-1.054822	0.5384226-2.503596

Lake density	B0.25	5.51665	1.00007	0.73779	0.98118
	2.5%-97.5%	2.3937183-12.713888	0.9998931-1.000252	0.5146735-1.057638	0.9012237-1.068233
	B0.5	5.50607	1.00008	0.73118	0.99469
	2.5%-97.5%	2.3913433-12.677738	0.9999056-1.000261	0.5090025-1.050342	0.8721373-1.134456
	B0.75	5.54573	1.0001	0.718	1.0407
	2.5%-97.5%	2.4161513-12.728977	0.9999220-1.000274	0.5008676-1.029272	0.8882440-1.219319
	B1	5.58441	1.0001	0.71572	1.0496
	2.5%-97.5%	2.4327485-12.819101	0.9999233-1.000272	0.4988642-1.026841	0.8830066-1.247629
	B2	5.56047	1.00011	0.70618	1.17277
	2.5%-97.5%	2.4292964-12.727481	0.9999355-1.000281	0.4931695-1.011201	0.8848055-1.554452
	B2.5	5.55555	1.00011	0.70253	1.2376
	2.5%-97.5%	2.4267798-12.718150	0.9999389-1.000283	0.4906857-1.005846	0.9036877-1.694884
	B5	5.33493	1.00011	0.71713	1.30376
	2.5%-97.5%	2.3177106-12.279986	0.9999346-1.000277	0.5019928-1.024474	0.8536439-1.991214
	B7.5	5.24518	1.0001	0.72139	1.35054
	2.5%-97.5%	2.2722304-12.107871	0.9999336-1.000274	0.5051289-1.030246	0.8462745-2.155289
	B10	5.24404	1.0001	0.72104	1.3698
	2.5%-97.5%	2.2741599-12.092354	0.9999338-1.000274	0.5050766-1.029351	0.8436641-2.224054
Lake coverage	B0.25	5.07594	1.00005	0.73533	1.00217
	2.5%-97.5%	2.0817289-12.376797	0.9998392-1.000266	0.5145597-1.050821	0.9938813-1.010533
	B0.5	5.1991	1.00005	0.73145	1.00279
	2.5%-97.5%	2.1869464-12.359987	0.9998254-1.000275	0.5126257-1.043675	0.9914562-1.014258
	B0.75	5.20926	1.00004	0.72818	1.00435
	2.5%-97.5%	2.2225211-12.209752	0.9998090-1.000270	0.5106352-1.038400	0.9900623-1.018847
	B1	5.19121	1.00002	0.72358	1.00691
	2.5%-97.5%	2.2342413-12.061658	0.9997915-1.000255	0.5073290-1.032009	0.9899587-1.024153
	B2	5.18634	1.00001	0.71583	1.01405
	2.5%-97.5%	2.2478658-11.966069	0.9997946-1.000223	0.5013389-1.022081	0.9911639-1.037460
	B2.5	5.21453	1	0.70558	1.0191

	2.5%-97.5%	2.2656283-12.001652	0.9998015-1.000201	0.4933585-1.009092	0.9963120-1.042413
	B5	5.38283	1.00004	0.70535	1.01838
	2.5%-97.5%	2.3382006-12.391965	0.9998626-1.000221	0.4923774-1.010439	0.9954975-1.041778
	B7.5	5.1852	1.00004	0.71529	1.02215
	2.5%-97.5%	2.2475305-11.962610	0.9998634-1.000221	0.5005233-1.022201	0.9943618-1.050717
	B10	5.06295	1.00004	0.71942	1.02621
	2.5%-97.5%	2.1921170-11.693466	0.9998604-1.000218	0.5040324-1.026853	0.9952790-1.058095
Lake fractal index	B0.25	23.8688	1.0001	0.7197	0.26838
	2.5%-97.5%	0.2502709-2276.4134	0.9999248-1.000266	0.5034696-1.028806	0.0048125-14.96708
	B0.5	7.5854	1.00009	0.72642	0.75215
	2.5%-97.5%	0.0508425-1131.6969	0.9999160-1.000258	0.5067147-1.041396	0.0091553-61.79297
	B0.75	17.9771	1.00009	0.72022	0.34673
	2.5%-97.5%	0.1150476-2809.0892	0.9999205-1.000260	0.5025958-1.032079	0.0039811-30.19793
	B1	21.5526	1.00009	0.71862	0.29435
	2.5%-97.5%	0.1168169-3976.4599	0.9999214-1.000262	0.5013213-1.030095	0.0028917-29.96267
	B2	40.3681	1.00009	0.72602	0.16064
	2.5%-97.5%	0.1801356-9046.4369	0.9999225-1.000262	0.5089975-1.035575	0.0011822-21.82879
	B2.5	809.891	1.0001	0.74351	0.00949
	2.5%-97.5%	1.3851060-473555.50	0.9999280-1.000265	0.5214138-1.060210	0.0000263-3.426501
	B5	71.3759	1.00009	0.73457	0.09167
	2.5%-97.5%	0.0767982-66336.434	0.9999194-1.000257	0.5144445-1.048883	0.0001643-51.15482
	B7.5	41.1108	1.00009	0.73496	0.15222
	2.5%-97.5%	0.0200033-84491.171	0.9999197-1.000259	0.5143156-1.050250	0.0001254-184.6432
	B10	221.994	1.00009	0.73926	0.03132
	2.5%-97.5%	0.0756594-651362.50	0.9999243-1.000264	0.5172140-1.056631	0.0000184-53.12401
Agriculture	B0.25	8.08131	1.00009	0.6083	1.00373
	2.5%-97.5%	2.2500117-29.025449	0.9999030-1.000276	0.3392776-1.090648	0.9863920-1.021382
	B0.5	7.53839	1.00009	0.6302	1.00191
	2.5%-97.5%	2.1701338-26.186091	0.9999010-1.000273	0.3559204-1.115847	0.9880578-1.015959

	B0.75	7.76071	1.00009	0.61826	1.00236
	2.5%-97.5%	2.2407846-26.878327	0.9999065-1.000276	0.3509530-1.089179	0.9904081-1.014458
	B1	7.07333	1.00009	0.65071	1.00112
	2.5%-97.5%	2.1234118-23.562112	0.9999042-1.000268	0.3756359-1.127224	0.9902096-1.012141
	B2	7.00858	1.0001	0.64333	1.00218
	2.5%-97.5%	2.1278746-23.084168	0.9999180-1.000277	0.3766098-1.098953	0.9920959-1.012363
	B2.5	7.22752	1.0001	0.63051	1.00273
	2.5%-97.5%	2.1555641-24.233573	0.9999221-1.000280	0.3664265-1.084920	0.9927639-1.012794
	B5	6.65805	1.00009	0.66428	1.00118
	2.5%-97.5%	2.1295960-20.815973	0.9999135-1.000268	0.3995211-1.104508	0.9916931-1.010759
	B7.5	6.29505	1.00009	0.68351	1.00037
	2.5%-97.5%	2.0441177-19.386210	0.9999134-1.000268	0.4157178-1.123813	0.9906680-1.010162
	B10	5.80849	1.00009	0.71145	0.99903
	2.5%-97.5%	1.9164501-17.604730	0.9999140-1.000268	0.4371533-1.157844	0.9889475-1.009217
Urban	B0.25	19.1484	1.00009	0.42452	1.00623
	2.5%-97.5%	3.9645949-92.484423	0.9998839-1.000304	0.2200726-0.818901	0.9761988-1.037182
	B0.5	18.3835	1.00008	0.4346	1.01008
	2.5%-97.5%	4.1694881-81.054383	0.9998770-1.000288	0.2318103-0.814784	0.9598698-1.062906
	B0.75	16.3754	1.0001	0.44541	1.01788
	2.5%-97.5%	4.1694881-81.054383	0.9998770-1.000288	0.2318103-0.814784	0.9598698-1.062906
	B1	10.644	1.00009	0.54836	1.00457
	2.5%-97.5%	2.6459930-42.818016	0.9998861-1.000291	0.3018493-0.996179	0.9371690-1.076822
	B2	8.18446	1.00008	0.62421	0.98355
	2.5%-97.5%	2.0886639-32.070917	0.9998811-1.000285	0.3476035-1.120923	0.9001979-1.074622
	B2.5	9.78167	1.00006	0.58748	0.98871
	2.5%-97.5%	2.6075887-36.693334	0.9998644-1.000262	0.3329574-1.036563	0.9103863-1.073783
	B5	10.7918	1.00009	0.54419	1.00999
	2.5%-97.5%	2.8266207-41.202298	0.9998900-1.000285	0.3073843-0.963415	0.9234402-1.104648
	B7.5	11.3759	1.00008	0.53473	1.01758

	2.5%-97.5%	2.9191310-44.332695	0.9998817-1.000269	0.2981885-0.958928	0.9045982-1.144663
	B10	11.5888	1.00007	0.53005	1.02378
	2.5%-97.5%	2.9174451-46.033933	0.9998809-1.000268	0.2926919-0.959888	0.8896972-1.178079

(7) The coefficients of the floating species richness/ Landscape buffers

Landscape variables		**Intercept**	**Lake conductivity**	**Added variable**
Original Model		2.59201	0.99964	
2.5%-97.5%		2.218796-3.028009	0.9988090-1.000476	
Stream density	B0.25	1.91266	0.99965	1.22715
	2.5%-97.5%	1.2495460-2.927673	0.9988347-1.000470	0.9434583-1.596157
	B0.5	1.65375	0.99968	1.46605
	2.5%-97.5%	1.0532219-2.596691	0.9988578-1.000507	1.0296955-2.087307
	B0.75	1.53389	0.99969	1.67827
	2.5%-97.5%	0.9556637-2.461987	0.9988773-1.000513	1.0897919-2.584508
	B1	1.3456	0.99973	2.00737
	2.5%-97.5%	0.8245030-2.196040	0.9989276-1.000538	1.2395423-3.250809
	B2	1.49128	0.99982	1.94396
	2.5%-97.5%	0.9150008-2.430523	0.9989905-1.000642	1.1269573-3.353249
	B2.5	1.60254	0.99982	1.81292
	2.5%-97.5%	0.9329119-2.752806	0.9989803-1.000656	0.9637920-3.410168
	B5	1.65443	0.99983	1.80509
	2.5%-97.5%	0.8828527-3.100345	0.9989811-1.000678	0.8171523-3.987453
	B7.5	1.67805	0.99983	1.78275
	2.5%-97.5%	0.8939733-3.149834	0.9989801-1.000683	0.7980332-3.982523
	B10	1.62369	0.99987	1.86953
	2.5%-97.5%	0.8476883-3.110056	0.9990039-1.000729	0.8101334-4.314276

Lake density	B0.25	2.49115	0.99942	1.05574
	2.5%-97.5%	2.0910989-2.967730	0.9984953-1.000355	0.9483064-1.175355
	B0.5	2.46162	0.99931	1.12773
	2.5%-97.5%	2.0664296-2.932377	0.9983409-1.000271	0.9347421-1.360566
	B0.75	2.53013	0.99953	1.06764
	2.5%-97.5%	2.1190590-3.020952	0.9986226-1.000440	0.8485063-1.343368
	B1	2.52315	0.9995	1.09633
	2.5%-97.5%	2.1195574-3.003581	0.9985836-1.000417	0.8371606-1.435730
	B2	2.46322	0.99945	1.27386
	2.5%-97.5%	2.0553039-2.952096	0.9985679-1.000334	0.8242537-1.968722
	B2.5	2.45044	0.99944	1.34803
	2.5%-97.5%	2.0418979-2.940718	0.9985604-1.000327	0.8205211-2.214666
	B5	2.44559	0.9995	1.44907
	2.5%-97.5%	2.0237818-2.955312	0.9986444-1.000364	0.7400152-2.837518
	B7.5	2.4602	0.99955	1.42886
	2.5%-97.5%	2.0231542-2.991646	0.9986951-1.000400	0.6453428-3.163649
	B10	2.45574	0.99956	1.49951
	2.5%-97.5%	2.0089632-3.001880	0.9987064-1.000406	0.5888536-3.818478
Lake coverage	B0.25	2.93696	0.99957	0.99649
	2.5%-97.5%	2.1809227-3.955078	0.9986995-1.000433	0.9893012-1.003726
	B0.5	2.90125	0.99959	0.99504
	2.5%-97.5%	2.2194163-3.792564	0.9987326-1.000446	0.9853522-1.004820
	B0.75	2.89521	0.9996	0.99331
	2.5%-97.5%	2.2463159-3.731563	0.9987512-1.000457	0.9810725-1.005703
	B1	2.92224	0.99961	0.99079
	2.5%-97.5%	2.2806044-3.744386	0.9987569-1.000462	0.9758001-1.006001
	B2	3.02254	0.99962	0.97888
	2.5%-97.5%	2.3631176-3.865984	0.9987701-1.000478	0.9525097-1.005973
	B2.5	2.92956	0.99962	0.98032

	2.5%-97.5%	2.2844065-3.756907	0.9987772-1.000472	0.9491720-1.012483
	B5	2.71755	0.99965	0.988
	2.5%-97.5%	2.1369119-3.455946	0.9988060-1.000488	0.9424148-1.035796
	B7.5	2.58647	0.99964	1.00067
	2.5%-97.5%	2.0209703-3.310203	0.9988093-1.000476	0.9428968-1.061973
	B10	2.36424	0.99966	1.03217
	2.5%-97.5%	1.8353784-3.045485	0.9988513-1.000471	0.9643727-1.104739
Lake fractal index	B0.25	16.06364	0.99958	0.18995
	2.5%-97.5%	0.1583313-1629.750	0.9987131-1.000438	0.0028286-12.75559
	B0.5	32.06626	0.99959	0.09964
	2.5%-97.5%	0.1857998-5534.152	0.9987256-1.000450	0.0008848-11.22000
	B0.75	5.66134	0.99963	0.48844
	2.5%-97.5%	0.0232541-1378.281	0.9987933-1.000474	0.0031650-75.37736
	B1	5.72861	0.99963	0.4831
	2.5%-97.5%	0.0143773-2282.551	0.9987882-1.000473	0.0019900-117.2789
	B2	0.20893	0.99965	10.2472
	2.5%-97.5%	0.0001510-289.0915	0.9988261-1.000478	0.0128750-8155.743
	B2.5	3.09324	0.99964	0.84915
	2.5%-97.5%	0.0011816-8097.168	0.9988086-1.000476	0.0005862-1229.982
	B5	0.02303	0.99959	80.5596
	2.5%-97.5%	0.0000160-330.4806	0.9987523-1.000436	0.0111070-584297.9
	B7.5	0.0036	0.9996	453.276
	2.5%-97.5%	0.00008588-151.089	0.9987683-1.000436	0.0229339-8958777
	B10	0.00057	0.99958	182659.4
	2.5%-97.5%	1.997575E-11-1.617	0.9987468-1.000417	1.564084-2133162000
Agriculture	B0.25	2.32647	0.99936	1.0102
	2.5%-97.5%	1.8388462-2.943400	0.9983267-1.000392	0.9969089-1.023662
	B0.5	2.28971	0.99948	1.0073
	2.5%-97.5%	1.7979929-2.915914	0.9984909-1.000475	0.9961899-1.018528

	B0.75	2.32689	0.99944	1.00626
	2.5%-97.5%	1.8535817-2.921047	0.9984399-1.000443	0.9968662-1.015745
	B1	2.36321	0.99948	1.00523
	2.5%-97.5%	1.8864694-2.960419	0.9984951-1.000463	0.9966159-1.013916
	B2	2.42081	0.99951	1.00411
	2.5%-97.5%	1.9808606-2.958467	0.9985477-1.000481	0.9964173-1.011852
	B2.5	2.42793	0.99952	1.00374
	2.5%-97.5%	2.0031984-2.942722	0.9985576-1.000487	0.9963810-1.011146
	B5	2.49668	0.99958	1.00201
	2.5%-97.5%	2.0980819-2.970994	0.9986364-1.000517	0.9949425-1.009122
	B7.5	2.55533	0.99962	1.00088
	2.5%-97.5%	2.1590977-3.024282	0.9987074-1.000528	0.9936652-1.008146
	B10	2.57909	0.99963	1.00035
	2.5%-97.5%	2.1843832-3.045127	0.9987305-1.000528	0.9931331-1.007614
Urban	B0.25	2.6972	0.99867	1.01402
	2.5%-97.5%	1.9344931-3.760606	0.9964447-1.000899	0.9874986-1.041246
	B0.5	2.69819	0.99881	1.02714
	2.5%-97.5%	1.9743420-3.687430	0.9968750-1.000745	0.9842518-1.071889
	B0.75	2.51181	0.99871	1.04602
	2.5%-97.5%	1.8338080-3.440491	0.9966939-1.000721	0.9952852-1.099350
	B1	2.62216	0.99872	1.04503
	2.5%-97.5%	1.9496785-3.526597	0.9967465-1.000699	0.9867614-1.106736
	B2	2.32299	0.9997	1.03047
	2.5%-97.5%	1.7903255-3.014147	0.9987773-1.000617	0.9625834-1.103147
	B2.5	2.4815	0.99966	1.02125
	2.5%-97.5%	1.9753593-3.117320	0.9987458-1.000576	0.9477429-1.100468
	B5	2.35707	0.9996	1.06633
	2.5%-97.5%	1.9187645-2.895496	0.9986392-1.000560	0.9774439-1.163292
	B7.5	2.41725	0.99974	1.05028

	2.5%-97.5%	1.9964118-2.926809	0.9988922-1.000583	0.9660294-1.141889
	B10	2.48336	0.99974	1.03321
	2.5%-97.5%	2.0770937-2.969081	0.9989047-1.000580	0.9461963-1.128230

(8) The coefficients of the floating species richness/ Catchment buffers

Catchment variables		Intercept	Lake conductivity	Added variable
Original Model		2.59201	0.99964	
2.5%-97.5%		2.218796-3.028009	0.9988090-1.000476	
Stream density	B0.25	2.20674	0.99961	1.11632
	2.5%-97.5%	1.4756143-3.300119	0.9987805-1.000447	0.8680972-1.435510
	B0.5	2.09667	0.99961	1.20319
	2.5%-97.5%	1.3919811-3.158093	0.9987755-1.000454	0.8681090-1.667619
	B0.75	2.08309	0.99962	1.24303
	2.5%-97.5%	1.3739040-3.158358	0.9987808-1.000469	0.8505741-1.816566
	B1	1.91023	0.99962	1.38194
	2.5%-97.5%	1.2480242-2.923817	0.9987729-1.000458	0.9144067-2.088511
	B2	1.97685	0.99964	1.37675
	2.5%-97.5%	1.3017914-3.001964	0.9988029-1.000481	0.8774427-2.160199
	B2.5	1.9894	0.99964	1.37595
	2.5%-97.5%	1.2762369-3.101077	0.9988054-1.000479	0.8387226-2.257274
	B5	2.0078	0.99962	1.38944
	2.5%-97.5%	1.1422995-3.529074	0.9987919-1.000452	0.6945358-2.779629
	B7.5	2.16721	0.99963	1.25962
	2.5%-97.5%	1.1778371-3.987644	0.9987978-1.000465	0.5908355-2.685404
	B10	1.90807	0.99963	1.48649
	2.5%-97.5%	1.0093320-3.607069	0.9988002-1.000460	0.6721470-3.287459

Lake density	B0.25	2.59937	0.99966	0.99637
	2.5%-97.5%	2.1923135-3.082013	0.9987397-1.000577	0.9109316-1.089816
	B0.5	2.56591	0.99957	1.02231
	2.5%-97.5%	2.1654213-3.040479	0.9986108-1.000532	0.8826979-1.184010
	B0.75	2.56847	0.99959	1.0238
	2.5%-97.5%	2.1648915-3.047284	0.9986542-1.000522	0.8539357-1.227452
	B1	2.55878	0.99954	1.04512
	2.5%-97.5%	2.1656494-3.023277	0.9985891-1.000495	0.8506793-1.284012
	B2	2.5134	0.99949	1.14162
	2.5%-97.5%	2.1140771-2.988137	0.9985801-1.000397	0.8297656-1.570675
	B2.5	2.49862	0.99947	1.18549
	2.5%-97.5%	2.0988514-2.974526	0.9985717-1.000376	0.8315237-1.690127
	B5	2.49241	0.99955	1.22568
	2.5%-97.5%	2.0833520-2.981788	0.9986971-1.000407	0.7829441-1.918775
	B7.5	2.48159	0.99955	1.26668
	2.5%-97.5%	2.0689998-2.976455	0.9987007-1.000407	0.7721470-2.077930
	B10	2.4824	0.99955	1.27534
	2.5%-97.5%	2.0692197-2.978072	0.9986953-1.000406	0.7612997-2.136454
Lake coverage	B0.25	2.90158	0.99957	0.99688
	2.5%-97.5%	2.1551226-3.906584	0.9987029-1.000439	0.9898123-1.003988
	B0.5	2.9254	0.99958	0.99487
	2.5%-97.5%	2.2382317-3.823531	0.9987164-1.000440	0.9855505-1.004282
	B0.75	2.93695	0.9996	0.9929
	2.5%-97.5%	2.2762746-3.789385	0.9987399-1.000456	0.9813108-1.004624
	B1	2.9758	0.99961	0.99031
	2.5%-97.5%	2.3194569-3.817872	0.9987565-1.000468	0.9764858-1.004329
	B2	3.00681	0.99963	0.98346
	2.5%-97.5%	2.3728651-3.810130	0.9987835-1.000475	0.9632843-1.004056
	B2.5	2.93145	0.99964	0.98472

	2.5%-97.5%	2.3241808-3.697382	0.9988049-1.000477	0.9630560-1.006869
	B5	2.80613	0.99964	0.98678
	2.5%-97.5%	2.2632058-3.479309	0.9988145-1.000472	0.9618041-1.012398
	B7.5	2.71336	0.99964	0.99141
	2.5%-97.5%	2.1757782-3.383764	0.9988051-1.000470	0.9620874-1.021620
	B10	2.65798	0.99964	0.99494
	2.5%-97.5%	2.1232663-3.327355	0.9988055-1.000473	0.9627019-1.028266
Lake fractal index	B0.25	9.75045	0.9996	0.29895
	2.5%-97.5%	0.1070006-888.5109	0.9987432-1.000457	0.0048951-18.25686
	B0.5	17.34324	0.9996	0.17567
	2.5%-97.5%	0.1184394-2539.593	0.9987413-1.000456	0.0018323-16.84186
	B0.75	9.34046	0.99962	0.30918
	2.5%-97.5%	0.0621745-1403.214	0.9987719-1.000469	0.0031417-30.42607
	B1	9.08619	0.99961	0.3168
	2.5%-97.5%	0.0506414-1630.262	0.9987636-1.000465	0.0027257-36.82023
	B2	10.25676	0.99963	0.28177
	2.5%-97.5%	0.0443531-2371.902	0.9987831-1.000470	0.0018752-42.34091
	B2.5	180.3226	0.99965	0.01981
	2.5%-97.5%	0.2820812-115272.7	0.9988073-1.000488	0.0000503-7.794502
	B5	43.94042	0.99966	0.07247
	2.5%-97.5%	0.0417605-46234.09	0.9988248-1.000497	0.0001141-46.03879
	B7.5	11.13293	0.99966	0.25831
	2.5%-97.5%	0.0047594-26041.74	0.9988199-1.000492	0.0001919-347.5579
	B10	6.25448	0.99965	0.44114
	2.5%-97.5%	0.0020501-19081.39	0.9988142-1.000487	0.0002556-761.4045
Agriculture	B0.25	2.32756	0.99936	1.01033
	2.5%-97.5%	1.8400250-2.944277	0.9983255-1.000391	0.9968381-1.024006
	B0.5	2.39608	0.99951	1.00544
	2.5%-97.5%	1.8887727-3.039638	0.9985276-1.000501	0.9945076-1.016488

	B0.75	2.34864	0.99953	1.00528
	2.5%-97.5%	1.8527290-2.977285	0.9985575-1.000510	0.9959213-1.014735
	B1	2.42411	0.99954	1.00419
	2.5%-97.5%	1.9343336-3.037902	0.9985684-1.000506	0.9957608-1.012684
	B2	2.36278	0.99945	1.00527
	2.5%-97.5%	1.9016617-2.935713	0.9984364-1.000472	0.9974425-1.013159
	B2.5	2.3094	0.99944	1.00582
	2.5%-97.5%	1.8657129-2.858589	0.9984053-1.000476	0.9981655-1.013542
	B5	2.37729	0.9995	1.00425
	2.5%-97.5%	1.9440245-2.907113	0.9984920-1.000513	0.9967312-1.011830
	B7.5	2.4077	0.99954	1.00353
	2.5%-97.5%	1.9776687-2.931246	0.9985394-1.000535	0.9956808-1.011435
	B10	2.42653	0.99957	1.0029
	2.5%-97.5%	1.9980926-2.946833	0.9985874-1.000552	0.9946735-1.011201
Urban	B0.25	2.70349	0.99866	1.01278
	2.5%-97.5%	1.9418076-3.763943	0.9964361-1.000895	0.9893156-1.036811
	B0.5	2.75923	0.99838	1.02653
	2.5%-97.5%	2.0093050-3.789048	0.9961478-1.000625	0.9891360-1.065329
	B0.75	2.51374	0.99882	1.0406
	2.5%-97.5%	1.8353551-3.442870	0.9968464-1.000801	0.9947633-1.088546
	B1	2.65371	0.99878	1.03768
	2.5%-97.5%	1.9676129-3.579045	0.9968330-1.000737	0.9884507-1.089357
	B2	2.54075	0.99962	1.02161
	2.5%-97.5%	1.9402497-3.327098	0.9986899-1.000550	0.9587619-1.088577
	B2.5	2.62154	0.99962	1.01171
	2.5%-97.5%	2.0390896-3.370358	0.9987002-1.000542	0.9510263-1.076260
	B5	2.45918	0.99966	1.02088
	2.5%-97.5%	1.9238558-3.143470	0.9987252-1.000588	0.9506803-1.096268
	B7.5	2.45822	0.99963	1.02964

	2.5%-97.5%	1.9362180-3.120959	0.9986849-1.000584	0.9384969-1.129630
	B10	2.46027	0.99963	1.03432
	2.5%-97.5%	1.9387066-3.122146	0.9986671-1.000589	0.9268609-1.154242

Appendix 5.4 c

The estimates of coefficients for GLM models in Figure 3.3, including measures of confidence (2.5%-97.5%) in those coefficients

(1) the coefficients of models predicting the total richness for catchment buffers

Buffer Distance (km)	Confidence interval	Coefficeints			
0.25		(Intercept)	PCA1	PCA4	
		2.5513294	0.09171078	0.07115405	
	2.5 %-97.5 %	(2.457699051, 2.6449597)	(-0.002570819, 0.1859924)	(-0.021214800, 0.1635229)	
0.5		(Intercept)	PCA1	PCA4	PCA5
		2.55139446	0.08388017	0.02437674	0.07521357
	2.5 %-97.5 %	(2.45774986,2.6450391)	(-0.01072365, 0.1784840)	(-0.07598744, 0.1247409)	(-0.01545588, 0.1658830)
0.75		(Intercept)	PCA1	PCA4	
		2.55427292	0.07257594	0.05332233	
	2.5 %-97.5 %	(2.45929106, 2.6492548)	(-0.02225736, 0.1674092)	(-0.04171019, 0.1483549)	
1		(Intercept)	PCA1	PCA3	
		2.55489397	0.06435768	0.05159555	
	2.5 %-97.5 %	(2.45965536, 2.6501326)	(-0.03056776, 0.1592831)	(-0.04417270, 0.1473638)	

2		(Intercept)	PCA1	PCA2	PCA4
		2.55611702	0.04052748	0.04778965	0.01724651
	2.5%-97.5%	(2.46038042, 2.6518536)	(-0.05464573, 0.1357007)	(-0.04697288, 0.1425522)	(-0.07885369, 0.1133467)
2.5		(Intercept)	PCA1	PCA3	PCA4
		2.55756142	0.03214544	0.01505552	-0.00192094
	2.5 %-97.5 %	(2.46121487, 2.65390798)	(-0.06408132, 0.12837221)	(-0.08221815, 0.11232919)	(-0.09897075, 0.09512887)
5		(Intercept)	PCA2	PCA3	PCA4
		2.557194429	-0.001436159	0.02676208	-0.031768786
	2.5 %-97.5 %	(2.46103895, 2.65334990)	(-0.09813004, 0.09525772)	(-0.07060773, 0.12413189)	(-0.12807918, 0.06454161)
7.5		(Intercept)	PCA2	PCA3	PCA4
		2.555656958	0.003270755	0.011671163	0.064749926
	2.5 %-97.5 %	(2.46022852, 2.65108539)	(-0.09327750, 0.09981901)	(-0.08493571, 0.10827804)	(-0.02935617, 0.15885602)
10		(Intercept)	PCA2	PCA3	
		2.557982633	0.019788104	-0.002766607	
	2.5 %-97.5 %	(2.46146056, 2.65450471)	(-0.07663803, 0.11621424)	(-0.09988070, 0.09434749)	

(2) the coefficients of models predicting the total richness for landscape buffers

Buffer Distance (km)	Confidence interval	Coefficeints		
0.25		(Intercept)	PCA1	PCA4
		2.55196416	0.08232441	0.07023477
	2.5 %-97.5 %	(2.45813726, 2.6457911)	(-0.01206132, 0.1767101)	(-0.02123550, 0.1617050)

0.5		(Intercept)	PCA1	PCA4	
		2.55339047	0.07846132	0.05637233	
	2.5 %-97.5 %	(2.45887116, 2.6479098)	(-0.01608049, 0.1730031)	(-0.03639865, 0.1491433)	
0.75		(Intercept)	PCA1	PCA4	
		2.55066361	0.07100329	0.09578619	
	2.5 %-97.5 %	(2.457433789, 2.6438934)	(-0.022375454, 0.1643820)	(0.004863706, 0.1867087)	
1		(Intercept)	PCA1	PCA3	PCA5
		2.54621908	0.0807304	0.02225025	0.15370752
	2.5 %-97.5 %	(2.45726239, 2.6351758)	(-0.00715511, 0.1686159)	(-0.06545957, 0.1099601)	(0.06647911, 0.2409359)
2		(Intercept)	PCA1	PCA3	PCA4
		2.55450526	0.05067544	0.0212131	0.06275099
	2.5%-97.5%	(2.45952510, 2.6494854)	(-0.04404076, 0.1453916)	(-0.07521726, 0.1176435)	(-0.03097461, 0.1564766)
2.5		(Intercept)	PCA1	PCA3	PCA4
		2.55632095	0.05008415	0.01840744	0.03102544
	2.5 %-97.5 %	(2.46049260, 2.6521493)	(-0.04540600, 0.1455743)	(-0.07862100, 0.1154359)	(-0.06485824, 0.1269091)
5		(Intercept)	PCA2	PCA3	PCA4
		2.55322152	0.03730915	0.03425901	0.08408555
	2.5 %-97.5 %	(2.458781443, 2.6476616)	(-0.057197732, 0.1318160)	(-0.061713483, 0.1302315)	(-0.009511238, 0.1776823)
7.5		(Intercept)	PCA2	PCA3	PCA4
		2.550601667	0.03668068	-0.00055263	0.128571803
	2.5 %-97.5 %	(2.45847382, 2.64272951)	(-0.05573693, 0.12909829)	(-0.09327001, 0.09216475)	(0.03769168, 0.21945193)
10		(Intercept)	PCA2	PCA3	PCA4
		2.54577054	0.08535278	0.08449171	0.09928679
	2.5 %-97.5 %	(2.454688986, 2.6368521)	(-0.005016034, 0.1757216)	(-0.009418885, 0.1784023)	(0.010678615, 0.1878950)

Appendix 5.4 d

The estimates of coefficients for OLS models of species turnover related to catchment-scale hydrological and land use variables.in Figure 4.7, including measures of confidence (2.5%-97.5%) in those coefficients

coefficient	Intercept	Land use
	-0.2343006	0.8550338
2.5%-97.5%	(-0.643855, 0.175253)	(0.030543, 1.679523)
coefficient	Intercept	Lake density
	-0.7033715	11.1214207
2.5%-97.5%	(-1.162074, -0.244668)	(5.197695,17.045146)
coefficient	Intercept	Stream density
	1.2725053	-0.00157885
2.5%-97.5%	(-0.555766,3.100776)	(-0.003799,0.000642)
coefficient	Intercept	Proximity index
	0.1047454	-0.00244037
2.5%-97.5%	(-0.478621,0.688112)	(-0.012303,0.007422)

Appendix 5.4 e

The estimates of the coefficients for GAM models in Table 4.2, including measures of confidence (2.5%-97.5%) in those coefficients

(1) the coefficient of GAM models (Null model)

NULL MODEL	coefficient
(Intercept)	0.6584323
2.5 %-97.5 %	(0.6355605, 0.6813042)

(2) the coefficient of GAM models (part 1)

MODEL 1	Catchment	MODEL 2	Catchment+Altitude	MODEL 3	Catchment+Conductivity	MODEL 4	Catchment+pH
parameter	COEFFICEINT	parameter	COEFFICEINT	parameter	COEFFICEINT	parameter	COEFFICEINT
(Intercept)	0.78903768	(Intercept)	2.1457103	(Intercept)	2.1673903	(Intercept)	2.2083638
(2.5 %, 97.5 %)	(0.73385486, 0.84422049)	(2.5 %, 97.5 %)	(2.0330154, 2.2646522)	2.5 %-97.5 %	(2.0540912, 2.2869387)	2.5 %-97.5 %	(2.0932025, 2.3298610)
watershed28955	0.07107262	factor(watershed)28955	1.0704672	factor(watershed)28955	1.080969	factor(watershed)28955	1.0511478
(2.5 %, 97.5 %)	(-0.04598780, 0.18813304)	(2.5 %, 97.5 %)	(0.9567342, 1.1977203)	2.5 %-97.5 %	(0.9654477, 1.2103130)	2.5 %-97.5 %	(0.9345773, 1.1822583)
watershed29000	-0.27164149	factor(watershed)29000	0.7781928	factor(watershed)29000	0.7557843	factor(watershed)29000	0.7437991
(2.5 %, 97.5 %)	(-0.38352947, -0.15975351)	(2.5 %, 97.5 %)	(0.6987457, 0.8666729)	2.5 %-97.5 %	(0.6783778, 0.8420234)	2.5 %-97.5 %	(0.6669306, 0.8295273)
watershed29233	-0.01268804	factor(watershed)29233	1.0316419	factor(watershed)29233	0.9696802	factor(watershed)29233	0.9877098
(2.5 %, 97.5 %)	(-0.09221494, 0.06683886)	(2.5 %, 97.5 %)	(0.9539039, 1.1157151)	2.5 %-97.5 %	(0.8976706, 1.0474664)	2.5 %-97.5 %	(0.9135062, 1.0679409)
watershedA	-0.1822428	factor(watershed)A	0.846461	factor(watershed)A	0.8514674	factor(watershed)A	0.822527
(2.5 %, 97.5 %)	(-0.25457122, -0.10991439)	(2.5 %, 97.5 %)	(0.7894847, 0.9075492)	2.5 %-97.5 %	(0.7935575, 0.9136034)	2.5 %-97.5 %	(0.7666179, 0.8825135)
watershedB	-0.14572998	factor(watershed)B	0.9253518	factor(watershed)B	0.8912715	factor(watershed)B	0.8758997
(2.5 %, 97.5 %)	(-0.24372953, -0.04773043)	(2.5 %, 97.5 %)	(0.8389716, 1.0206257)	2.5 %-97.5 %	(0.8100704, 0.9806121)	2.5 %-97.5 %	(0.7957103, 0.9641703)
watershedC	-0.28097316	factor(watershed)C	0.7702394	factor(watershed)C	0.7864714	factor(watershed)C	0.7609212
(2.5 %, 97.5 %)	(-0.35710196, -0.20484436)	(2.5 %, 97.5 %)	(0.7156650, 0.8289755)	2.5 %-97.5 %	(0.7292009, 0.8482398)	2.5 %-97.5 %	(0.7064304, 0.8196152)

watershedD	-0.19668768	factor(watershed)D	0.8336332	factor(watershed)D	0.8561073	factor(watershed)D	0.8178968
(2.5 %, 97.5 %)	(-0.28217652, -0.11119883)	(2.5 %, 97.5 %)	(0.7678168, 0.9050913)	2.5 %-97.5 %	(0.7867661, 0.9315598)	2.5 %-97.5 %	(0.7526628, 0.8887848)
watershedE	-0.22997101	factor(watershed)E	0.8147583	factor(watershed)E	0.8237117	factor(watershed)E	0.7880746
(2.5 %, 97.5 %)	(-0.32340232, -0.13653970)	(2.5 %, 97.5 %)	(0.7444682, 0.8916849)	2.5 %-97.5 %	(0.7516562, 0.9026746)	2.5 %-97.5 %	(0.7196445, 0.8630117)
watershedF	-0.04159031	factor(watershed)F	0.9984946	factor(watershed)F	0.9576842	factor(watershed)F	0.9636835
(2.5 %, 97.5 %)	(-0.11431535, 0.03113474)	(2.5 %, 97.5 %)	(0.9294619, 1.0726545)	2.5 %-97.5 %	(0.8927645, 1.0273246)	2.5 %-97.5 %	(0.8973809, 1.0348848)
watershedG	-0.41143768	factor(watershed)G	0.7079953	factor(watershed)G	0.6681062	factor(watershed)G	0.6694218
(2.5 %, 97.5 %)	(-0.50486898, -0.31800637)	(2.5 %, 97.5 %)	(0.6447590, 0.7774337)	2.5 %-97.5 %	(0.6104527, 0.7312047)	2.5 %-97.5 %	(0.6108969, 0.7335535)
watershedH	-0.01570434	factor(watershed)H	0.9961174	factor(watershed)H	1.0105596	factor(watershed)H	0.9678019
(2.5 %, 97.5 %)	(-0.09243293, 0.06102425)	(2.5 %, 97.5 %)	(0.9252734, 1.0723856)	2.5 %-97.5 %	(0.9375999, 1.0891968)	2.5 %-97.5 %	(0.8968976, 1.0443116)
		s(Al1).1	0.9999996	s(con1).1	1.0000007	s(ph1).1	0.9842129
		(2.5 %, 97.5 %)	(0.9996966, 1.0003027)	2.5 %-97.5 %	(0.9997051, 1.0002965)	2.5 %-97.5 %	(0.9305243, 1.0409993)
		s(Al1).2	1.0000001	s(con1).2	0.9999999	s(ph1).2	1.0099984
		(2.5 %, 97.5 %)	(0.9996324, 1.0003680)	2.5 %-97.5 %	(0.9996480, 1.0003520)	2.5 %-97.5 %	(0.8754185, 1.1652674)
		s(Al1).3	1	s(con1).3	1	s(ph1).3	1.0018224
		(2.5 %, 97.5 %)	(0.9998704, 1.0001296)	2.5 %-97.5 %	(0.9998992, 1.0001008)	2.5 %-97.5 %	(0.9728271, 1.0316818)
		s(Al1).4	1.0000001	s(con1).4	1	s(ph1).4	0.9898184
		(2.5 %, 97.5 %)	(0.9997567, 1.0002435)	2.5 %-97.5 %	(0.9998200, 1.0001800)	2.5 %-97.5 %	(0.9123862, 1.0738220)
		s(Al1).5	1	s(con1).5	1	s(ph1).5	0.999722
		(2.5 %, 97.5 %)	(0.9999091, 1.0000908)	2.5 %-97.5 %	(0.9999323, 1.0000677)	2.5 %-97.5 %	(0.9808159, 1.0189926)
		s(Al1).6	0.9999999	s(con1).6	1	s(ph1).6	1.0085774
		(2.5 %, 97.5 %)	(0.9997849, 1.0002150)	2.5 %-97.5 %	(0.9998431, 1.0001569)	2.5 %-97.5 %	(0.9425504, 1.0792297)
		s(Al1).7	1	s(con1).7	1	s(ph1).7	0.9949013
		(2.5 %, 97.5 %)	(0.9999507, 1.0000493)	2.5 %-97.5 %	(0.9998909, 1.0001091)	2.5 %-97.5 %	(0.9515603, 1.0402162)
		s(Al1).8	0.9999997	s(con1).8	0.9999997	s(ph1).8	1.0765611
		(2.5 %, 97.5 %)	(0.9989517, 1.0010489)	2.5 %-97.5 %	(0.9987299, 1.0012712)	2.5 %-97.5 %	(0.8141886, 1.4234833)

	s(Al1).9	1.0473188	s(con1).9	1.0445537	s(ph1).9	1.0072849
	(2.5 %, 97.5 %)	(1.0278871, 1.0671179)	2.5 %-97.5 %	(1.0248372, 1.0646497)	2.5 %-97.5 %	(0.9191030, 1.1039273)

(3) the coefficient of GAM models (part 2)

MODEL5	Catchment+Alkalinity	MODEL6	Catchment+Depth	MODEL7	Catchment+Area
parameter	COEFFICEINT	parameter	COEFFICEINT	parameter	COEFFICEINT
(Intercept)	2.1862083	(Intercept)	2.2000078	(Intercept)	2.2120207
2.5 %-97.5 %	(2.0700357, 2.3089006)	2.5 %-97.5 %	(2.0832397, 2.3233208)	2.5%-97.5%	(2.0955181, 2.3350005)
factor(watershed)28955	1.0854753	factor(watershed)28955	1.0508767	factor(watershed)28955	1.0508984
2.5 %-97.5 %	(0.9669171, 1.2185704)	2.5 %-97.5 %	(0.9369727, 1.1786275)	2.5%-97.5%	(0.9364921, 1.1792811)
factor(watershed)29000	0.7480627	factor(watershed)29000	0.7733604	factor(watershed)29000	0.7570427
2.5 %-97.5 %	(0.6686211, 0.8369430)	2.5 %-97.5 %	(0.6928775, 0.8631920)	2.5%-97.5%	(0.6784370, 0.8447559)
factor(watershed)29233	0.9792003	factor(watershed)29233	1.0384451	factor(watershed)29233	0.9695697
2.5 %-97.5 %	(0.9051118, 1.0593533)	2.5 %-97.5 %	(0.9572989, 1.1264697)	2.5%-97.5%	(0.8963286, 1.0487953)
factor(watershed)A	0.8457748	factor(watershed)A	0.8353659	factor(watershed)A	0.8364483
2.5 %-97.5 %	(0.7869993, 0.9089399)	2.5 %-97.5 %	(0.7784564, 0.8964357)	2.5%-97.5%	(0.7792323, 0.8978654)
factor(watershed)B	0.8871747	factor(watershed)B	0.8614041	factor(watershed)B	0.8596192
2.5 %-97.5 %	(0.8043211, 0.9785630)	2.5 %-97.5 %	(0.7817871, 0.9491293)	2.5%-97.5%	(0.7809220, 0.9462472)
factor(watershed)C	0.7696302	factor(watershed)C	0.7453351	factor(watershed)C	0.7528096
2.5 %-97.5 %	(0.7132083, 0.8305156)	2.5 %-97.5 %	(0.6903150, 0.8047405)	2.5%-97.5%	(0.6987168, 0.8110901)
factor(watershed)D	0.8363032	factor(watershed)D	0.8247466	factor(watershed)D	0.8293806
2.5 %-97.5 %	(0.7681330, 0.9105233)	2.5 %-97.5 %	(0.7563287, 0.8993537)	2.5%-97.5%	(0.7626439, 0.9019572)
factor(watershed)E	0.8031742	factor(watershed)E	0.7524129	factor(watershed)E	0.7658145
2.5 %-97.5 %	(0.7322384, 0.8809820)	2.5 %-97.5 %	(0.6767648, 0.8365170)	2.5%-97.5%	(0.6972420, 0.8411310)
factor(watershed)F	0.9552179	factor(watershed)F	0.9852369	factor(watershed)F	0.9833563
2.5 %-97.5 %	(0.8890718, 1.0262852)	2.5 %-97.5 %	(0.9172116, 1.0583073)	2.5%-97.5%	(0.9145246, 1.0573686)

factor(watershed)G	0.6835722	factor(watershed)G	0.6298826	factor(watershed)G	0.6421766
2.5 %-97.5 %	(0.6220893, 0.7511315)	2.5 %-97.5 %	(0.5699568, 0.6961092)	2.5%-97.5%	(0.5850396, 0.7048938)
factor(watershed)H	0.978988	factor(watershed)H	0.9754144	factor(watershed)H	0.9614624
2.5 %-97.5 %	(0.9075844, 1.0560091)	2.5 %-97.5 %	(0.9028565, 1.0538034)	2.5%-97.5%	(0.8908345, 1.0376898)
s(alk1).1	1.0040172	s(mndp1).1	1.0786639	s(area1).1	1.0000009
2.5 %-97.5 %	(0.9764481, 1.0323647)	2.5 %-97.5 %	(1.0071913, 1.1552083)	2.5%-97.5%	(0.9993545, 1.0006477)
s(alk1).2	0.9977978	s(mndp1).2	1.0169398	s(area1).2	1.0000013
2.5 %-97.5 %	(0.9717139, 1.0245819)	2.5 %-97.5 %	(0.8421779, 1.2279669)	2.5%-97.5%	(0.9991997, 1.0008035)
s(alk1).3	1.000444	s(mndp1).3	0.9950231	s(area1).3	1.0000003
2.5 %-97.5 %	(0.9911693, 1.0098054)	2.5 %-97.5 %	(0.9517197, 1.0402968)	2.5%-97.5%	(0.9997254, 1.0002753)
s(alk1).4	1.0016611	s(mndp1).4	1.0009772	s(area1).4	0.9999998
2.5 %-97.5 %	(0.9876492, 1.0158718)	2.5 %-97.5 %	(0.8836819, 1.1338417)	2.5%-97.5%	(0.9995062, 1.0004936)
s(alk1).5	0.9999733	s(mndp1).5	0.9936001	s(area1).5	0.9999999
2.5 %-97.5 %	(0.9952025, 1.0047671)	2.5 %-97.5 %	(0.9617304, 1.0265260)	2.5%-97.5%	(0.9997912, 1.0002086)
s(alk1).6	0.9986128	s(mndp1).6	0.997903	s(area1).6	1.0000003
2.5 %-97.5 %	(0.9858880, 1.0115018)	2.5 %-97.5 %	(0.9189448, 1.0836456)	2.5%-97.5%	(0.9995916, 1.0004091)
s(alk1).7	1.0003891	s(mndp1).7	0.998192	s(area1).7	0.9999999
2.5 %-97.5 %	(0.9954324, 1.0053704)	2.5 %-97.5 %	(0.9482513, 1.0507629)	2.5%-97.5%	(0.9998779, 1.0001220)
s(alk1).8	0.9873879	s(mndp1).8	0.991307	s(area1).8	1.000002
2.5 %-97.5 %	(0.8933969, 1.0912672)	2.5 %-97.5 %	(0.7111773, 1.3817786)	2.5%-97.5%	(0.9980481, 1.0019597)
s(alk1).9	1.0243621	s(mndp1).9	1.1090384	s(area1).9	1.0361605
2.5 %-97.5 %	(0.9870620, 1.0630718)	2.5 %-97.5 %	(0.9922846, 1.2395297)	2.5%-97.5%	(1.0156593, 1.0570757)

(4) the coefficient of GAM models (part 3)

MODEL8	Catchment+Geography	MODEL9	Catchment+Hydrology
parameter	COEFFICEINT	PARAMETER	COEFFICEINT
(Intercept)	2.1617044	(Intercept)	2.1531037
2.5 %-97.5 %	(2.0479719, 2.2817529)	2.5 %-97.5 %	(2.0374936, 2.2752737)
factor(watershed)28955	1.0811637	factor(watershed)28955	1.1194509
2.5 %-97.5 %	(0.9644526, 1.2119984)	2.5 %-97.5 %	(0.9957436, 1.2585272)
factor(watershed)29000	0.7940605	factor(watershed)29000	0.8039607
2.5 %-97.5 %	(0.7108132, 0.8870573)	2.5 %-97.5 %	(0.7180702, 0.9001248)
factor(watershed)29233	1.0189242	factor(watershed)29233	1.0370365
2.5 %-97.5 %	(0.9417771, 1.1023908)	2.5 %-97.5 %	(0.9552767, 1.1257939)
factor(watershed)A	0.8613917	factor(watershed)A	0.8618664
2.5 %-97.5 %	(0.8025700, 0.9245245)	2.5 %-97.5 %	(0.8014107, 0.9268827)
factor(watershed)B	0.9061407	factor(watershed)B	0.9025361
2.5 %-97.5 %	(0.8224341, 0.9983668)	2.5 %-97.5 %	(0.8179993, 0.9958095)
factor(watershed)C	0.7643691	factor(watershed)C	0.7721146
2.5 %-97.5 %	(0.7103289, 0.8225206)	2.5 %-97.5 %	(0.7159334, 0.8327045)
factor(watershed)D	0.83797	factor(watershed)D	0.831923
2.5 %-97.5 %	(0.7711830, 0.9105410)	2.5 %-97.5 %	(0.7652125, 0.9044492)
factor(watershed)E	0.8221604	factor(watershed)E	0.8357662
2.5 %-97.5 %	(0.7508894, 0.9001960)	2.5 %-97.5 %	(0.7599544, 0.9191409)
factor(watershed)F	0.9713606	factor(watershed)F	0.9636174
2.5 %-97.5 %	(0.9044833, 1.0431828)	2.5 %-97.5 %	(0.8974443, 1.0346697)
factor(watershed)G	0.6646754	factor(watershed)G	0.6739643
2.5 %-97.5 %	(0.6046783, 0.7306254)	2.5 %-97.5 %	(0.6125778, 0.7415023)
factor(watershed)H	0.9837073	factor(watershed)H	0.9820266

2.5 %-97.5 %	(0.9104014, 1.0629158)	2.5 %-97.5 %	(0.9106148, 1.0590386)
s(over).1	0.9668079	s(hydro).1	0.9930257
2.5 %-97.5 %	(0.9028514, 1.0352949)	2.5 %-97.5 %	(0.9483897, 1.0397625)
s(over).2	1.2188588	s(hydro).2	1.04072
2.5 %-97.5 %	(0.9985799, 1.4877296)	2.5 %-97.5 %	(0.9445997, 1.1466212)
s(over).3	1.0134252	s(hydro).3	0.99669
2.5 %-97.5 %	(0.9733042, 1.0552000)	2.5 %-97.5 %	(0.9798546, 1.0138148)
s(over).4	0.9190847	s(hydro).4	0.9799337
2.5 %-97.5 %	(0.8050343, 1.0492928)	2.5 %-97.5 %	(0.9167230, 1.0475030)
s(over).5	0.9922972	s(hydro).5	0.9936396
2.5 %-97.5 %	(0.9617185, 1.0238482)	2.5 %-97.5 %	(0.9698141, 1.0180504)
s(over).6	1.084621	s(hydro).6	1.0202562
2.5 %-97.5 %	(0.9623735, 1.2223972)	2.5 %-97.5 %	(0.9682951, 1.0750058)
s(over).7	1.0236608	s(hydro).7	0.9964655
2.5 %-97.5 %	(0.9792704, 1.0700634)	2.5 %-97.5 %	(0.9857604, 1.0072867)
s(over).8	1.4394913	s(hydro).8	1.1014486
2.5 %-97.5 %	(0.8895366, 2.3294548)	2.5 %-97.5 %	(0.8708508, 1.3931077)
s(over).9	1.0684658	s(hydro).9	1.0394425
2.5 %-97.5 %	(0.9365826, 1.2189200)	2.5 %-97.5 %	(0.9686014, 1.1154647)

(2) the coefficient of GAM models (part 5)

Multiple model: catchment+altitude+conductivity+depth+area

parameter	coefficient	2.5％-97.5％
(Intercept)	2.149781	(2.0371862, 2.2685990)
factor(watershed)28955	1.0543174	(0.9431131, 1.1786341)
factor(watershed)29000	0.7704098	(0.6922310, 0.8574178)
factor(watershed)29233	1.0166917	(0.9341293, 1.1065513)
factor(watershed)A	0.8564636	(0.7998741, 0.9170567)
factor(watershed)B	0.9114723	(0.8269390, 1.0046469)
factor(watershed)C	0.7777755	(0.7212187, 0.8387673)
factor(watershed)D	0.857574	(0.7880064, 0.9332834)
factor(watershed)E	0.7986401	(0.7202060, 0.8856161)
factor(watershed)F	1.0032446	(0.9348678, 1.0766226)
factor(watershed)G	0.6692236	(0.6040979, 0.7413701)
factor(watershed)H	0.993148	(0.9189975, 1.0732815)
s(Al1).1	0.9999999	(0.9998862, 1.0001136)
s(Al1).2	1	(0.9998620, 1.0001380)
s(Al1).3	1	(0.9999514, 1.0000486)
s(Al1).4	1	(0.9999087, 1.0000913)
s(Al1).5	1	(0.9999659, 1.0000341)
s(Al1).6	1	(0.9999193, 1.0000807)
s(Al1).7	1	(0.9999815, 1.0000185)
s(Al1).8	1.0000001	(0.9996067, 1.0003936)
s(Al1).9	1.0258206	(1.0051170, 1.0469507)
s(con1).1	1.0000017	(0.9996176, 1.0003860)
s(con1).2	0.9999999	(0.9995427, 1.0004573)

s(con1).3	0.9999999	(0.9998690, 1.0001309)
s(con1).4	0.9999998	(0.9997660, 1.0002337)
s(con1).5	1	(0.9999121, 1.0000879)
s(con1).6	0.9999998	(0.9997960, 1.0002037)
s(con1).7	0.9999999	(0.9998582, 1.0001416)
s(con1).8	0.999998	(0.9983487, 1.0016500)
s(con1).9	1.0294607	(1.0096178, 1.0496937)
s(mndp1).1	1.0337392	(0.9850561, 1.0848282)
s(mndp1).2	1.0040759	(0.9001790, 1.1199643)
s(mndp1).3	0.9993738	(0.9754010, 1.0239358)
s(mndp1).4	0.9987472	(0.9323972, 1.0698188)
s(mndp1).5	0.998529	(0.9806321, 1.0167526)
s(mndp1).6	0.9983626	(0.9528645, 1.0460331)
s(mndp1).7	1.0001096	(0.9715041, 1.0295574)
s(mndp1).8	1.0028307	(0.8253856, 1.2184237)
s(mndp1).9	1.0472646	(0.9734015, 1.1267325)
s(area1).1	1.0000003	(0.9997530, 1.0002476)
s(area1).2	1	(0.9996934, 1.0003068)
s(area1).3	1.0000001	(0.9998949, 1.0001052)
s(area1).4	0.9999999	(0.9998111, 1.0001887)
s(area1).5	0.9999999	(0.9999201, 1.0000798)
s(area1).6	1.0000001	(0.9998438, 1.0001565)
s(area1).7	1	(0.9999533, 1.0000466)
s(area1).8	1.0000008	(0.9992530, 1.0007492)
s(area1).9	1.0161903	(0.9942475, 1.0386175)

Appendix 5.4 f

The estimates of coefficients for GAM models in Figure 4.7, including measures of confidence (2.5%-97.5%) in those coefficients

(1) the coefficient of GAM models for the total lake pairs

Environmental similarity		Hydrology distance		Geography distance	
PARAMETER	coefficients	PARAMETER	coefficients	parameter	coefficients
(Intercept)	2.155188	(Intercept)	2.1531037	(Intercept)	2.1617044
2.5 %-97.5 %	(2.0451614, 2.2711340)	2.5 %-97.5 %	(2.0374936, 2.2752737)	2.5 %-97.5 %	(2.0479719, 2.2817529)
watershed28955	1.0683527	factor(watershed)28955	1.1194509	factor(watershed)28955	1.0811637
2.5 %-97.5 %	(0.9588857, 1.1903166)	2.5 %-97.5 %	(0.9957436, 1.2585272)	2.5 %-97.5 %	(0.9644526, 1.2119984)
watershed29000	0.7662957	factor(watershed)29000	0.8039607	factor(watershed)29000	0.7940605
2.5 %-97.5 %	(0.6903529, 0.8505925)	2.5 %-97.5 %	(0.7180702, 0.9001248)	2.5 %-97.5 %	(0.7108132, 0.8870573)
watershed29233	1.0065794	factor(watershed)29233	1.0370365	factor(watershed)29233	1.0189242
2.5 %-97.5 %	(0.9343717, 1.0843672)	2.5 %-97.5 %	(0.9552767, 1.1257939)	2.5 %-97.5 %	(0.9417771, 1.1023908)
watershedA	0.8656459	factor(watershed)A	0.8618664	factor(watershed)A	0.8613917
2.5 %-97.5 %	(0.8052813, 0.9305354)	2.5 %-97.5 %	(0.8014107, 0.9268827)	2.5 %-97.5 %	(0.8025700, 0.9245245)
watershedB	0.8904503	factor(watershed)B	0.9025361	factor(watershed)B	0.9061407
2.5 %-97.5 %	(0.8111011, 0.9775623)	2.5 %-97.5 %	(0.8179993, 0.9958095)	2.5 %-97.5 %	(0.8224341, 0.9983668)
watershedC	0.7645801	factor(watershed)C	0.7721146	factor(watershed)C	0.7643691
2.5 %-97.5 %	(0.7112208, 0.8219426)	2.5 %-97.5 %	(0.7159334, 0.8327045)	2.5 %-97.5 %	(0.7103289, 0.8225206)
watershedD	0.8361949	factor(watershed)D	0.831923	factor(watershed)D	0.83797
2.5 %-97.5 %	(0.7722033, 0.9054893)	2.5 %-97.5 %	(0.7652125, 0.9044492)	2.5 %-97.5 %	(0.7711830, 0.9105410)
watershedE	0.8117998	factor(watershed)E	0.8357662	factor(watershed)E	0.8221604
2.5 %-97.5 %	(0.7380963, 0.8928631)	2.5 %-97.5 %	(0.7599544, 0.9191409)	2.5 %-97.5 %	(0.7508894, 0.9001960)
watershedF	1.0103001	factor(watershed)F	0.9636174	factor(watershed)F	0.9713606
2.5 %-97.5 %	(0.9417168, 1.0838781)	2.5 %-97.5 %	(0.8974443, 1.0346697)	2.5 %-97.5 %	(0.9044833, 1.0431828)

watershedG	0.6713304	factor(watershed)G	0.6739643	factor(watershed)G	0.6646754
2.5 %-97.5 %	(0.6157012, 0.7319858)	2.5 %-97.5 %	(0.6125778, 0.7415023)	2.5 %-97.5 %	(0.6046783, 0.7306254)
watershedH	0.9892899	factor(watershed)H	0.9820266	factor(watershed)H	0.9837073
2.5 %-97.5 %	(0.9213475, 1.0622426)	2.5 %-97.5 %	(0.9106148, 1.0590386)	2.5 %-97.5 %	(0.9104014, 1.0629158)
s(envi_nmds).1	1.0601149	s(hydro).1	0.9930257	s(over).1	0.9668079
2.5 %-97.5 %	(0.9845955, 1.1414266)	2.5 %-97.5 %	(0.9483897, 1.0397625)	2.5 %-97.5 %	(0.9028514, 1.0352949)
s(envi_nmds).2	1.060555	s(hydro).2	1.04072	s(over).2	1.2188588
2.5 %-97.5 %	(0.9074318, 1.2395168)	2.5 %-97.5 %	(0.9445997, 1.1466212)	2.5 %-97.5 %	(0.9985799, 1.4877296)
s(envi_nmds).3	1.0096443	s(hydro).3	0.99669	s(over).3	1.0134252
2.5 %-97.5 %	(0.9695357, 1.0514121)	2.5 %-97.5 %	(0.9798546, 1.0138148)	2.5 %-97.5 %	(0.9733042, 1.0552000)
s(envi_nmds).4	1.0390367	s(hydro).4	0.9799337	s(over).4	0.9190847
2.5 %-97.5 %	(0.9417605, 1.1463608)	2.5 %-97.5 %	(0.9167230, 1.0475030)	2.5 %-97.5 %	(0.8050343, 1.0492928)
s(envi_nmds).5	1.0083648	s(hydro).5	0.9936396	s(over).5	0.9922972
2.5 %-97.5 %	(0.9678675, 1.0505566)	2.5 %-97.5 %	(0.9698141, 1.0180504)	2.5 %-97.5 %	(0.9617185, 1.0238482)
s(envi_nmds).6	0.9690886	s(hydro).6	1.0202562	s(over).6	1.084621
2.5 %-97.5 %	(0.8980021, 1.0458025)	2.5 %-97.5 %	(0.9682951, 1.0750058)	2.5 %-97.5 %	(0.9623735, 1.2223972)
s(envi_nmds).7	0.9939306	s(hydro).7	0.9964655	s(over).7	1.0236608
2.5 %-97.5 %	(0.9713810, 1.0170036)	2.5 %-97.5 %	(0.9857604, 1.0072867)	2.5 %-97.5 %	(0.9792704, 1.0700634)
s(envi_nmds).8	1.1773755	s(hydro).8	1.1014486	s(over).8	1.4394913
2.5 %-97.5 %	(0.8916233, 1.5547072)	2.5 %-97.5 %	(0.8708508, 1.3931077)	2.5 %-97.5 %	(0.8895366, 2.3294548)
s(envi_nmds).9	1.1156242	s(hydro).9	1.0394425	s(over).9	1.0684658
2.5 %-97.5 %	(1.0076259, 1.2351979)	2.5 %-97.5 %	(0.9686014, 1.1154647)	2.5 %-97.5 %	(0.9365826, 1.2189200)

(2) the coefficient of GAM models explaining species turnover by environmental similarity

LAKE PAIRS WITH LOW DISTURBANCE		LAKE PAIRS WITH MODERATE DISTURBANCE		LAKE PAIRS WITH HIGH DISTURBANCE	
parameter	environment similarity	parameter	environment similarity	parameter	environment similarity
(Intercept)	1.9993975	(Intercept)	1.8772416	(Intercept)	2.1973303
2.5 %-97.5 %	(1.8388635, 2.1739463)	2.5 %-97.5 %	(1.7920888, 1.9664405)	2.5 %-97.5 %	(2.0965205, 2.302987)
watershedC	0.8486461	watershedF	1.1336771	watershed28955	1.0681557
2.5 %-97.5 %	(0.7707194, 0.9344518)	2.5 %-97.5 %	(1.0609962, 1.2113368)	2.5 %-97.5 %	(0.9680124, 1.178659)
watershedD	0.9110891	watershedG	0.7586872	watershed29000	0.766576
2.5 %-97.5 %	(0.8204213, 1.0117770)	2.5 %-97.5 %	(0.6960231, 0.8269931)	2.5 %-97.5 %	(0.6965863, 0.843598)
watershedE	0.7951149	watershedH	1.1226493	watershed29233	0.9918128
2.5 %-97.5 %	(0.6891085, 0.9174284)	2.5 %-97.5 %	(1.0450033, 1.2060646)	2.5 %-97.5 %	(0.9249880, 1.063465)
s(envi_nmds).1	1.0007389	s(envi_nmds).1	1.0802329	s(envi_nmds).1	1.0617616
2.5 %-97.5 %	(0.9442733, 1.0605809)	2.5 %-97.5 %	(0.9606537, 1.2146971)	2.5 %-97.5 %	(0.9718860, 1.159948)
s(envi_nmds).2	1.0351004	s(envi_nmds).2	1.0575712	s(envi_nmds).2	0.9842549
2.5 %-97.5 %	(0.9079686, 1.1800328)	2.5 %-97.5 %	(0.8161712, 1.3703703)	2.5 %-97.5 %	(0.8614963, 1.124506)
s(envi_nmds).3	0.9990353	s(envi_nmds).3	0.9622681	s(envi_nmds).3	0.9967352
2.5 %-97.5 %	(0.9686277, 1.0303975)	2.5 %-97.5 %	(0.9031837, 1.0252178)	2.5 %-97.5 %	(0.9446498, 1.051692)
s(envi_nmds).4	0.9812221	s(envi_nmds).4	1.0310169	s(envi_nmds).4	0.9881603
2.5 %-97.5 %	(0.9227064, 1.0434488)	2.5 %-97.5 %	(0.8679487, 1.2247220)	2.5 %-97.5 %	(0.9209156, 1.060315)
s(envi_nmds).5	1.0095696	s(envi_nmds).5	1.0021624	s(envi_nmds).5	1.0059582
2.5 %-97.5 %	(0.9761967, 1.0440835)	2.5 %-97.5 %	(0.9438225, 1.0641085)	2.5 %-97.5 %	(0.9767464, 1.036044)
s(envi_nmds).6	1.0188242	s(envi_nmds).6	1.0272562	s(envi_nmds).6	1.0111588
2.5 %-97.5 %	(0.9659845, 1.0745542)	2.5 %-97.5 %	(0.9032607, 1.1682733)	2.5 %-97.5 %	(0.9494363, 1.076894)
s(envi_nmds).7	1.0047519	s(envi_nmds).7	1.0208641	s(envi_nmds).7	0.9972074
2.5 %-97.5 %	(0.9900182, 1.0197049)	2.5 %-97.5 %	(0.9485196, 1.0987263)	2.5 %-97.5 %	(0.9793266, 1.015415)
s(envi_nmds).8	1.0917457	s(envi_nmds).8	1.1644368	s(envi_nmds).8	1.0459994

2.5 %-97.5 %	(0.8890862, 1.3405997)	2.5 %-97.5 %	(0.7576431, 1.7896460)	2.5 %-97.5 %	(0.7881837, 1.388147)
s(envi_nmds).9	1.1051963	s(envi_nmds).9	1.1492542	s(envi_nmds).9	1.0790042
2.5 %-97.5 %	(1.0170764, 1.2009510)	2.5 %-97.5 %	(0.9802822, 1.3473520)	2.5 %-97.5 %	(0.9668474, 1.204171)

(3) the coefficient of GAM models explaining species turnover by hydrological distance

LAKE PAIRS WITH LOW DISTURBANCE		LAKE PAIRS WITH MODERATE DISTURBANCE		LAKE PAIRS WITH HIGH DISTURBANCE	
parameter	hydrological distance	parameter	hydrological distance	parameter	hydrological distance
(Intercept)	1.9307658	(Intercept)	1.882415	(Intercept)	2.1499428
2.5 %-97.5 %	(1.7573163, 2.1213349)	2.5 %-97.5 %	(1.7996043, 1.9690364)	2.5 %-97.5 %	(2.0221364, 2.2858270)
watershedC	0.8580779	watershedF	1.1094627	watershed28955	1.1135718
2.5 %-97.5 %	(0.7669755, 0.9600015)	2.5 %-97.5 %	(1.0399297, 1.1836449)	2.5 %-97.5 %	(0.9897867, 1.2528377)
watershedD	0.9176059	watershedG	0.7808669	watershed29000	0.7945076
2.5 %-97.5 %	(0.8087608, 1.0410997)	2.5 %-97.5 %	(0.7162188, 0.8513503)	2.5 %-97.5 %	(0.7058258, 0.8943316)
watershedE	0.9252851	watershedH	1.1246141	watershed29233	1.0264586
2.5 %-97.5 %	(0.8153376, 1.0500590)	2.5 %-97.5 %	(1.0493001, 1.2053338)	2.5 %-97.5 %	(0.9350522, 1.1268005)
s(hydro).1	0.9999998	s(hydro).1	0.9991087	s(hydro).1	1
2.5 %-97.5 %	(0.9996489, 1.0003508)	2.5 %-97.5 %	(0.8721429, 1.1445581)	2.5 %-97.5 %	(0.9997678, 1.0002323)
s(hydro).2	0.9999997	s(hydro).2	1.1915456	s(hydro).2	1
2.5 %-97.5 %	(0.9995677, 1.0004319)	2.5 %-97.5 %	(0.9182508, 1.5461800)	2.5 %-97.5 %	(0.9995652, 1.0004351)
s(hydro).3	1	s(hydro).3	0.9956826	s(hydro).3	1
2.5 %-97.5 %	(0.9999141, 1.0000859)	2.5 %-97.5 %	(0.8754435, 1.1324362)	2.5 %-97.5 %	(0.9998533, 1.0001467)
s(hydro).4	1.0000001	s(hydro).4	1.0624184	s(hydro).4	1
2.5 %-97.5 %	(0.9997077, 1.0002926)	2.5 %-97.5 %	(0.9011559, 1.2525389)	2.5 %-97.5 %	(0.9997419, 1.0002582)
s(hydro).5	1	s(hydro).5	1.0113912	s(hydro).5	1

2.5 %-97.5 %	(0.9999050, 1.0000949)	2.5 %-97.5 %	(0.9602792, 1.0652238)	2.5 %-97.5 %	(0.9998713, 1.0001287)
s(hydro).6	0.9999999	s(hydro).6	0.9385954	s(hydro).6	1
2.5 %-97.5 %	(0.9997091, 1.0002907)	2.5 %-97.5 %	(0.8185199, 1.0762858)	2.5 %-97.5 %	(0.9997799, 1.0002202)
s(hydro).7	1	s(hydro).7	1.0280753	s(hydro).7	1
2.5 %-97.5 %	(0.9999446, 1.0000554)	2.5 %-97.5 %	(0.9597039, 1.1013176)	2.5 %-97.5 %	(0.9999504, 1.0000496)
s(hydro).8	1.0000006	s(hydro).8	1.2910663	s(hydro).8	1.0000001
2.5 %-97.5 %	(0.9988382, 1.0011642)	2.5 %-97.5 %	(0.7483793, 2.2272827)	2.5 %-97.5 %	(0.9992291, 1.0007718)
s(hydro).9	1.0346283	s(hydro).9	1.1176118	s(hydro).9	1.0272104
2.5 %-97.5 %	(0.9922042, 1.0788664)	2.5 %-97.5 %	(0.9355616, 1.3350871)	2.5 %-97.5 %	(0.9839312, 1.0723933)

(4) the coefficient of GAM models explaining species turnover by geographical distance

LAKE PAIRS WITH LOW DISTURBANCE		LAKE PAIRS WITH MODERATE DISTURBANCE		LAKE PAIRS WITH HIGH DISTURBANCE	
parameter	geographical distance	parameter	geographical distance	parameter	geographical distance
(Intercept)	1.9510274	(Intercept)	1.8671895	(Intercept)	2.1709926
2.5 %-97.5 %	(1.7723976, 2.1476604)	2.5 %-97.5 %	(1.7854065, 1.9527188)	2.5 %-97.5 %	(2.0545824, 2.2939984)
watershedC	0.8483115	watershedF	1.1270342	watershed28955	1.0779922
2.5 %-97.5 %	(0.7567471, 0.9509549)	2.5 %-97.5 %	(1.0581648, 1.2003860)	2.5 %-97.5 %	(0.9664690, 1.2023843)
watershedD	0.9135102	watershedG	0.7769164	watershed29000	0.7889513
2.5 %-97.5 %	(0.8054605, 1.0360543)	2.5 %-97.5 %	(0.7134869, 0.8459848)	2.5 %-97.5 %	(0.7046112, 0.8833867)
watershedE	0.9021155	watershedH	1.1423619	watershed29233	1.0120003
2.5 %-97.5 %	(0.7942207, 1.0246679)	2.5 %-97.5 %	(1.0642118, 1.2262509)	2.5 %-97.5 %	(0.9325493, 1.0982203)
s(over).1	0.9999993	s(over).1	1.0139279	s(over).1	0.9704239
2.5 %-97.5 %	(0.9994627, 1.0005361)	2.5 %-97.5 %	(0.9244781, 1.1120325)	2.5 %-97.5 %	(0.8886795, 1.0596875)
s(over).2	0.9999992	s(over).2	1.1481421	s(over).2	0.9383667
2.5 %-97.5 %	(0.9992563, 1.0007425)	2.5 %-97.5 %	(0.9384360, 1.4047099)	2.5 %-97.5 %	(0.7984253, 1.1028360)

s(over).3	1.0000002	s(over).3	1.0135686	s(over).3	1.0079933
2.5 %-97.5 %	(0.9998279, 1.0001724)	2.5 %-97.5 %	(0.9638615, 1.0658392)	2.5 %-97.5 %	(0.9726502, 1.0446207)
s(over).4	0.9999995	s(over).4	1.0557746	s(over).4	0.9677382
2.5 %-97.5 %	(0.9995741, 1.0004250)	2.5 %-97.5 %	(0.9299354, 1.1986424)	2.5 %-97.5 %	(0.8770249, 1.0678343)
s(over).5	0.9999999	s(over).5	1.0037129	s(over).5	1.0034528
2.5 %-97.5 %	(0.9998617, 1.0001380)	2.5 %-97.5 %	(0.9670304, 1.0417869)	2.5 %-97.5 %	(0.9773480, 1.0302548)
s(over).6	1.0000006	s(over).6	0.9392133	s(over).6	1.031804
2.5 %-97.5 %	(0.9995995, 1.0004018)	2.5 %-97.5 %	(0.8361447, 1.0549867)	2.5 %-97.5 %	(0.9507788, 1.1197341)
s(over).7	1	s(over).7	0.9684182	s(over).7	1.0023339
2.5 %-97.5 %	(0.9999155, 1.0000845)	2.5 %-97.5 %	(0.9040602, 1.0373576)	2.5 %-97.5 %	(0.9860130, 1.0189251)
s(over).8	1.0000028	s(over).8	1.3011851	s(over).8	1.145656
2.5 %-97.5 %	(0.9984273, 1.0015807)	2.5 %-97.5 %	(0.8677493, 1.9511196)	2.5 %-97.5 %	(0.8650826, 1.5172281)
s(over).9	1.0371155	s(over).9	1.0463158	s(over).9	1.0503513
2.5 %-97.5 %	(0.9964662, 1.0794230)	2.5 %-97.5 %	(0.9093325, 1.2039345)	2.5 %-97.5 %	(0.9323835, 1.1832446)

Appendix 5.4 g

The estimates of coefficients for mixed effect model in Figure 5.7.

Catchment	(Intercept)	logalk
2270	-1.589875	0.4719306
2490	-1.430254	0.4596188
3458	-1.853659	0.6583305
4672	-1.980378	0.7883874
5350	-1.67797	0.4985617
6297	-1.670235	0.5576479
6405	-1.728601	0.5571173
8455	-1.911114	0.6173391
8751	-1.757555	0.692295
10719	-1.79853	0.8206073
10786	-1.672354	0.5534388
11611	-1.769283	0.6725591
13470	-1.57035	0.7168506
14057	-1.598039	0.5052831
14462	-1.593038	0.5609778
16206	-1.932539	0.633846
18563	-1.912765	0.7781108
18714	-1.711748	0.6577551
20860	-1.735533	0.8177485
21925	-1.833026	0.4574358
24025	-1.329754	0.5641405
25284	-1.572036	0.7313365
27782	-1.840282	0.5839337
28003	-1.010612	0.5142878
28847	-1.778293	0.8967235
28955	-2.102485	1.0774958
29000	-1.568035	0.7440616
29233	-2.723091	1.4443283
29321	-1.789074	0.9369718

35953	-1.580913	1.4818421

Appendix 5.4 h

The estimates of coefficients of significant parameters for GLM in Table 5.3.

model 1		(Intercept)	Stream density
	coefficient	0.4125201	-1.140626
	2.5%-97.5%	(-0.269827, 1.0948673)	(-1.960907, -0.3203455)
model 2		(Intercept)	Catchment mean slope
	coefficient	-0.93409364	0.04255303
	2.5%-97.5%	(-1.2822646, -0.585922)	(0.0097595, 0.0753465)
model 3		(Intercept)	Lake density
	coefficient	-0.2455308	-1.6624608
	2.5%-97.5%	(-0.5202312, 0.02916968)	(-3.110819, -0.21410266)
model 4		(Intercept)	Distance to sea
	coefficient	-0.77619332	0.01919735
	2.5%-97.5%	(-1.0017585, -0.550628)	(0.00566074, 0.03273395)
model 5		(Intercept)	Patch density
	coefficient	-0.81492438	0.05035254
	2.5%-97.5%	(-1.0181433, -0.6117053)	(0.02307111, 0.07763397)
model 6		(Intercept)	Contig index
	coefficient	1.160744	-2.482957
	2.5%-97.5%	(-0.1170905, 2.4385787)	(-4.362446, -0.6034673)
model 7		(Intercept)	Land use coverage

	coefficient	-0.6227684	0.04161004
	2.5%-97.5%	(-0.7538161, -0.49172073)	(0.02102551, 0.06219457)

Appendix 5.4 j

The coefficient of the final parameters using the stepwise Logistic Regression with GLM models in Table 5.4

Model 1 Hydrological dataset

Hydrological dataset	(Intercept)	C_LD	C_Slope
coefficient	-0.65764636	-1.55478362	0.04033463
2.5 %-97.5 %	(-1.058167922, -0.2571248)	(-2.877915497, -0.23165174)	(0.009745607, 0.07092365)

Model 2 landscape dataset

Landscape dataset	(Intercept)	M_PD	M_land.use
coefficient	-0.78509536	0.03254175	0.02985559
2.5 %-97.5 %	(-0.96996855, -0.60022217)	(0.004713743, 0.06036976)	(0.008201786, 0.05150939)

Model 3 Hydrological + landscape dataset

Hydrological + Landscape dataset	(Intercept)	C_LD	C_SDI	C_AI	M_PD	M_land.use
coefficient	-0.42934372	-0.43918731	-0.16448184	0.01466788	0.01983521	0.02581804
2.5 %-97.5 %	(-2.293234, 1.434546)	(-0.980609, 0.102235)	(-0.3442895, 0.015325)	(-0.00598, 0.0353249)	(0.0070833, 0.032587)	(0.0139105, 0.037725)

Appendix 5.5

The GAM analyses with the non-replication lake pairs. Association between dissimilarity of lake macrophytes based on Jaccard's index and the difference in lake environment for hydrologically-connected lake pairs. Each parameter tested for its influence on species turnover in the reference lake pairs was supplemented with the catchment identity. s represents the smoothing function. The GAM model with lowest AIC value was fitted using a step forward procedure for variable selection.

Variables (log(x))	Terms with s	ResDf	Dev	AIC	BIC	Deviance explained (%) with catchment	Unique contribution
NULL	1	110	4.57	-35.15	-29.73	0	-
Catchment	1 + factor(catchment)	99	2.68	-72.23	-37.01	0.413	0.35
Altitude difference (x1)	s(x1,1)	98	2.51	-77.41	-39.47	0.449	0.036
Conductivity different (x2)	s(x2,3)	97.27	2.44	-78.17	-37.01	0.465	0.052
pH difference (x3)	s(x3,3.25)	96.44	2.45	-75.44	-31.44	0.462	0.049
Alkalinity difference (x4)	s(x4,3.31)	98	2.54	-76.21	-38.28	0.444	0.031
Area difference (x5)	s(x5,1.95)	97.99	2.34	-85.45	-47.52	0.488	0.075
Depth difference(x6)	s(x6,5.54)	96.79	2.39	-79.27	-36.67	0.475	0.062
Geographical distance(x7)	s(x7,4.21)	96.35	2.43	-76.56	-32.49	0.467	0.054
Hydrological distance(x8)	s(x8,2.44)	97.91	2.59	-73.78	-35.35	0.433	0.021
Multiple regression	x1+x2+x5+x6+factor(catchment)	92.9	2.03	-88.44	-33.86	0.554	-