THE RELATIVE IMPORTANCE OF EUTROPHICATION AND CONNECTIVITY IN STRUCTURING BIOLOGICAL COMMUNITIES OF THE UPPER LOUGH ERNE SYSTEM, NORTHERN IRELAND

Thesis submitted for the degree of Doctor of Philosophy

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by

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I, JORGE SALGADO confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

JORGE SALGADO B.

Abstract

This study investigates the relative importance of eutrophication and connectivity (dispersal) in structuring macrophyte and invertebrate lake assemblages across spatial and temporal scales in the Upper Lough Erne (ULE) system, Northern Ireland.

Riverine systems and their associated flood-plains and lakes comprise dynamic diverse landscapes in which water flow plays a key role in affecting connectivity. However, as for many other freshwater systems, their ecological integrity is threatened by eutrophication and hydrological alteration. Eutrophication results in a shift from primarily benthic to primarily pelagic primary production and reductions in species diversity, while flow regulation often reduces water level fluctuation and hydrological connectivity in linked riverine systems. Low water levels promote isolation between areas and increases the importance of local driving forces (e.g. eutrophication). Conversely, enhanced water flow and flooding events promote connectivity in systems thus potentially increasing local diversity and homogenising habitats through the exchange of species. Therefore, connectivity may help to override the local effects of eutrophication.

Attempts at testing the above ideas are rare and typically involve the examination of current community patterns using space for time substitution. However, biological community responses to eutrophication and changes in hydrological connectivity may involve lags, historical contingency, and may be manifested over intergenerational timescales (10s -100s of years), rendering modern studies less than satisfactory for building an understanding of processes that drive community structure and effect change. By combining contemporary and palaeolimnological data this study demonstrates that the ULE system is far from its pre-disturbance state as an oligotrophic-mesotrophic system. Furthermore, contemporary and palaeo-data suggest there has been a strong interaction between eutrophication and hydrological change, which influences the distributions and abundances of representative taxa in the ULE system. Thus, while eutrophication has promoted a decrease in compositional heterogeneity of organisms and has exerted a homogenising effect over time, connectivity has buffered the effects of eutrophication helping to maintain local diversity via re-introductions.

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1 Chapter 1 – Introduction

1.1 Background

The factors controlling the distribution and abundance of organisms in communities have long been of interest (see Stokstad 2009 for review) and historically these forces have been widely investigated at two levels (Pianka 1966, MacArthur and Levins 1967, MacArthur and Wilson 1967, Loreau and Mouquet 1999). First, variation in the distribution and abundance of species has been examined at a local scale, where fluctuations have been attributed to local biotic processes like competition, predation and environmental heterogeneity (MacArthur and Levins 1967). Second, species diversities and distributions have been investigated at the regional scale by focusing on processes of emigration and immigration and population extinction (MacArthur and Wilson 1967, Hanski 1999, Hubbell 2001).

Due to the island-like nature of lakes, which are distinctly bounded habitats, most studies of community structure have addressed the local within-lake scale. Particular focus has been on eutrophication, which is widely recognized as a key driver of ecological change in these ecosystems (Moss et al. 1996; Jeppesen et al. 2000). Over the last decade, however, it has been recognised that limnetic ecosystems (e.g. lake districts, riverine landscapes and wetlands consisting of many shallow lakes and ponds) can be understood using the framework of "metacommunities", in which species distributions and abundances reflect both regional processes (e.g. dispersal) and local processes (e.g. Cottenie et al. 2003; Beisner et al. 2006; Capers et al. 2010).

The term ‘metacommunity’ refers to a set of local communities that are connected by dispersal of multiple, potentially interacting species (Gilpin and Hanski 1991, Wilson 1992) (see Glossary of Terms at end of chapter) (Fig. 1-1). Metacommunity theory constitutes a theoretical framework to explain the interdependence of local processes (e.g. between species and the environment) and regional processes (e.g. dispersal) in explaining local and regional diversity (Leibold et al 2004; Holyoak et al. 2005; Logue et al. 2011).

Figure 1-1. Visual example of pond metacommunities. The metacommunities consists of multiple local communities (ponds) connected by dispersal of individuals among ponds.Aerial of tundra ponds Arctic Coast near Colville River Alaska (http://www.nationalgeographicstock.com)

Dispersal plays a key role in influencing local communities in two ways: (1) by providing a source of colonists; and (2) by altering local population dynamics via emigration and immigration (Leibold and Nornberg 2004). Dispersal rates depend on the degree of connectedness between sites in a metacommunity and environmental heterogeneity (Leibold and Nornberg 2004). If dispersal rates are low relative to environmental change (e.g. disturbances, altered abiotic conditions), the latter will be the main factor regulating species assemblyat local sites (Kneitel et al. 2001, Leibold and Nornberg 2004, Leibold et al. 2004). Nonetheless, dispersal events will still influence the species present at local sites in a metacommunity especially after a "favourable" environmental change. In contrast, when dispersal is high, local population abundances will be affected by both the emigration and immigration of individuals from other sites via "source-sink" relations between sites (Shmida and Wilson 1996). Under these conditions, dispersal will influence community assembly by supplementing local populations that, in an unfavourable environment, will not be self-sustaining (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002). As a consequence, at a regional scale, dispersal may enhance the degree to which communities respond to favourable environmental change or may override local

effects of environmental change by maintaining local populations through source-sink dynamics.

Based on the relationship between dispersal rates and habitat and species characteristics, four theoretical paradigms have been developed to describe metacommunities (Holyoak et al. 2005, Leibold et al. 2004). Each paradigm evokes different mechanisms of community assembly to explain local assembly within a metacommunity and predicts changes in local community composition as follow (Fig. 1-2):

(i) *The species-sorting paradigm* assumes that habitat patches differ in environmental conditions. Here, connectedness (dispersal) is low but not limited (i.e. species can arrive at all habitat patches) and differences in the tolerance of species to novel environmental conditions will enable species to coexist regionally. In this case, local diversity will be low, as sites will be dominated by few competitive species. However, these competitive taxa will differ between sites, so β-diversity is relatively high.

(ii) The *mass-effects* paradigm assumes that environmentally heterogeneous habitat patches are highly interconnected via frequent dispersal. Here, source habitats allow for persistence within a sink habitat (Shmida and Wilson 1996). Consequently, local diversity will be relatively high and no particular species will dominate. At the regional-scale β-diversity will be low.

(iii) *The patch-dynamic paradigm* assumes environmentally homogeneous patches that are inhabited by species exhibiting a trade-off between dispersal and local dominance. Under this scenario, the colonisation–competition trade-off (i.e. successful competitors are poor colonisers and vice versa) will determine community structure.

(iv) *The neutral paradigm* assumes species equivalence. Community assembly reflects stochastic events, immigration and speciation, which counteracts local extinction processes (Hubbell 2001).

Figure 1-2. Schematic representation of the four paradigms for metacommunity theory (species pool consist of two competing species with populations A and B). The degree to which a species is the competitive dominant in a site is shown by the matching of the smaller box or oval (denoting its habitat type niche) with the site symbol. (a) *Patch dynamic paradigm* - is shown with conditions that permit coexistence: a competition-colonization trade-off is illustrated with species A being a superior competitor but species B being a superior colonist; the third patch is vacant and could become occupied by either species. (b) *Species-sorting paradigm* - species are separated into spatial niches and dispersal is not sufficient to alter their distribution. (c) *Mass-effectparadigm* - cause species to be present in both source and sink habitats; the smaller letters and symbols indicate smaller sized populations. (d) *Neutral paradigm* - all species are currently present in all patches; species would gradually be lost from the region and would be replaced by speciation (Figure obtained from Leibold et al. 2004).

1.2 Riverine systems

Riverine systems (henceforth referred to as riverscapes following Amoros and Bornette 2002) include all floodplain water bodies (side arms, backwaters, cut-off braided channels, oxbow lakes, floodplain shallow lakes, ponds and marshes) that are more or less connected through surface or subsurface waterways to a main river. They are active ecosystems characterised by variable environmental and fluvial dynamics that create complex habitats and connectivity gradients (Ward 1999). Hydrological connectivity, the transfer of water and matter between water bodies, acts as a homogenising force at the landscape level. At intermediate levels, connectivity will

enhance diversity within water bodies (α-diversity) (Amoros and Bornette 2002). In contrast, environmental heterogeneity will determine local conditions and create differences in diversity (β-diversity) between habitats and water bodies. The interrelationship between connectivity and environmental heterogeneity jointly contribute to the level of biodiversity in riverscapes (Junk et al., 1989; Ward et al. 1998).

Riverscapes may harbour high levels of biodiversity, including numerous rare and highly specialized species, and may therefore be of high conservation value. They also provide important ecological services such as flood mitigation and nutrient retention (Tockner and Standford, 2002, Van Diggelen et al., 2006, Brauman et al., 2007, Tockner et al., 2008 Klaus et al. 2011). Nevertheless, as with many other freshwater systems, the ecological integrity of European riverscapes has been heavily diminished (Paillex et al. 2009). Increasing demands for water regulation and drainage schemes, and increased nutrient-loading (eutrophication), emerge as the most pervasive causes of degradation in riverscapes (Pringle 2001, Paillex et al 2009, Klaus et al. 2011).

1.2.1 Eutrophication

Eutrophication stimulates primary productivity causing a shift in community assemblages from the low levels of diversity, which characterise nutrient-poor habitats, to more diverse communities of submerged macrophytes, and associated fauna, which characterise intermediate levels of eutrophication. This is followed by a strong reduction in diversity at high levels of eutrophication (Jeppesen et al. 2000, Sayer et al. 2010a) (Fig. 1-3). In addition to these direct shifts in community composition, eutrophication indirectly affects the biota by influencing other environmental processes (Donohue et al. 2009; Chase 2007). Increased levels of nutrients can reduce availability of light, oxygen and carbon dioxide, and modify habitat structure (changes in macrophyte assemblages), food webs (greater reliance on open-water planktonic productivity) and predation pressure (reduction in macrophyte cover) (e.g. Cadotte et al. 2006, Fukami et al. 2006, Brauns et al. 2007, Declerck et al. 2007).

1.2.2 Hydrological alteration

Hydrological alteration can be defined as any natural or anthropogenic disruption in the magnitude or timing of natural water flows (Rosenberg et al. 1997, Pringle 2001). Impacts of hydrological alteration include habitat fragmentation and isolation (Rosenberg et al. 1997) and upstream or downstream habitat modifications, including loss of floodplains, riparian zones and adjacent wetlands, and modification and/or loss of river deltas and estuaries (Rosenberg et al. 1997). All these alterations substantially impact aquatic biodiversity by affecting the movement of organisms (Rosenberg et al. 1997, Pringle 2001, Paillex et al. 2009). Conversely, hydrological alteration in the form of flood events enhances connectivity, resulting in a homogenisation of biological communities across the habitats that comprise a riverscape (Thomaz et al. 1999).

1.2.3 Riverscapes and metacommunities

Currently the independent effects of eutrophication and connectivity are relatively well-known. However, due to inherent difficulties in measuring the effects of eutrophication and connectivity, the joint interaction of these two processes, and how this influences riverscape biodiversity, has rarely been addressed. Recent studies, however, have emphasised the striking metacommunity structure of limnetic systems in which species respond to both regional processes and local environmental changes (e.g. Cottenie et al. 2003; Leibold and Norberg 2004, Beisner et al. 2006). For instance, Cottenie et al. (2003) showed that zooplankton communities in a system of highly interconnected Belgium ponds were structured by both eutrophication and site connectivity and provided evidence for the importance of emigration-immigration events in maintaining zooplankton diversity. Nevertheless, this study revealed that even under high connectedness, local nutrient-enrichment was strong enough to act as the main driver structuring the zooplankton assemblages.In contrast,in a study of 18 Canadian lakes (Beisner et al. 2006), the distributions and abundances of poor-dispersing species (e.g. zooplankton and fish) were better predicted by spatial relationships (dispersal and connectivity) than by local environmental factors. Brown and Swan (2011) found macroinvertebrate communities varied according to river configuration in North America. Here the balance of both environmental variation and spatial factors changed according to location within the network and environmental

components dictated community structure in headwaters, while dispersal dominated the structuring of main-stem communities.

Figure 1-3. Visual example of a well-connected system (metacommunity) affected by eutrophication. Pantanal lagoons, Barzil. (http://travel.nationalgeographic.com)

To date, inherent difficulties in measuring the combined effects of eutrophication and dispersal over time have limited studiesof their influence on structuring freshwater communities to a snapshot in time (Allen et al. 2011). Consequently, a space for time assumption has been implicit in understanding metacommunity dynamics (e.g. Cottenie et al. 2003; Cottenie 2005, Brown and Swan 2011). However, riverscapes are ecosystems that change constantly over time (Amoros and Bornette 2002). Likewise, eutrophication is a gradual process that progresses over time (Schindler 1974, Davidson et al. 2005, Conley et al. 2009, Sayer et al. 2010a). Thus, to fully understand the interaction of connectivity and eutrophication, it is vital to focus research at both spatial and temporal scales, the latter ranging from decades to centuries.

1.2.4 Long-term records and metacommunity

A problem for many long-term metacommunity studies is the frequent lack of long-term monitoring data (Allen et al. 2011). Shallow lakes, however, offer a unique

opportunity for such investigations since their sediment records allow the detection of changes in the distribution and abundance of taxa over long periods of time(Brodersen et al. 2001, Odgaard and Rasmussen, 2001, Rasmussen and Anderson, 2005, Ayres et al., 2008, Salgado et al. 2010, Allen et al. 2011). The presence of plant leaf and animal body remains and resistant stages, such as seeds, spores and eggs in lake sediments, thus provides unique insights into temporal changes in communities (Jeppesen et al. 2001, Birks 2001). Such palaeolimnological data can provide evidence of local community changes, historical dynamics of communities, population turnover via extinction and re-colonization, and biotic responses to anthropogenic impacts (Jeppesen et al. 2001, Odgaard and Rassmussen, 2001, Hill et al. 2007, Birks et al. 2000, Okamura et al. submitted).

Aquatic plant macrofossils have long been analysed alone or together with other proxies, to reconstruct long-term changes in catchment vegetation (Birks 1973, Birks et al. 2000) and to infer water level change in lakes (Hannon and Gaillard 1997, Dieffenbacher-Krall and Halteman 2000). More recently, plant remains have been used to infer historical dynamics of submerged macrophyte communities (Rasmussen and Anderson, 2005, Davidson et al. 2005; Salgado et al. 2010), to reconstruct primary producer responses to eutrophication (Davis 1985, Sayer et al. 2010b), and to reconstruct associations between macrophyte community changes and freshwater invertebrate community structure (Davis 1985, Brodersen et al. 2001, Davidson et al. 2010, Davidson et al. 2011).

1.3 Overall aim and specific research questions

The primary aim of this thesis is to investigate the relative importance of eutrophication and connectivity (dispersal) in structuring freshwater communities in the Upper Lough Erne (ULE) system, a riverscape of well-connected satellite lakes in Northern Ireland, at both spatial and temporal scales. To this end, the following specific research questions are addressed:

- Do eutrophication and dispersal processes structure contemporary community assemblages? If so, does the effect of these structuring processes vary across different taxonomic groups?

- What is/are the best metacommunity paradigm(s) to describe the structure of the ULE system biological assemblages? Do they vary through time?

- Do eutrophication and dispersal influence different aspects of species diversity (α-diversity, β-diversity and γ-diversity)? If so how are they related? Are there other attributes of the riverscape (e.g. lake size and lake maximum water depth) that contribute?

- Can palaeolimnological techniques be used to track metacommunity dynamics over time?

1.4 Study site

The Upper Lough Erne (ULE) system is situated in Co. Fermanagh, Northern Ireland (Fig. 1-4). It is a complex and dynamic riverscape that offers a unique opportunity to assess the effects of eutrophication and connectivity in structuring riverscape biotic assemblages. The system is formed as the channel of the River Erne splits and widens across a landscape of drumlins creating the main Upper Lough Erne (ULE), a large (34.5 km^2) mainly shallow (mean depth 2.3 m) and eutrophic (TP 70 µg/L) lake (Table 1). Associated with this large water body is a complex of interconnected smaller (range of 1-50 ha), shallow (mean depth < 2 m) satellite lakes that vary in degree of nutrient-enrichment and hydrological connectivity (mediated by rivers, streams and agricultural channels).

The shores of ULE and the associated satellite lakes are mostly thickly wooded, and the contiguous drumlins are divided by a dense patchwork of fields and hedges. Small settlements are scattered throughout the area, which is otherwise characterized by arable farmland, improved and unimproved grassland, meadows, swamps and deciduous forest. The ULE system has an extraordinary biodiversity. It is designated as a Special Area of Conservation (SAC) under the EC Habitats Directive (www.ni-

environment.gov.uk) and is divided into four major Sites of Special Scientific Interest (SSSI) (Belleisle in the North, Trannish in the middle part of the ULE, and Crom and Galloon in the southern part), each supporting many plant and animal species of restricted distribution in the British Isles. These include whiskered bat (*Myotis mystacinus*), shoveler (*Anas clypeata* L.), pochard (A*ythya* spp.), brook lamprey (*Lampetra planeri*), white-clawed crayfish (*Austropotamobius pallipes*), lunar hornet moth (*Sesia apiformis*), the pondskater (*Limnoporus rufoscutellatus*) and the water beetles, *Donacia aquatica, Donacia bicolora, Gyrinus distinctus, Gyrinus natator* and *Hydroporus glabriusculus.* Uncommonor locally rare plant species include arrowhead (*Sagittaria sagittifolia),* narrow-leaved water plantain (*Alisma lanceolatum),* needle-spike rush *(Eleocharis acicularis)* and the nationally (N. Ireland) rare frogbit (*Hydrocharis morsus-ranae).* Populations of European otter (*Lutra lutra*) and wintering whooper swan (*Cygnus cygnus*) further enhance the conservation value of the system.

Figure 1-4. Aerial photo of the Lough Erne system, County Fermanagh, Northern Ireland. (http://www.nationalgeographicstock.com)

1.4.1 A history of eutrophication and connectivity

Previous research and historical records demonstrate that over the last 150 years, the ULE system has been subject to processes of hydrological change and eutrophication that may have influenced its ecology(Price 1890, Battarbee 1986, Gibson et al. 1995,

Smith et al. 2005). Frequent flood events in the ULE catchment caused by high rainfall (annual average of 6.3 mm day^{-1}) (Price 1890) and an inability of the River Erne to discharge the incoming water back to the sea (Cunningham 1992) led to a major drainage scheme between 1880-1890 (Fig. 2). The main ULE and associated channels were excavated to increase water depth and, as consequence, water levels dropped from around 48 to 46 m above sea level (Price 1890). Recurrent flood events prompted a second attempt at water level regulation under the Erne Drainage and Development Act (Northern Ireland) in the early 1950s. At this time 30 km of channel were dredged between the ULE system and the Lower Lough Erne system. Since this time water levels in the ULE system have been maintained between around 43-45 m above sea level (Mathers et al. 2002, Smith et al. 2005). Despite these efforts, the ULE system is still prone to flood events (Cunningham 1992). A flood impact map of 2009 showsthat extensive floodingstill occurs, which connects most satellite lakes and the main ULE (http://safer.emergencyresponse.eu, OFMDFM 2010) (see Chapter 2).

Diatom-based palaeolimnological studies in the main ULE indicate a gradual increase in nutrient-enrichment since the 1900s and a further acceleration of this process after 1950 (Battarbee 1986, Gibson et al. 1995, Smith et al. 2005) (Fig. 1-5). Early eutrophication probably arose from domestic effluents from storm drains that were introduced in the local towns (Battarbee 1986). The acceleration of eutrophication in the 1950s likely resulted from the interaction of various factors including post-war agricultural intensification, increased sewage and synthetic detergent inputs, development of rural septic-tank sanitation, and increased organic pollution from industry (Battarbee 1986).

Figure 1-5. Summary diagram showing a three-stage eutrophication of Lough Erne, with periods of initial change between 1900 and 1910 and rapid change between 1950 and 1960. (Figure obtained from Battarbee 1986).

1.5 Structure and outline of thesis

This thesis presents results and analyses in four chapters that describe studies on both temporal and spatial dynamics in the ULE system and its associated water bodies. Each chapter contains an introduction, description and assessment of the methods employed, including results, discussion and conclusions.

1.5.1 Spatial contemporary dynamics:

CHAPTER 2 – The factors determining the composition of contemporary assemblages of actively dispersing (chironomids) and passively dispersing (macrophytes and filter-feeding invertebrates) taxa from a set of 20 satellite shallow lakes are analysed. Multivariate Redundancy Analyses (RDA) and partial RDA are employed to identify the relative contributions of eutrophication and dispersal in structuring the species assemblages. Mantel tests are employed to examine whether community similarity is correlated with environmental and geographical gradients.

CHAPTER 3 – The effects of eutrophication and connectivity on macrophyte species diversity within and between the Upper Lough Erne (ULE) and a set of 20 well-connected shallow satellite lakes are examined. A combination of permutational analyses of multivariate dispersions and permutational multivariate analyses of variance are employed to quantify within- and between-lake compositional heterogeneity. To test predictable patterns of within- and between-lake macrophyte compositional heterogeneity along environmental and spatial gradients, least squares regression analyses between the distance to centroid for each lake and a set of different local and regional variables are conducted.

1.5.2 Spatial-temporal dynamics

CHAPTER 4 –The long-term effects of nutrient-enrichment on species turnover, community compositional heterogeneity and the potential mechanisms of coexistence of submerged macrophytes and invertebrates from three areas of Castle Lough are investigated. More specifically, this study tests: (1) whether nutrient-enrichment promoted local dominance by some species and reduced compositional heterogeneity between sub-localities over time; and (2) whether there is a complex within-lake

continuum of “sub-metacommunities”. A combination of permutational analyses of multivariate dispersions, permutational multivariate analyses of variance and non-metric multivariate analyses are employed to quantify species turnover and changes in dominance over time.

CHAPTER 5 – By using a multi-proxy, multi-lake palaeoecological approach, this final chapter addresses how species turnover and compositional heterogeneity developed through time in five lakes in response to eutrophication and hydrological alterations. Non-metric multivariate analyses and principal curve analyses are used to visualise trajectories of community change and to identify major phases of compositional change. A combination of permutational analyses of multivariate dispersions and permutational multivariate analyses of variance is employed to quantify variability in compositional heterogeneity over time.

1.6 Glossary of Terms

A list of terms commonly used in this thesis to define species diversity and metacommunities.

Terms	Definition
Community	The individuals of all species that potentially interact within a single patch or local area of habitat
Metacommunity	A set of local communities that are linked by dispersal of multiple, interacting species (Wilson 1992)
Source–sink effects	A mechanism for spatial dynamics in which there is enhancement of local populations by immigration to sink localities due to migration of individuals from other localities where emigration reduces populations
Dispersal	Movement of individuals from a site (emigration) to another (immigration)
Species-sorting perspective	A perspective associated with metacommunity dynamics that emphasizes that resource gradients or patch types cause sufficiently strong differences in the local demography of species and the outcomes of local species interactions that patch quality and dispersal jointly affect local community composition. This perspective emphasizes spatial niche separation as a driver of assemblage structure above and beyond spatial dynamics. Dispersal is important because it allows compositional changes to track changes in local environmental conditions.
Mass-effect perspective	A perspective associated with metacommunity dynamics that focuses on the effect of immigration and emigration on local population dynamics. In such a system species can be rescued from local competitive exclusion in communities where they are bad competitors, via immigration from communities where they are good competitors. This

	perspective emphasizes a role for spatial dynamics in affecting local population densities
Riverscapes	Riverine landscapes that include all floodplain water bodies (side arms, backwaters, cut-off braided channels, oxbow lakes, floodplain shallow lakes and ponds and marshes) that are more or less connected through surface waterways to a main river.
Compositional heterogeneity	Any variability in species relative abundances or species identities within a given area.
α-diversity	The number of species present within a given area.
β-diversity	Between-community diversity attributed to spatial turn-over of species or spatial differences in within-lake compositional heterogeneity.
γ-diversity	The total diversity at a given scale.
Evenness	The variability of a trait (e.g. relative abundances of individuals within a species) within a community.
Eutrophication	Excessive richness of nutrients in a lake or other water body, due to run off of fertilizers, sewage or via natural sources.
Hydrological connectivity	The transfer of water and matter between water bodies.

2 Chapter 2 – The relative importance of local and regional processes in structuring shallow lake metacommunities

2.1 Abstract

Recent metacommunity approaches are recognising that diversity in freshwater habitats can be regulated by local environmental factors and regional processes, such as dispersal. This study assesses the relative importance of eutrophication and connectedness (dispersal) in structuring actively (chironomids) and passively (macrophytes and filter-feeder invertebrates) dispersing assemblages for a set of satellite shallow lakes in the Upper Lough Erne system, Northern Ireland. Using species abundances and occurrences, lake environmental variables (water chemistry and physical parameters) and dispersal predictors (overland and watercourse distances between lakes) this study aims to: (1) examine the relative importance of dispersal and environment in structuring actively and passively dispersing assemblages; (2) evaluate whether patterns observed are consistent with metacommunity perspectives (i.e. species-sorting and/or mass-effects); and (3) explore variability in community similarity along spatial and environmental gradients. This study suggest that eutrophication, lake surface area and lake maximum water depth have played a significant role in structuring communities and that the relative importance of spatial predictors (overland and watercourse distances) have varied according to dispersal mode. Submerged macrophyte distributions were explained by both overland and watercourse distances, while watercourse distances bestpredicted benthic and planktonicinvertebrate and overland distances best predicted chironomid distributions. There was no spatial autocorrelation between community similarity and environmental or spatial gradients, implying that the main Upper Lough Erne mediates extensive dispersal. This study indicates that metacommunity structure varied among sampling years from a combined species-sorting and mass-effect perspective to a species-sorting perspective.

2.2 Introduction

Increased nutrient loading and other human activities over the last two centuries have caused a dramatic decline in the biodiversity of most European lowland shallow lakes (Jeppesen et al. 2000, Arts 2002, Roelofs 2002). Scientific investigation of this problem has historically taken an approach that is strongly centred on a local or site-based perspective to understand the major compositional changes caused by eutrophication (e.g. Jeppesen et al. 2000, Davidson et al. 2005, Rasmussen and Anderson 2005, Sayer et al. 2010b). Eutrophication initially elevates diversity above the low levels that characterise nutrient-poor habitats. At intermediate levels a diverse community of submerged elodeid macrophytes and associated fauna develops. As nutrient-enrichment progresses, however, diversity is reduced as planktonic groups associated with high nutrient levels start to dominate (Jeppesen et al. 2000, Arts 2002, Sayer et al. 2010b).

Recent metacommunity studies are challenging this exclusive focus on local dynamics by incorporating spatial processes such as dispersal that operate at a regional scale (e.g. Cottenie et al. 2003, Kneitel and Miller 2003, Leibold et al. 2004, Leibold and Norberg 2004, Cadotte 2005, Cadotte 2006b, Cottenie 2005). Within this framework, the relative importance of local and spatial factors in determining local community structure depends on the combination of dispersal rates, the extent to which sites are connected to each other and the degree and frequency of environmental change (Chase 2003, Kneitel and Miller 2003, Leibold and Norberg 2004). For instance, if the environment is heterogeneous and dispersal is low but nonetheless relatively frequent, species may sort according to their preferred environment. In this case, local community dynamics will reflect spatial variation in the abiotic environment (i.e. the species-sorting metacommunity perspective) (Leibold et al. 2004, Chase et al. 2005). However, if environmental heterogeneity is associated with high connectedness among sites, dispersal may swamp or interact with these local influences (i.e. the mass-effect perspective) (Shmida and Wilson 1985, Amarasekare and Nisbet 2001, Mouquet and Loreau 2002, Mouquet and Loreau 2003). In this case, poor competitors can be rescued from local competitive exclusion by immigration (Shmida and Wilson 1985, Mouquet and Loreau 2003). In well-connected lake systems it is possible that two major forces (local and regional effects) may contribute to community structure.

In particular, local anthropogenic effects such as eutrophication may be relaxed or enhanced depending on rates of dispersal.

Research attempting to disentangle the proportion of variation in freshwater community composition that is related to regional versus local environmental processes has largely focused on planktonic organisms inhabiting large lakes or small ponds (e.g. Shurin 2000, Shurin et al. 2000, Cottenie et al. 2003, Havel and Shurin 2004, Crump et al. 2007). For instance, Pinel-Alloul et al. (1995) surveyed zooplankton across a large region in Canada and found that both space (distance) and environmental heterogeneity influenced patterns of community structure. However spatial and environmental variation was confounded as community and environmental dissimilarity increased with distance. Jenkins and Buikema (1998) studied the role of dispersal in structuring zooplankton communities that developed in newly formed ponds. They found that ponds with very similar abiotic conditions nevertheless developed different zooplankton communities over the first year resulting from dispersal limitations. More recently, (Cottenie et al. 2003) examined a series of well-connected ponds and found that although there was significant effect of space, local environmental conditions played a large role in determining zooplankton diversity.

Although the above-mentioned studies provide important insights about freshwater metacommunity dynamics, the relative roles of local versus regional conditions have rarely been compared for non-planktonic residents of shallow lakes (but see Heegaard 2004, Capers et. 2010 and Logue et al. 2010). In this respect, recent studies have demonstrated that metacommunity dynamics are far more complex when other taxonomic groups and landscapes are incorporated (e.g. Cottenie 2005, Beisner et al. 2006, Brown and Swan 2010, Capers et al. 2010). For example, Beisner et al. (2006) found that variation in community composition of bacteria, zooplankton and fish in 18 connected lakes partly reflected the ability of a particular group of organisms to disperse. They also found that environmental conditions affected community composition of bacteria, both environmental and spatial factors influenced crustacean zooplankton, while fish community composition was influenced only by spatial factors. Furthermore, for riverine systems in North America, Brown and Swan (2011) found macroinvertebrate community structure to vary according to the nature and network of river configuration. They demonstrated that the balance of both

environmental variation and spatial factors changed in harmony with location within the network and that environmental components dictated community structure in headwaters while dispersal dominated at mainstems.

The current study examines the relative influence on biological communities of local environmental variables and spatial configuration on a series of well-connected, shallow, eutrophic satellite lakes in the Upper Lough Erne (ULE) system, Northern Ireland, in order to: (1) characterise the relative influence of dispersal and environmental variation in structuring communities of overland and/orwatercourse dispersing organisms (macrophytes, chironomidsand other benthic and planktonic macro invertebrates); (2) assess whether patterns observed are consistent with the species-sorting and/or mass-effects metacommunity perspectives; and (3) explore community similarity patterns along spatial and environmental gradients.

2.3 Study site

The Upper Lough Erne (ULE) lake system is situated in Co. Fermanagh in the west of Northern Ireland (Fig. 2-1). It comprises an intricate network of small (generally <13 ha.), shallow (<5 m), satellite lakes set in anagricultural drumlin-dominated landscape. The lakes are linked by channels and rivers to two large mainly shallow lakes: Lower Lough Erne, situated in the north west (54^{o}30' N 7^{o}50'W) (mean depth 11.9 m and surface area 109.5 km^{2}); and Upper Lough Erne in the south (54^{o}14' N 7^{o}32' W) (mean water depth 2.3 m and surface area 34.5 km^{2}) (Battarbee 1986, Gibson et al. 1995) (Fig.2-1). The shores of the ULE and its associated satellite lakes are mostly thickly wooded and the contiguous drumlins are divided by a dense patchwork of fields and hedges. Small settlements are scattered throughout the area and land-use is arable farmland, improved and unimproved grassland, meadows, swamps and deciduous forest. The ULE system is designated as a Special Area of Conservation (SAC) under the EC Habitats Directive SAC (www.ni-environment.gov.uk). By the standards of Great Britain and Ireland, it has rich wetland flora, with over 50-recorded species of submerged and floating aquatic plant (Goldsmith et al. 2008). This large and complex freshwater system is of particular interest as, despite its conservation status, the main Lough and most of its satellite

lakes are affected by eutrophication (Table 2-1). Additionally, since the end of the 1990s, the zebra mussel (*Dreissena polymorpha* Pallas) has invaded much of the system, thus displacing other native mussel species and creating shifts in water clarity and alterations in the freshwater communities (Rosell et al. 1999, Minchin et al. 2003). Over the last 150 years, the catchment has been subjected to several schemes to improve drainage and prevent winter flooding (Price 1890, Battarbee 1986, Cunningham 1992, Gibson et al. 1995). Despite these efforts, the ULE system is still prone to major flood events (Cunningham 1992). A flood impact map from 2009shows current extensive flooding areas that connected most satellite lakes and the main ULE (http://safer.emergencyresponse.eu) (Fig.2-1).

The system occupies a large lowland depression in a region mainly composed of Carboniferous limestone rocks (Gibson et al. 1995). The drumlin-dominated lowland landscape is underlain by Late Midlandian till, shaped principally during the last glacial (the Midlandian). Subsequent modification throughout the post-glacial Holocene period resulted in a thick layer of Upper (younger) till overlying a core of Lower (older) till (Gibson et al. 1995). Within the landscape are numerous inter-drumlin hollows, which, in the majority of cases, have likely functioned as lakes since the end of the last Glaciation (10,000 years BP). Many others have been infilled by sediment washing off the surrounding drumlins probably early in the Holocene, as the landscape adjusted to increasingly temperate conditions (Gibson et al. 1995). These processes have typically created flat-bottomed, marshy areas between the drumlins (www.nienvironment.gov).

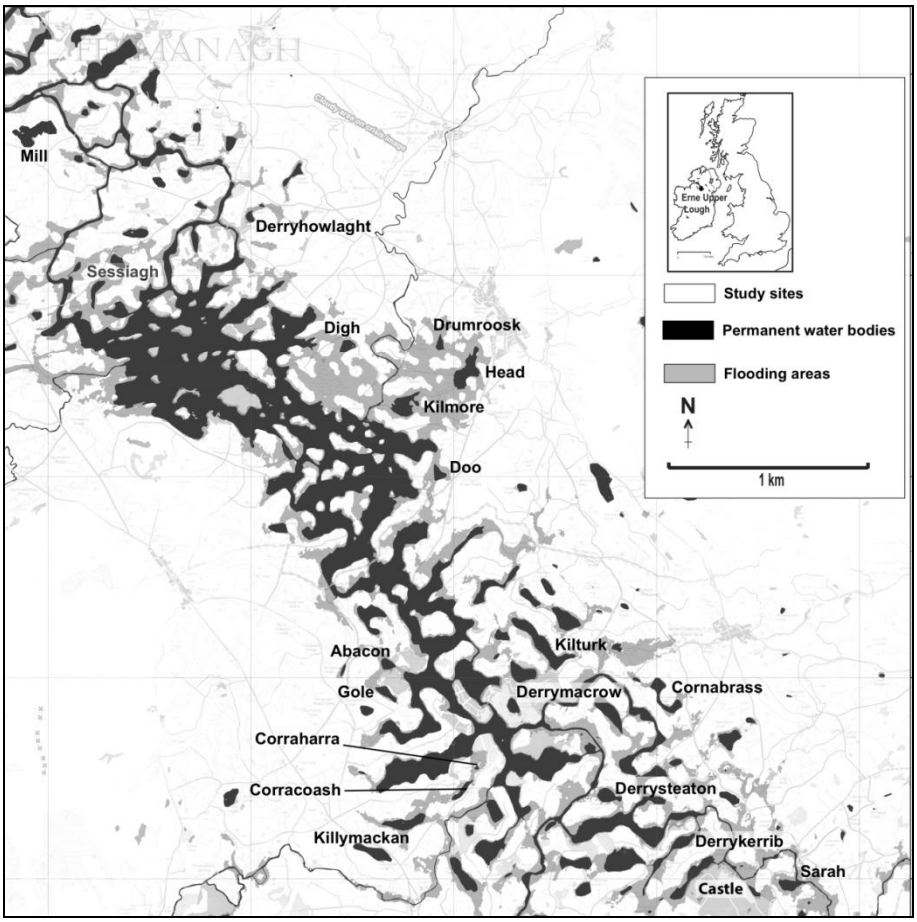

Figure 2-1. Map of the study sites, Upper Lough Erne (ULE) system. Permanent water bodies are shown in black and flooding areas in grey.

2.4 Materials and methods

Twenty satellite shallow lakes in the ULE system were selected for this study (Table 2-1 and Fig. 2-1). Selection criteria for lakes included replication along an enrichment gradient (mostly TP and TN), position in geographical space and watercourse connectivity between the satellite lakes and the ULE (Table 2-1 and Fig. 2-1).

Water chemistry variables were measured at each site on a quarterly basis by Environmental Scientific Services (ENSIS) consultancy staff in March, June/July and September 2006 and January 2007. Chemistry data included: pH, conductivity, alkalinity, watercolour, chlorophyll-a, total phosphorus (TP) and total nitrogen (TN). Two water samples were collected from each site using the "beach throw" methodthat consists of a weighted acid-washed (rinsed with deionised, distilled water)

polypropylene sample bottle, with a buoy attached to a rope 50 cm below the mouth of the bottle (Goldsmith et al. 2008). The bottle is thrown into the lake from an open area of shore to a distance in excess of 10 m. The buoy holds the full bottle 50 cm below the water surface and then by pulling the rope the sample is retrieved. All samples, with the exception of those for chlorophyll-a, TP, and total alkalinity were filtered on-site and refrigerated prior to analysis.

TP was determined by solution spectrometry (phosphomolybdate), after digestion by acid persulphate (Johnes and Heathwaite 1992). TN was determined by solution spectrometry (sulphosalicylic acid) after alkaline persulphate digestion (Wetzel and Likens 1991). Total alkalinity was determined by acidimetric titration. Water samples (250–1000 mL) for the analysis of chlorophyll-a were filtered through Whatman GF/F (0.7 m) filter papers (Whatman, Clifton, New Jersey, USA) and chlorophyll-a was determined spectrophotometrically (Pye Unicam SP6– 550 UV/VIS, Philips, Cambridge, UK) by cold extraction in 90% acetone (Talling and Driver 1961). Conductivity and pH were measured in the laboratory by electrometry.

Watercolour was determined spectrophotmetrically against standard platinum solutions (Wetzel and Likens 1991). All water chemical analyses were conducted by The Freshwater Sciences Research Group in the University of Ulster, Coleraine.

Lake morphometric variables, including secchi depth and maximum water depth, were recorded at each site during the summer. A site measurement was recorded from the deepest point of each lake. A standard 20 cm diameter secchi plate was used and the secchi depth expressed in cm. Lake area data was derived from the Northern Ireland Lake Inventory supplied by NIEA and quoted in hectares (ha). An additional exploratory dataset of TP, TN and chlorophyll-a was acquired during the summer of 2009 to identify any change in the water chemistry of the satellite lakes (Table 2-1). All analytical work for this second set of sampling was conducted in the water chemistry laboratories of the Geography Department of University College London (UCL) using the above mentioned methods.

Table 2-1. Mean annual values of environmental data collected from the 20 satellite shallow lakes at 2006-2007 (Goldsmith et al. 2008) and summer values of TP, TN and Chlorophyll-a data collected for 13 satellite lakes in 2009. To allow for comparisons, average values of June (2006) and September (2006) are given next to 2009 data.

2006-2007

LAKE	TP (ug/L)	TN (mg/L)	Chlorophyll-a (ug/L)	Colour (mgPt/L)	pH	Alk (mgCaCO3/L)	Cond (uS/cm)	Area (Ha)	Depth (cm)	Secchi (cm)
Abacon Lough	100	1,63	24,2	82	7,90	86	231	7	600	105
Castle Lough	29	1,03	4,2	55	8,00	118	302	13	450	160
Cornabrass Lough	96	1,05	5,3	77	8,00	135	353	18	430	70
Corracoash Lough	119	1,73	9,3	63	7,80	117	285	6,5	160	100
Corraharra Lough	130	1,29	21,9	71	7,80	120	275	1,5	150	100
Derryhowlaght Lough	159	1,75	18,3	91	7,60	143	316	4	190	55
Derrykerrib Lough	36	0,97	8,6	49	7,80	114	269	10,5	245	170
Derrymacrow Lough	83	1,00	8,2	54	7,70	106	263	21	610	75
Derrysteaton Lough	124	1,03	7,1	68	7,40	78	247	12	720	125
Drumroosk Lough	168	1,99	12,9	79	7,90	101	272	4	50	50
Gole Lough	128	1,35	13,8	76	7,80	117	285	8	310	55
Killymackan Lough	111	0,80	17,4	73	7,50	37	248	19,2	170	132
Kilmore Lough	186	1,09	6,5	83	7,90	112	297	20	90	80
Kilturk Lough	111	0,92	9,0	59	8,10	90	303	43	290	80
Lough Digh	82	1,44	10,2	76	7,70	120	228	9	400	130
Lough Doo	54	1,18	5,0	136	8,10	99	298	5	260	120
Lough Head	383	1,79	9,0	153	8,30	125	327	31	85	85
Lough Sarah	61	0,98	7,0	66	7,80	104	262	1,6	160	105
Mill Lough	23	0,47	11,1	23	7,80	108	226	33	930	285
Sessiagh East	45	0,92	7,9	63	7,50	56	195	8	100	90

LAKE	Summer values of 2006 TP (ug/L)	TN (mg/L)	Chlorophyll-a (ug/L)	Summer values of 2009 TP (ug/L)	TN (mg/L)	Chlorophyll-a (ug/L)
Castle Lough	27	1,03	5,9	37,5	0,00	5,97
Cornabrass Lough	86	0,54	6,1	434	0,01	69,47
Derryhowlaght Lough	160,5	1,00	32,3	228	0,01	59,18
Derrykerrib Lough	43,5	0,45	13,05	68	0,00	21,79
Derrysteaton Lough	199,5	0,76	11,05	84	0,00	34,64
Gole Lough	172	0,47	22	200	0,03	108,20
Killymackan Lough	159	0,40	30,1	198	1,64	37,38
Kilturk Lough	145	1,28	15,05	114	0,04	4,48
Lough Digh	61,5	1,20	11,8	86	0,00	17,76
Lough Doo	45	0,60	8,65	50	0,00	6,81
Lough Head	326,5	0,51	8,65	286	0,07	49,62
Mill Lough	16	0,28	9,85	42	0,01	17,02

As dispersal rates are inherently difficult to measure, a surrogate was adopted by quantifying the abundances of three taxonomic groups that differ in their dispersal mode: (1) chironomids – mainly overland dispersal; (2) submerged and floating leaved macrophytes (henceforth referred to as macrophytes) -overland and watercourse dispersal; and (3) bryozoans, molluscs and cladocerans (henceforth referred to as invertebrates)–mainly overland and/or water course dispersal.

Macrophyte species data were obtained from two different sources. For 2006 and 2007 data for all of the lakes were derived from the Northern Ireland Environmental Agency (NIEA) Water Framework Directive (European Parliament 2000) field campaign of Goldsmith et al. (2008). For 2008 and 2009 data were obtained for 13 of the 20 selected lakes as part of the current study. Macrophyte data from Goldsmith et al. (2008) were collected using Lake Common Standard Monitoring methods (JNCC 2005). These surveys consisted of three components: (i) a strandline survey of discrete 100 m sections considered as representative of the lake; (ii) a shoreline survey from 25 cm to ≥ 75 cm water depth; and (ii) a survey from a boat in deeper water. Twenty points per 100 m section were recorded and a minimum of three sections per site was surveyed. Due to their small size (< 5 ha), only a single 100 m section of lake was surveyed at Corracoash, Corrahara and Drumrusk lakes (see Table 2-1). Surveying was performed using a bathyscope or a long-handled double-headed rake (grapnel) where poor water clarity restricted visibility. Macrophyte abundances were recorded on a semi-quantitative scale of 0 – 3, where 3 was very abundant and zero was absent. The location of all survey sections and boat transects was recorded using Global Positioning System (GPS), backed up with digital photographs where necessary. The boat surveys were conducted from small boats, through all areas shallow enough to support aquatic plants, recording all submerged and floating-leaved species. Macrophyte species abundance data from Goldsmith et al. (2008) were reported on species occurrences at each lake.

In 2008 and 2009 sampling was conducted from a boat using a combination of grapnel and bathyscope in haphazard zigzag movements across each lake in order to cover most areas and not over-represent the lake margins. Data were recorded for ≥ 30 points in each lake. Macrophyte density and composition at each point was

recorded for an estimated area of 1 m^2 using the percentage volume infestation (PVI) method (Canfield et al. 1984).

PVI = (Percentage coverage of macrophytes X Average height of macrophytes)/ Water depth.

As macrophyte data from Goldsmith et al. (2008) were reported in species percentage frequency of occurrences, PVI data for 2008-2009 were standardised into species percentage frequencyoccurrences. Macrophyte species occurrences were calculated for both NIEA and PVI data sets, as the total number of observations of a species on a given lake divided by the total number of sampling points of that lake. The positive interspecific abundance–occupancy relationship across different species is one of the most robust patterns in macroecology (Gaston et al. 2000; Blackburn, Cassey and Gaston 2006; Verberk et al. 2010) and thus a trustworthy surrogate for species abundances estimation.

Due to the lack of data on chironomids and invertebrates from 2006 and 2007 and in view of the difficulties of directly quantifying the abundances of benthic invertebrates having patchy distributions and seasonal variation, an indirect method to estimate contemporary species abundances was adopted by counting organismal remains from surface sediment samples collected at each of the 13 lakes surveyed in 2008 and 2009. Each sample comprised the uppermost 3 cm of sediment thus averaging across current assemblages and those of the previous ~ 3-5 years. For invertebrates, this study focused on bryozoans, bivalves and cladocerans. The remains of these groups are well preserved in the sediments and should thus provide a reliable source of information about contemporary assemblages (Aldridge and Horne 1998, Hill et al. 2007, Jeppesen et al. 2001). Bryozoans abundance was characterised by examination of statoblasts (dormant propagules) (Hill et al. 2007), cladoceran assemblages were characterised using ephippial resting stages (Jeppesen et al. 2001) and bivalve assemblages by analysis of whole shells, shell fragments and larvae (glochidia) (Aldridge and Horne 1998). Chironomid assemblages were characterised by counting larval head capsules, which offer a consistent and accurate representation of the extant larvae and are well preserved in sediment cores (Brodersen and Lindegaard 1999).

2.4.1 Data analysis

To analyse the relative importance of environmental and regional factors in structuring the active and passive dispersal assemblages, a variance partitioning analysis (pRDA) was conducted using macrophyte species occurrence and chironomid and invertebrate taxa relative abundances (Fig. 2-2).. Using this approach the total percentage of variation explained by a redundancy analysis (RDA) is partitioned into unique and common contributions for the sets of environmental and dispersal predictors, the latter related to space (Borcard et al. 1992). Dispersal predictors were constructed using the Principal Coordinate Neighbour Matrix (PCNM) analysis (Borcard and Legendre 2002) from two sources and run as two separate variation partitioning analyses: (1) the direct overland distances between given satellite lakes measured from the midpoint (XY coordinates) of each satellite lake. Lake midpoints were visual approximations of the centre of each lake assessed with the open source Google Earth software for Macintosh version 6.0.3.2197 (earth.google.com); and (2) actual watercourse distances between lakes that were connected by streams, rivers and channels to assess the potential role of dispersal by the fluvial vector (Beisner et al. 2006). This element was calculated by measuring the distance between the midpoints of given lakes considering the distances of any of the above-mentioned hydrological connecting vectors. Watercourse length was determined using the path tool in Google Earth software. The PCNM method uses the XY coordinates or watercourse distances to compute a matrix of geographic (i.e. Euclidean) distances between the sites (Borcard and Legendre 2002). Principal coordinate analysis (PCoA) is then conducted on the modified distance matrix and the positive eigenvalues of the PCoA are used as the set of PCNM variables (dispersal predictors) for the pRDA. Prior to pRDA species data were subject to Hellinger transformation (Legendre and Gallagher 2001). Hellinger transformation provides one of the best estimates of the variation partitioning based on RDA (Peres-Neto et al. 2006; Bocard and Legendre 2002, Beisner et al. 2006).

To separate the effects of both environmental (E) and spatial (S) predictors, the following analyses were calculated:

1. Two RDA using both sets of predictors, E and S, to calculate first, the total amount of species occurrence variation explained by the environment

including any spatial component [S] and, second, to calculate the total amount of variation in macrophyte species occurrence and invertebrate and chironomid relative abundance explained by the spatial component including any environmental component [E]. The total proportion of variation explained by both [E] and [S] is then [E+S];

2. A pRDA using [S] as a covariable of [E] to calculate the unique fraction that is explained by environmental variables, defined as [E|S].

3. A pRDA with [E] as a covariable of [S] to determine the amount of macrophyte species occurrence and invertebrate and chironomid relative abundance variation that is explained only by spatial predictors, defined as [S|E].

4. The common fraction shared by environment and space is then [E+S]-[E|S] - [S|E] and the residual fraction of variation not explained by environment and space is [1- ([E|S] + [S|E] + [E+S])].

The significance ($P \leq 0.05$) of the environmental variables alone (analysis 2) and spatial variables alone (analysis 3) was then used to determine the metacommunity type for each taxonomic group according to Cottenie (2005) (Table 2-2). These are: (1) *species-sorting* perspective - if only the macrophyte species occurrence and invertebrate and chironomid relative abundance variation that is explained by the environmental component is significant (i.e. $P[E|S] \leq 0.05$ and $P[S|E] > 0.05$); (2) *mass-effect* perspective - if both environment and space fractions are significant but spatial variables explain larger variation than environment variables (i.e. $P[E|S]$ and $P[S|E] \leq 0.05$ and $[S|E] > [E|S]$); (3) *species-sorting* and *mass-effect* perspective - when both environment and space fractions are significant and explain equally the amount of species occurrence variation (i.e. $P[E|S]$ and $P[S|E] \leq 0.05$ and $[S|E] \approx [E|S]$); and (4) other perspective - if only the spatial fraction is significant ($P[S|E] \leq 0.05$).

As the environmental data in 2009 were collected only in summer and values showed a similar pattern as those collected in 2006-2007 by Goldsmith et al. (2008) all statistical analysis were calculated using the more complete set of 2006-2007 data. The mean values from all quarterly water chemistry data of 2006-2007 were used for

pRDA. Environmental and invertebrate relative abundance matrices were first centred by subtracting the column means (omitting zeros or data absences) of species/environmental-variables from their corresponding columns and subsequently scaled by dividing the (centred) columns by their standard deviations (scale in R; R Core Development Team 2011).

Because the number of environmental variables, spatial predictors and sample size all influence pRDA analysis, the results of this study are given asadjusted fractions of the variation (Peres-Neto et al. 2006). These adjusted fractions are analogous to adjusted R^2 in multiple regressions. The significance of [E+S], [E|S] and [S|E] fractions were tested by permutation tests using 999 stratified (within each lake) randomizations (Borcard et al. 1992). When the number of environmental and spatial predictors is greater than the number of sites, collinearity between variables and covariables is expected (Borcard et al. 1992). Therefore, the number of both environmental and PCNM components was reduced via preliminary RDA (Cottenie 2005). The selected variables were then tested over a series of other preliminary pRDA where uninformative environmental and spatial variables were discarded at each step until a final pRDA presenting the best solution was reached. All RDA and pRDA were conducted in the program R version 2.13 for Macintosh (R Core Development Team 2011) using the algorithm *varpart* in vegan library.

pRDA determines how much of the variation in species occurrence is explained by the respective effects of environmental conditions and space but does not allow estimation of how lake community similarity varies along the spatial and environmental gradient (Tuomisto and Ruokolainen 2006). Therefore, to determine whether connectedness between lakes was correlated with community similarity (Legendre & Fortin, 1989), Mantel tests on geographical distance and community similarity matrices were calculated. The geographical distance matrix contained the pairwise Euclidean distances between all lakes measured from watercourses. The community dissimilarity matrices contained the pairwise Bray-Curtis dissimilarity index of macrophyte, chironomid and invertebrate assemblages between lakes.

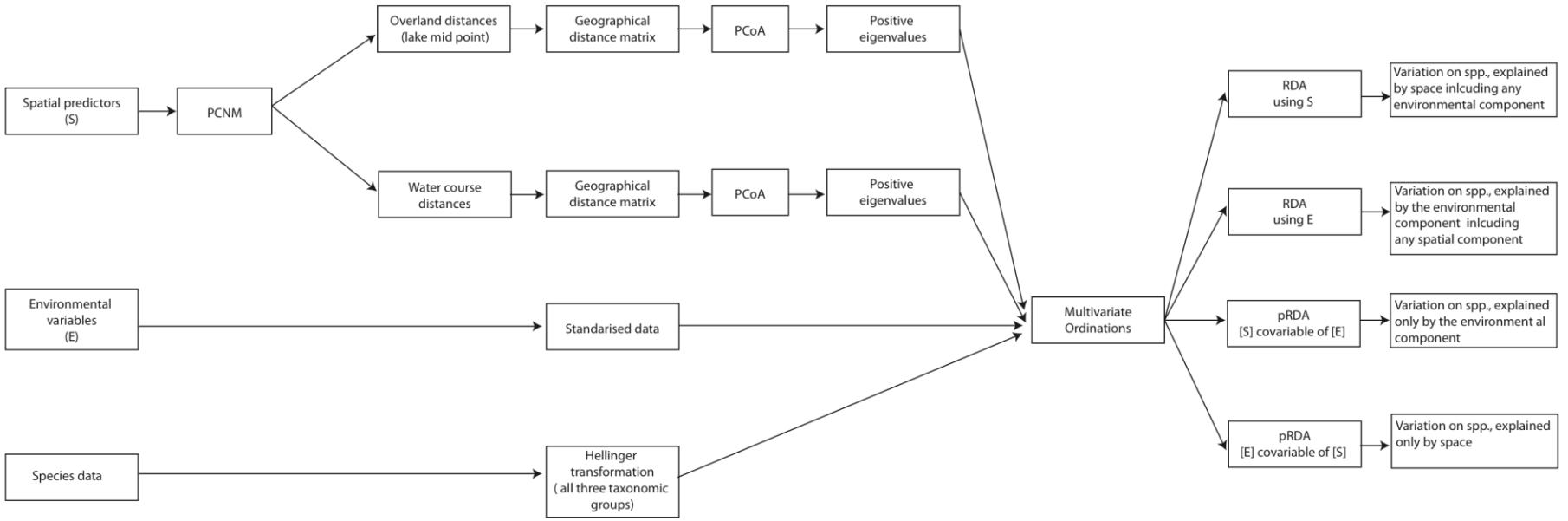

Figure 2-2. Flow diagram visualising each step of the Principal Coordinate Neighbour Matrix (PCNM) and constraint Redundancy Analysis (pRDA).

Table 2-2. Theoretical relationship between significance structure of the four important variation components and associated metacommunity types. The components are environment [E], space [S], environment independent of space [E|S], and space independent of environment [S|E]. $P \leq 0.05$ explains a significant part of the variation in species structure. Table modified from Cottenie (2005).

Components		Species-sorting		Mass-effect		Species-sorting + Mass effect		Other
		P	*Adj R*	*P*	*Adj R*	*P*	*Adj R*	
Total amount of species occurrence variation explained by the environment including any spatial component	[E]		-		-	-		-
Total amount of species occurrence variation explained by the spatial component including any environmental component	[S]		-		-	-		-
Total proportion of variation explained by both [E] and [S]	[E+S]		-		-	-		-
Unique fraction that is explained by environmental variables	[E|S]	P ≤ 0.05		P ≤ 0.05	[S|E] > [E|S]	P ≤ 0.05	[S|E] = [E|S]	-
Unique fraction that is explained by spatial variables	[S|E]		-	P ≤ 0.05		P ≤ 0.05		P ≤ 0.05
The common fraction shared by environment and space	[E+S]-[E|S]-[S|E]		-		-	-		-
The residual fraction of variation not explained by environment and space	[1- ([E|S] + [S|E] + [E+S])		-		-	-		-

To establish whether distance between lakes was also correlated with pairwise differences between values of the environmental variables another Mantel test was calculated. Subsequently partial Mantel tests (Legendre and Fortin 1989) were used to determine whether distance and community similarity were correlated after removing the potentially confounding effects of the significant environmental variables. To calculate an environmental dissimilarity index, a preliminary principal component analysis (PCA) of all environmental variables was calculated. Highly redundant variables were excluded and the remaining variables were subject to a principal curve (PC) analysis (De'ath 1999). By using nonlinear regressions and smoothers this ordination method extracts one principal gradient from the multidimensional space. This has an advantage over other ordination methods by providing compositional changes in only two components whilst capturing the information of all axes (De'ath 1999). The analysis provides a value for each sample location along the curve (lambda) that can be used as an indicator of environmental variability. A pairwise distance (Euclidean) of lambda was then calculated. The significance of correlations of all analyses was tested with 999 permutations in R (vegan package).

2.5 Results

A total of 44 submerged and floating-leaved macrophytes species were recorded in the surveys for 2006-2007 (Goldsmith et al. 2008 and Fig. 2-3). Castle Lough, Kilturk Lough and Mill Lough had the greatest number of species with 21, 18 and 18 species, respectively. The lowest number of species was recorded in Derrysteaton Lough and Gole Lough which both had just 6 species. In 2008-2009 a total of 36 species were recorded with an average of 13 species per lake and 10 lakes having 10 or more species (Fig. 2-3). The highest number of species was recorded in Kilturk Lough, which had 24 species, while low numbers of species (n = 4) were again found in Derrysteaton and Gole Lough. Overall, the most commonly recorded species in both surveys for all lakes were *Elodea canadensis* Michx., *Lemna minor* L., *Lemna trisulca* L., *Nuphar lutea* (L.) Smith., *Potamogeton obtusifolius* Mert. & Koch., *Sparganium emersum* Rehmann and *Stratiotes aloides* L. (Appendix 1). Other species such as *Fontinalis antipyretica* Hedw., *Potamogeton pusillus* L., *Potamogeton pectinatus* L.,

Sagittaria sagittifolia L. and *Utricularia vulgaris* L. agg., were also frequently recorded.

Surface sediment samples included 44 chironomid taxa. There was an average of 20 taxa per lake and the lowest diversity was recorded at Cornabrass Lough and Kilturk Lough, which possessed 16 and 15 taxa respectively (Fig. 2-4). The greatest diversity was at Killymackan, which had 26 taxa. In general the most common taxa were *Procladius*type, *Chironomus plumosus*type, *Dicrotendipes nervosus*type, *Endochironomus albipennis*type, *Glyptotendipes pallens*type, *Polypedilum nubeculosum*type, *Cladotanytarsus mancus*type, *Tanytarsus lugens*type, *Cricotopus intersectus*typeand *Cricotopus laricomalis*type(Fig. 2-4). Surface sediment samples contained a total of 12 invertebrate taxa with an average of 7 taxa per lake (Fig. 2-5). Castle Lough had 10 types and Lough Doo only 5. The most abundant taxa were the bryozoans *Plumatella* spp. and *Paludicella articulata* Ehren., together with *Anodonta cygnea* L., *Daphnia pulex/hyalina* and *Ceriodaphnia* sp.

2.5.1 Relative contributions of spatial and environmental variables

For the 2006-2007 macrophyte data, the overland distance analysis showed that both the environment [E|S] and spatial fractions [S|E] were significant (P = 0.04 and P = 0.039, respectively) and each explained 14% of the adjusted total variation (Table 3). The combined fraction of environmental and spatial factors [E+S] explained 22% of the total variation. The preliminary RDA and pRDA identified five significant environmental variables that were used in the final pRDA: TP, TN, conductivity, area and water depth (Table 2-3). Among the spatial variables, the first six PCNM's variables were also significant in explaining species occurrence and were included in the pRDA (Table 2-3). In 2008-2009 the environmental component was significant (P = 0.015) and explained 22% of the adjusted variation. TP, TN, area and water depth were identified as the most important variables in explaining species occurrence and distribution (Table 2-3). The spatial component explained around 13% of the adjusted variation in species occurrence but was not significant (P = 0.09). Among the spatial variables, preliminary pRDA only identified the first two components (PCNM1 and PCNM2) as significant. Both environmental and spatial factors [E+S] explained 26% of the total variation.

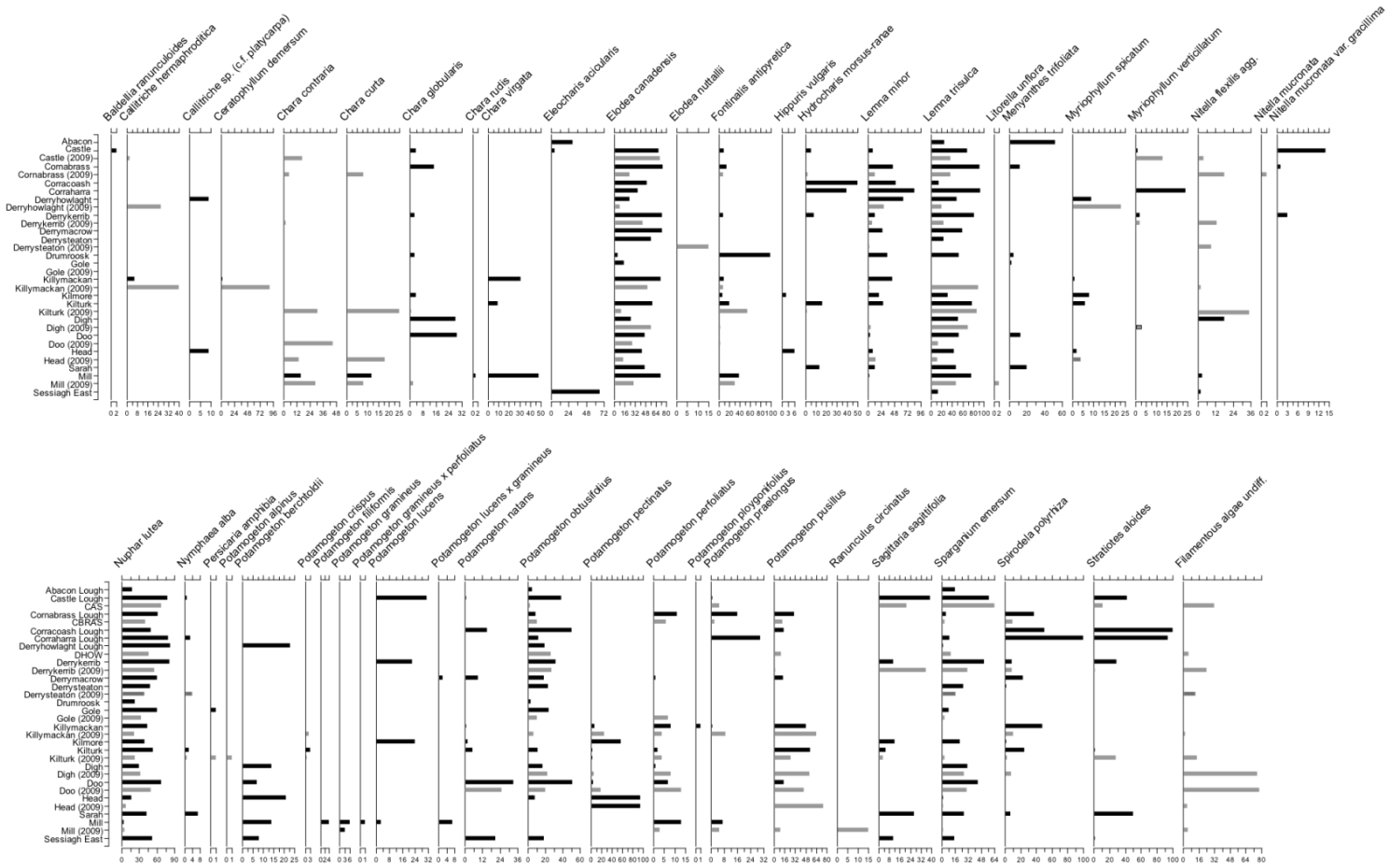

Figure 2-3. Macrophyte species occurrences in the study sites. Data from 2006-2007 are shown in black and in grey for 2008-2009.

The watercourse analysis of 2006-2007 showed that both environmental and spatial factors were significant in explaining macrophyte species occurrence (Table 2-3). The environmental component [E|S] explained 24% of the adjusted total variation (P = 0.02) and the spatial component ([S|E]) 22% of the variation (P = 0.01). The combined environmental and spatial components [E+S] accounted for 24% of the total variation. Preliminary pRDA identified TP, TN, conductivity, area, water depth and watercolour as the most important environmental variables to explain variation in species occurrence. The first seven PCNM components were also significant. The analysis of 2008-2009 showed similar trends in species occurrence variation to those found in the analysis of overland distances over the same time period. The environmental component was significant (P = 0.025) explaining 23% of the total species occurrence variation. The spatial component explained 15% of the total variation but was not significant (P = 0.09) (Table 2-3). The combined environmental and spatial fraction [E+S] explained 29% of the total variation in species occurrence. Three environmental variables (TP, TN and area) and the first three spatial components PCNM1, PCNM2 and PCNM3 were identified as significant explanatory variables.

With regard to invertebrate abundances, when direct overland distance between lakes was included in the analysis, only the environmental component was identified as significant (P = 0.042) and this factor explained 35% of the adjusted total taxa relative abundance variation (Table 2-3). Here, macrophyte PVI, chlorophyll-a and water depth were identified as significant. In contrast, when watercourse distance between lakes was included in the analysis, both environment [E|S] and space [S|E] were significant (P = 0.039 and P = 0.05 respectively) and explained 27% of the adjusted variation in total taxon relative abundances. Again macrophyte PVI, chlorophyll-a and water depth and the first three spatial predictors were identified as significant explanatory variables that entered in the pRDA.

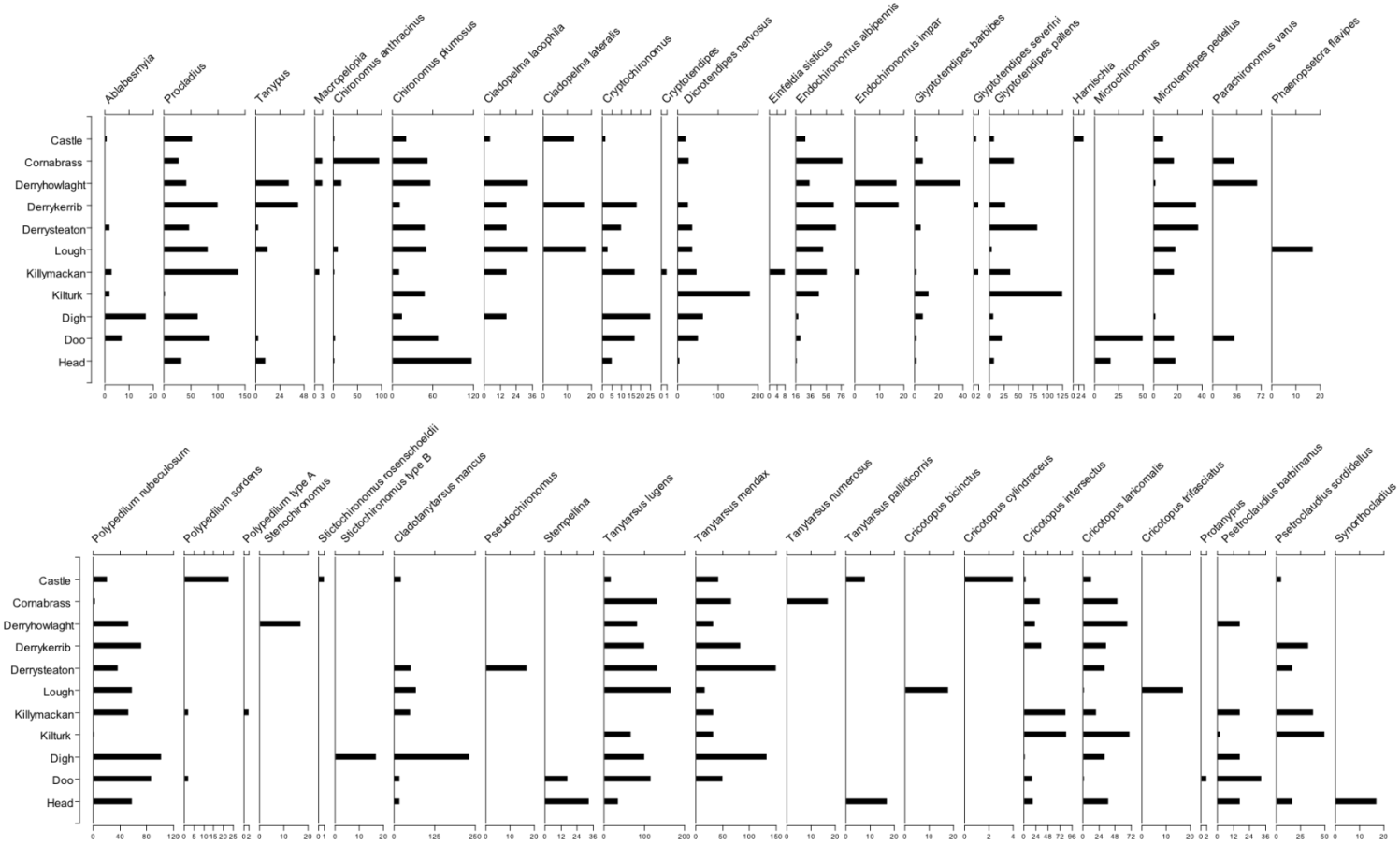

Figure 2-4. Larval chironomid head capsules abundances obtained from surface-sediments samples of eleven satellite lakes in 2008-2009..

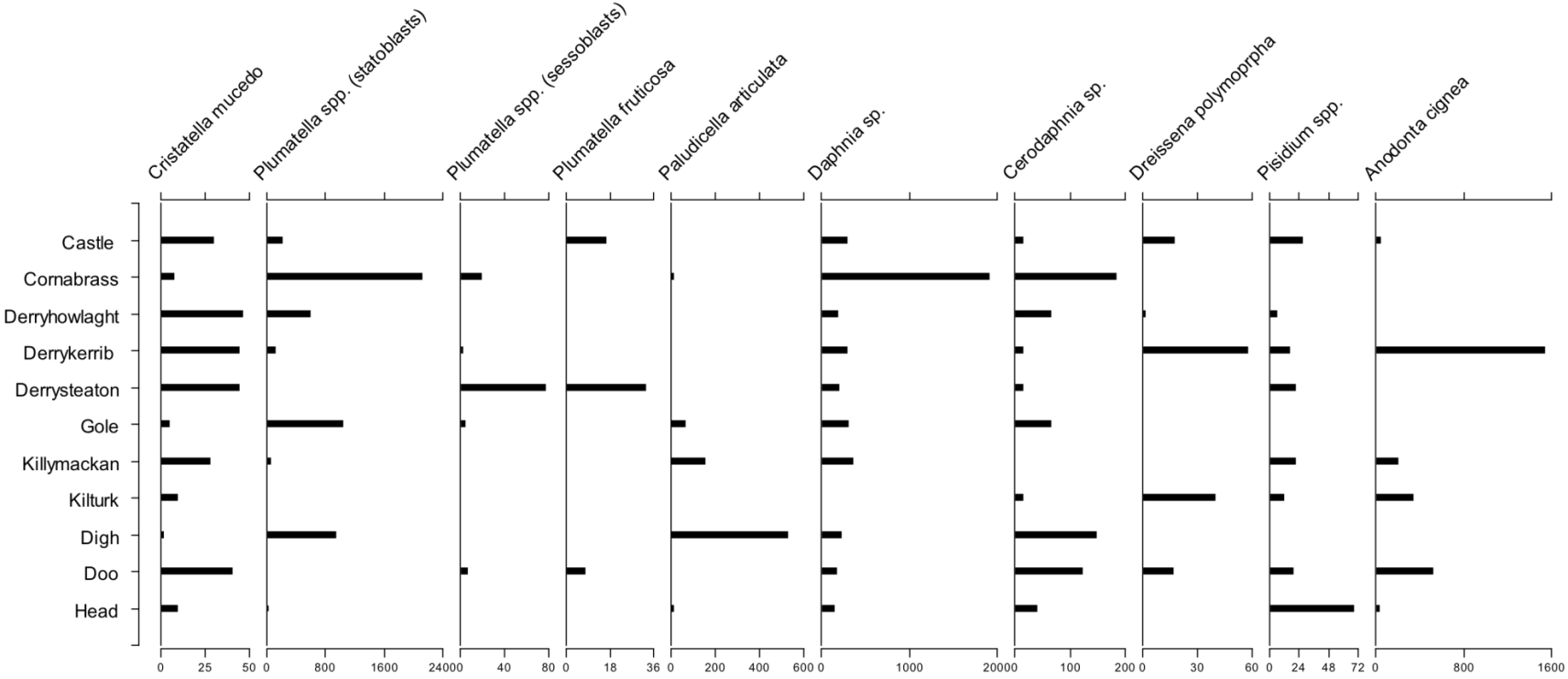

Figure 2-5. Invertebrate macrofossil abundances from surface-sediment samples of 11 satellite lakes obtained in 2008-2009.

For chironomid abundances, analysis using direct distance identified both environment and space factors as significant (P = 0.01 and P = 0.02 respectively) (Table 2-3). The environmental component [E|S] explained 22% of the adjusted total variation in taxon relative abundance, while space [S|E] explained 18% of the adjusted total species relative abundance variation. The combined fraction of environment and space [E+S] accounted for 33% of the adjusted total variation. The analysis indicated that macrophyte PVI and area and the first three spatial predictors (PCNM1, PCNM2 and PCNM3) were the most important variables that entered in the pRDA. Analysis using watercourse distance, on the other hand, identified only the environmental component as significant (P = 0.047), explaining 13% of the adjusted total variation in taxon abundance. Again area and macrophyte PVI were the only two variables identified by preliminary pRDA as significant variables explaining distribution and abundance of chironomid taxa.

2.5.2 Community similarity along environmental and spatial gradients

Mantel and partial Mantel test results regarding community similarity along environmental and spatial gradients are given in Table 2-4. Overall, the results indicated that there was no specific and predictable pattern of community similarity along environmental or spatial gradients in the system. The only case that indicated a significant trend was between the aquatic flora dissimilarities (2008-2009) and the environmental dissimilarities (r = 0.38, P = 0.035) in the partial Mantel test (i.e. when excluding any spatial component). Preliminary PCA analysis identified TP, TN, area, water depth, chlorophyll-a and conductivity as significant variables. The other variables (water colour, secchi depth, pH and alkalinity) were redundant or non-significant. Mantel test examination of the environmental component (lambda values from PC analysis of the above-mentioned six significant environmental variables) over macrophyte assemblages in 2006-2007 resulted in P just above the significant boundary (0.053). The Mantel and partial Mantel tests between invertebrate community similarity and the environmental gradient showed similar results with a regression coefficient of around 0.30 and a P value above the 0.05 confidence level (P = 0.08).

Table 2-3. Results of variation partition analysis (pRDA) for species assemblages of actively (chironomids) and passively (macrophytes and invertebrates) dispersing organisms, using direct linear overland distances between lakes and watercourse distance lengths via river and channels connections between lakes. '*'= P< 0.05; '**'= P< 0.01. Environmental variables and spatial components that enter in each pRDA are given in the lower part of the table.

	Macrophytes (2006-2007)		Macrophytes (2008-2009)		Chironomids (2006-2009)		Invertebrates (2006-2009)	
Effect	Adj.R^2	*P*	Adj.R^2	*P*	Adj.R^2	*P*	Adj.R^2	*P*
Overland distances								
[E]	0.08	0.058	0.14	0.053	0.15	0.005 **	0.16	0.11
[S]	0.08	0.056	0.04	0.215	0.11	0.048 *	0.00	0.485
[E+S]	0.22		0.26		0.33		0.35	
[E|S]	0.14	0.044 *	0.23	0.015 *	0.23	0.0175 *	0.35	0.042 *
[E+S]-[E|S]-[S|E]	-0.06							
[S|E]	0.15	0.039 *	0.13	0.085	0.18	0.0225 *	0.19	0.22
Resididuals	0.78		0.74		0.67			
Watercourse distances								
[E]	0.12	0.015 *	0.14	0.031 *	0.15	0.005 **	0.13	0.085
[S]	0.10	0.047 *	0.05	0.215	0.01	0.45	0.14	0.092
[E+S]	0.34		0.29		0.14		0.40	
[E|S]	0.24	0.022 *	0.24	0.025 *	0.13	0.047 *	0.27	0.039 *
[E+S]-[E|S]-[S|E]								
[S|E]	0.22	0.01 **	0.15	0.0875 .	0.01	0.48	0.27	0.05 *
Resididuals	0.66		0.71		0.86		0.60	
Environmental and spatial variables (overland distances)								
	TP TN Conductivty Area Water depth		TP TN Area Water depth		Area PVI		Water depth PVI Chlorophyll-a PCNM1-PCNM3	
	PCNM1-PCNM6		PCNM1-PCNM2		PCNM1-PCNM3			
Environmental and spatial variables (watercourse distances)								
	TP TN Conductivty Water colour Area Water depth PCNM1-PCNM7		TP TN Area		Area PVI PCNM1-PCNM3		PVI Chlorophyll-a PCNM1-PCNM3	

Table 2-4. Results of Mantel and partial Mantel test analyses between community dissimilarities (Bray-Curtis distances) of macrophyte, chironomid and invertebrate assemblages and environmental and watercourse dissimilarities (Euclidean distances).'*' = P< 0.05.

	2006-2007		2008-2009	
	R	*P*	R	*P*
Mantel test				
Environmental variables vs. watercourse distances	0.060	0.285	0.241	0.116
Macrophytes vs. environmental variables	-0.016	0.531	0.359	0.053(*)
Macrophytes vs. watercourse distances	0.096	0.198	-0.015	0.508
Chironomids vs. environmental variables			0.137	0.309
Chironomids vs. watercourse distances			0.075	0.322
Invertebrates vs. environmental variables			0.292	0.085
Invertebrates vs. watercourse distances			0.106	0.244
Partial Mantel				
Macrophytes vs. environmental variables	0.097	0.211	0.380	0.035*
Macrophytes vs. watercourse distances	-0.022	0.539	-0.114	0.774
Chironomids vs. environmental variables			0.142	0.290
Chironomids vs. watercourse distances			0.084	0.348
Invertebrates vs. environmental variables			0.301	0.077
Invertebrates vs. watercourse distances			0.129	0.182

2.6 Discussion

2.6.1 Environmental variables and assemblage variation

The results of this study demonstrate a strong association between local environmental conditions and species composition. In both 2006-2007 and 2008-2009, the environmental fraction alone [E|S] explained a significant portion of the variation in the occurrence of the aquatic plants, chironomids and invertebrates (Table 2-3). For macrophytes, the key factors were TP and TN, indicating a strong influence of eutrophication. Lake morphological characteristics (size and water depth) exerted a weaker influence. The influence of TP and TN in structuring lake macrophyte communities has been well documented (Spence 1967, Carpenter 1984, Arts 2002). Increased concentrations of TP and TN typically reduce availability of light and oxygen and modify sediment characteristics from low organic matter and high sand content to more unconsolidated and organic sediments (Spence 1967, Barko and Smart 1983, Salgado et al. 2010). These changes in the environment commonly lead to a shift in the aquatic vegetation from one dominated by an isoetid community to an

elodeid and floating-leaved species assemblage, and subsequently to phytoplankton dominance (Spence 1967, Arts 2002).

The relationship between water depth and macrophyte abundance could be attributed to an indirect alteration of light availability in the water column due to an increasing input of TN and TP (Spence 1967, Spence 1982, Canfield 1985). The maximum colonisation depth of macrophytes is usually ascribed to light attenuation in the water column and minimum light requirements of the plants (Canfield, 1985, Middelboe and Markager 1997). Highly transparent waters allow macrophytes to colonise at greater depth than in more turbid waters (Canfield 1985, Middelboe and Markager 1997, Capers et al. 2010). The association between lake area and macrophyte species richness, is widely attributed to an array of factors such as greater habitat heterogeneity in large lakes, larger areas for colonisation and greater sampling and likelihood (Leibold and Norberg 2004, Matias et al. 2010, Chapter 3).

Variation in the occurrences of chironomids and invertebrates was also attributed to environmental variables and particularly by macrophyte PVI and phytoplankton biomass expressed as chlorophyll-a. The association between chlorophyll-a and chironomid and invertebrate assemblage composition has been universally attributed to food availability (Rasmusen 1984, Rasmusen 1985, Armitage et al. 1995, Caraco et al. 1997, Jeppesen and Jensen 2000, De Haas et al. 2006, Hartikeinen et al. 2008). The role of submerged macrophytes in structuring chironomid and invertebrate communities in shallow lakes has also been well recognised. Macrophytes act as a direct or indirect (epyphitic growth on leaves and stems) food source, provide predation refuges, and substrata for egg-laying (Sculthopre 1967, Jeppesen et al. 1998, Brodersen et al. 2001, Langdon et al. 2010, Jones et al. 1998). Several studies have demonstrated a positive relationship between the presence of macrophytes and the abundance and diversity of chironomids (e.g. Moore 1980, Brodersen et al. 2001, Langdon et al. 2010). For example, a study of a set of 25 Danish lakes by Brodersen et al. (2001) showed a strong relationship between chironomid community change and macrophyte assemblages. More recently, an analysis of chironomids in surface sediments from a set of 39 UK and Danish shallow lakes by Langdon et al. (2010) found that the most important explanatory variable for changes in chironomid assemblage was macrophyte abundance.

A strong association between macrophytes and cladocerans has also been widely demonstrated due to the use of plants as a refuge from fish predation by cladocerans (Stansfield et al. 1997, Burks and Jeppesen 2001). For instance, Stansfield et al. (1997) showed that *Daphnia* spp. persisted in extensive macrophyte stands in three shallow lakes in the UK after their elimination in open water by fish, indicating some refuge effect. By measuring the reaction of *Daphnia pulex* to macrophytes in the presence and absence of chemical cues from two commonly occurring European fishes, roach (*Rutilus rutilus*) and perch (*Perca fluvialitis*), Burks and Jeppesen (2001) found that *D. pulex* sought macrophyte refuge in the presence of both fishes and that the effectiveness of the refuge depended on macrophyte density and predator identity.

Few attempts (e.g. Bushnell 1966, Okland and Okland 2000) have been made to assess the interaction of macrophytes and bryozoans. Nevertheless, the available data suggest that in general the presence of macrophytes enhances bryozoan abundances either by modifying food resource availability or by providing substrata for attachment of colonies (Bushnell 1966, Økland and Økland 2000).

2.6.2 Spatial variables and assemblage variation

The significance of spatial predictors (overland or watercourse) varied amongst groups. For instance, submerged macrophyte compositional changes were significantly explained by both overland and watercourse distance. Aquatic plants are capable of producing different reproductive vegetative fragments (e.g. leaf fragments, turions, stolons) and seeds that allow them to disperse passively via hydrochory, across land by assisted transportation and to a lesser extent by wind (Sculthorpe 1967, Cook 1987, Barrat-Segretain 1996, Green et al. 2002, Santamaría 2002). Water flow offers a general means of dispersal in riverine systems (Dawson 1988, Barrat-Segretain 1996, Green et al. 2002, Santamaría 2002) for all types of propagules (seeds, fruits and vegetative fragments) (Sculthrope 1967, Cook 1987, Abernethy and Willby 1999, Green et al. 2002, Santamaría 2002) and propagules may float for several days or weeks, dispersing over long distances (Cook 1987, Barrat-Segretain 1996). Since flowering may be uncommon among submerged macrophytes, dispersal by means of vegetative parts tends to be much more significant than dispersal by seeds (Keddy 1976). In riverine systems most flow-mediated dispersal is downstream, and very little transport occurs between separated water bodies (Barrat-Segretain

1996). Therefore, dispersal via water is frequently an important method over relatively short distances.

Other agents of dispersal, such as waterfowl, are more likely to effect long distance dispersal of propagules, especially to permanently isolated waters (Sculthorpe 1967, Cook 1987, Barrat-Segretain 1996). Compelling evidence from migration routes, field observations and experimental feeding experiments indicates that both internal and external dispersal of sexual macrophyte propagules is common and largely attributed to migratory water fowl (Hutchinson, 1975, Cook, 1987, Santamaría 2002). Likewise, many species of waterfowl are known to consume large amounts of aquatic plant seeds (Thomas 1982, Green et al. 2002, Figuerola and Green 2002, Santamaría 2002). The hydrological connectivity in ULE system is very high (Fig. 2-1) and macrophyte-feeding waterfowl, including whooper and mute swan, and mallard, are present in large numbers (www.doeni.gov.uk/niea/ramsar/). Given the abundance of waterfowl, it is not surprising that both dispersal predictors are significant. Nevertheless, watercourse distances explained the highest proportion of species occurrence variation. This suggests that the dispersal of aquatic flora of the system is achived mostly by hydrochory.

For chironomids, direct distances alone were significant in explaining a large proportion in their occurrence variation. This result is consistent with their dispersal mode as in this diverse group adults can disperse widely by wind-assisted movements, especially over open landscapes (Armitage et al. 1995, Delettre and Morvan 2008). Even though most chironomid species are weak flyers, with a mean self-generated dispersal distance of around 500 m (Armitage et al. 1995, Delettre and Morvan 2008), wind can disperse large numbers over long distances (Nielsen and Nielsen 1962, Davies 1967, Armitage et al. 1995, Delettre and Morvan 2008).

Analyses indicated that watercourse distance was the only significant dispersal predictor for occurrence variation in the invertebrate taxa (Table 2-3). Unionid mussels, for example, produce free-floating larvae that can disperse freely through the water column or as obligate parasites on the gills of fish during later stages of development (Zale and Neves 1982, Ricciardi and Neves 1998). Fish hosts are also restricted to dispersing through connecting water courses (e.g. Beisner et al. 2006). Zebra mussels can disperse quickly by both natural and human mediated mechanisms

(Johnson and Carlton 1996). Their planktotrophic larvae develop over weeks in the plankton and therefore ensure widespread dissemination by water and wind-driven currents (Johnson and Carlton 1996). At juvenile and adult stages, this species can disperse by fouling submerged objects that subsequently drift (e.g. aquatic macrophytes). Aquatic birds and boats offer other mechanisms of dispersal. Thus larval, juvenile or adult zebra mussels can disperse broadly, even colonising in up-current regions and disconnected nearby water bodies (Johnson and Carlton 1996).

Bryozoan colonies reproduce by colony fission, fragmentation, larvae and statoblasts (dormant propagules). Larvae are short-lived so generally should not disperse far (Bilton et al. 2001). Long distance dispersal is mainly expected to be achieved by statoblasts (Bilton et al. 2001, Okamura and Freeland 2002) many of which float and are carried by wind and water currents (Bilton et al. 2001). However, rafting colonies on detached floating surfaces (e.g. vegetation) may sometimes be important for dispersal (Bilton et al. 2001). Some statoblasts, like those produced by *C. mucedo*, have hooks that increase the likelihood of attachment to animal vectors for dispersal across land (Okamura and Freeland 2002). Such dispersal is supported by evidence of gene flow (Freeland et al. 2000, Figuerola et al. 2005). However, both spined and unspined statoblasts are collected in waterfowl faeces (Charalambidou et al. 2003) and studies suggest that a proportion remains viable after excretion (Charalambidou and Santamaría 2002).

Studies on dispersal pathways in zooplankton have shown that *Daphnia* spp. can disperse through both watercourses as living or resting stages (ephippia) (Pace 1992, Walks and Cyr 2004, Beisner et al. 2006) and by overland movement as desiccation-resistant ephippia (Brendonck and Riddoch 1999, Louette and De Meester 2005, Figuerola et al. 2005).

By focusing on three different biological groups (chironomids, macrophytes and invertebrates) and two possible routes of dispersal (overland and by watercourse) the evidence from this study highlights the importance of regional processes in driving freshwater diversity. The study also illustrates how a comparative analysis of distinct biological groups can distinguish the relative importance of dispersal modes for organisms residing in the same system.

2.6.3 Metacommunity perspectives

pRDA shows that over the 4 years of this study two types of metacommunities were found (Tables 2-3 and 2-4): (1) a metacommunity structured by the significant influence of both environmental variables alone and spatial variables alone (*species-sorting* and *mass-effect* perspective); and (2) a metacommunity structured by environmental variables alone (species-sorting perspective). These results may be attributed to differences in dispersal modes employed by the study groups. Variable results however, were obtained for the submerged macrophytes in 2006-2007 and in 2008-2009. The pRDA of macrophyte data in 2006-2007 suggests that macrophyte communities had a metacommunity structure consistent with both the environmental variables and dispersal being influential on macrophyte abundance. In contrast, in2008-2009 pRDA analysis revealed that position in space was not significant while environmental variables explained a significant portion of the community variation (Table 2-3). This shift in macrophyte metacommunity structure could be attributed to differences in water chemistry, but this is unlikely since water chemistry data for both time periods were largely simliar. Another explanation is inter-annual variation in the macrophyte community as has been commonly shown in studies of shallow lakes (Søndergaard et al. 2010, Sayer et al. 2010a).

Alternatively, the greater influence of environmental variables in 2008-2009 could reflect the effects of advancing eutrophication swamping the influence of dispersal. Palaeolimnological analyses of the macrophyte communities (chapter 4 and 5) suggest that since the 1960s changes in species assemblages correspond to increasing eutrophication and a concomitant decline in the effects of regional forces. Thus the differences in macrophyte assemblages between 2006-2007 and 2008-2009 may result from incremental changes due to over-enrichment of the system. The variation in metacommunity structure between years shown here and similarly in other studies (e.g. Cottenie et al. 2003) provides evidence that over time different drivers may act alone or in combination to structure species assemblages. In the ULE system, environmental heterogeneity (*species-sorting*) appears to play a fundamental role in structuring local communities with its effects modulated by the independent influence of dispersal (Cottenie 2005).

2.6.4 Community similarity along environmental and spatial gradients

Mantel and partial mantel test analyses showed few significant relationships between community similarity and environmental and spatial gradients (Table 4). This suggests that, in most cases, in the ULE system neither community similarity nor environmental heterogeneity were autocorrelated with geographical distance. Thus, those satellite lakes that are close together are not necessarily more similar in community composition or in local environmental conditions than lakes that are further apart. This lack of spatial autocorrelation could be attributed to extensive dispersal in the system (Chase et al. 2005) mediated by the main ULE Lough. The ULE spans the entire range of the satellite lakes and is either directly or indirectly connected to them through rivers, small streams or agricultural channels (Fig. 2-1). Thus, it is probable that the ULE Lough acts as both, a main sink that receives a large variety of species that inhabit in its associated eutrophic satellite lakes, and as a main dispersal route. As illustrated in Figure 2-1 the whole ULE region effectively becomes a single large inter-lake hydrological system following a flood event. This increases the connectedness of the system and hence dispersal rates of many different species during particular time periods (autumn and winter). In turn, these hydrological changes may help to override any potential influences of specific local environmental variables alone (*species-sorting*) (Shmida and Wilson 1985, Cottenie 2005). Several studies have investigated the effects of high connectivity in river flood-plain systems and have concluded that high connectedness may act as a homogenising force decreasing the variability of composition between lakes along spatial gradients (Amoros and Bornette 2002, Robach et al. 1997, Bornette et al. 1998).

It is noticeable that Mantel and partial Mantel tests between macrophyte assemblages and environmental gradients for 2008-2009 analysis showed a positive and significant slope (Table 2- 4). This pattern has been previously attributed to provide support for a metacommunity species-sorting perspective (Chase et al. 2005, Brown and Swan 2010). This positive trend suggests further a suspected rapid change in nutrient-enrichment in the system. Notably, a positive trend (though no significant $P = 0.08$) was also observed for the partial Mantel test analysis between invertebrate community similarity and the environmental gradient (Table 2-4). Invertebrate assemblages showed a positive significant trend in the pRDA in response to rising chlorophyll-a, which may therefore providefurther evidence of over-enrichment. In this regard, if

dispersal of many groups in the ULE system is facilitated mainly through the ULE Lough, the apparent rapid over-enrichment could soon counter the buffering capacity of the ULE-mediated dispersal. Thus, the effects of connectedness of the ULE system may no longer swamp the local effects of enrichment in the associated satellite lakes.

2.7 Conclusions

By undertaking comparative analyses of three taxonomic groups, which differ in their dispersal mode, in shallow satellite lakes in the ULE system, this study indicates that eutrophication and hydrological connectedness play fundamental and complex roles in determining community structure. The relative importance of the spatial predictors (overland and watercourse distances) varied according to dispersal mode and has resulted in distinct metacommunity types in recent years (*species-sorting* and *species-sorting + mass-effect*). The lack of spatial autocorrelation between lake community similarity and environmental and spatial gradients suggests that dispersal events in the system are global mediated by the main ULE Lough. Future management and restoration strategies for the ULE system must therefore focus on the whole system, rather than individual lakes, with special attention to the main ULE.

3 Chapter 3 – Environmental and spatial processes determine lake macrophyte diversity and compositional heterogeneity in a metacommunity landscape.

3.1 Abstract

This study examines patterns of submerged and floating-leaved macrophyte species diversity and compositional heterogeneity within and between a large shallow lake (Upper Lough Erne - ULE) and a set of 20 well-connected shallow eutrophic satellite lakes in Northern Ireland. Despite high nutrient levels, most sites (16) were characterized by high macrophyte α-diversity, a pattern attributed to the high hydrological connectedness of the system. Within-lake variation in the macrophyte assemblages was reflected by differences in relative abundances and composition. Compositional heterogeneity was measured as the mean distance to the site-specific centroid in multivariate space, using Bray-Curtis dissimilarity, and ranged from 0.3 – 0.6. Chlorophyll-a, surface area and water depth were the most significant variables explaining within-lake macrophyte assemblage variability at the regional scale. Macrophyte within-lake heterogeneity was inversely related to nutrient enrichment (as indicated by measurements of chlorophyll-a, total phosphorus and total nitrogen). Nutrient-rich lakes had more homogeneous macrophyte assemblages than lakes with lower nutrient levels. Lake surface area and water depth were positively associated with macrophyte within-lake compositional heterogeneity. Homogenous lakes were mostly associated with higher levels of chlorophyll-a, low α-diversity and were relatively small and shallow. Low chlorophyll-a, high α-diversity, large surface area and deeper waters generally characterized highly heterogeneous lakes. Differences in within-lake compositional heterogeneity in the ULE system (regional β-diversity) varied in a U-shaped relationship, where regional β-diversity was minimized at intermediate levels of within-lake compositional heterogeneity.

3.2 Introduction

Since the seminal papers of Whitaker (1960, 1972) ecologists have long distinguished three different components of species diversity: local species richness, regional species richness and spatial turnover or differentiation diversity (Whittaker et al., 2001). Local species richness describes the total number of species within an area and is commonly referred to as alpha (α) diversity (Whittaker 1960, 1972, 2001). Regional species richness refers to the number of species in a landscape unit and is commonly referred to as gamma (γ) diversity (Whittaker 1960, 1972, 2001). Spatial turnover or differentiation diversity refers to the differences in species composition between communities or habitat types. It is recognised as the turnover between the α-diversity of communities or habitat types that gives rise to γ-diversity and is generally referred to as beta (β) diversity (Whittaker, 1960, 1972).

With the increasing degradation of ecosystems, understanding species turnover has become one of the central goals for conservation strategies. In response, different measures of β-diversity have been introduced (e.g. Koleff et al. 2003, Anderson et al. 2006b, Tuomisto 2010a, 2010b). Three main types of β-diversity estimation are recognised and these fall into three levels of abstraction. Raw-data tables describe the first level (community composition or α-diversity). These consist of observations of the abundances of one or more species in more than one site, in which the values of one or more environmental variables and spatial coordinates have also been measured (Legendre et al. 2005, Tuomisto and Ruokolainen 2006). The second level of abstraction is derived from the first level and consists of the variation in the raw-data tables (variation in community composition or β-diversity) (Legendre et al. 2005, Tuomisto and Ruokolainen 2006). The third level of abstraction is derived from the second level and consists of the variation in the variationwithin the raw-data tables (e.g. differences between two or more regions in the within-region β-diversity) (Legendre et al. 2005, Tuomisto and Ruokolainen 2006). Within this framework, the levels of abstraction can are recognised as: (1) community composition or α diversity; (2) β-diversity; and (3) regional variation in β-diversity (Legendre et al. 2005, Tuomisto and Ruokolainen 2006). Note that there is a distinction between community composition and α-diversity. Thus, if two sites have exactly the same numbers of species, their α-diversities are identical, but their community compositions can be

anything from identical to completely different. Accordingly, β-diversity can be anything between 0% (if all species are shared between the sites in similar abundances) and 100% (if no species are shared) (Tuomisto and Ruokolainen 2006).

Submerged macrophyte assemblages play a key role in the biological structure and ecological functioning of shallow lakes (Sculthorpe 1967; Jeppessen et al. 1998). Consequently, considerable attention has been placed on understanding the effects of environmental change (especially eutrophication), on the composition of macrophyte assemblages (i.e. β-diversity). As a consequence, the sequence of macrophyte species turnover is well known (Jeppesen et al. 2000, Arts 2002, Davidson et al. 2005, Sand-Jensen et al. 2008). Eutrophication promotes a shift in the vegetation community composition from an isoetid, rosette-like, assemblage characteristic of nutrient-poor habitats to a diverse community of submerged elodeid macrophytes at intermediate nutrient levels. With greater eutrophication abundances of tall elodeid plants are commonly reduced whereas those of floating-leaved species increase. Ultimately, phytoplankton tends to dominate lakes and submerged macrophytes are sparse to non-existent (Arts 2002, Sand-Jensen et al. 2008, Salgado et al. 2010, Sayer et al. 2010a).

Recognition of the importance of spatial processes that operate at the regional scale (e.g. dispersal) and the application of new multivariate techniques (e.g. Borcard et al. 1992, Borcard et al. 2002, Peres-Neto et al. 2006, Legendre et al. 2010) together indicate that macrophyte species turnover may be influenced by the interaction of both local and regional processes (Heegaard 2004, Capers et al. 2010). For instance, Capers et al. (2010) examined the relative importance of local environmental conditions and regional spatial processes for aquatic plant assemblages in a set of 98 lakes in Connecticut. They found that macrophyte community structure was influenced by the joint action of local conditions (pH, conductivity, water clarity, lake area, maximum depth) and regional processes such as dispersal. Of the total explained variation, 45% was related to environmental conditions and 40% to spatial processes (Capers et al. 2010). They also found that the distribution of species in the lakes was influenced by the distance between lakes and was associated with dispersal-related functional traits, thereby providing additional evidence that dispersal ability of species affects community composition. Similarly, Heegaard (2004) found that macrophyte species turnover in Northern Ireland was determined by a combination of chemical

conditions (mostly associated with enrichment) and distance between lakes, a factor that is commonly used as an indirect measure for dispersal processes (Borcard et al. 1992, Nekola and White 1999, Borcard et al. 2002, Beisner et al. 2006, Peres-Neto et al. 2006, Legendre et al. 2010). In particular, Heegaard (2004) found that macrophyte species turnover was lower in the southwest of Northern Ireland where distances between lakes are lower, and lakes are more connected. Chapter 2 details how the relative importance of local and regional processes in structuring contemporary macrophyte communities varied over time in a set of 20 satellite shallow lakes of the Upper Lough Erne system, Northern Ireland. In 2006 both factors significantly contributed to variation in species turnover whereas environmental variables alone explained variation in species turnover in 2009.

The development of the so-called before-after-control-impact design approach to monitoring (BACI; Underwood 1990, 1991,1994 Underwood et al. 2000) and, more recently, permutational multivariate techniques (Anderson 2001, Anderson 2006), have enabled studies to explore the causes of differences in species assemblages. Such studies indicate that species turnover is just one aspect of β-diversity that is affected by environmental change. In addition to altering species-richness or which species are present (turnover), environmental change may also impact on the variation of species identities and abundances(Fig. 3-1). This is manifested as temporal and spatial variability (heterogeneity) in community composition (Underwood 1990, 1991,1994, Underwood et al. 2000, Anderson 2001, Anderson et al. 2006). For instance, Warwick et al. (1990) found much greater heterogeneity in coral assemblages in a 1983 survey, compared to either before (1981) or after (1985) El Niño events. Warwick and Clarke (1993) found a similar pattern for meiobenthos, macrobenthos, and fish communities that were subjected to different levels of disturbance. For this reason, they proposed that a greater spatial and temporal variation in community composition could generally characterise assemblages in stressed environments and hence may be an important diagnostic feature (Warwick and Clarke, 1993). In contrast, Chapman et al. (1995) found a decline in species compositional heterogeneity as sewage discharge pressure increase and hence no evidence to support the hypothesized positive relationship between variation in community composition and environmental stress.

The extent to which regional processes and local environmental stressors impact β-diversity in the form of compositional heterogeneity of macrophyte communities within and between lakes has received surprisingly limited attention (but see Carpenter and Titus 1984). The aim of this study is therefore to examine patterns of macrophyte species diversity and compositional heterogeneity within and between the main Upper Lough Erne (ULE) Lake and a set of 21 well-connected satellite shallow eutrophic lakes in Northern Ireland. Particular focus is on testing whether eutrophication homogenises macrophyte assemblages across the system and whether dispersal may counteract these homogenising effects.

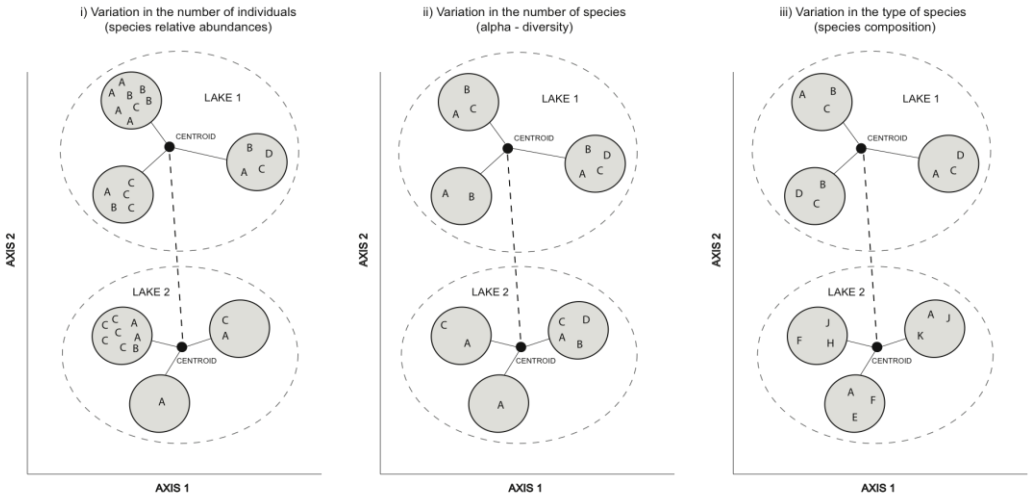

Figure 3-1. Schematic diagram of causes of variability on community compositional heterogeneity.

3.3 Study site

The Upper Lough Erne (ULE) system is situated in Co. Fermanagh in the west of Northern Ireland (Fig. 3-2). It is a complex and dynamic riverine landscape formed as the channel of the River Erne splits and widens across a landscape of drumlins. The main Upper Lough Erne, a large (34.5 km^2), shallow (mean depth 2.3 m) and eutrophic (TP 70 µg L^{-1}) lake is surrounded by a series of interconnected, smaller, shallow satellite lakes that vary in degree of enrichment and are linked to the main Lough by streams and agricultural channels.

The ULE system has a diverse aquatic flora and over 50 recorded species of

submerged and floating plants have been recorded for the system (Goldsmith et al. 2008). It is designated as a Special Area of Conservation (SAC) under the EC Habitats Directive SAC (www.ni-environment.gov.uk) and divided into four major areas (Belleisle, Trannish, Crom and Galloon) that contain many species of restricted distribution in the British Isles. These include the Arrowhead *Sagittaria sagittifolia*, the narrow-leaved water plantain *Alisma lanceolatum*, the needle-spike rush *Eleocharis acicularis* and the nationally rare frogbit *Hydrocharis morsus-ranae*. The Belleisle area (ULE-B) in the northern part of the system includes the open water of the ULE and a range of satellite lakes (Fig. 3-2). The Trannish area (ULE-T) is in the middle part of the ULE system includes the open water of the ULE system and a series of swamp, fen and satellite lake communities (Fig. 3-2). The Crom area (ULE-C) is an area in southern Upper Lough Erne, which includes the open waters of the Lough, and a range of associated wetlands. The Galloon area (ULE-G) is in the extreme southern part of the ULE system and is characterized by more sheltered habitats where open waters often give way to swamp and floodplain zones.

Figure 3-2. Map of the study sites, Upper Lough Erne (ULE) system. Hydrological connectivity categories are shown in brackets: (1)- areas within the Upper Lough Erne (ULE-B, ULE-C, ULE-G and ULE-T); (2)- lakes in the south connected to the ULE through the Rivers Finn and Erne (Castle Lough, Derrykerrib Lough, Derrysteaton and Sarah Lough); Category (3)- lakes directly connected to the ULE through small streams or marshlands (Abacon LoughCorraharra Lough, Derryhowlaght Lough, Digh Lough and Lough Doo); (4) - lakes connected to the ULE through another satellite lake (Corracoash Lough, Cornabrass Lough, Derrymacrow Lough Gole Lough, Head Lough and Sessiagh East); and (5) - lakes that are connected to the ULE through two or more satellite lakes or completely isolated (Drumroosk Lough, Killymackan Lough, Kilturk Lough and Mill Lough). Permanent water bodies are shown in black and flooding areas in grey. Picture modify from http://safer.emergencyresponse.eu

3.4 Material and methods

3.4.1 Environmental variables sampling

Three water chemistry and two lake morphometric variables were measured for this study: Chlorophyll-a, total phosphorus (TP), total nitrogen (TN), water depth and lake surface area (Table 3-1). These are the more widely used variables to represent eutrophication and the more likely to influence macrophyte communities in temperate

lakes (Spence 1967, Spence 1982, Sayer et al. 2010a, Capers et al. 2010). Measurements for Period 1 were taken at each site on a quarterly basis by ENSIS staff in March, June/July and September 2006 and January 2007. Two water samples were collected from each site using the "beach throw" method that consists of a weighted acid-washed (rinsed with deionised, distilled water) polypropylene sample bottle, with a buoy attached to a rope 50 cm below the mouth of the bottle (Goldsmith et al. 2008). The bottle is thrown into the lake from an open area of shore to a distance in excess of 10 m. The buoy holds the full bottle 50 cm below the water surface and then by pulling the rope the sample is retrieved. Water samples for TN were filtered on-site and refrigerated along with the unfiltered samples for chlorophyll-a and TP prior to analysis.

TP was determined by solution spectrometry (phosphomolybdate), after digestion by acid persulphate (Johnes and Heathwaite 1992). TN was determined by solution spectrometry (sulphosalicylic acid) after alkaline persulphate digestion (Wetzel and Likens 1991). Water samples (250–1000 mL) for the analysis of chlorophyll-a were filtered through Whatman GF/F (0.7 m) filter papers (Whatman, Clifton, New Jersey, USA) and chlorophyll-a was determined spectrophotometrically (Pye Unicam SP6–550 UV/VIS, Philips, Cambridge, UK) by cold extraction in 90% acetone (Talling and Driver 1961). Maximum water depth was recorded at each site during the summer and lake area data was derived from the Northern Ireland Lake Inventory supplied by NIEA and quoted in hectares (ha). The Freshwater Sciences Research Group in the University of Ulster, Coleraine, conducted all water chemistry data for Period 1.

Measurements of TP, TN and chlorophyll-a for Period 2 were acquired during the summer of 2009 (Table 1). All analytical work for this second set of sampling was conducted using the above-mentioned methods and analysed in the water chemistry laboratories of the Geography Department of University College London (UCL).

3.4.2 Macrophyte sampling

Macrophyte abundance data were obtained from a database of Environmental Scientific Services (ENSIS) and two sampling field trips. These two sources provided information of aquatic flora abundances over two periods of time, 2006-2007 (ENSIS) and 2008-2009 (Field trips). Twenty satellite shallow lakes and four areas of the main Upper Lough Erne were selected for this study (Table 3-1 and Fig. 3-2).Selection

criteria for lakes included replication along an enrichment gradient (total phosphorus, total nitrogen and chlorophyll-a), availability of multiple macrophyte data points from each lake and watercourse connectivity between the satellite lakes and the main ULE. Connectivity criteria were based on hydrological features described by Goldsmith et al. (2008) as follow (Fig. 3-2): Category 1 - sites within the ULE (ULE-B, ULE-C, ULE-G and ULE-T); Category 2 - lakes in the south connected to the ULE through the Rivers Finn and Erne (Castle Lough, Derrykerrib Lough, Derrysteaton and Sarah Lough); Category 3 - lakes directly connected to the ULE through small streams or marshlands (Abacon Lough, Corraharra Lough, Derryhowlaght Lough, Lough Digh and Lough Doo); Category 4 - lakes connected to the ULE through another satellite lake (Corracoash Lough, Cornabrass Lough, Derrymacrow Lough Gole Lough, Head Lough and Sessiagh East); and Category 5 – lakes connected to the ULE through two or more satellite lakes or completely isolated (Drumroosk Lough, Killymackan Lough, Kilturk Lough and Mill Lough).

Period 1 data (ENSIS) were collected between June and September in both 2006 and 2007 using Site Condition Monitoring methods (JNCC, 2005) to conduct: (1) an emergent and marginal survey; (2) a shoreline wader survey; and (3) a boat survey. Data collection was carried out at each lake on discrete 100 m sections of shoreline considered to be representative of the lake. Twenty points per 100 m section were recorded and a minimum of three sections per site were surveyed with the exception of Corracoash, Corraharra and Drumroosk lakes for which a single 100 m section was surveyed due to their small size (> 5 ha.) (see Table 3-1). Surveying was performed using a bathyscope and a double-headed rake (grapnel) where poor water clarity restricted visibility. Macrophyte abundances were recorded on a semi-quantitative scale of 0-3, where 3 indicated highly abundant and zero absence. The location of all survey sections and boat transects was recorded using a Global Positioning System(GPS). The boat surveys were conducted from a small inflatable boat for each 100m section. The point of start was at the midpoint of each transect at a depth of > 75 cm. Surveys consisted of 10 sampling points taken from increasing water depths. All 24 selected sites were sampled over this period.

Table 3-1. Mean average values of environmental data collected from 20 satellite lakes and 4 areas of the Upper Lough Erne (ULE) at 2006-2007. Data obtained from Goldsmith et al. (2008).

LAKE	TP (ug/L)	TN (mg/L)	Chlorophyll-a (ug/L)	Area (Ha)	Depth (cm)
Abacon Lough	100	1,63	24,2	7	600
Castle Lough	29	1,03	4,2	13	450
Cornabrass Lough	96	1,05	5,3	18	430
Corracoash Lough	119	1,73	9,3	6,5	160
Corraharra Lough	130	1,29	21,9	1,5	150
Derryhowlaght Lough	159	1,75	18,3	4	190
Derrykerrib Lough	36	0,97	8,6	10,5	245
Derrymacrow Lough	83	1,00	8,2	21	610
Derrysteaton Lough	124	1,03	7,1	12	720
Drumroosk Lough	168	1,99	12,9	4	50
Gole Lough	128	1,35	13,8	8	310
Killymackan Lough	111	0,80	17,4	19,2	170
Kilmore Lough	186	1,09	6,5	20	90
Kilturk Lough	111	0,92	9,0	43	290
Lough Digh	82	1,44	10,2	9	400
Lough Doo	54	1,18	5,0	5	260
Lough Head	383	1,79	9,0	31	85
Lough Sarah	61	0,98	7,0	1,6	160
Mill Lough	23	0,47	11,1	33	930
Sessiagh East	45	0,92	7,9	8	100
ULE-B	63	-	3.85	80	227
ULE-T	68	-	5.8	80	860
ULE-C	72	-	6.05	80	840
ULE-G	-	-	-	60	870
Average	107,16	1,22	10,84	19,79	340,32
Min	28,5	0,47	194,75	1,5	50
Max	383	1,79	353,25	80	870

Period 2 data were collected between June and August of both 2008 and 2009 from 15 of the 24 sites sampled in Period 1 (see Table 3-3). Macrophyte data from 2008 and 2009 were recorded for ≥ 30 points in each site. All sampling efforts were made from a boat using a combination of grapnel and bathyscope in haphazard zigzag movements across each lake in order to cover most areas and not over-represent the lake margins. Macrophyte density and composition at each point were recorded for an estimated area of 1-2 m^2 using the percentage volume infestation (PVI) method (Canfield et al. 1984) as follows:

PVI = (Percentage coverage of macrophytes x average height of macrophytes)/ Water depth.

3.4.3 Data analysis

Two levels of β-diversity were measured that correspond to two different levels of abstraction (see introduction): (1) within-lake variation - defined as the compositional heterogeneity among different sampling points within each satellite lake (level of abstraction 2); and (2) regional variation - measured as the between site variability of within-lake compositional heterogeneity (third level of abstraction).

To quantify within-lake compositional heterogeneity, a combination of permutational analysis of multivariate dispersions (perMANOVA; Anderson 2001)and permutational multivariate analysis of variance (HMD; Anderson 2006, Anderson et al. 2006) was used. HMD analysis is suitable for assessing the significance of compositional heterogeneity that is attributed to variation in species relative abundances. PerMANOVA analysis enables assessments of the significance of the compositional heterogeneity attributed to variation in the identity of species present.

HMD analysis is a non-parametric method that compares variability of mean distance to centroid (dispersion) within groups versus variability in this distance among different groups. This analysis examines the ratio of the *F*-statistic through permutation tests (Anderson 2006, Anderson et al. 2006) and will be referred to as $\sigma^2_{\text{Lake-HMD}}$ (*sensu* Anderson et al. 2011). For this analysis, each lake was treated as an independent group and species samples dissimilarities were calculated using the Bray-Curtis index of dissimilarity with a principal coordinate analysis (PCO) (Anderson 2006). Groups presenting greater multivariate dispersion (higher values of mean distance to group centroid) will be associated with more heterogeneous assemblages and thus greater $\sigma^2_{\text{Lake-HMD}}$. As the data from 2006-2007 is to some extent "standardised" by the semi-quantitative abundance categories (assignment to 0-3 scale) and PVI data from 2008-2009 have a similar intrinsic standardisation by calculating the abundance of each species in relation to the average height of all plants at a sampling point, data were not transformed prior to analysis. The absence of all macrophytes species in some areas within a lake is a common feature and thus an indication of heterogeneity (or homogeneity). Consequently, sampling points that had an absence of macrophyte species were used initially to calculate the Bray-Curtis dissimilarity distances matrix. However, as pairwise dissimilarity between two observations that have absence of species are meaningless in Bray-Curtis distances,

dissimilarities between zero joint absences were excluded subsequently for the HMD and perMANOVA analyses.

To explore if within-lake species richness was influencing the outcome of compositional heterogeneity attributed to species relative abundances and to establish direct comparisons between the two different data sets (Period 1 and Period 2) a second HMD analysis on presence/absence data was conducted for both time periods (subsequently referred to as Period 1 and Period 2). Species samples dissimilarities were calculated using the Sørensen dissimilarity index.

To test whether $\sigma^2_{\text{Lake-HMD}}$ was an artefact of varying sampling effort between lakes of different sizes, a subset of equal randomly-chosen number of points per lake for both data sets was selected. Each sub-set data was subsequently tested by HMD analysis. For Period 1 only lakes with three or more sections were chosen and a total subset of 40 randomly-chosen points per lake was used. For Period 2 all sampling sites were included and a total subset of 30 randomly-chosen sampling points per lake was used. The number of points comprising the subset data was based on the minimum number of sampling points recorded for a lake during each period. Subset data were randomly generated in R version 2.13 for Machintosh (R Core Development Team 2011) using the *set.seed* and *sample* algorithms. An integer of 5 was chosen for all cases in order to set the seed for the computer to choose a random subset of all possible numbers. This has the advantage that the procedure can be repeated with an exact outcome every time.

Although HMD analysis provides a robust measure of compositional variability in terms of the average distances of dissimilarity to centroid, it does not discriminate between samples that differ in the identity of species composition (i.e. two areas could be equally homogeneous/heterogeneous but differ in species composition). Therefore, permutational multivariate analysis of variance (perMANOVA) (Anderson 2001) was conducted, henceforth referred to as $\sigma^2_{\text{Lake-perM}}$ (*sensu* Anderson et al 2011). This is a non-parametric method for multivariate analysis of variance that compares the variability of average dissimilarity within groups versus the variability among other groups, using the ratio of the *F*-statistic through permutational tests. Here, larger values of *F* reflect higher compositional differences between groups. Species samples dissimilarities were calculated using the Bray-Curtis dissimilarity index

(perMANOVA). Owing to analytical requirements for equal numbers of sampling points per lake (Anderson 2005), perMANOVA analysis were calculated on the subset data of equal numbers of samplinging points for each period (40 and 30 points respectively for each period - see above).

To address if there were differences in the within-lake variability in the ULE system (referred as to σ^2_{ULE}), post-hoc pairwise permutation tests (number of permutations = 999) under the reduced model for both HMD ($\sigma^2_{ULE\text{-}HMD}$) and perMANOVA ($\sigma^2_{ULE\text{-}perM}$) test were conducted. As riverine systems can be seen as hierarchical entities (areas embedded within lakes and lakes embedded within a catchment) (Amoros and Bornette 2002) permutational tests were nested allowing random permutations only within each lake data set. These analyses generate a permutation distribution of F under the Null hypotheses of no differences in average dispersion ($\sigma^2_{ULE\text{-}HMD}$) and in average dissimilarity ($\sigma^2_{ULE\text{-}perM}$) among lakes (Anderson 2001). Here, the total number of significant cases for each analysis (HMD and perMANOVA) represents the regional β-diversity. Hence, larger number of significant cases reflects high β-diversity whilst low significance represents low β-diversity. An integer of 5 was chosen to set the seed for the computer to choose a random subset of all possible permutations for all post-hoc permutation tests. This has the advantage that the procedure can be repeated with an exact outcome every time. A different choice for the random seed will give a different random subset of the possible permutations (Anderson 2001). As Type I error asymptotically approaches to a significance level of 0.05 with increases in sample size, a significance value of 0.01 was considered.

To test whether within-lake compositional heterogeneity was influenced by the degree of hydrological connectivity, a combination of HMD and perMANOVA approaches was adopted. For Period 1, four lakes, and for Period 2, three lakes of each connectivity category were selected randomly and aggregated into a single group within each connectivity category. To allow for comparisons between time periods, both analyses (HMD and perMANOVA) were calculated on presence/absence in a sub-set of Period 1 and Period 2 data using Bray-Curtis dissimilarities. Post-hoc pairwise comparisons between groups were then calculated using the reduced model with 4999 permutations.

To test if there was a predictable pattern of within-lake macrophyte compositional heterogeneity ($\sigma^2_{Lake\text{-}HMD}$) along the environmental and spatial gradients in the ULE system, Least squares regression analyses between the average distances to centroid for each lake and each of the environmental, morphometric and spatial variables were performed. In order to explore other relationships, least squares regression analyses between α-diversity and the set of environmental and morphometric variables and between environmental and morphometric variables were conducted. A summary of all statistical analysis techniques and their applications is summarised in Table 3-2.

Table 3-2. Summary of all statistical analysis techniques and their applications

Statistical method	Symbol	Application
Homogeneity of multivariate dispersion analysis (HMD)	$\sigma^2_{Lake\text{-}HMD}$	Assess the within-lake compositional heterogeneity that is attributed to variation in relative abundances.The method compares variability of mean distance to centroids (dispersion) within groups versus variability in this distance among different groups.
HMD post-hoc pairwise comparisons	$\sigma^2_{ULE\text{-}HMD}$	Assess the variation of within-lake compositional heterogeneity attributed to variation in relative abundances in the ULE system.
Permutational multivariate analysis of variance (perMNOVA)	$\sigma^2_{Lake\text{-}perM}$	Assess the within-lake compositional heterogeneity that is attributed to variation in the identity of species. The method compares the variability of average dissimilarity within groups versus the variability among other groups
perMNOVA post-hoc pairwise comparisons	$\sigma^2_{ULE\text{-}perM}$	Assess the variation of within-lake compositional heterogeneity attributed to variation in the identity of species in the ULE system.
Least sqaure regressions		Assess the variation in within-lake compositional heterogeneity (meassured as average distance to centroid) along difrent environmental and spatial gradients

3.5 Results

3.5.1 Patterns of species richness

A total of 51 (γ-diversity) submerged and floating-leaved aquatic plants were selected for Period 1 (Table 3-3; Fig. 3-3). During this period, there was median value of 14.5 species per lake with 20 lakes possessing 10 or more species. The four areas of the

ULE were the most speciose sites, with 30 species for ULE-G, 27 for ULE-C and 23 for both ULE-T and ULE-B (Table 3-3, Fig. 3-3). Amongst the satellite lakes, Castle Lough and Mill Lough had the highest local α-diversity with 22 and 21-recorded taxa. Lowest α-diversity was recorded for Abacon Lough, Derrysteaton Lough and Gole Lough with 7 species observed for the first two lakes and 8 for the latter. The median species richness recorded per sampling point varied from lake to lake (range = 7-1) and there was a median value of 3 species for all the sampling lakes (Table 3-3).

Regional species richness (γ-diversity) in Period 2 was of a total of 38-recorded species. A median value of 15 macrophyte species per lake was retained (Table 3-3). Over this period, 13 lakes presented 10 or more species. The highest α-diversity was recorded in Kilturk Lough and ULE-T, with 24 and 20 species, respectively. The lowest levels of α-diversity were recorded again in Gole and Derrysteaton Lough with 4 and 7 species, respectively. During Period 2 the median species richness per sampling point for all lakes was of 4.0 and ranged from 1-5 species per sampling point (Table 3-3).

Mean values of macrophyte species abundances from each lake are shown in Figures 2 and 3. Several species dominated in some instances (e.g. Mill, Castle, Derrykerrib, Doo, Kilturk), while in others cases, especially in the ULE, many species occur at similar abundances. In a few lakes (e.g. Gole, Derrysteaton, Drumroosk, Abacon) only one or two species dominated the assemblages with a few other occurring in much lower values (Fig. 3-3 and 3-3). Overall, the most common and abundant species in both time periods were *Elodea canadensis* Michx., and the floating-leaved species *Lemna minor* L., *Lemna trisulca* L., *Nuphar lutea* (L.) Smith., and *Sparganium emersum* Rehmann. Broad-leaved *Potamogeton* species occurred regularly (e.g. *Potamogeton praelongus* Wulfen, *Potamogeton perfoliatus* L., *Potamogeton lucens* L., *Potamogeton natans* L. and *Potamogeton lucens* L.). Fine-leaved *Potamogeton* species were also frequently recorded (e.g. *Potamogeton obtusifolius* Mert. & Koch., *Potamogeton berchtoldii* Fieber, *Potamogeton pusillus* L. and *Potamogeton pectinatus* L.). Other species like *Stratiotes aloides* L. *Fontinalis antipyretica* Hedw., *Sagittaria sagittifolia* L. and *Utricularia vulgaris* agg. (L.) were also frequently observed but with a patchier distribution.

3.5.2 Within- and between-lake variability

HMDanalysis of the macrophyte data for Period 1 indicated that within-lake variation ($\sigma^2_{Lake\text{-}HMD}$) varied considerably between lakes with a median value of 0.47 (Table 3-3) (Fig. 3-5). According to $\sigma^2_{Lake\text{-}HMD}$ values three main groups of lakes were obtained (Fig. 3-5a). The first group was composed of Corracoash, Corraharra, Derryhowlaght and Derrykerrib and was characterised by $\sigma^2_{Lakes\text{-}HMD}$ values < 0.4. The second group was the most diverse and was associated with $\sigma^2_{Lake\text{-}HMD}$ with values of between 0.4 and 0.5. Lakes in this group included Cornabrass, Killymackan, Castle, Derrymacrow, Drumroosk, Mill, Kilturk, Sarah, Gole, Doo, Derrysteaton and Sessiagh (Fig. 3-5a). Abacon, ULE-C, Kilmore, ULE-B and ULE-T composed the third group which was characterised by $\sigma^2_{Lake\text{-}HMD}$> 0.5.

For Period 2, HMD analysis resulted in a higher median value of $\sigma^2_{Lake\text{-}HMD}$ (0.56) with only Head having a value below 0.4 (0.36) (Table 3-3, Fig. 3-5b). The analysis showed a similar pattern to the analysis of Period 1 data, identifying three clusters of lakes. These groups were characterised by lakes with $\sigma^2_{Lake\text{-}HMD}$ values below 0.45 (Head and Gole), lakes having $\sigma^2_{Lake\text{-}HMD}$ values between 0.45-0.6 (Derryhowlaght, Digh, Castle, Killymackan, Doo, Kilturk, Derrykerrib, Derrysteaton and Mill) and lakes with $\sigma^2_{Lake\text{-}HMD}$ above 0.6 (Cornabrass, ULE-T, ULE-C, ULE-B) (Fig. 3-5b).

Table 3-3. Study lakes associated diversity and results of HMD and PERMANOVA analyses examining compositional heterogeneity of macrophyte at within-lake scale. (σ2Lakes-HMD) - Within-lake compositional heterogeneity attributed to variation in relative abundances; (σ2Lakes-perM) -Within-lake compositional heterogeneity attributed to variation in species identities. (P/A) - presence/absence data; (Subset) - subset of equally random number of sampling points for each period; P1 – Period 1; P2 – Period 2.

Lake	Lake code	No. of sampling points		α-diversity (Lake)		α-diversity (Sampling points)		Regional diversity (γ)		$\sigma^2_{Lakes\text{-}HMD}$ (Abundance)		$\sigma^2_{Lakes\text{-}HMD}$ (P/A)		$\sigma^2_{Lakes\text{-}HMD}$ (Subset)		$\sigma^2_{Lakes\text{-}perM}$	
		Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
Abacon Lough	Abc	80	-	7	-	2	-	57	38	0,52	-	0,50	-	0,56		0,75	
Castle Lough	Cas	80	180	22	15	5	4	57	38	0,44	0,53	0,39	0,36	0,43	0,5426	0,67	0,80
Cornabrass Lough	Cbr	80	61	16	16	5	3	57	38	0,40	0,61	0,33	0,45	0,37	0,6083	0,69	0,81
Corracoash Lough	Crc	20	-	11	-	4	-	57	38	0,34	-	0,39	-	-	-	-	-
Corraharra Lough	Crh	20	-	14	-	7	-	57	38	0,34	-	0,23	-	-	-	-	-
Derryhowlaght Lough	Dhow	80	35	10	10	3	4	57	38	0,34	0,49	0,35	0,35	0,32	0,4955	0,66	0,69
Derrykerrib Lough	Dker	80	41	17	15	5	5	57	38	0,39	0,57	0,34	0,41	0,40	0,5758	0,69	0,84
Derrymacrow Lough	Dmac	80	-	13	-	2	-	57	38	0,44	-	0,37	-	0,43		0,71	
Derrysteaton Lough	Dst	80	46	7	7	2	2	57	38	0,49	0,59	0,45	0,38	0,49	0,5146	0,77	0,70
Digh Lough	Dgh	80	37	14	13	2	4	57	38	0,49	0,52	0,48	0,35	0,49	0,5151	0,76	0,73
Doo Lough	Doo	80	41	15	14	3	4	57	38	0,47	0,54	0,43	0,41	0,47	0,5424	0,75	0,78
Drumroosk Lough	Drum	20	-	9	-	2	-	57	38	0,44	-	0,42	-	-	-	-	-
Gole Lough	Gol	120	30	8	4	1	1	57	38	0,47	0,4662	0,43	0,16	0,46	0,4239	0,64	0,52
Head Lough	Hed	60	55	12	11	2	2	57	38	0,38	0,36	0,33	0,28	0,38	0,3549	0,60	0,51
Killymackan Lough	Killy	80	52	18	16	4	4	57	38	0,42	0,53	0,35	0,28	0,56	0,5587	0,71	0,79
Kilmore Lough	Kilm	80	-	16	-	3	-	57	38	0,57	-	0,56	-	0,46	-	0,77	-
Kilturk Lough	Kilt	80	74	19	24	4	4	57	38	0,46	0,57	0,41	0,40	0,41	0,58	0,75	0,85
Mill Lough	Mill	120	66	21	15	4	4	57	38	0,46	0,59	0,39	0,38	0,49	0,5905	0,76	0,69
Sarah Lough	Sar	40	-	12	-	4	-	57	38	0,47	-	0,43	-	0,46	-	0,75	-
Sessiagh East Lough	Ses	120	-	13	-	3	-	57	38	0,50	-	0,46	-	0,49	-	0,77	-
Upper Lough Erne-Belleisle	ULE-B	200	30	23	15	2	2	57	38	0,58	0,63	0,57	0,56	0,55	0,6344	0,80	0,90
Upper Lough Erne-Crom	ULE-C	320	30	27	15	2	4	57	38	0,57	0,61	0,55	0,53	0,58	0,61	0,83	0,91
Upper Lough Erne-Gallon	ULE-G	160	-	30	-	4	-	57	38	0,50	0,63	0,47	0,50	0,52	-	0,84	0,89
Upper Lough Erne-Trannish	ULE-T	320	55	23	20	2	3	57	38	0,60	-	0,59	-	0,56	0,6344	0,80	-
MEDIAN				**14,5**	**15,0**	**3,0**	**4,0**			**0,47**	**0,56**	**0,42**	**0,38**	**0,47**	**0,56**	**0,75**	**0,78**

In Period 1, presence/absence data showed no major variation amongst sites with a slightly lower median of $\sigma^2_{\text{Lake-HMD}}$ values (0.42) (Table 3) (Fig 3-5c). In contrast, for Period 2, the same analysis resulted in reduced $\sigma^2_{\text{Lake-HMD}}$ with a median value of 0.38 (Table 2, Fig 3-5d). Although separation into three clusters was indicated, patterns were more obvious by PVI analysis. Analysis of presence/absence data also revealed differences in the distribution of lakes among the clusters with Killymackan having lower $\sigma^2_{\text{Lake-HMD}}$ values and Cornabrass having intermediate $\sigma^2_{\text{Lake-HMD}}$ values (Fig. 3-5d).

HMD analysis of subsets of Period 1 and Period 2 data showed close agreement between $\sigma^2_{\text{Lake-HMD}}$ values for the full datasets (Fig. 3-5a, b). The median $\sigma^2_{\text{Lake-HMD}}$ values for both datasets within each time period did not vary, being 0.46 and 0.56, respectively (Table 3-3). The only $\sigma^2_{\text{Lake-HMD}}$ value that was underrepresented by the PVI subset data was for Derrysteaton (for the full PVI dataset, $\sigma^2_{\text{Lake-HMD}}$ = 0.59, for subset = 0.51) (Fig. 3-5b).

The perMANOVA analysis for the two periods showed that compositional dissimilarity within lakes ($\sigma^2_{\text{Lake-perM}}$) was very high with a median value of 0.75in Period 1 and of 0.78 in Period 2 (Table 2). Both data sets showed a similar trend with Head and Gole Loughs presenting the lowest average dissimilarity values (0.60 and 0.64 in Period 1 and 0.50 and 0.52 in Period 2). The four ULE sites had the greatest $\sigma^2_{\text{Lake-perM}}$ with values ranging around 0.82 for Period 1 and to 0.89 for Period 2 (Table 3-3).

3.5.3 Regional variability of within-lake compositional heterogeneity

The overall HMD analysis for Period 1, showed that $\sigma^2_{\text{ULE-HMD}}$ varied significantly across the ULE system (F= 22.72; P = 0.001) (Table 3-4). Post-hoc pairwise permutation analysis revealed that 51% (140 pairwise comparisons out of a total of 276) of comparisons were significantly different ($P \leq 0.01$) (Table 3-4). Similarly, the overall HMD test on the Period 2 data revealed a significant variation of $\sigma^2_{\text{ULE-HMD}}$ among the study sites (F= 14.5; P = 0.001) (Table 3-5), although only 36% (43 out of 120) of the post-hoc comparisons were significant during this time period ($P \leq 0.01$) (Table 3-5).

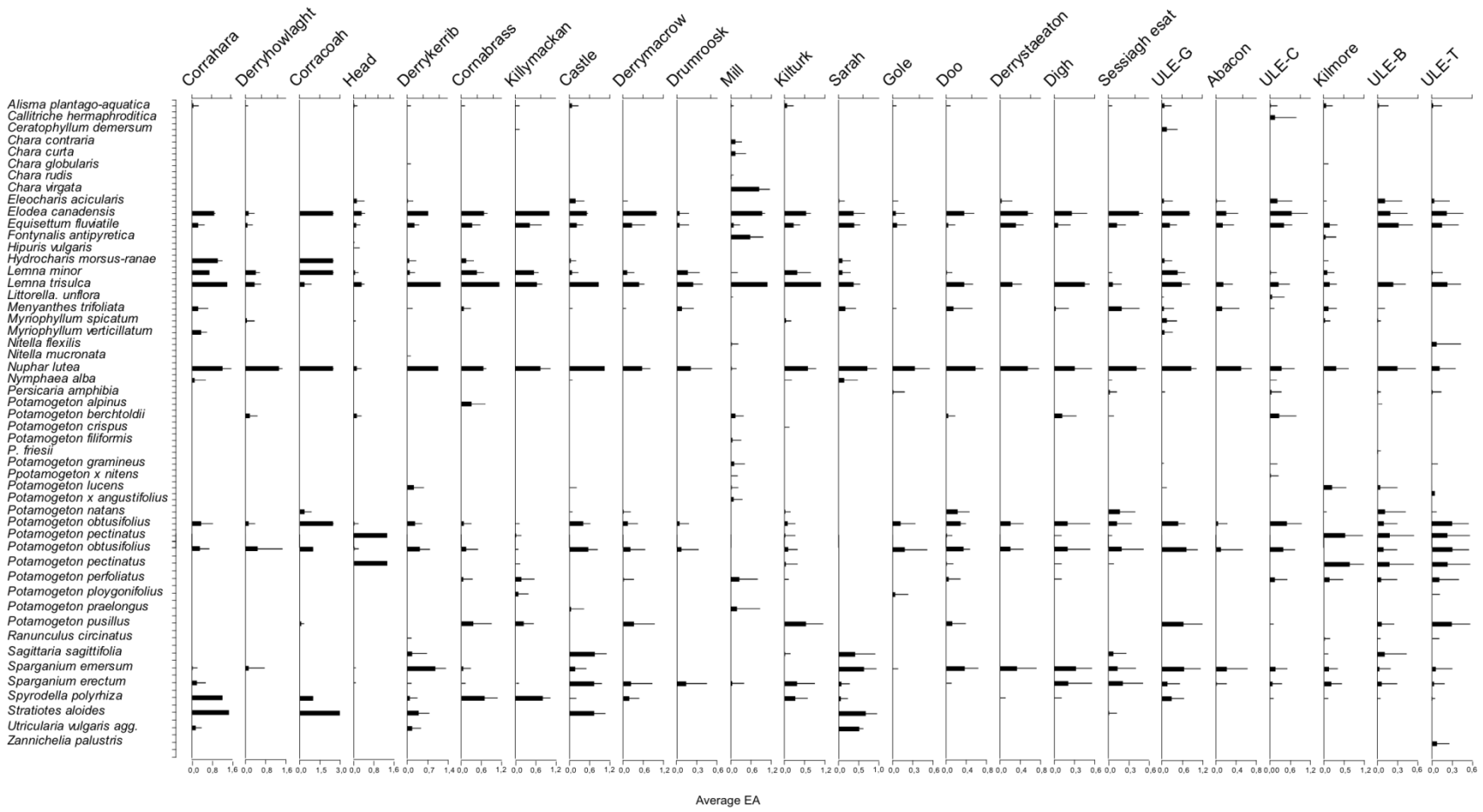

Figure 3-3. Average and standard deviations of within-lake macrophyte species relative abundances for Period.

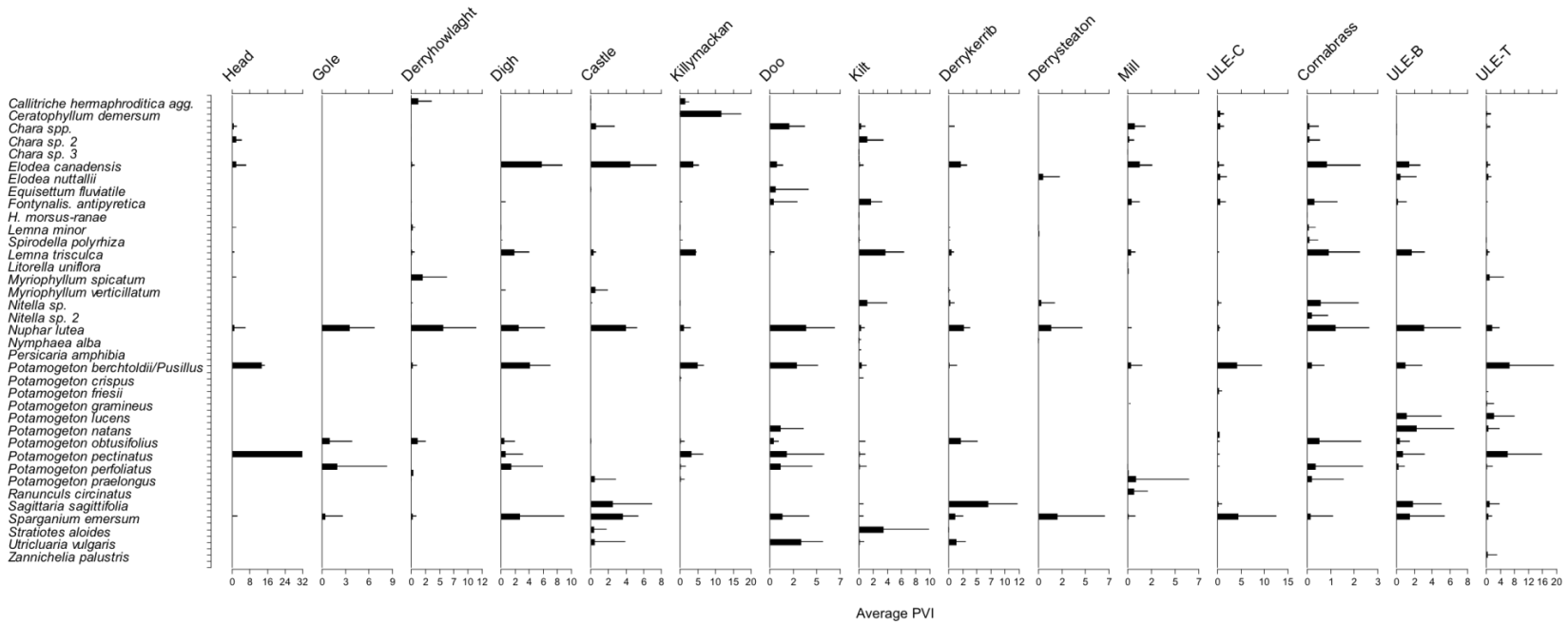

Figure 3-4. Average and standard deviations of within-lake macrophyte species relative abundances for Period 2.

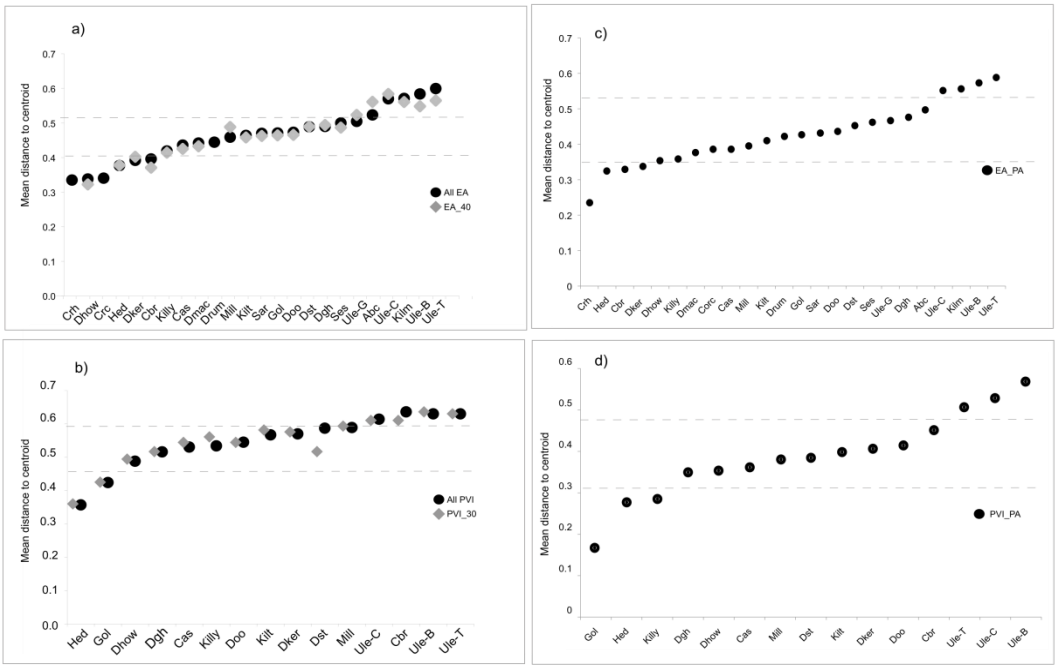

Figure 3-5. Mean distance to centroid of macrophyte assemblages in 20 shallow sampling lakes and four areas of the ULE using Bray-Curtis dissimilarity distances. (a) Period 1- Abundance macrophyte data (black circles = all sampling points; grey squares = Subset of 40 random abundance sampling point per lake); (b) Period 2 – abundance macrophyte data (black circles = all sampling points; grey squares = Subset of 30 random abundance sampling point per lake); (c) Presence/absence macrophyte data for Period 1; (d) Presence/absence macrophyte data for Period 2. Dotted lines reflect visual separation of lakes into three clusters (see results). For lake abbreviations see Table 1.

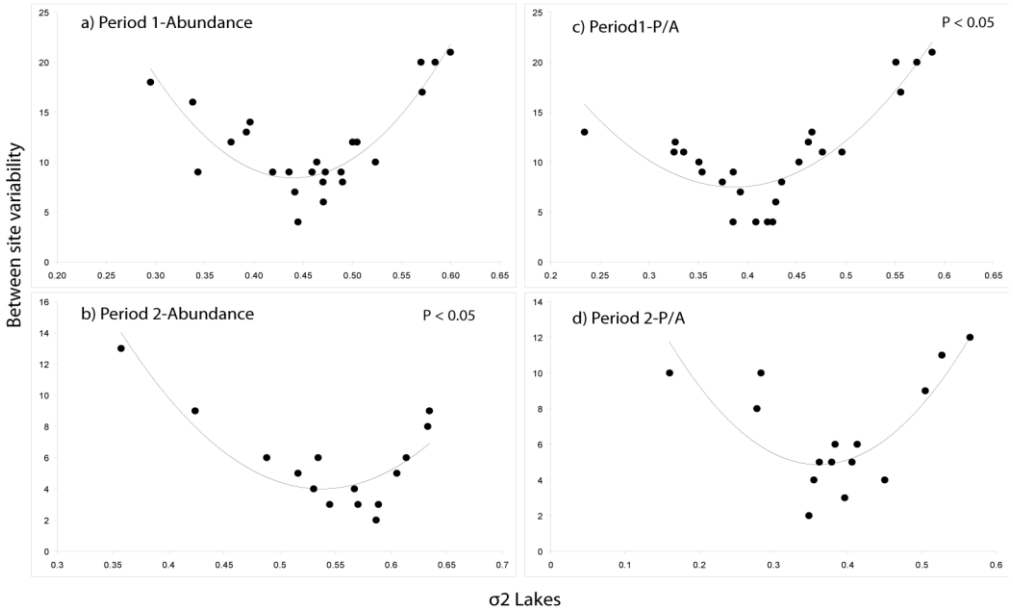

Figure 3-6. Regional variability (σ2 ULE-HMD) as a function of within-lake variability (σ2 Lakes) measured as the mean distance to centroid. Regional variability was determined as the number of significant ($P \leq 0.01$) pairwise comparisons between lakes revealed by HMD analysis. (a) NIEA macrophyte data (Period 1); (b) PVI data (Period 2); (c) presence/absence data (Period 1) (d) presence/absence data (Period 2). A 0.05 level of confidence was used to test the significance of each pattern.

Analyses of presence/absence data resulted in good agreement with the abundance data. For all data sets (EA and presence/absence for Period 1 and PVI and presence/absence for Period 2) a U-shaped relationship consistently described the number of cases of significant pairwise comparisons between lakes (see last column, Tables 3-4 and 5) (Fig. 3-6). Furthermore the plots consistently suggest three major clusters of lakes associated with within-lake macrophyte compositional heterogeneity ($\sigma^2_{\text{Lake-HMD}}$). Thus, the number of significant pairwise comparisons ($\sigma^2_{\text{ULE-HMD}}$) associated with moderate $\sigma^2_{\text{Lake-HMD}}$ values was low, whereas lakes associated with lower or higher values of $\sigma^2_{\text{Lake-HMD}}$ had a much greater number of significant pairwise comparisons ($\sigma^2_{\text{ULE-HMD}}$) (Fig. 3-6). Lakes belonging to these groups correspond with the groups previously described in Figure 3-4.

The perMANOVA analyses on Period 1 and Period 2 abundance data identified significant variation in the identity of species present ($\sigma^2_{\text{ULE-perM}}$) among the study sites for Periods 1 and 2 (F= 7.27; P = 0.001; F= 9.15; P = 0.001, respectively). For Period 1, 80% of the pairwise comparisons were significant ($P \leq 0.01$), while for Period 2, 87% of the comparisons were significant (pairwise comparisons are showed in Appendix 1).

3.5.4 Species variability along environmental and spatial gradients

The overall HMD analyses revealed significant differences in macrophyte compositional heterogeneity associated with the different connectivity categories for Period 1 (F = 12.64, P = 0.001; Table 3-6). Category 2 had the lowest mean distance to centroid value (0.44), followed by category 4 (0.5), category 5 (0.5), category 3 (0.52) and category 1 (0.58), respectively. Pairwise comparison showed that categories 1 and 2 were significantly different from the other three categories (P < 0.01 for all cases; Table 3-6). perMANOVA analysis revealed significant differences in compositional heterogeneity attributed to the identity of species during this period (F= 9.4105, P = 0.0002; Table 3-6). Pairwise comparisons indicated significant differences among all five connectivity types (P = 0.01 for all cases). For Period 2, the overall HMD test showed significant differences between connectivity types (F = 11.21, P = 0.001; Table 3-6). Pairwise comparisons showed that Category 1 was significantly more heterogeneous (P < 0.01 for all cases) than the other connectivity types. In addition, Category 2 was significantly more heterogeneous than Categories 4

and 5 ($P \leq 0.01$),Category 3 less heterogeneous than Category 5 ($P = 0.03$), and Category 4 was less heterogeneous than Category 5.

Least square regression analysis on Period 1 species abundance data revealed a significant positive relationship between $\sigma^2_{\text{Lake-HMD}}$ and water depth and lake surface area variables and a significant negative relationship between $\sigma^2_{\text{Lake-HMD}}$ and chlorophyll-a (Table 3-7). Regressions on $\sigma^2_{\text{Lake-HMD}}$ derived from the Period 2 data resulted again in a significant positive relationship with water depth and lake surface area and a significant negative relationship with TP, TN and chlorophyll-a (Table 3-7). Abacon Lough was identified as an outlier for the regression between $\sigma^2_{\text{Lake-HMD}}$ and chlorophyll-a for Period 1 and Cornabrass for Period 2 for the regressions between $\sigma^2_{\text{Lake-HMD}}$ and chlorophyll-a and $\sigma^2_{\text{Lake-HMD}}$ and TP. Both lakes were then excluded from the analyses. Least square regression analysis on within lake heterogeneity based on presence-absence data found lake surface area and chlorophyll-a to have a significant effect in bothperiods (Table 5). Least square regressions on environmental vs. lake morphological variables, on α-diversity vs. environmental, and on α-diversity vs. lake morphological variables revealed the following significant trends for both the Period 1 and Period 2 data sets (Table 6): (1) chlorophyll-a concentrations decline as lake area increases and water depth increases as lake area increases for Period 1; (2) α-diversity increases with area and water depth for Period 1; (3) α-diversity decline with TN, TP and chlorophyll-aconcentrations for Period 1 and only with chlorophyll-a for Period 2 .

Table 3-4. Results of multivariate homogeneity test (HMD) analysis and post-hoc pairwise comparisons on EA macrophyte data (Period 1). Significant values (under $P \leq 0.01$) are showed. The number of significant cases per lake is shown on the right hand side of the permutational table along with the total percentage of significant cases. (-) Not significant comparisons.

Overall test:

	Df	S. Sq	M. Sq	F	P
Groups	23	10,94	0,476	22,722	0,001
Residuals	1802	37,74	0,021		

Pairwise comparisons:

	Abc	Cas	Cbr	Crc	Crh	Dmac	Dhow	Dker	Dst	Digh	Doo	DruM	Gole	Hed	Kily	Kil	Kilt	Mill	Sar	Ses	ULE-B	ULE-T	ULE-C	ULE-G	**TOTAL (p<0.01)**
Abc		0,003	0,001	0,008	0,001	-	0,001	0,001	-	-	-	-	-	0,001	0,004	-	-	-	-	-	0,001	0,001	-	-	**10**
Cas			-	-	0,001	-	0,004	-	-	-	-	-	-	-	-	0,001	-	-	-	0,006	0,001	0,001	0,001	0,001	**8**
Cbr				-	0,005	-	-	-	0,001	0,003	0,006	-	-	-	-	0,001	0,005	0,006	0,009	0,001	0,001	0,001	0,001	0,001	**13**
Crc					-	-	-	-	-	-	-	-	-	-	-	0,001	-	-	-	0,004	0,001	0,001	0,001	0,001	**6**
Crh						0,001	-	-	0,001	0,001	0,002	-	0,008	-	0,004	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	0,001	**15**
Dmac							0,003	-	-	-	-	-	-	-	-	0,001	-	-	-	-	0,001	0,001	0,001	0,002	**6**
Dhow								-	0,001	0,001	0,003	-	0,003	-	-	0,001	0,001	0,001	0,006	0,001	0,001	0,001	0,001	0,001	**13**
Dker									0,001	0,005	0,006	-	-	-	-	0,001	0,005	0,002	0,010	0,001	0,001	0,001	0,001	0,001	**12**
Dst										-	-	-	-	0,003	-	0,001	-	-	-	-	0,001	0,001	0,003	-	**5**
Digh											-	-	-	0,005	-	-	-	-	-	-	0,001	0,001	0,001	-	**4**
Doo												-	-	0,009	-	0,001	-	-	-	-	0,001	0,001	0,001	-	**5**
DruM													-	-	-	0,003	-	-	-	-	0,001	0,001	0,002	-	**4**
Gole														-	-	0,010	-	-	-	-	0,001	0,001	0,001	-	**4**
Hed															-	0,001	0,008	0,005	-	0,001	0,001	0,001	0,001	0,001	**8**
Kily																0,001	0,100	-	-	0,003	0,001	0,001	0,001	0,001	**7**
Kil																	0,001	0,001	0,001	0,004	-	-	-	-	**4**
Kilt																		-	-	-	0,001	0,001	0,001	-	**3**
Mill																			-	-	0,001	0,001	0,001	-	**3**
Sar																				-	0,001	0,001	0,001	-	**3**
Ses																					0,001	0,001	0,001	-	**3**
ULE-B																						-	-	0,001	**1**
ULE-T																							0,004	0,001	**2**
ULE-C																								0,001	**1**
ULE-G																								**Total**	**140**
																								%	**50,7**

Table 3-5. Results of multivariate homogeneity test (HMD) analysis and post-hoc pairwise comparisons on PVI macrophyte data (Period 2). Significant values (under $P \leq 0.01$) are showed. The number of significant cases per lake is shown on the right hand side of the permutational table along with the total percentage of significant cases. (-) Not significant comparisons.

Overall test:

	Df	S. Sq	M. Sq	F	P
Groups	14	3,23	0,23	14,5	0,001
Residuals	660	10,51	0,02		

Pairwise comparisons:

	Cas	Cbr	Dhow	Digh	Dker	Dst	Gole	Hed	Killy	Kilt	Doo	Mill	ULE-B	ULE-T	ULE-C	**TOTAL (p<0.01)**
Cas		0,002	-	-	-	-	-	0,001	-	-	-	-	0,002	0,001	-	**4**
Cbr			0,002	0,005	-	-	0,001	0,001	0,002	-	-	-	-	-	-	**5**
Dhow				-	-	-	-	0,002	-	-	-	0,002	0,001	0,001	0,001	**5**
Digh					-	-	-	0,001	-	-	-	-	0,001	0,001	0,011	**4**
Dker						-	0,007	0,001	-	-	-	-	-	0,005	-	**3**
Dst							0,002	0,001	-	-	-	-	-	-	-	**2**
Gole								-	0,010	0,002	-	0,001	0,001	0,001	0,001	**6**
Hed									0,001	0,001	0,001	0,001	0,001	0,001	0,001	**7**
Killy										-	-	-	0,001	0,001	0,008	**3**
Kilt											-	-	0,008	0,001	-	**2**
Doo												-	0,002	0,001	-	**2**
Mill													-	-	-	**0**
ULE-B														-	-	**0**
ULE-T															-	**0**
ULE-C															**Total**	**43**
															%	**36**

Table 3-6. Results of Homogeneity test of multivariate dispersion (HMD) examining the effects of 5 hydrological connectivity categories on the compositional heterogeneity of macrophyte assemblages. Category 1- areas within the Upper Lough Erne (ULE-B, ULE-C, ULE-G and ULE-T); Category 2- lakes in the south connected to the ULE through the Rivers Finn and Erne (Castle, Derrykerrib, Derrysteaton and Sarah); Category 3- lakes directly connected to the ULE through small streams or marshlands (Abacon, Corraharra, Derryhowlaght, Digh and Doo); Category 4- lakes connected to the ULE through another satellite lake (Corracoash, Cornabrass, Derrymacrow Gole, Head and Sessiagh East); and Category 5- lakes that are connected to the ULE through two or more satellite lakes or completely isolated (Drumroosk, Killymackan, Kilturk and Mill).

Period 1

Avg. distance to centroid	
Category 1	0,58
Category 2	0,44
Category 3	0,52
Category 4	0,50
Category 5	0,49

Overall test:

	Df	S. Sq	M. Sq	F	P
Groups	4	1,20	0,300	12,64	0
Residuals	571	13,56	0,024		

Pairwise comparis	*P*
Cat. 1 vs. Cat. 2	0,001
Cat. 1 vs. Cat. 3	0,002
Cat. 1 vs. Cat. 4	0,001
Cat. 1 vs. Cat. 5	0,001
Cat. 2 vs. Cat. 3	0,001
Cat. 2 vs. Cat. 4	0,009
Cat. 2 vs. Cat. 5	0,016
Cat. 3 vs. Cat. 4	0,386
Cat. 3 vs. Cat. 5	0,274
Cat. 4 vs. Cat. 5	0,863

Period 2

Avg. distance to centroid	
Category 1	0,64
Category 2	0,59
Category 3	0,58
Category 4	0,59
Category 5	0,62

Overall test:

	Df	S. Sq	M. Sq	F	P
Groups	4	0,94	0,24	11,22	0,001
Residuals	345	7,25	0,02		

Pairwise comparis	*P*
Cat. 1 vs. Cat. 2	0,001
Cat. 1 vs. Cat. 3	0,001
Cat. 1 vs. Cat. 4	0,051
Cat. 1 vs. Cat. 5	0,001
Cat. 2 vs. Cat. 3	0,104
Cat. 2 vs. Cat. 4	0,005
Cat. 2 vs. Cat. 5	0,392
Cat. 3 vs. Cat. 4	0,036
Cat. 3 vs. Cat. 5	0,376
Cat. 4 vs. Cat. 5	0,005

Table 3-7. Partial least squares regressions results between within-lake variability and local and regional variables ($P \leq 0.05$). (Cent) - Mean distance to centroid; (WC) - watercourse distances; (XY) - overland distances. Numbers in brackets represent values including outliers lakes in the analysis (Gole for 2006 and Coranbrass dor 2009).

Period 1 (abundance)	F	P	R^2 adj	Period 1 (P/A)	F	P	R^2 adj
Depth vs. Cent	9.196	0.006	0.2714	Depth vs. Cent	NS	NS	NS
TP vs. Cent	NS	NS	NS	TP vs. Cent	NS	NS	NS
TN vs. Cent	NS	NS	NS	TN vs. Cent	NS	NS	NS
Chla vs. Cent*	13.17	0.002 (0.04)	0.3668	Chla vs. Cent*	6.039	0.02325 (NS)	0.1935
Area vs. Cent	17.31	0.0004	0.4258	Area vs. Cent	13.18	0.001	0.3462
Dist (WC) vs. Cent	NS	NS	NS	Dist (WC) vs. Cent	NS	NS	NS
Dist (XY) vs. Cent	NS	NS	NS	Dist (XY) vs. Cent	NS	NS	NS
Other relationships							
Alpha vs. TN*	13.55	0.002	0.3977				
Alpha vs. Depth	6.508	0.02	0.1932				
Alpha vs. Area	34.53	0.00001	0.5931				
Alpha vs. Chla	6.17	0.02	0.1903				
Alpha vs. TP	4.04	0.057(*)	0.1214				
TN vs. Area*	NS	NS	NS				
TP vs. Area	NS	NS	NS				
Depth vs. Area	8.562	0.008	0.2474				
Chla vs. Area	4.428	0.047	0.1348				
Chla vs. Depth	NS	NS	NS				
Period 2 (abundance)	F	P	R^2 adj	Period 2 (P/A)	F	P	R^2 adj
Depth vs. Cent	6.161	0.027	0.2694	Depth vs. Cent	NS	NS	NS
TP vs. Cent	22.3	0.0004 (NS)	0.621	TP vs. Cent	NS	NS	NS
TN vs. Cent	13.02	0.0047	0.5221	TN vs. Cent	NS	NS	NS
Chla vs. Cent*	12.89	0.0037 (0.028)	0.4778	Chla vs. Cent*	22.22	0.0005 (0.005)	0.6201
Area vs. Cent	4.433	0.0553(*)	0.1969	Area vs. Cent	7.376	0.0177	0.3129
Dist (WC) vs. Cent	NS	NS	NS	Dist (WC) vs. Cent	NS	NS	NS
Dist (XY) vs. Cent	NS	NS	NS	Dist (XY) vs. Cent	NS	NS	NS
Other relationships							
Alpha vs. TN*	NS	NS	NS				
Alpha vs. Depth	NS	NS	NS				
Alpha vs. Area	NS	NS	NS				
Alpha vs. TP	NS	NS	NS				
Alpha vs. Chla	17.55	0.001 (0.005)	0.56				
Chla vs. Depth	NS	NS	NS				
Chla vs. Area	NS	NS	NS				
TP vs. Area	NS	NS	NS				

3.6 Discussion

3.6.1 Patterns of species richness

This study demonstrates that the ULE system has a remarkably rich submerged and floating-leaved flora (n = 51) despite high nutrient concentrations of most constituent lakes. In both sampling periods, the median number of species per sampling point (3-4 species) and per lake (15 species) was high (Table 3-3) compared to previous studies of other temperate eutrophic shallow lakes in Europe. For example, a recent study by Sayer et al. (2010a) recorded 30 species in total with a median of only five species per lake in a set of 39 shallow lakes of similar annual average TP concentrations (112 µg L^{-1}) from UK and Denmark. Further, Jeppesen et al. (2000) found relatively few submerged and floating-leaved macrophytes species (n = 25) in a

data set of more than 600 lakes in Denmark with annual mean TP concentrations of 210 µg L^{-1} . They found an average of 12 species per lake among sites with lower TP values (0-50 µg L^{-1}) and $\leq$ 5 species when TP values exceeded 100 µg TP L^{-1}. TP values for the set of lakes in the ULE system had an annual average concentration of 110µg L^{-1} (Table 3-1). Differences in macrophyte diversity between other lakes and those in the ULE system could be attributed to a variety of factors that influence macrophyte distributions such as alkalinity, surface area, altitude and lake morphology (Spence 1967, 1982, Rørslett 1991, Jones et al. 2003), but none of these are compelling.

Another explanation for the high macrophyte diversity of the ULE system might lie with the fact that it is organized as a metacommunity in which lakes are linked to differing degrees by dispersal (Leibold et al. 2004, Leibold and Norberg 2004). Within flood plains research has shown that connectivity is common and, if high, it could contribute to increases in macrophyte α-diversity (Amoros and Bornette 2002). Theoretical metacommunity models have demonstrated occupancy by both dominant competitors and less abundant poor competitors under intermediate rates of dispersal, (Loreau and Mouquet 1999, Mouquet 2003, Leibold and Norberg 2004). Data collected in the current study over both time periods showed that, despite eutrophic conditions, most lakes presented occupancy patterns supporting metacommunity model predictions. For instance species like *M. verticillatum, P. lucens, P. praelongus, S. aloides* and *U. vulgaris* co-occurred at many of the sites. These species are commonly reported to decline or disappear following high enrichment (Arts 2002, Smolders et al. 2003, Davidson et al. 2005, Sand-Jensen et al. 2008, Salgado et al. 2010; Madgwick et al. 2011).

Comparison with macrophyte species richness and occupancy of lakes in the Norfolk Broads, England, is also of relevance. Previous studies indicate that historically (c. pre-1900), macrophyte assemblages in the fenlands of Northern Ireland and in the Norfolk Broads were highly similar (Small 1931; Forbes 2000). To date however, in spite of similar contemporary water chemistry conditions and comparable histories of eutrophication in the Broads and ULE, *P. lucens, P. praelongus, S. aloides* and *U. vulgaris*have disappeared from most of the former lakes (Kennison et al. 1998, Ayres et al. 2008, Madgwick et al. 2011). This differential response to eutrophication might

be explained by greater connectivity and dispersal in the ULE. Although connectivity in the Broads is common, the ULE system has a higher degree of hydrological connectedness between lakes mediated by the presence of a "mothership" lake (the ULE) that is linked to almost all sites. This permanent connectivity to the ULE, which is mediated by rivers, streams and agricultural channels, is further enhanced by more regular flood events (Fig. 3-2). Furthermore, as discussed below, the complex and large size of the ULE also helps to sustain higher macrophyte species-richness, and thus acts as a source and a refuge for poor competitors. The data from Kilmore Lough further exemplifies the role of dispersal. This lake has the second highest annual average levels of TP (186 μg L^{-1}) in the ULE system, yet 16 species were recorded in Period 1 including *P. lucens,* a species associated with low regional dispersal capacities (Riis and Sand-Jensen 2001) (Fig. 3-3). Kilmore Lough is not directly connected to the main ULE but is located in an area that is highly prone to flooding (Fig. 3-2) (http://safer.emergencyresponse.eu), and its relative position may therefore prevent species extinction through constant propagule inputs. As a consequence, despite eutrophication, poor competitor species may persist longer in nutrient-rich conditions in the ULE system due to metacommunity processes of mass effects (Shmida and Wilson 1985).

3.6.2 Within- and between-lake macrophyte compositional heterogeneity

Along with the high levels of α-diversity, the quantitative analyses (HMD and perMANOVA) of macrophyte abundance and presence/absence data revealed that in the periods of study there was substantial within-lake compositional heterogeneity in the ULE system that was largely attributed to variation in relative abundances ($\sigma^2_{\text{Lake-HMD}}$) and species identity ($\sigma^2_{\text{Lake-perM}}$) (Table 2). Overall, most macrophyte species showed a high variation between minimum and maximum abundance values in each lake (see Figs. 3-3 and 3-4), indicating substantial variation in mean abundances between sampling points.

Data for both time periods revealed that, with the exception of the almost ubiquitous *E. canadensis*, a patchy distribution was common in most of the submerged species, especially *P. alpinus, P. praelongus, P. lucens, P. natans, M. verticillatum, M. spicatum, S. aloides* and *U. vulgaris*. Previous research has shown that *Myriophyllum* species are highly sensitive to changes in sediment characteristics responding poorly

to the unconsolidated and organic sediments that result from eutrophication (Barko and Smart 1996). The differences in relative abundance of different broad-leaved *Potamogeton* species are suggested to reflect the influence of impoverished light and physical disturbance (Riis and Sand-Jensen 2001). Although broad-leaved *Potamogeton* species presumably have a high competitive ability for light and space under relatively stable conditions in deep waters, they can be intolerant of physical disturbance (Preston 1995, Riis and Sand-Jensen 2001). The unsteady hydrological conditions derived from frequent floods in the ULE system and the increasing turbidity imposed by eutrophication are therefore likely to impose harsher conditions on these species.

Although *P. natans* and *S. aloides* are capable of withstanding considerable physical disturbance as well as turbid conditions (Mesters, 1995; Grasmück et al. 1995, Riis and Sand-Jensen 2001, Smolders et al. 2003), they typically grow in slow-moving and wind-protected waters. Their observed patchy distribution is probably then attributable to a preference for more protected areas (Smolders et al. 2003). In addition, *S. aloides* is highly sensitive to changes in iron and sulphate concentration (Smolders and Roelofs 1996, Smolders et al. 2003) and these are quickly altered with enrichment. *E. canadensis* has been described as a disturbance-tolerant and with a high dispersal capacity (Nichols and Shaw 1986, Grime et al. 1988; Abernethy et al. 1996 Barrat-Segretain et al. 1998). The aggressive vegetative reproduction by shoot fragments allows this species to continually colonise new areas and maintain stable populations after disturbances (Barko 1982, Barrat-Segretain and Amoros 1996, Barrat-Segretain et al. 1998).

3.6.3 Within-lake compositional heterogeneity and regional environmental gradients

Least square regressions between within-lake compositional heterogeneity and nutrient concentrations identified that compositional heterogeneity declined significantly along the nutrient gradient (especially for chlorophyll-a) for both time periods (Table 3-5). Demonstration of compositional heterogeneity changes in response to eutrophication is relatively novel and the mechanisms behind this process are still poorly known. Chase (2007) proposes that severe ‘‘ecological filters’’, such as those resulting from strong anthropogenic eutrophication, reduce the importance of

key processes in structuring biotic communities and thus homogenise biotic assemblages within sites. This process is mediated by specific niche preferences (species-sorting) that result in the exclusion of poor competitors, the local dominance of good competitors and an increase in differences in species composition between lakes (β-diversity) (Loreau and Mouquet 1999, Leibold and Nornberg 2004, Cadotte 2006).

A recent study by Sayer et al. (2010a), suggest that for macrophytes, species sorting-mechanism may happen over long-term periods (10-100 years) through a feedback loop of nutrients-phytoplankton-macrophyte abundance interactions. The increase in nutrients promotes macrophyte species loss and enhances phytoplankton production. In turn, the increase in phytoplankton places further pressure on less adapted species by reducing summer macrophyte cover. At last, the dominance of few competitive species makes the system more prone to a midsummer crash in the plant population.

The methodological sampling differences between the two periods of time used in this study, constrains interpretations as tothe possible mechanisms behind the homogenisation of communities with increasing nutrient supply. However, four key trends were revealed by the data that strongly suggest that in the ULE system, changes in compositional heterogeneity might have been driven by species-sorting processes as suggested by Chase (2007) and Sayer et al. (2010a). First, chlorophyll-a emerged as the main nutrient variable to explain reductions in compositional heterogeneity for both periods (Table 3-7). Second, within-lake occupancy macrophyte patterns showed an increase in dominance with nutrients (Table 3-7). Third, and closely associated therewith, HMD analyses showed a reduction in regional β-diversity in the variation of relative abundances for Period 2 (a stronger correlation between within-lake compositional heterogeneity and nutrients was obtained for Period 2; (Table 3-7). Last, perMANOVA analyses showed an increase in regional β-diversity in the within-lake variation in the identity of species for Period 2 (Tables 3-3 and 3-4). These trends are supported by palaeolimnological research presented in Chapter 4 and 5. Both studies showed that as eutrophication develops, there is an increase in species dominance, a reduction in among-lake variation of relative abundances and an increase in among-lake variation in the identity of species.

It is possible that variations in lake size and water depth are both confounding factors, since they also emerged as the main variables explaining species richness and assemblage variability. The relationship between species-richness and area is well-founded in island biogeography (MacArthur and Wilson 1967) and has been consistently demonstrated across a wide variety of habitats and organisms (Lomolino 2000). For instance, lake area contributed most significantly to the variation in macrophyte species-richness in 641 lakes in Scandinavia (Rørslett 1991). Similar results were obtained by Vestergaard and Sand-Jensen (2000) for 73 Danish lakes and by Jones et al. (2003) for 300 lakes in the UK.

Generally, the relationship between area and species-richness have been attributed to an array of factors such as a greater diversity of niches, (MacArthur and MacArthur 1961), larger areas for colonization (MacArthur and Wilson 1967) and, more recently, by sampling and likelihood; increased sampling increases the likelihood of encountering more species (e.g. Connor and McCoy 1979). The latter idea can be discounted in this study, however, as even when a reduced and equal number of sampling points per lake were used, within-lake compositional heterogeneity values ($\sigma^2_{\text{Lakes-HMD}}$) did not differ from those based on a greater number of points (Fig. 3-4).

The differences obtained between the two time periods for the relationship of area and other variables like chloprophyll-a and α-diversity makes interpretation of the influence of surface area on compositional heterogeneity rather difficult. However, the positive significant association between surface area and water depth and between α-diversity and lake size (Period 1) may reflect both a greater diversity of niches and an increase area for colonisation. This appears to pertain to the main ULE Lake, which had the largest surface area and the greatest diversity and compositional heterogeneity. The main lake also offers a complex geomorphology (meanders of more protected riverine areas in the South, open areas in the North and numerous islands and shelter bays throughout; Fig. 3-2). The positive relationship between surface area and compositional heterogeneity and the inverse relationship between surface area and nutrient concentrations highlights the key role of the ULE in acting as a species source and as a refuge for poor competitors thus likely counteracting the homogenising effects of eutrophication.

The relationship between water depth and macrophyte community structure is widely attributed to a maximum colonisation depth, which in turn is determined by light attenuation in the water column and minimum light requirements of the plants (Canfield, 1985, Middelboe and Markager 1997, Spence 1967, Spence 1982). Highly transparent waters allow macrophytes to colonise to greater depth than in more turbid waters (Canfield 1985, Middelboe and Markager 1997, Capers et al. 2010). However, the significant positive relationship between lake surface area and water depth obtained for this study precludes any further interpretation.

3.6.4 Compositional heterogeneity and connectivity

The comparisons between connectivity types (Fig. 3-2) and macrophyte compositional heterogeneity further revealed the interaction of connectivity and eutrophication on macrophyte compositional heterogeneity. For instance, analyses indicated that the ULE macrophyte assemblages were more heterogeneous than the satellite lakes for both periods, a pattern likely ascribable to its larger surface area. The data also revealed that for Period 1, compositional heterogeneity values were relatively lower than Period 2 and no significant differences in macrophyte assemblages between most of the other categories of hydrological connectivity (see Fig. 3-2) were observed. Nonetheless, for Period 2, compositional heterogeneity values declined moderately while differences between macrophyte assemblages in sites in different categories increased.

Previous theoretical (Loreau and Mouquet 1999, Mouquet 2003, Shurin and Allen, 2001, Cadotte 2006), laboratory microcosm (Holyoak and Lawler 1996; Cadotte and Fukami 2005), and field (Forbes and Chase 2002; Kneitel and Miller 2003) metacommunity studies have demonstrated a close relationship between connectivity (dispersal) and α and β-diversity. When dispersal is intermediate α-diversity (and hence heterogeneity) increases and β-diversity declines. An inverse trend is observed when dispersal rates decline. Taken together, the observed trends in this study suggest that over Period 1, the influence of hydrological connectivity was relatively high, promoting compositional heterogeneity amongst macrophyte assemblages in sites that varied in connectivity and lower β-diversity. For period 2, the data suggest a lower influence of dispersal and a higher influence of local variables, which results in high β-diversity. Variation in the influence of local and regional processes in structuring

local communities have been described for other metacommunity systems (Cottenie et al. 2003, Cottenie and De Meester 2005) and coincides with a suspected acceleration of eutrophication over a short time-span of just two years as described in Chapter 2.

3.6.5 Trends in within-lake compositional variability in the ULE system

Theoretical studies predict that connectivity between sites acts as a regional homogenising force on diversity resulting in a hump-shaped relationship (Mouquet 2003, Kneitel and Miller 2003, Cadotte 2006b). At low levels of dispersal α-diversity is low but differences between sites (β-diversity) are high. At intermediate levels of dispersal α-diversity is high and differences between sites are reduced. At high rates of dispersal both α-diversity and β- diversity decline (Mouquet 2003, Kneitel and Miller 2003, Leibold and Norberg 2004, Cadotte 2006b). This means that, as α-diversity increases, the number of species from the regional pool (γ-diversity) shared between sites increases and hence differences between sites decline (Mouquet 2003, Leibold and Norberg 2004, Cadotte 2006b).

The data from this study partially agree with the above-described theoretical relationship when comparing the regional variability of within-lake compositional heterogeneity attributed to variation in relative abundances (Fig. 3-6). At low levels of within-lake macrophyte compositional heterogeneity (measured as the mean distance from centroid), differences between lakes were high, while at intermediate levels of within-lake compositional heterogeneity, differences between lakes declined. However, there was a notable difference from the above-mentioned theoretical hump-shaped relationship at intermediate to high levels of compositional heterogeneity. Because of the relatively linear nature of the observed gradient of within-lake compositional heterogeneity (Fig. 3-5), differences between lakes increase as within-lake heterogeneity increases from intermediate levels (Fig. 3-7). This U-shaped pattern suggests that lakes that have intermediate values of macrophyte assemblage heterogeneity are more likely to share more typical features of the regional species pool than those sites that are at both extremes (low or extreme high compositional heterogeneity).

As demonstrated by least-square regression analyses, multiple factors explain the U-shaped relationship for regional within-lake variability (Fig. 3-6). Overall, both data sets (Period 1 and Period 2) coincide and suggest that lakes that presented low

compositional heterogeneity were lakes mostly associated with higher levels of chlorophyll-a, low α-diversity and were relatively small and shallow (Tables 3-1 and 3-3). Contrastingly, highly heterogeneous lakes were mostly associated with low values of chlorophyll-a, high α-diversity, higher water depth and largesurface area. It is noticeable however, that there was a temporal (between year) variation in within-lake heterogeneity. For instance, presence/absence data in Period 1 for Gole Lough had moderate macrophyte assemblage heterogeneity (0.47) and in Period 2 it was low (0.16) (Fig. 3-5). Similarly, Cornabrass Lough had relatively low values of within-lake heterogeneity in Period 1 and a diverse assemblage in Period 2 (Fig. 3-5). These results may be attributed to the variation in the influence of these variables between time periods observed in least-square regression analyses (Table 3-5). Nevertheless, regardless of the forces that may drive the regional within-lake variability in the ULE, the U-shaped relationship was fairly consistent over the Periods indicating that regional β-diversity is minimised at intermediate levels of within-lake assemblage heterogeneity.

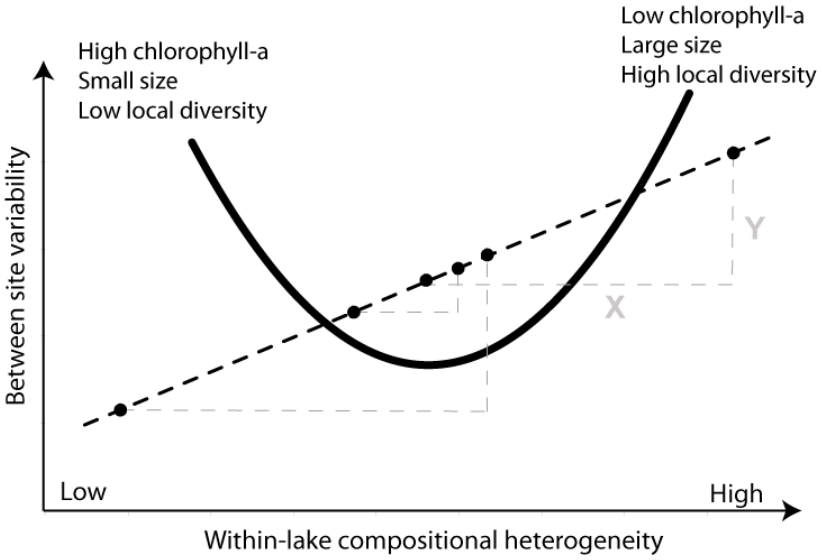

Figure 3-7. Conceptual diagram of how the regional variability of macrophyte assemblages varies as a function of within-lake heterogeneity. Black dotted line represents the observed linear gradient in within-lake macrophyte compositional heterogeneity of the 25 sampling sites. Grey dotted lines indicate the distances between any given pair of sites (black points). Sites that are farther apart in the gradient are more dissimilar based on XY distances.

3.7 Conclusions

As a result of an increase in nutrient loading over the last century there has been a marked decline in the ecological integrity of most temperate shallow lakes (Roelofs

2002). As this process continues, plant-less lakes or lakes with mono-specific macrophyte stands are becoming increasingly common and diverse, structurally complex, macrophyte-dominated lakes are becoming rare. This study illustrates that the ULE system is one of those rare remaining hydrological systems with diverse macrophyte assemblages in most of its associated lakes. Nonetheless, reductions in the number of species in some of the lakes, especially in the main ULE in Period 2 (Table 3-3), the high variability in the identities of species assemblages between lakes and the significant negative trend observed between variability of within-lake species relative abundances and nutrient concentration provide evidence that the system is vulnerable to and may be experiencing detrimental change due to eutrophication.

By incorporating metacommunity theories, this study has revealed four key issues relevant to macrophyte community studies and future conservation strategies, both in ULE and elsewhere. First, despite eutrophication, the high connectedness of the system is helping to maintain high levels of local diversity. Although, dispersal rates were not quantified *per se*, the occurrence, at most sites, of species usually lost in the early stages of eutrophication agrees with previous theoretical and experimental work that demonstrate similar patterns driven by intermediate dispersal rates. Second, variability in species assemblages revealed a significant negative association with nutrient concentrations. This is a poorly studied area for shallow lakes and requires future attention. Underwood (1994) highlighted how environmental stressors may not affect the number of species but can influence mean variability in species abundances. Hence the use of common procedures that only identify changes in species richness and turnover may not detect other compositional changes. Eutrophication exerts a continuous effect that is likely to influence both variability in mean abundances and changes in species richness. Third, this study also identified a strong influence of lake surface area and water depth in determining macrophyte species diversity and assemblage variability. This finding suggests that the main ULE plays a vital role in maintaining macrophyte species diversity, by acting as a species refuge and/or as a source of colonists within the system. Consequently, strong efforts should be made to maintain the integrity of this lake. Nevertheless, the associated satellite lakes may also play important roles in the system by acting as species refuges and sources of species back to the main ULE. Finally, by using the number of significant post-hoc pair-wise comparisons from HMD analysis as a measure of regional within-lake compositional

heterogeneity (β-diversity), this study demonstrates that β-diversity changes in such a way that macrophyte compositional differences between lakes are minimised at intermediate levels of within-lake compositional heterogeneity.

4 Chapter 4 – Temporal and spatial dynamics in the community dominance structure of a shallow lake during eutrophication

4.1 Abstract

Recent work has suggested that nutrient enrichment in freshwater systems reduces the relative abundances of certain species and thereby the dominance (or evenness) structure of communities. This study investigates the long-term effects of nutrient enrichment and dispersal on community composition heterogeneity and the potential mechanisms promoting coexistence of submerged macrophytes, invertebrates and chironomids in three areas of Castle Lough, a eutrophic and well-connected shallow lake, in Northern Ireland, UK. More specifically, this study tests: (1) whether nutrient enrichment promotes local dominance by some species and reduces compositional heterogeneity between sub-localities; and (2) whether the same metacommunity dynamics that affect diversity at the lake-landscape scale occur at the within-lake scale (i.e. an existence of a continuum of "sub-metacommunities"). Contemporary and palaeolimnological data revealed changes in community composition and in the relative abundances of species. Temporal assembly dynamics showed that communities in each lake area changed from c. pre-1900 being heterogeneous to being more homogenous (dominated by a few species) in the present day. This change was accompanied by an increase in temporal β-diversity and little extinction over time. These trends are consistent with transitions that would be expected as a result of dispersal and advancing eutrophication. Spatial assembly dynamics revealed that c. pre- 1900 differences between areas (spatial β-diversity) were low and increased over time being highest from c. 1950 to present. This trend supports the notion of a continuum of "sub-metacommunities" where species sorting processes also occur at the within-lake scale of small and shallow vegetated lakes. In addition, temporal and spatial dynamics revealed that changes in dominance occurred more rapidly than changes in species richness, which appeared to be driven by source-sink dynamics.

These findings have profound implications for restoration initiatives since they demonstrate that concentrating exclusively on changes in species richness in metacommunity landscapes may be insufficient to fully appreciate the response of shallow lake ecosystems to eutrophication.

4.2 Introduction

Recent meta-analyses have shown that local and regional processes jointly structure aquatic metacommunities (i.e. a set of local communities that are linked by dispersal) (Cottenie et al. 2003, Leibold et al. 2004, Leibold and Norberg 2004, Brown and Swan 2010, Capers et al. 2010). Environmental heterogeneity and biotic interactions (competition, predation, parasitism) regulate the local capacity of species to persist, while dispersal and adaptation influence species turnover via extinction-colonisation events and species-sorting along environmental gradients (Leibold and Norberg 2004). Nonetheless, the degree to which dispersal and adaptation maintain local diversity depends upon the connectedness of the system and will be reflected in species dominance or evenness in a hump-shaped relationship (Loreau and Mouquet 1999, Kneitel et al. 2003, Cadotte 2006). Thus, if connectedness is low, dispersal events will be less regular and local factors will be the main structuring driver. In this case species will sort according to their environmental optima and single or a few competitive species will dominate local communities. At intermediate levels of connectedness, both local and regional factors will influence community structure and local communities will be composed of both dominant species and rare species that are maintained by immigration. When connectedness is largely high, local processes will be swamped, and one or few competitive species will dominate locally and regionally. Thus, by this scenario there are two extremes: local processes result in dominance by one or a few species at one end of the spectrum and regional processes result in the same scenario at the other end (Loreau and Mouquet 1999, Kneitel and Miller 2003, Leibold et al. 2004, Leibold and Norberg 2004).

To date, most meta-analyses on freshwater aquatic systems have focused on what are generally regarded as well-mixed populations of mobile planktonic organisms in small water-bodies, especially ponds and shallow lakes (Cottenie et al. 2003, Cottenie

and De Meester 2004, Leibold and Norberg 2004). The effects of metacommunity processes in terms of maintaining local diversity and structuring assemblages in space may therefore be oversimplified because the dynamics of less mobile taxa have been overlooked. Submerged macrophytes, for example, lack active mobility and their immediate local distribution depends upon competition for space and tolerance of, rather than escape from, environmental constraints (Bradshaw 1965). Consequently, it is likely that variation in local attributes (environmental change) or regional attributes (dispersal) may promote significant and variable differences between areas within a lake in accordance to the above-mentioned connectedness scenarios. For instance, if a local factor such as eutrophication is strong and is the main driver at the metacommunity landscape, it can homogenise any other local variation in the environment of a lake such as substrate types and variation in nutrient levels along with reductions of CO_2 concentration in the lake (Jepessen et al. 2001). Consequently macrophyte assemblages between given areas of a lake should become relatively homogeneous as one or few competitive species will dominate among areas. However, when local and regional factors act together, dispersal should promote more even macrophyte assemblages (different species occurring with relatively similar abundances) at each site and maintain heterogeneity between different areas through source sink dynamics. The joint action of both local and regional factors may therefore promote within-lake continuum of sub-metacommunities (Leibold and Norberg 2004), even in small lakes. As submerged macrophyte assemblages provide a wide range of structurally complex habitats, from the micro- (plant architecture) to the meso-scale (plant stands) (Sculthorpe 1967, Jeppesen et al. 1998) heterogeneity in macrophyte assemblages may also influence the distribution and abundance of co-occurring species. Thus, by assuming that small water-bodies are homogeneous, well-mixed entities, freshwater metacommunity studies may have missed vital information (at least for vegetated lakes) on how metacommunity processes maintain local diversity.

Increasing human influences on ecosystems have led to dramatic changes in the composition of biological communities. As a consequence, there has been an increased focus on understanding the relationship between species richness and ecosystem function (Hillebrand et al. 2011). However, species richness is only one aspect of diversity (Anderson et al. 2011). Increasingly it is being recognised that

anthropogenic stressors, such as eutrophication, reduce also the variation in species identities and relative abundance and thus promotes the dominance of communities (Hillebrand et al. 2008, Donohue et al. 2009, Wittebolle et al. 2009). To date however, how anthropogenic stressors, especially eutrophication, interact with hydrological connectivity to influence lake species richness and dominancein connected systems has received little research. Indeed, due to inherent difficulties of measuring the effects of eutrophication and dispersal over time, most studies have limited their scope and realm of inference to a snapshot in time (e.g. Cottenie et al. 2003). Classically, therefore, a space-for-time assumption has been implicit in the understanding of community dynamics and research has centred almost entirely on contemporary datasets (Jeppesen et al. 2000). Nevertheless, well-connected ecosystems (e.g. riverine landscapes) are dynamic and change constantly over time (Amoros and Bornette 2002). Likewise, eutrophication is usually a gradual process that is manifested over long-term (decadal to centennial) scales (Schindler 1974, Davidson et al. 2005, Conley et al. 2009, Sayer et al 2010b). Therefore, to fully understand the joint effects of connectivity and eutrophication in effecting diversity, it is vital to focus research at both spatial and temporal scales.

Sediment core records from shallow lakes have demonstrated their suitability to detect changes in community structure over long time spans(Brodersen et al. 2001; Odgaard and Rasmussen 2001, Rasmussen and Anderson 2005 Ayres et al. 2008, Salgado et al. 2010, Allen et al. 2011). Sediment core records also offer the opportunity to investigate long-term metacommunity dynamics (Allen et al. 2011). These long-term perspectives are often lacking in metacommunity studies and are especially relevant to systems characterised by high connectivity. By using contemporary and palaeolimnological data, this study aims to enhance understanding of how spatial processes and mechanisms of coexistence may vary in a metacommunity landscape altered by eutrophication. In particular, the study investigates patterns of variation in dominance of submerged macrophytes and co-occurring invertebrate assemblages in time (contemporary and decadal to centennial) from three areas of Castle Lough, a eutrophic, specious and well-connected shallow lake, in the Upper Lough Erne system, Northern Ireland, UK. Specifically, the study tests: (1) whether nutrient enrichment promotes patch-scale dominance by some species and reduces compositional heterogeneity between sub-localities over time; (2) whether the same

metacommunity dynamics that effect diversity at the lake-landscape scale occur similarly at the intra-lake scale (i.e. within-lake continuum of "sub-metacommunities"). Based on eutrophication knowledge and metacommunity and dispersal theory I made the following predictions related to changes in species dominance (Fig. 4-1):

Spatial assembly dynamics:

i. *Low dispersal - high influence of eutrophication*: If eutrophication is the main driver structuring lake communities, all three areas should be homogeneous and the same few species adapted to eutrophic conditions should dominate in all three areas (Fig. 4-1a). Low differences between areas (spatial β-diversity) would be expected in this scenario.

ii. *Low dispersal – variable influence of eutrophication among patches*: If there is an environmental difference between lake patches that is ascribed to eutrophication or other lake physical attributes (e.g. water depth, substrate) and a relatively low influence of dispersal, a low number of different competitive species should dominate at different lake areas (Fig. 4-1a). High differences between areas (β-diversity) would be expected in this scenario.

iii. *High dispersal - high influence of eutrophication*: If both eutrophication and dispersal influence communities, all three areas should be characterised by the presence of several species having similar relative abundances. According to the strength of variation in eutrophication between areas, differences in diversity between areas (β-diversity) could be low (same species pool at each area – high dispersal and no differences in eutrophication), intermediate (some shared species between areas – high dispersal and intermediate variation in eutrophication) or high (no shared species between areas – high dispersal and strong differences in eutrophication) (Fig. 4-1a).

iv. *High dispersal - low influence of eutrophication*: If dispersal is effective and eutrophication is low or swamped by dispersal, all three communities should be homogeneous and the same few species should dominate in all three areas (Fig. 4-1a). Low differences between different areas (β-diversity) would be expected in this scenario. This scenario differs from (i) by the type of species that dominates. That is, in this scenario dominant species should have high dispersal strategies rather than environmental tolerance strategies.

Temporal assembly dynamics

i. *Low dispersal – high influence of a constant eutrophication*: If local factors (e.g. eutrophication) are constant over time and there is no influence of dispersal, assemblages among time periods should be dominated by the same few good competitor species (Fig. 4-1 b).

ii. *Low dispersal – variable influence of eutrophication among time periods*: If there is an increase/decrease in the strength of eutrophication between time periods and relatively low influence of dispersal, a few good but different competitive species would dominate each period (Fig. 4-1b). High differences between time periods (temporal β-diversity) would be expected in this scenario.

iii. *High dispersal – high influence of eutrophication*: If there is an increase/decrease in the strength of eutrophication between time periods and dispersal is high, time periods should be characterised by the presence of several species having similar relative abundances. According to the rate of temporal variation in eutrophication, differences between time periods (temporal β-diversity) could be low (same species pool at each period - high dispersal and high but constant eutrophication), intermediate (a given number of shared species between periods - high dispersal and high variable eutrophication) or high (no shared species between periods – high dispersal- strong variation in eutrophication) (Fig. 4-1b).

iv. *High dispersal – low influence of eutrophication:* If dispersal is large and eutrophication is low or swamped by dispersal, all time periods should be homogeneous and the same few species highly capable of dispersing should dominate in all three areas (Fig. 4-1b). Low differences between areas (β-diversity) should be expected in this scenario. This scenario differs from (i) by the type of dominant species. That is, in this scenario dominant species should have high dispersal strategies rather than environmental tolerance strategies.

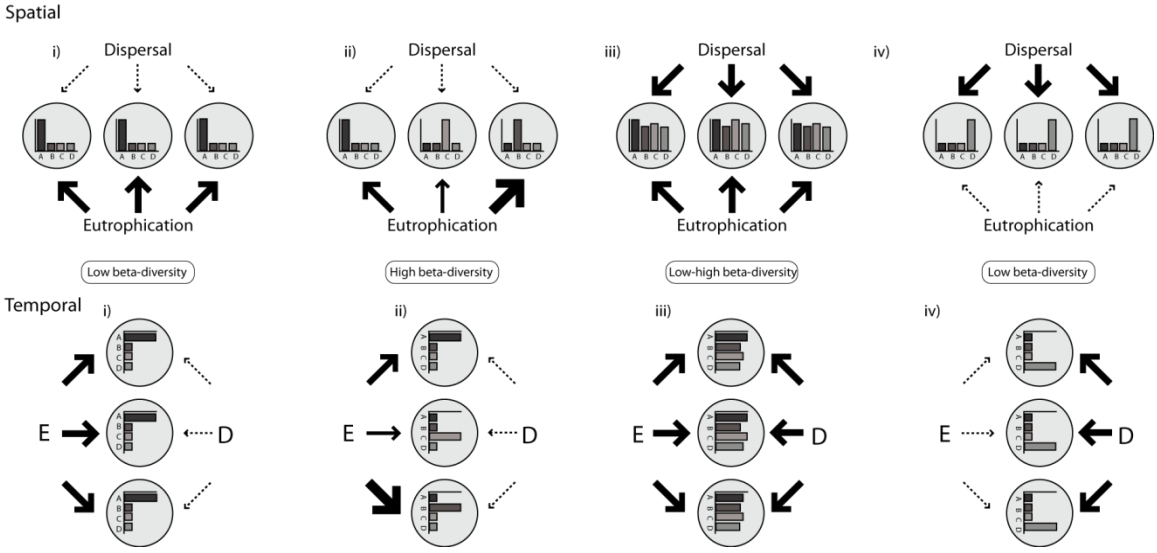

Figure 4-1. Predicted patterns in community dominance in response to eutrophication and dispersal strength at spatial (a) and temporal (b) scales. In this diagram, the lake species pool is of four species (A-D), but their relative abundances vary among patches. The strength of dispersal and eutrophication is represented by the width of the arrows (greater means stronger influence). For temporal scale eutrophication and dispersal terms are abbreviated by E and D respectively. Figure modified from Hillebrand et al. 2009.

4.3 Study site

Castle Lough is a small (surface area of 13 ha), shallow (5 m maximum depth), lowland (45 m above sea level) lake located in the Upper Lough Erne (ULE) system, Fermanagh Co, Northern Ireland (54°12'N, 007°37'W) (Fig. 2). It has a moderate annual mean total phosphorus (TP 29 μg L^{-1}) and mean total nitrogen (TN 1.03 mg L^{-}

^{1}) concentrations (Goldsmith et al. 2008) and is considered to be in "good" ecological condition but at risk due to the presence of the invasive zebra mussel *Dreissena polymorpha* Pallas (European Directive 2004). The lake has a distinctive river-like morphology with three distinctive basins. It is connected to the main ULE system, a highly connected system of shallow riverine lakes, to the south through the River Finn (Fig. 4-2).

Previous research and historical records provide evidence that over the last 150 years the ULE system has been subject to hydrological change and eutrophication processes that have influenced its ecology (Price 1890, Battarbee 1986, Gibson et al. 1995, Smith et al. 2005). Frequent flood events in the ULE catchment caused by high rainfall (63 mm day^{-1}) (Price 1890) and an inability of the River Erne to discharge the incoming water back to the sea (Cunningham 1992) led to a major drainage scheme in the ULE system (including Castle Lough's outflow) between 1880-1890. Water levels in the ULE dropped from around 48 to 46 m above sea level (Price 1890). Continuing flood events prompted a second attempt at water-level regulation under the Erne Drainage and Development Act (Northern Ireland) in the early 1950's. At this time 30 km of channel were dredged between the ULE system and the Lower Lough Erne system. Since this time water levels in the ULE system have been maintained between around 43-45 m (Mathers et al. 2002, Smith et al. 2005). Despite these efforts, the ULE system is still prone to major flood events (Cunningham 1992). A map reconstruction of 2009 floods shows how most satellite lakes, including Castle Lough, and the main ULEbecome a single large lake http://safer.emergencyresponse.eu).

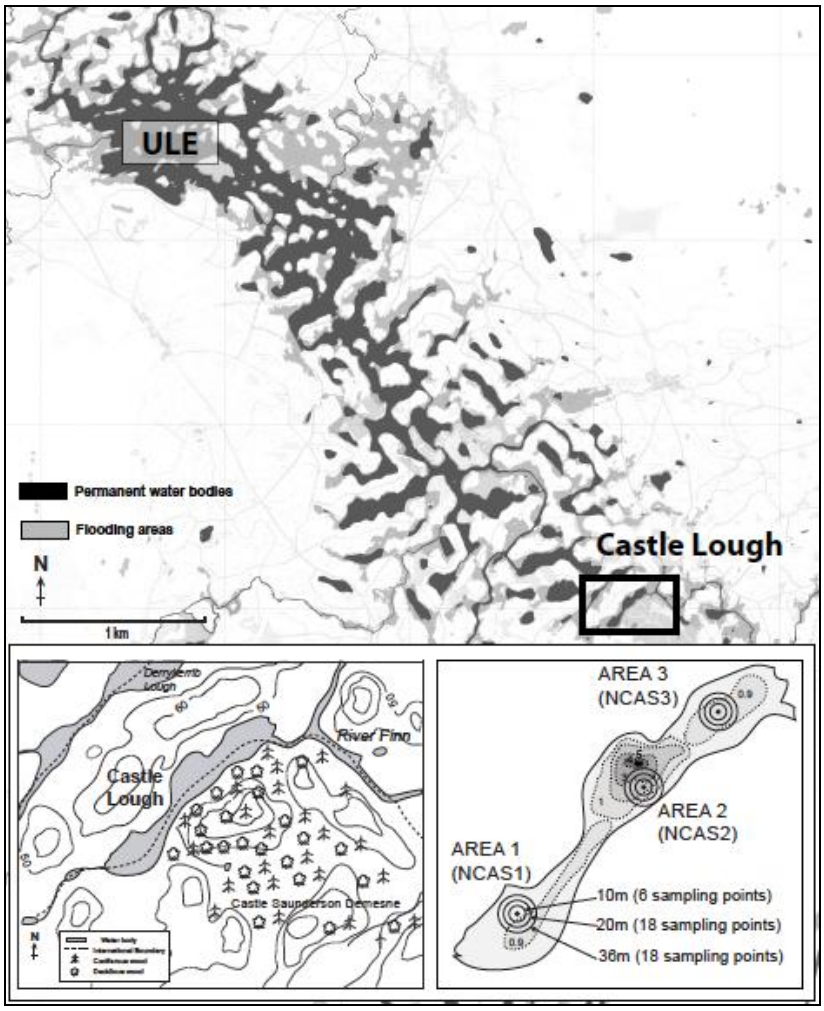

Figure 4-2. Location of Castle Lough. Contemporary sampling areas, number of sampling points per area and cores locations (Black circles) are indicated.

Diatom-based palaeolimnological studies in the ULE indicate a gradual acceleration of nutrient enrichment since the 1900's with a more pronounced phase of eutrophication after c. 1950 (Battarbee 1986, Gibson et al. 1995, Smith et al. 2005). Early nutrient enrichment (1900) of the ULE system is thought to be due to domestic effluent inputs after storm drains were introduced to local towns (Battarbee 1986). The acceleration of eutrophication in the 1950's likely resulted from the interaction of various factors including post-war agricultural intensification, increased sewage input, development of rural septic-tank sanitation and increased organic pollution from industry (Battarbee 1986).

4.4 Materials and methods

As dispersal rates are inherently difficult to measure, dispersal was inferred indirectly by quantifying species dominance patterns at different stages of eutrophication and by researching three different groups that differ in their dispersal mode: (1) "active" dispersers – chironomids; and (2) passive dispersers - submerged and floating-leaved macrophytes (henceforth referred to as macrophytes); and bryozoans, molluscs and cladocerans (henceforth referred to as invertebrates). Chironomids are commonly classified as passive dispersers (Armitage et al. 1997), however they can fly by themselves on a mean dispersal distance of around 500 m (Armitage et al. 1995, Delettre and Morvan 2008), and therefore put themselves actively into a position where wind currents can then passively disperse them in large numbers over longer distances (Nielsen and Nielsen 1962, Davies 1967, Armitage et al. 1995, Delettre and Morvan 2008). Furthermore, first-instar larvae of Orthocladiinae and Chironominae are vigorous swimmers that effect dispersal from the site of hatching (Armitage et al. 1995). These combined effects of planktonic and adult activities are predicted to confer greater dispersal than that achieved by the passively dispersing macrophytes and invertebrates examined in this study.

To characterise current macrophyte communities in Castle Lough, three circular areas (Area 1, Area 2 and Area 3; Fig. 4-2), each with a 30 m radius, were sampled. The areas were of a similar depth (1.5 m on average) and were located in each major basin of the lake. To ensure broad sampling, each area was divided into three sub-areas delimited by 10 m radii (Fig. 4-2). A total of 60 points per area were sampled, and, to ensure equivalent sampling of sub-areas, six points were surveyed from the innermost area, and 18 and 36 points for the successively larger sub-areas, respectively (see Fig. 4-2). Macrophyte density and composition were recorded for each point using the percentage volume infestation (PVI) system (Canfield et al. 1984). This entailed surveying macrophytes from a boat using a combination of grapnel sampling and visual observations made with an underwater viewe (bathyscope). At each point water depth, average plant height and the percentage cover of each species were measured for an estimated area of 1 m^2. PVI was calculated as:

PVI = (Percentage coverage of macrophytes X Average height of macrophytes) / Water depth

To characterise temporal changes in macrophytes, invertebrates and chironomids for each lake area, three sediment cores (NCAS 1, NCAS 2 and NCAS3) were collected in June 2008 from the centre of Area 1, Area 2 and Area 3 (Fig. 4-2) using a wide-bore (14 cm) "Big-Ben" piston corer (Patmore et al. in prep). Cores NCAS1, NCAS2 and NCAS3 were collected from water depths of 117 cm, 180 cm and 160 cm respectively and were extruded in the field at 1-cm intervals. Lithostratigraphic changes for the cores were recorded in the field.

Chronologies for each sediment core were established by radiometric dating. Sediment samples from each core were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay in the Bloomsbury Environment Institute at University College London (UCL), using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. ^{210}Pbwas determined via its gamma emissions at 46.5keV, and 226Ra by the 295keV and 352keV gamma rays emitted by its daughter isotope ^{214}Pb following storage for three weeks in sealed containers to allow radioactive equilibration. ^{137}Csand ^{241}Am were measured by their emissions at 662keV and 59.5keV. The absolute efficiencies of the detector were determined using calibrated sources and sediment samples of known activity (Appleby et al. 1986, 1992, Appleby 2001). Corrections were made for the effect of self-absorption of low energy gamma rays within the sample (Appleby et al. 1992). No attempt was made to date sediments beyond the range of the ^{210}Pb dating analyses as the focus of interest was the last 150 years. Dates were ascribed using the constant rate of supply (CRS) model (Appleby and Oldfield, 1978). The CRS model assumes a constant rate of supply of unsupported 210^{Pb}, no post-depositional mixing and a variable sediment accumulation rate.

Macrophyte assemblages were estimated using macrofossils; leaves, seeds, spines and a range of other vegetative fragments (Birks 2001). Bryozoan composition was characterised using statoblasts (dormant propagules) which have been shown to provide a reliable source of information on contemporary bryozoan abundances (Hartikainen et al. 2009). Cladoceran and molluscan compositions were determined using ephippial remains (Jeppesen et al. 2001) and whole shells, shell-fragments and

larvae (glochidia), respectively (Aldridge and Horne 1998, Ayres et al. 2008). Chironomid composition was estimated by counting larval head capsules which offer a consistent representation of extant larvae and are well-preserved in sediments (Brodersen and Lindegaard 1999). Macrofossil remains were identified to the lowest practicable taxonomic level (mostly genus or morphotype) and counted.

Twenty 1-cm slices were sampled from core NCAS1 (95 cm long), fourteen from core NCAS2 (85 cm long) and fifteen from core NCAS3 (95 cm long) core at a resolution of 1-5 cm depth intervals. The whole length of core NCAS1 was sampled while for NCAS2 and NCAS3 only the top 30 cm (c. 150 years) were studied. Sampling resolution was dictated by intrinsic sedimentation rates within each core (see results) as follows: every 2-3 cm over the uppermost 30 cm for core NCAS1 and every 10 cm onwards; every 1 cm for the upper 8 cm and every 3 cm below for NCAS2; between 1-3 cm for core NCAS3. All samples were disaggregated in 10% potassium hydroxide (KOH) before sieving.

Macrofossil analyses were performed using an adaptation of standard methods (Birks 2001, Davidson et al. 2005). Three sieves with different mesh sizes (355 µm, 125 µm and 90 µm) were used to separate macrofossil and chironomids remains (Brooks et al. 2007). Due to the high volume of sediment retained at 125 µm and 90 µm both samples were mixed after sieving to provide a total volume of 200 mL per core sample. Subsequently a subsample of 20 mL was analysed. Chironomid head-capsules were picked simultaneously with other macrofossils and a minimum of 50 head capsules enumerated in each sample (Heiri and Lotter 2001). Chironomid larval head-capsules were prepared using standard methods, mounted in Euparal and identified using Brooks et al. (2007). All macrofossil data were standardized as numbers of fossils per 100 cm^3 (raw and standardized data are provided in Appendix 1). The 125 µm and 90 µm subsamples (20 mL) were standardized first up to 200 mL and then to 100 cm^3. Macrofossils were identified by comparison with reference material held at the ECRC, UCL and the Natural History Museum, London and using relevant taxonomic keys (e.g. Birks 2001, Wood and Okamura 2005, Aldridge and Horne 1998, Preston 1995).

4.4.1 Data analysis

Evenness is the variability of a community attribute (e.g. relative abundances of individuals within a species or identity of species within a location) (Hillebrand et al. 2008). If communities are heterogeneous in composition, (i.e. many species represented by relatively similar number of individuals) there is high assemblage evenness (Fig. 4-1). In contrast, if community composition is homogenous (i.e. one or few species have many individuals, while other species have very few individuals), evenness is low (Fig. 4-1). As a consequence, any variation in compositional heterogeneity (evenness) among sampling units for a given area or period of time at a given spatial scale can be referred to as a measure of β-diversity (Anderson et al. 2006; Anderson et al. 2011).

As the experimental design of this study was based at two scales, space and time,two different classes of β-diversity were considered: (1) spatial β-diversity - defined as the variability in community compositional heterogeneity between sampling areas; (2) temporal β-diversity - measured as the variability in community compositional heterogeneity among defined time intervals (see below) within the three sediment cores.

To quantify changes in community compositional heterogeneity (evenness) over space and time, a combination of permutational analysis of multivariate dispersions (perMANOVA, Anderson 2001)and permutational multivariate analysis of variance (Anderson 2006, Anderson et al. 2006) was used. Due to the minimum number of samples required for these analyses ($n \geq 3$ samples; Anderson 2005) and to allow for comparisons between cores that differ in sedimentation rates, the macrofossil data were divided into three time series. Two time series were of approximately 50-years (c. present -1950 and c. 1950-1900) and a third comprised the remaining sediment samples beyond the radiometric dates (c. pre-1900).

Permutational multivariate analysis of variance (perMANOVA) is a non-parametric method for multivariate analysis of variance that compares variability of dissimilarity distances within groups versus variability among groups, using the ratio of the *F*-statistic. With this procedure larger values of *F* indicate greater compositional differences between groups, which in this case is attributed to the identities of species present among sampling units. For this analysis, each area and time interval were

treated as an independent group. Species dissimilarities were calculated using the Bray-Curtis dissimilarity index. Of many potential measures of dissimilarity, the Bray–Curtis has been shown to have one of the strongest relationships between site dissimilarity and ecological distance (Faith et al. 1987). Due to varying sedimentation rates in the three cores, pairwise permutation comparisons were calculated with strata, as suggested by Anderson (2005). Each core was nested within its respective location and permutation of residuals was calculated under a reduced model (4999 permutations) (Anderson 2001). PerMANOVA analyses were calculated using perMANOVA software version 1.6 (Anderson 2005). Owing to analytical requirements for equal numbers of samples for perMANOVA analysis (Anderson 2005), a set of 4 representative sediment samples per compositional phase were used.

Homogeneity in Multivariate Dispersions analysis (HMD) (Betadisper in R; R Core Development Team 2011) comprises a distance-based test of the homogeneity of multivariate dispersions among groups to their group centroid (Anderson 2006, Anderson et al. 2006). For this analysis each area and time interval for each core was treated as an independent group and species dissimilarities were calculated using the Bray-Curtis index of dissimilarity with a principal coordinate analysis (PCO) (Anderson 2006). To test if the variance between groups was significant, distances of group members to the group centroid were subject to nested pairwise comparisons using random permutation tests within each core (number of permutations = 4999) under the reduce model. HMD analysis generates a permutation distribution of F under the null hypothesis of no difference in dispersion between groups (i.e. no difference in relative abundance variability). The assumption here is that groups with a large multivariate dispersion will have a heterogeneous species composition (evenness) (Anderson 2006).

To test if varying sedimentation rates between cores influenced macrofossil abundances over time, the macrofossil data were examined in terms of flux (flux = sedimentation rate x macrofossil concentrations) by assuming a constant rate of sedimentation beyond the radiometric-dating limits. Flux relationships produced no change in quantitative results and therefore only macrofossil concentration data are reported here. As these analyses do not account for differences in sedimentation rates

within a core, they were conducted under the assumption of equivalent time periods per sample. The temporal scale is therefore relative rather than exact.

4.5 Results

4.5.1 Core chronologies and sedimentation rates

Radiometric chronologies for Cores NCAS1, NCAS2 and NCAS3 are given in Fig. 4-3. The final ^{210}Pb dates were calculated using the CRS model. For core NCAS1 the model placed c. 1950 and c. 1900 at 11 cm and 20 cm, respectively. Sedimentation rates based on the revised ^{210}Pb dates exhibited a fairly stable pattern with a mean of 0.032 g cm^{-2} yr^{-1} from the c. 1880s to the c.1980s and an increase over the last two decades at 0.05 g cm^{-2} yr^{-1}. For core NCAS2 c. 1950 was placed at 4 cm and c. 1900 at 7 cm. ^{210}Pb dating suggested a low sedimentation rate from the c.1870s to c. 1960 and a subsequent increase from post c. 1960 to the present day (0.036 g cm^{-2} yr^{-1}). For core NCAS3 c. 1950 and c. 1900 were placed at 6 cm and 16 cm. Two brief episodes of rapid sedimentation are suggested at c. 1917 and c. 1934. Excluding these episodes of rapid accumulation, the mean sedimentation rate during the past 70 years was 0.019 g cm^{-2} yr^{-1}.

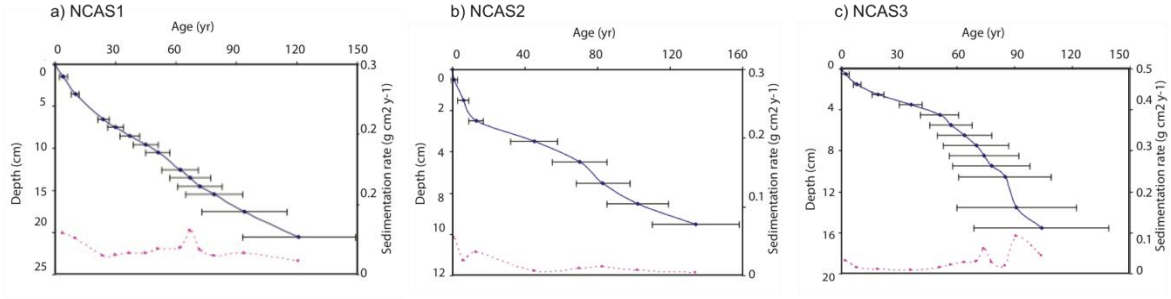

Figure 4-3. Radiometric chronology of cores NCAS1, NCAS2 and NCAS3 taken from Castle Lough, showing the CRS model 210Pb dates and sedimentation rates. The solid line shows age while the dashed line indicates sedimentation rate.

4.5.2 Temporal dynamics

Figures 4, 5 and 6 provide data on macrophyte, invertebrate and chironomid abundances of individual taxa respectively within the cores. For the c. pre-1900 period plant macrofossil data in all three cores demonstrated a prevalence of

bryophytes (including *Sphagnum* leaf remains). Subsequently, there was a predominance of *Apium inundatum* L.,*Alisma plantago-aquatica* L., *Ranunculus section Batrachium,Chara* spp. *Nitella* spp. *Najas flexilis* Willd., *Stratiotes aloides* L., and *Callitriche* remains. *Isoetes lacustris* L. was also observed in core NCAS3. Period c. 1950-1900 is characterised by the appearance of *Potamogeton praelongus* Wulfen., *Potamogeton obtusifolius* Mertens & Koch and *Myriophyllum* spp. and an increase in remains from floating-leaved species remains in c. present-1950 samples, including Nymphaeaceae and *Lemna trisulca* L..

The c. pre-1900 invertebrate (Fig. 4-5) and chironomid (Fig. 4-6) macrofossil assemblages were in general characterised by the bryozoans *Paludicella articulata* Gervais and *Plumatella fruticosa* Allman and the chironomid taxa *Tanypus, Protanypus, Orthocladius consobrinus, Stempellina, Tanytarsus pallidicornis,* and *Pseudochironomus*. Over this period most mollusc taxa were absent remains. Subsequently from c. 1950-1900 there was a prevalence of the bryozoan *Cristatella mucedo* Cuvier and the chironomid taxa, *Chironomus plumosus, Chironomus anthracinus* and *Microtendipes pedellus*. From c. 1950 to the present-day assemblages were characterised by bryozoans in the genus *Plumatella* sp. (but not *P.fruticosa*) and the molluscs *Bithynia tentaculata* L., *Pisidium* spp., *Anodonta cygnea* L. and *Dreissena polymorpha* Pallas. The chironomid taxa *Endochironomus albipennis, Dicrotendipes nervosus, Glyptotendipes pallens, Cricotopus,Tanytarsus mendax*and *Tanytarsus lugens* and the cladocerans *Daphnia* spp., and *Ceriodaphnia* spp., also showed high abundances. Over this period there was a strong decline in most of the species that were historically-recorded (c. pre-1900), especially the bryozoans *P.articulata, P. fruticosa* and the chironomids *Protanypus* and *O. consobrinus*.

perMANOVA analyses on macrophyte, invertebrate and chironomid macrofossils indicated that compositional heterogeneity attributed to the variation in the identity of species varied substantially between the different time intervals (*overall test P* = 0.0002 for all three groups; Table 4-1). Nested pair-wise comparison tests indicated significant differences in macrophyte compositional heterogeneity between all three-time periods for core NCAS1 and NCAS3 cores ($P < 0.05$) (Table 4-1). For core NCAS2 core the comparison between c. present-1950 vs. c. 1950-1900 was not significant. Nested pairwise comparisons of invertebrate assemblages demonstrated

significant differences in core NCAS1 for period c. present-1950 vs. c. pre-1900 ($P< 0.05$), and in cores NCAS2 and NCAS3 for present-1950 vs. c. pre-1900 and for c. 1950-1900 vs. c. pre-1900 ($P< 0.05$ respectively) (Table 4-1). The comparisons for chironomid assemblages for cores NCAS1 and NCAS2 were significant for periods c. present-1950 vs. c. 1950-1900 ($P< 0.05$), c. present-1950 vs. c. pre-1900 ($P< 0.05$) and for all three time period in NCAS3 ($P< 0.05$) (Table 4-1).

HMDanalysis of the plant macrofossils revealed a decline in community compositional heterogeneity (measured as the mean distance to centroid) with time for all three cores (Table 4-2). The overall test indicated that there was a significant influence of time in the variation of compositional heterogeneity attributed to species relative abundances (P = 0.00124) (Table 4-2). However, pairwise analyses were only significant for core NCAS1 for c. present-1950, 1950-1900 (P = 0.03) and for core NCAS2 for c. present-1950, pre-1900. The HMD analysis for invertebrates showed that compositional heterogeneity in cores NCAS1 and NCAS3 was equally high during c.present-1950 and c.pre-1900 but lower at c. 1950-1900 (Table 4-2). For core NCAS2 compositional heterogeneity declined with time. HMD tests on chironomid assemblages indicated a contrary pattern for cores NCAS1 and NCAS2 to those observed

Table 4-1. Results of perMANOVA analysis examining compositional heterogeneity of macrophyte, invertebrate and chironomid assemblages within and among three different areas of Castle Lough.

	Macrophytes					**Invertebrates**					**Chironomids**				
	Source	df	SS	MS	F	P	df	SS	MS	F	P	df	SS	MS	F	P
	Lo	2	17243.13	8621.56	11.62	0,0002	2	13664.15	6832.07	7.20	0.0002	2	11794.54	5897.27	9.30	0.0002
	Ti	2	24819.05	12409.52	16.73	0,0002	2	17649.10	8824.55	9.30	0.0002	2	10293.63	5146.80	8.11	0.0002
	LoxTi	4	20124.12	5031.03	6.78	0,0002	4	11206.58	2801.64	2.95	0.0004	4	7819.21	1954.80	3.08	0.0002
	Residual	27	20026.15	741.70			27	25616.40	948.75			27	17119.78	634.06		
	Total	35	82212.47				35	68136.25				35	47027.16			
Spatial dynamics pairwise comparison																
	Groups		t	P	Avg. dissim.		t	P	Avg. dissim			t	P	Avg. dissim		
c. present-1950	(NCAS1, NCAS2)		2.041	0.033	40,77		2.738	0.033	60.58			1.9044	0.033*	38.43		
	(NCAS1, NCAS3)		1.716	0.062	40,01		2.069	0.029	66.44			2.3927	0.029*	25.85		
	(NCAS2, NCAS3)		2.322	0.028	29,63		1.998	0.028	42.88			1.8188	0.028*	27.84		
c. 1950-1900	(NCAS1, NCAS2)		2.600	0.033	73,39		1.559	0.121	41.51			1.6195	0.033*	47.69		
	(NCAS1, NCAS3)		2.657	0.026	69,02		3.365	0.026	64.22			1.8917	0.026*	56.01		
	(NCAS2, NCAS3)		5.484	0.030	75,21		2.821	0.030	58.98			1.6888	0.030*	44.08		
c.pre-1900	(NCAS1, NCAS2)		2.357	0.030	67.09		1.318	0.175	55.14			1.3099	0.118	41.57		
	(NCAS1, NCAS3)		3.281	0.030	83.98		1.973	0.056	52.22			3.8847	0.030*	68.6		
	(NCAS2, NCAS3)		3.272	0.029	76.13		1.516	0.108	55.57			3.3694	0.029*	65.9		
Temporal dynamics pairwise comparison																
NCAS1	Average dissimilarities						Average dissimilarities					Average dissimilarities				
	(present-1950)	38.48					(present-1950)	49.73				(present-1950)	31.78			
	(1950-1900)	54.67					(1950-1900)	34.78				(1950-1900)	46.16			
	(pre-1900)	48.72					(pre-1900)	51.41				(pre-1900)	35.89			
	Groups		t	P	Avg. dissim.		t	P	Avg. dissim			t	P	Avg. dissim		
	(present-1950, 1950-1900)		2.698	0.033	78.88		1.886	0.033	56.32			1.5115	0.062	45.69		
	(present-1950, pre-1900)		3.925	0.029	97.20		1.346	0.252	56.33			2.5003	0.029*	53.21		
	(1950-1900, pre-1900)		2.241	0.028	75.09		1.012	0.360	44.07			1.3918	0.115	46.45		
NCAS2	Average dissimilarities						Average dissimilarities					Average dissimilarities				
	(present-1950)	15.36					(present-1950)	15.82				(present-1950)	25.85			
	(1950-1900)	29.57					(1950-1900)	36.58				(1950-1900)	29.56			
	(pre-1900)	40.83					(pre-1900)	52.24				(pre-1900)	40.58			
	Groups		t	P	Avg. dissim.		t	P	Avg. dissim			t	P	Avg. dissim		
	(present-1950, 1950-1900)		0.887	0.468	22.75		3.237	0.033	53.21			2.2371	0.034*	40.78		
	(present-1950, pre-1900)		4.685	0.026	80.47		3.816	0.026	82.22			2.6205	0.026*	54.51		
	(1950-1900, pre-1900)		3.776	0.030	77.05		1.819	0.061	55.03			1.6104	0.065	43.03		
NCAS3	Average dissimilarities						Average dissimilarities					Average dissimilarities				
	(present-1950)	22.53					(present-1950)	44.52				(present-1950)	27.84			
	(1950-1900)	18.13					(1950-1900)	30.14				(1950-1900)	39.05			
	(pre-1900)	35.35					(pre-1900)	43.89				(pre-1900)	25.86			
	Groups		t	P	Avg. dissim.		t	P	Avg. dissim			t	P	Avg. dissim		
	(present-1950, 1950-1900)		4.767	0.030	55.27		2.3677	0.0300	56.36			2.4903	0.030*	52.69		
	(present-1950, pre-1900)		2.218	0.030	46.38		2.7682	0.0304	75.14			3.6923	0.030*	56.45		
	(1950-1900, pre-1900)		2.982	0.029	53.18		2.0258	0.0580	54.34			1.9568	0.029*	44.44		

Table 4-2. Results of HMD analysis examining compositional heterogeneity of macrophyte, invertebrate and chironomid assemblages within and among three different areas of Castle Lough.

	Macrophytes			**Invertebrates**			**Chironomids**		
Test statistic	P-val method	F	P	P-val method	F	P	P-val method	F	P
Devs from centroids	ANOVA tables	4.60	0.001	ANOVA tables	3.75	0.004	ANOVA tables	1.61365	0.16740
	Perm LS residuals		0.047	Perm LS residuals		0.0446	Perm LS residuals		0.52940
Spatial dynamics pairwise comparisons									
C. present-1950	t	P		t	P				
(NCAS1, NCAS2)	3.027	0.090		5.714	0.030*				
(NCAS1, NCAS3)	1.837	0.192		0.735	0.484				
(NCAS2, NCAS3)	0.924	0.425		6.510	0.032*				
c. 1950-1900									
(NCAS1, NCAS2)	3.289	0.031*		0.106	1.000				
(NCAS1, NCAS3)	4.246	0.028*		0.536	0.696				
(NCAS2, NCAS3)	0.789	0.432		0.525	0.758				
c.pre-1900									
(NCAS1, NCAS2)	0.720	0.515		0.037	0.912				
(NCAS1, NCAS3)	0.885	0.570		0.817	0.492				
(NCAS2, NCAS3)	0.361	0.882		1.091	0.401				
Temporal dynamics pairwise comparisons									
NCAS1	t	P		t	P				
(present-1950, 1950-1900)	2.247	0.030*		1.966	0.248				
(present-1950, pre-1900)	0.931	0.596		0.144	0.944				
(1950-1900, pre-1900)	1.096	0.339		1.734	0.219				
NCAS2									
(present-1950, 1950-1900)	1.798	0.139		1.792	0.168				
(present-1950, pre-1900)	3.373	0.055		7.408	0.023*				
(1950-1900, pre-1900)	1.261	0.273		1.539	0.245				
NCAS3									
(present-1950, 1950-1900)	0.605	0.629		2.455	0.028*				
(present-1950, pre-1900)	1.164	0.600		0.412	0.751				
(1950-1900, pre-1900)	1.664	0.420		1.443	0.294				
Average distances to centroid									
NCAS1	Average	SE		Average	SE				
present-1950	23.86155	3.94051		31.48693	3.03072				
1950-1900	35.54958	3.39308		21.07025	4.34495				
pre-1900	29.40587	4.46098		32.30668	4.80514				
NCAS2									
present-1950	9.36209	2.72174		9.49951	2.37055				
1950-1900	18.14931	4.05863		21.90078	6.50045				
pre-1900	25.17581	3.81710		32.35687	1.97464				
NCAS3									
present-1950	13.72844	3.85872		28.89229	1.80327				
1950-1900	10.90617	2.60875		17.85639	4.11719				
pre-1900	22.46747	6.43833		26.83225	4.66075				

for invertebrates with compositional heterogeneity being highest at c. 1950-1900. Again for core NCAS2 compositional heterogeneity declined with time.

4.5.3 Spatial dynamics

Contemporary macrophyte assemblages revealed substantial spatial variation in compositional heterogeneity between the three areas (perMANOVA: $P = 0.002$ for all cases, Table 4-1). HMD analysis showed that Area 2 was significantly more

heterogeneous than the other two areas (P = 0.002 for comparisons with Areas 1 and 2, respectively) (Table 4-2). Area 2 presented the greatest distance to centroid (80.99), followed by Area 1 (63.17) and Area 3 (61.14) (Table 4-2 and Fig. 4-7).

In Area 1, 13 species were recorded (Fig. 4-7). This area was fully covered by submerged macrophytes (99% of plant coverage) and species PVI values ranged between 0 and 50 (Fig. 4-7). More than 50% of the points sampled contained five or more species, the most abundant being *Elodea canadensis* Michx., *Nuphar lutea* (L.) Sm., *Sparganium emersum* Rehmann and *L. trisulca* Other species, e.g. *Chara* sp., *Myriophyllum verticillatum* L., *S. aloides*, *Sagittaria sagittifolia* L. and *Utricularia vulgaris* L., showed patchier distributions and intermediate PVI values (Fig. 4-7). Species such as *Callitriche* sp., *Nitellaflexilis* L. and *P. obtusifolius* were recorded at a few points only and had even patchier distributions and very low PVI values (Fig. 4-7).

In Area 2, 10 species were recorded and lower macrophyte coverage (83%) was observed. PVI values ranged from 0-45% while 5 or more specieswere recorded in around 40% of the sampling points. As in Area 1, *S. emersum* L., *N. lutea,E. canadensis* and *L. trisulca* were the most abundant species. Filamentous algae (undifferentiated) were recorded in a moderate number of points. *S. sagittifolia* presented the highest recorded PVI value (32%) for the area but its occurrence was very patchy. *Nitellaflexilis*, *U. vulgaris* and *Callitriche* sp. were observed in a few samples and had very low PVI values. *Chara* sp., *M. verticillatum* and *P. obtusifolius* were absent.

Area 3 contained 12 species and had macrophyte coverage of 96%. PVI values ranged from 0-37% and more than 50% of the sites had 5 or more species. *S. emersum*, *N. lutea*, *E. canadensis*, *S. sagittifolia* and filamentous algae were the most commonly recorded species. *L. trisulca*, *U. vulgaris* and *P. praelongus* were patchily distributed and their PVI values ranged from 1-27%. *S. aloides,P. obtusifolius* and *Chara* sp. were rare and *M. verticillatum* and *Callitriche* sp. were absent.

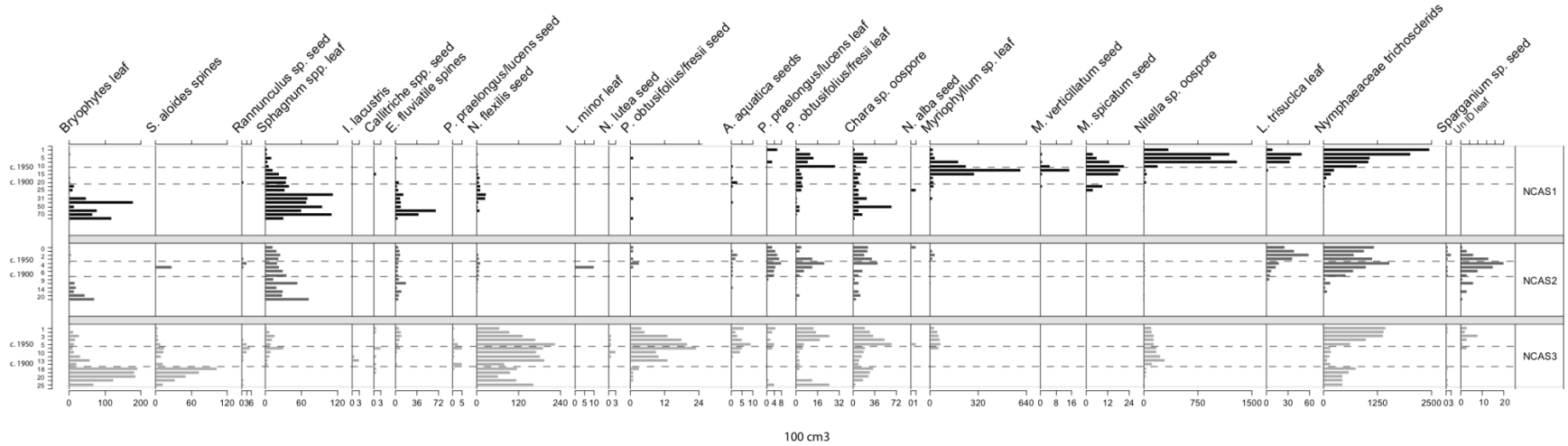

Figure 4-4. Plant-macrofossil stratigraphies for cores NCAS1, NCAS2 and NCAS3. Zones correspond to c. present-1950, c. 1950-1900 and c. pre-1900.

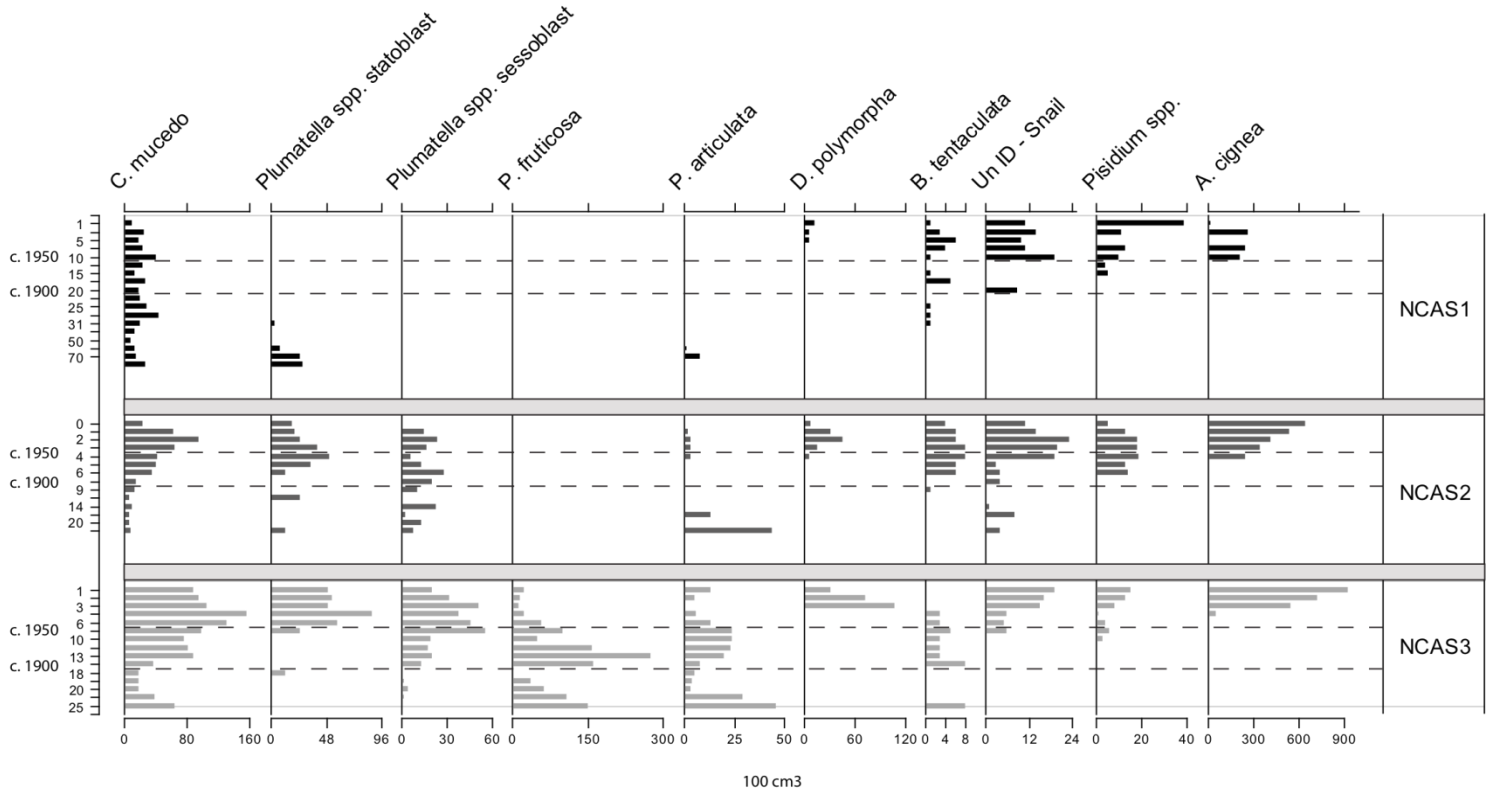

Figure 4-5. Invertebrate-macrofossil stratigraphies for cores NCAS1, NCAS2 and NCAS3. Zones correspond to c. present-1950, c. 1950-1900 and c. pre-1900.

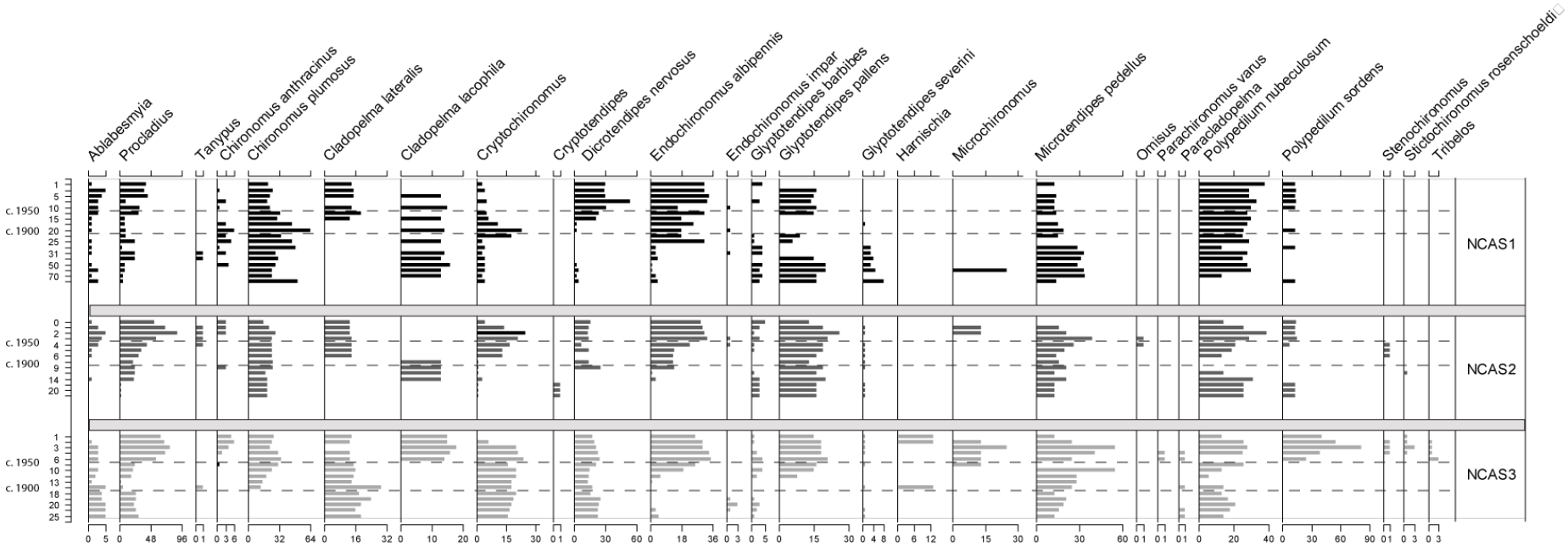

Figure 4-6. Chironomid-macrofossil stratigraphies for cores NCAS1, NCAS2 and NCAS3. Zones correspond to c. present-1950, c. 1950-1900 and c. pre-1900.

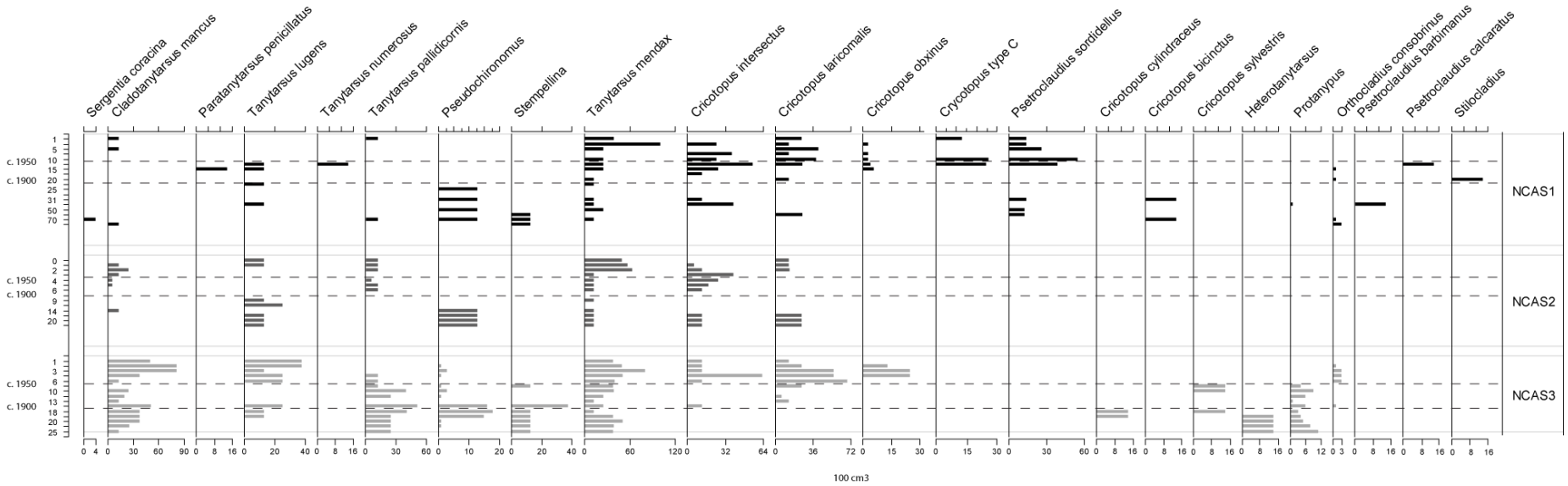

Figure 4-6. Continuation

PerMANOVA analyses of palaeo-data provided a similar picture to that revealed by analyses of contemporary data. The compositional heterogeneity attributed to the variation in the identity of species of macrophyte, invertebrate and chironomid assemblages between areas were significantly different in most cases for c. present-1950 (Table 4-1). The only exception was for macrophyte assemblages between NCAS1 and NCAS2 cores (P = 0.06). Pair-wise comparisons for the other two periods (c. 1950 and c. pre-1900) showed that these differences declined for most cases with time among all three biological groups (Table 4-1). HMD pair-wise analysis for macrophytes revealed significant differences between cores NCAS1 and NCAS2 for c. present-1950 and for cores NCAS1 and NCAS2 and cores NCAS1 and NCAS3 for c. 1950-1900. The analyses on invertebrates revealed that NCAS2 was different from both NCAS1 and NCAS3 for c. present-1950. Pairwise comparisons for chironomid assemblages did not show any differences in compositional heterogeneity attributable to variation in relative abundances between areas among all three-time periods (Table 4-2).

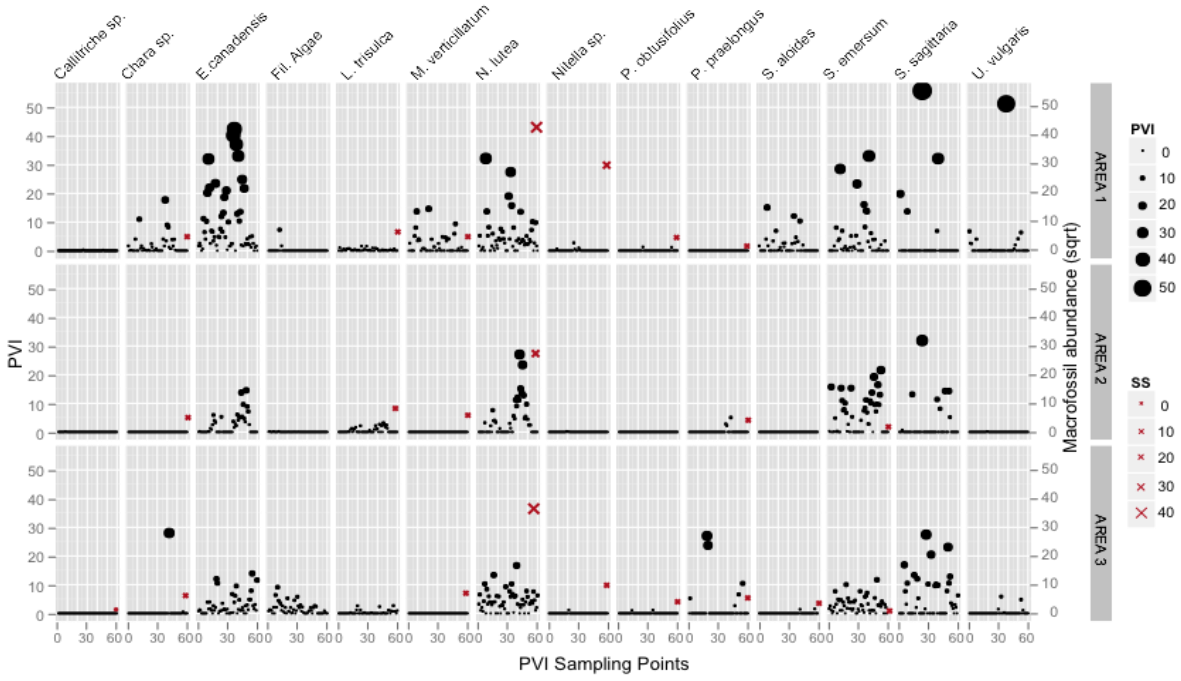

Figure 4-7. Macrophyte PVI data and surface sediment plant macrofossil data at Area 1, Area 2 and Area 3. Macrofossil data is square-root transformed.

4.6 Discussion

4.6.1 Temporal assembly dynamics

The goal of this study was to evaluate the effects of eutrophication and dispersal in dictating community evenness. Based on knowledge of eutrophication and metacommunity theory, a set of initial predictions was made about the possible patterns that should emerge according to the strength of influence of eutrophication and/or dispersal (Fig. 4-1). The data strongly support the view hat the best scenario to describe temporal community change in Castle Lough is through a combination of two predictions, low dispersal – high influence of a variable eutrophication (temporal prediction ii) and high dispersal – high influence of eutrophication (temporal prediction iii) (Fig. 4-1). Three lines of evidence were revealed from the analyses that support this combination of predictions at the temporal scale: (1) HMD analyses provide evidence for change from historically (c. pre1900) heterogeneous communities (temporal prediction iii) to more homogenous (dominated by few species) assemblages in the present day (temporal prediction ii)(Table 4-2); (2) perMANOVA analyses indicated that temporal β-diversity (differences in the variation in the identity of species between periods), increased significantly over time (prediction ii) (Table 4-1); and (3) despite an increase in dominance of competitive taxa adapted to nutrient-rich conditions over time, both contemporary and palaeolimnological data showed that extinctions have been rare and most of the species found historically still persist (prediction iii). As discussed next, these changes are consistent with transitions that would be expected as a result of increasing eutrophication (temporal environmental heterogeneity) and high dispersal.

4.6.2 Evidence for change in trophic status and dominance

Time series analyses of palaeo-data revealed that c. pre-1900 Castle Lough was characterised by having a community associated with mesotrophic conditions. In support of this *Najas flexilis,I. lacustris, P. praelongus/lucens,Chara* spp., and *S. aloides* were found abundantly in the cores c. pre-1900 samples. These species have been reported to grow vigorously at low to intermediate nutrient levels (Spence 1967, Carpenter and Titus 1984, Arts 2002, Sand-Jensen et al. 2008). Likewise the

chironomids present during this period, including *Stempellina*, *Pseudochironomus*, *O. consobrinus* and *Protanypus*,have been reported to inhabit low nutrient environments (Brodersen and Lindeegard 1999, Armitage 1995, Kansanen, 1985, Brundin 1949, Brodin 1982, Brodin 1986, Pinder and Reiss 1983, Brooks et al. 2007). Further evidence comes from two other key fossil invertebrates, the bryozoans *Plumatella fruticosa* and *Paludicella articulate*, both of which are noted to occur in oligo-mesotrophic conditions (Økland and Økland 2000, Wood and Okamura 2005).

Following this historical phase (c. pre-1900), characterised by heterogeneous local assemblages comprised of taxa associated with low nutrient environments, the macrophyte, invertebrate and chironomid assemblages converged towards those associated with meso-eutrophic conditions. For instance, macrophyte species, like *Nitella* spp., *L. trisulca* and Nymphaeaceae, increased considerably in numbers while abundances of bryophytes, *S. aloides* and *I. lacustris* declined noticeably. Furthermore, *Myriophyllum* sp. (probably *M. verticillatum*), which is generally observed at the transition between moderate and very high nutrient levels (e.g. Arts 2002, Smolders et al. 2003,Sand-Jensen et al. 2008, Salgado et al. 2010, Davidson et al. 2011), also increased in abundance during this period. These changes were accompanied by strong declines in the abundances of statoblasts from the bryozoans *P. articulata* and *P. fruticosa* statoblasts and an increase in abundances of other species within the genus *Plumatella*. Hartikainen et al. (2009) have shown that *Plumatella* statoblast abundances are positively correlated with high nutrient concentrations. The increase in the relative abundances of the chironomids, *E. albipennis, D. nervosus, G. pallens* and *Cricotopus* along with an abrupt decline in the chironomids *Stempellina*, *Pseudochironomus, O. consobrinus* and *Protanypus* brings further evidence of change towards a more nutrient-rich environment (Brodersen et al. 2001).

4.6.3 Evidence for dispersal over time

In this study dispersal was inferred indirectly from two sources: (1) the responses of actively dispersing (chironomids) and passively dispersing (macrophyte and invertebrates) taxa; and (2) patterns in species dominance and co-occurrences under different trophic conditions. Within this framework, the contemporary and palaeo-data from all three areas indicates two trends consistent with an influence of dispersal.

First extinctions have been rare and most of the species of both actively and passively dispersing groups found historically are still persisting among the areas. Metacommunity theory predicts that this pattern is expected at intermediate levels of dispersal, where competitively dominant species are widespread in response to environmental change but rare species co-exist in lower abundances through emigration (Loreau and Mouquet 1999, Mouquet 2003). Second, HMD analysis showed that compositional heterogeneity of macrophyte and invertebrate communities varied significantly over time (high temporal β-diversity between c. present-1950 and c. pre-1900) whilst for chironomids no significant differences between time periods were observed (Table 4-2). These trends concur with prediction (ii and iii) (see introduction and Fig.1).

4.6.4 Spatial assembly dynamics

In addition to a decline in compositional heterogeneity over time in each area, the contemporary and palaeo-data revealed that c. pre-1900 assemblages between areas changed from a high dispersal – high influence of eutrophication scenario (spatial prediction iii) towards a low-dispersal – high influence of a variable eutrophication (spatial prediction ii) scenario by c. 1950 -present (Fig. 4-1). This was supported by perMANOVA and HMD analyses that indicated that c. pre-1900 spatial β-diversity was low (spatial prediction iii) but increased over time (spatial prediction ii). These trends revealed two key aspects about the development of within-lake communities in response to environmental and dispersal processes that support the notion of a continuum of "sub-metacommunities" (*sensu* Leibold and Norberg 2004) within small shallow vegetated lakes in metacommunity landscapes.

The low spatial β-diversity of c. pre-1900 assemblages indicates that either environmental conditions other than nutrient concentrations (e.g. substrate type) were probably homogeneous or that dispersal would have been greater and acted as a homogenising vector within the lake (prediction iv; Fig. 4-1). Within this framework, the first scenario is less likely as substrate types tends to vary naturally in low-nutrient temperate lakes (Spence 1967, Spence 1982). On the other hand, c. pre-1900 flood events were large and highly frequent among the ULE system (Price 1890), which would have promoted large dispersal events between neighbouring lakes.

The increase in spatial β-diversity over time indicates that either the impact of eutrophication was different over time between areas (spatial prediction ii; Fig. 4-1), or that the impact of eutrophication was more even across the lake but dispersal would also have influenced assemblages through species sorting and sink-source dynamics (prediction ii + iii; Fig. 4-1). The first scenario is unlikely as the sedimentary analysis of the biota indicates parallel changes in community structure over time in the three cores. As discussed in the following section, the low extinctions in all three cores over time and the variation in relative abundances of some species between the cores suggest instead a joint influence of eutrophication and dispersal through source-sink dynamics.

4.6.5 Source-sink dynamics and 'sub-metacommunities'

The increase in spatial β-diversity over time and the fact that extinctions have been rare and that most species found historically still persist indicates that community assembly between areas might have been driven by dispersal through sink-source dynamics. In the absence of dispersal, competitive species are likely to dominate rapidly and competitive inferiors will be prone to extinction (Holyoaks et al. 2005, Hillebrand et al. 2008). However, between-patch dispersal may promote the persistence of rare species if populations receive immigrants from neighbouring high abundance patches (source–sink dynamics) (Chesson 2000, Hoopes et al. 2005, Mouquet 2003). Chapters 2 and 3 provided evidence that connectivity plays a key role in structuring the communities of the satellite lakes in the ULE system, including Castle Lough. The presence of species less well-adapted to eutrophic conditions may therefore be attributed to regional immigration processes over time from other lakes in the system.

The significant differences in compositional heterogeneity between areas revealed by perMANOVA analyses over time suggest, however, that source-sink dynamics may also pertain within the lake. For example, *Myriophyllum* sp. was abundant only in core NCAS1 (source) between the late c.1800s and c.1930. After the c.1930s it occurred more frequently in the other two cores while numbers in core NCAS1 declined (c. present-1950) (Fig. 4-5). Similarly, *Najas flexilis* was consistently abundant in Area 3 (source) at the same time as numbers declined considerably in Area 1 (sink) and remained constant in Area 2 (Fig. 4-5). The bryozoan *P. articulata*

presents another example, being common before c.1900 in all three cores but almost disappearing from cores NCAS1 and NCAS2 (sink) after the 1900s while persisting in relatively high numbers in NCAS3 (source) (Fig. 4-6). Bryozoans in the genus *Plumatella* were also entirely absent from core NCAS1 but were common (apart from *P. fruticosa*) in cores NCAS2 and NCAS3 after 1950. Finally, results from the contemporary macrophyte surveys are consistent with a species source-sink dynamic distribution as less competitive species like *S. aloides*, *M. verticillatum* and *P. praelongus* were recorded growing abundantly in some areas but were absent or poorly represented in others (Fig. 4-8). These trends indicate therefore, that different areas of the lake could harbour population "reservoirs" that help to sustain viable populations over time through within-lake dispersal events (Leibold and Norberg 2004).

4.6.6 Ecological implications of change in dominance structure

The results of this study support the idea that alteration of biotic communities by major anthropogenic stressors not only alters the number of species or composition assemblages, but also variability in their relative abundances and thus in dominance or evenness (e.g. Donohue et al. 2009, Hillebrand et al. 2008). More importantly this present study suggests that in human-altered metacommunity landscapes, changes in evenness might be prone to occur more rapidly than changes in species richness.

The increase in dominance of few groups, has profound implications for ecosystem function (Hillebrand et al. 2008, Wittebolle et al. 2009) includingchanges in community resistance (capacity to resist stress) and resilience (capacity to overcome stress) and species-invasion processes. For example, in aquatic microcosm experiments Steiner et al. (2006) showed that the resilience of algal communities following a perturbation increased with increasing dominance of a few species while resistance increased with evenness. Similarly Engelhardt and Kadlec (2001a,b) concluded that resistance of wetland macrophyte communities was mediated by diversity, whereas resilience was determined by the characteristics of the best competitor and the most productive species. The presence of low resistance-to-disturbance species, overall, decreases system resilience whereas high numbers of a disturbance-tolerant species may increase resilience. On the other hand, planted

grassland manipulation experiments suggest that invasion of grasslands decreased with increasing evenness (e.g. Wilsey and Polley 2002, Smith et al. 2004).

4.6.7 Constraints and caveats

There are methodological limitations to this study that should be taken into account when interpreting the results. The use of palaeolimnological data to infer past communities has some limitations. Due to taphonomy and a strong likelihood of rare taxa not being represented in the samples, especially when they grow far from the core site, not all historically-present species will leave remains in a sediment core. Closely associated therewith is the reflection of actual plant abundance from macrofossil data. Plant-macrofossil abundances come from an array of different sources (spines, leave fragments and seeds), which are difficult to interpret in a reliable single abundance way. Fortunately most of these issues are probably of little importance as around 60% of the current macrophyte species were recorded in the most-recent sediment samples (1-5 cm) from Castle Lough and surface sediments from all three cores recorded the dominance of floating-leaved species and the lower co-occurrence of species less well-adapted to enrichment conditions such as *P. praelongus* and *Myriophyllumverticillatum* as is characteristic of the current day (Fig. 4-8). In addition, the permutational analyses of sediment samples were also consistent with the contemporary surveys in identifying key differences in compositional heterogeneity between the three areas. Finally, the observed trends of change in dominance and species composition presented in this study, strongly coincides with what previous research on contemporary and historical monitoring data spanning a similar time period (last c. 100 years) and eutrophication history have shown for lakes and streams in Denmark (Riis and Sand-Jensen 2001, Sand-Jensen et al. 2008).

Another taphonomic caveat is the assumption that macrofossils are indicative of local (core-site) environments. This relationship has been demonstrated by previous work on macrophyte macrofossils in shallow lakes (Zhao et al. 2006). For the purposes of this study, the remains in each core sample were therefore assumed to be representative of the local community present at the time in each sampling area. It is also likely that the macrofossil record either over- or under-represented some taxa (e.g. Davidson et al. 2005). The importance of these issues was reduced through the use of c. 50-year time-series intervals, which helps to average out any possible effects

of spatial and short-term variation. Also notable is that, although macrophyte contemporary data was at higher taxonomic resolution, the sedimentary record provided evidence of taxa previously unrecorded in the lake (e.g. *N. flexilis* and *I. lacustris*).

A further methodological limitation is the lack of data on historical environmental variables (other than eutrophication, changing water-levels and connectivity), which may have played a role in structuring the community over space and time. Nonetheless it is strongly suspected that eutrophication, changing water-levels and connectivity were key drivers of community change in the ULE system (see Chapter 5).

4.7 Conclusions

By combining contemporary community data with a multi-taxon palaeoecological record from three areas of a shallow lake and testing a series of predictions, this study reveals four key aspects of how species evenness may have been influenced at the patch scale and at the lake scale by eutrophication and dispersal.

First, analysis of temporal assembly dynamics revealed that at the patch-scale (at each area) communities in Castle Lough changed from historically (c. pre-1900) heterogeneous (even with no dominant species) communities to more homogeneous (dominated by few species) assemblages in the present day. This was accompanied by an increase in temporal β-diversity and little extinction over time. These trends are consistent with transitions that would be expected as a result of dispersal and increasing eutrophication and are thus best described by a combination of low dispersal – high influence of a variable eutrophication and high dispersal – high variable eutrophication scenarios (Fig. 4-1).

Second, spatial assembly dynamics revealed that assemblages between areas changed from c. pre-1900 heterogeneous assemblages at the lake-scale with low spatial β-diversity to a relative dominance at the patch-scale and high spatial β-diversity by c. 1950-present (Fig. 4-1). The increase in differences between areas (spatial β-

diversity) over time suggest that either eutrophication developed differentially between the areas within the lake and promoted spatial environmental heterogeneity and species-sorting processes between areas, or a more likely jointly increasing influence of dispersal and eutrophication. These trends support the notion of a continuum of "sub-metacommunities" (*sensu* Leibold and Norberg 2004) within small shallow vegetated lakes in metacommunity landscapes.

Third, the high spatial β-diversity and the rare extinction over time suggest that community assembly between areas might have been driven by within-lake sink-source dynamics. This indicates that different areas of a shallow lake could harbour population "reservoirs" that help to sustain viable populations over time through within-lake dispersal events (Leibold and Norberg 2004). It also provides further indications that dispersal is likely to have a complex relationship with scale and thus a simple assignment to two scales (local and regional) in metacommunity theory may be an oversimplification (Cadotte and Fukami 2005).

Fourth, well-connected hydrosystems may be viewed as a hierarchical nested system, in which water bodies have different embeded areas; a locality (e.g. flood-plains) a series of water bodies and a region (e.g. a river catchment) a series of localities (Amoros and Bornette 2002, Ward et al. 1999). This nested hierarchy, in which one scale becomes the within-scale unit at the next highest scale (Amoros and Bornette 2002) permits the inference of processes across progressive scales into those at the next higher scale. Hence, the observed patterns from this study can be used as a model to understand regional processes in metacommunity landscapes.

This study demonstrates that despite a number of caveats in the fossil-record, palaeoecological techniques can provide a unique and reliable opportunity to track the local development of communities over decadal scales, a timeframe that is usually neglected by most current metacommunity studies. This study also suggests that in human-altered metacommunity landscapes, changes in evenness may occur more rapidly than changes in species richness. Therefore, concentrating exclusively on changes in species richness may limit our understanding of structure and function in ecosystems. Acknowledging that changes in both species richness and evenness may be signals of stress due to human impacts is imperative for meaningful conservation and restoration strategies.

5 Chapter 5 – Long-term changes linked with eutrophication and connectivity in a metacommunity system

5.1 Abstract

Riverine systems and their associated flood-plains and lakes comprise dynamic, hydrologically-connected landscapes. However, as for many other freshwater systems, the ecological integrity and biodiversity of these ecosystems is threatened by eutrophication. By using a multi-proxy, multi-lake palaeoecological approach, this study demonstrates that the Upper Lough Erne shallow lake system in Northern Ireland (UK) is far from its pre-industrial oligotrophic-mesotrophic ecological condition. Three relatively distinct phases that corresponded to c. pre-1900 (oligo-mesotrophic assemblages), to c. 1950-1900 (meso-eutrophic assemblages) and to c. present-day-1950 (eutrophic assemblages) were inferred from the long-term dynamics of passively (macrophytes and invertebrates) and actively (chironomids**)** dispersing organisms in the cores. These phases reflected a progressive increase in eutrophication since the early 1900s and to two hydrological dredging schemes that occurred at the end of the 1800s and 1950s. The data also revealed that within-lake compositional heterogeneity declined with eutrophication, while regional β-diversity attributable to within-lake variation in the identity of species increased. These findings accord well with previous studies that have found a decrease in the compositional variability of organisms within and between eutrophic lakes and bring new evidence of the homogenising effects of eutrophication at the local and regional scale. By incorporating metacommunity theory, this study also provides evidence that hydrological connectedness has buffered the effects of eutrophication and maintained local diversity over time via species re-introductions. These results have profound implications for the conservation and management of the ULE system and shallow lakes more generally as it shows that high connectivity may to some extent buffer the pervasive effects of nutrient-enrichment.

5.2 Introduction

Riverine systems and their associated flood-plains and lakes comprise dynamic hydrologically-connected landscapes in which water flow plays a key role in effecting connectivity (Amoros and Bornette 2002, Junk et al. 1989, Ward 1998). This hydrological connectivity represents a homogenising force at the landscape level, which, at intermediate levels of dispersal, reduces between-water body diversity (ß-diversity) and enhances within-water body diversity (α-diversity) (Amoros and Bornette 2002).

Research on the relationship between hydrological connectivity and α and β -diversity (e.g. Salo et al. 1986, Bornette et al. 2010, Ward et al. 1999) has identified four influential features associated with the landscape: (1) the distance between water bodies; (2) the presence of permanent versus temporary connections amongst water bodies; (3) the sizes and shapes of water bodies; and (4) the environmental characteristics of the water bodies. Distances between and temporal connectivity amongst patches (isolation) will influence dispersal rates (Holyoak et al. 2005) while variation in dispersal will determine regional persistence (Hanski 1999), the strength of interspecific interactions (Amarasekare 2003) and local and regional species diversity (Cadotte 2006a). The relationship between area and species richness is probably one of the few general laws of ecology (Lawton 1999) and a weight of evidence and theory demonstrates that species diversity increases as area increases (MacArthur and Wilson 1967, Rosenzweig 1995). On the other hand, environmental characteristics of water bodies also determine local population dynamics and may effect species sorting according to taxon environmental optima (Leibold and Norberg 2004, Cottenie 2005).

The degree to which landscape-related features contribute to local and regional diversity will depend on the connectedness of the system (Kneitel and Miller 2003, Leibold et al. 2004, Cadotte 2006). If connectedness is low, dispersal events are stochastic and local environmental factors become the main driver of community structure. In this case, diversity will be low and competitively dominant species will occupy most sites (Loreau and Mouquet 1999). At intermediate levels of connectivity, diversity is high as both local and regional factors (e.g. dispersal) are influential. In

this case, competitively dominant species are widespread but rare species co-exist in a few areas through emigration (Loreau and Mouquet 1999, Mouquet 2003). When connectedness is high, local processes are swamped and diversity is low as high dispersal creates what is effectively a single large community in which regionally dominant competitors constantly invade each local community (Forbes and Chase 2002, Mouquet and Loreau 2002, Amarasekare and Nisbet 2001).

As freshwater ecosystems become increasingly degraded, e.g. especially from eutrophication, local environmental change has become a key driver of ecosystem dynamics. Reductions in diversity are commonly reported even in well-connected systems (e.g. Cottenie et al. 2003, Chapter 3). The process of eutrophication causes major species turnover in lakes and initially eutrophication tends to increase species diversity. Indeed mesotrophic lakes usually possess species-rich communities of submerged macrophytes and associated fauna. With progressive eutrophication a strong reduction in local diversity is usually evident linked to the increasing prevalence of planktonic species and reductions in both macrophytes and macrophyte-associated invertebrates (Jeppesen and Jensen 2000, Sayer et al. 2010a).

Recent studies suggest that eutrophication can also homogenise the compositional structure of species assemblages within and between lakes (Donohue et al. 2009, Sayer et. al 2010b, Chapters 3 and 4). For instance, Donohue et al. (2009) investigated the effect of nutrient enrichment on the compositional heterogeneity of benthic invertebrate assemblages in Irish lakes. They found that compositional heterogeneity within and between lakes was inversely related to nutrient-enrichment. Chapter 3 describes a similar trend as macrophyte assemblages became more homogenous with the development of eutrophication in a set of 25 well-connected eutrophic and shallow lakes in Northern Ireland.

Although most effects of eutrophication are now well-known, the scientific focus on eutrophication is strongly centred on a local perspective where only within-lake dynamics are considered (Jeppesen et al. 2000, Davidson et al. 2005, Rasmussen and Anderson 2005). In addition, how eutrophication interacts with hydrological connectivity to influence lake biological communities in connected systems has received little investigation. Indeed, due to inherent difficulties in measuring the effects of eutrophication and regional processes such as dispersal over time, most

studies have limited their scope and period of inference to a snapshot in time (Allen et al. 2011). Typically, therefore, a space-for-time assumption has been implicit in our understanding of community dynamics and studies have focused almost entirely on contemporary datasets (Jeppesen et al. 2000). Nevertheless, riverscapes are ecosystems that change constantly over time (Amoros and Bornette 2002). Likewise, eutrophication is a gradual process that is manifested over time (Schindler 1974, Davidson et al. 2005, Conley et al. 2009, Sayer et al 2010a). Thus, to fully understand the joint effects of connectivity and eutrophication, it is vital to focus research at both spatial and temporal scales.

Sediment core records from shallow lakes have demonstrated their suitability to document changes in community structure over long time spans(Brodersen et al. 2001 Odgaard and Rasmussen 2001; Rasmussen and Anderson 2005; Ayres et al. 2008, Salgado et al. 2010, Allen et al. 2011) and the opportunity to investigate long-term metacomunity dynamics (Allen et al. 2011). These long-term perspectives are often lacking in metacommunity studies but are especially relevant to systems characterised by high connectivity. This study examines temporal (decade to centennial) patterns of species diversity at both local (within lake) and regional (between lake) scales from a set of five lakes that vary in degree of connectivity and nutrient enrichment in the Upper Lough Erne system, Northern Ireland. The study has two primary goals: (1) to understand how changes in eutrophication and/or hydrological connectivity influence within and between-lake community trajectories of change over time (species turnover); (2) to determine whether within – and among-lake communities become more homogeneous over time in response to nutrient enrichment and/or hydrological connectivity. Knowledge of eutrophication processes and metacommunity theory allows me to pose and test the following predictions related to two issues:

1. Trajectory of change

    i. If eutrophication was the only driver of community structure, similar trajectories of change should be observed within and between lakes through time and the length of trajectories should increased as nutrient enrichment concentration increases within each lake (species sorting) (Fig. 5-1a). In this scenario, the degree of hydrological connectivity should not influence the outcome.A

decline in local diversity (one or a few competitive dominants) in highly eutrophic lakes should be observed.

ii. If hydrological connectivity was the main driver of community structure little compositional change within and between lakes should be observed over time (mass effect). Here the degree of local enrichment should not influence the outcome and β-diversity should increase with isolation (Fig. 5-1b).Local diversity should be relatively high at intermediate levels of connectivity and no species dominate the assemblages over time. Increasing dispersal strength through very high levels of connectivity will reduce diversity with one or a few major regional species dominating all lakes.

iii. If both eutrophication and connectivity influence community structure trajectory of change should be similar to (i) but differences in length of trajectories should be less evident between lakes relative to that effected by eutrophication alone (Fig. 5-1c). Here the trajectory of change in multivariate space for more isolated lakes should be determined by nutrient concentration. Local diversity should be high reflecting the presence of a few competitive dominants and other less adapted species.

2. Compositional heterogeneity

i. If eutrophication is the main driver, within-lake compositional heterogeneity should decline strongly over time as enrichment progresses. Likewise, at between-lake scale more eutrophic sites should be less heterogeneous than less eutrophic sites at a given time period. (Fig. 5-1d).

ii. If dispersal is the main driver, a weak decline or no pattern in compositional heterogeneity within and between sites should be observed over time.

iii. If both connectivity and eutrophication are influential, a moderate decline in compositional heterogeneity within and between sites is expected over time.

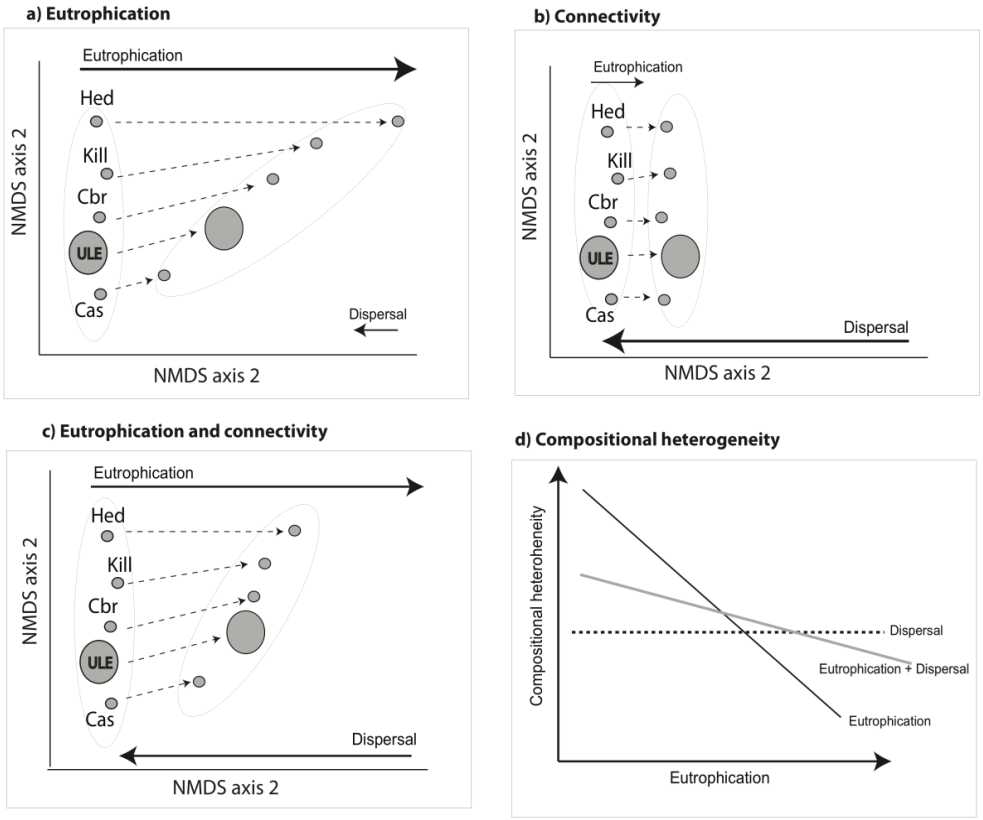

Figure 5-1. Predicted temporal metacommunity scenarios according to the influence of local vs. regional processes. a) Eutrophication is strong and hydrological connectivity (dispersal) low; b) Eutrophication is low and hydrological connectivity high; c) Both factors are strong; d) influence of eutrophication and dispersal in compositional heterogeneity.

5.3 Study Site

The Upper Lough Erne (ULE) system is situated in Co. Fermanagh, Northern Ireland, UK (Fig. 5-2). It is a complex and dynamic riverine landscape formed as the channel of the River Erne splits and widens across a landscape of drumlins creating two large mainly shallow lakes: Lower Lough Erne, situated in the north west (54^{o}30' N 7^{o}50'W) (mean depth 11.9 m and surface area 109.5 km^{2}); and Upper Lough Erne in the south (54^{o}14' N 7^{o}32' W) (mean water depth 2.3 m and surface area 34.5 km^{2}) (Battarbee 1986, Gibson et al. 1995) (Fig.5-1). Associated with the large ULE is a series of interconnected, smaller (area range 1-50 ha.), and shallow (mean depth <2

m) satellite lakes that vary in degree of enrichment and hydrological connectivity (mediated by rivers, streams and agricultural channels).

Previous research and historical records demonstrate that over the last 150 years, the ULE system has been subject to hydrological change and eutrophication (Price 1890, Battarbee 1986, Gibson et al. 1995, Smith et al. 2005). Frequent flood events during the 1800s in the ULE catchment caused by high rainfall (63 mm day^{-1}) and an inability of the River Erne to discharge the incoming water back to the sea led to a major drainage scheme between 1880-1890 (Price, 1890; Cunningham 1992). During this era the main ULE and associated channels were excavated to increase water depth and as consequence, water levels dropped from around 48 to 46 m above sea level (Price 1890). Recurrent flood events prompted a second attempt at water level regulation under the Erne Drainage and Development Act (Northern Ireland) in the early 1950's. At this time 30 km of channel were dredged between the ULE and the Lower Lough Erne system. Since this time water levels in the ULE system have been maintained between around 43-45 m above sea level (Mathers et al. 2002, Smith et al. 2005). Despite these efforts, the ULE system is still prone to flood events (Cunningham 1992). A flood impact map of 2009 showsthat extensive floodingstill occurs, which connects most satellite lakes and the main ULE (http://safer.emergencyresponse.eu, OFMDFM 2010) (Fig. 5- 2).

Diatom-based palaeolimnological studies in the main ULE system indicate a gradual increase in nutrient enrichment since the 1900s with a further acceleration of this process after the 1950s (Battarbee 1986, Gibson et al. 1995, Smith et al. 2005). Early eutrophication of ULE is thought to be due to domestic effluent inputs after storm drains were introduced to local towns (Battarbee 1986). The acceleration of eutrophication in the 1950s likely resulted from the interaction of various factors including post-war agricultural intensification, increased sewage input, synthetic detergent input, development of rural septic-tank sanitation, and increased organic pollution from industry (Battarbee 1986).

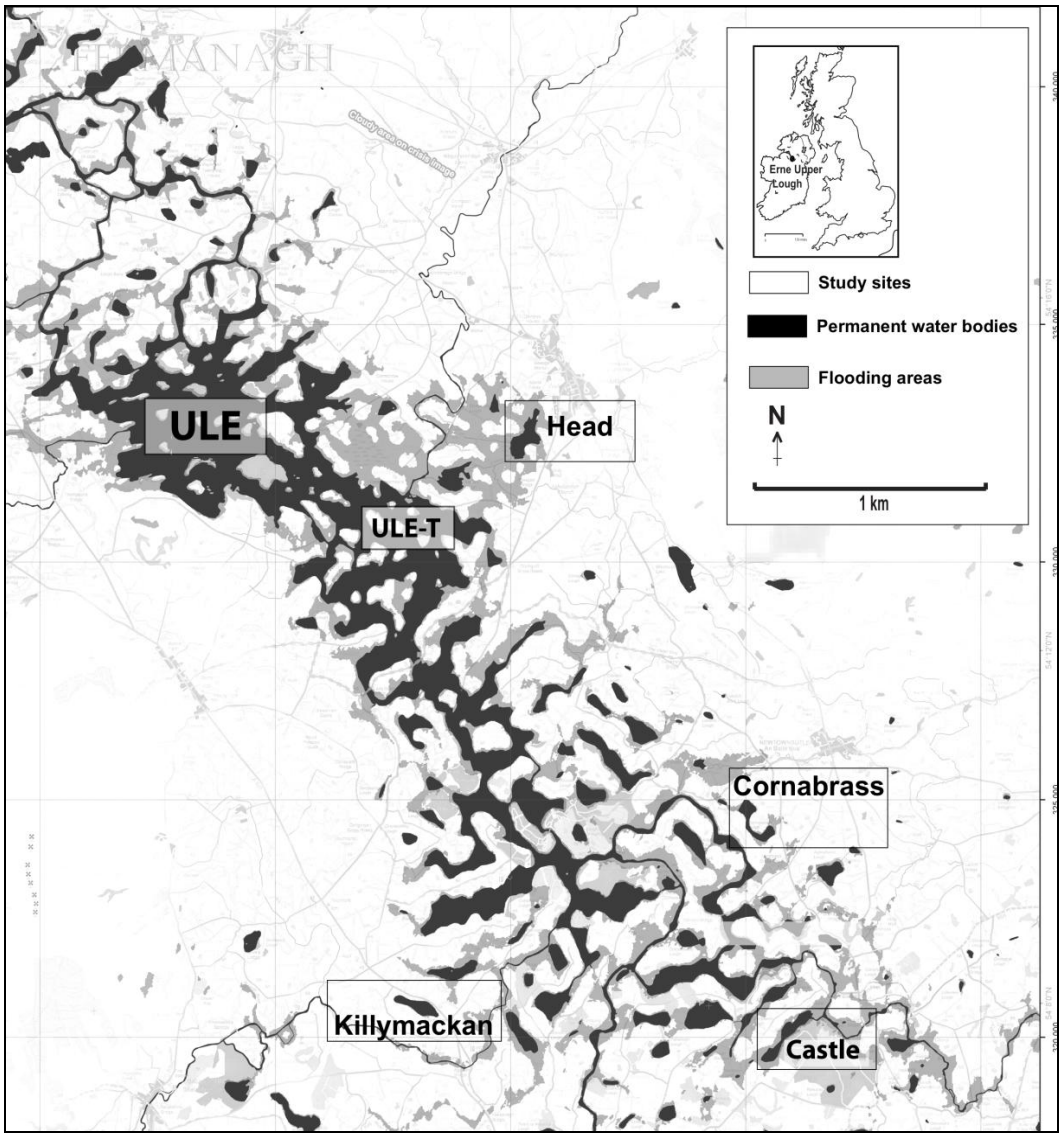

Figure 5-2. Map of the Upper Lough Erne System with the associated study satellite lakes.

5.4 Materials and methods

This study uses palaeolimnological techniques to examine five lakes from the ULE system. These lakes were Castle Lough, Cornabrass Lough, Killymackan Lough, Lough Head and the main ULE (Trannish area) (Fig. 5- 2). Selection criteria for these lakes included a nutrient-enrichment gradient, according to total phosphorus (TP) and total nitrogen (TN) concentrations (Table 1; data obtained from Goldsmith et al 2008) and a hydrological connectivity gradient to the main ULE. Connectivity was as follows: direct connection through a river, stream or agricultural channel (Castle Lough); indirect connection to the ULE through another water body (Cornabrass and

Head); connection to the ULE involving more than two intervening water bodies (Killymackan) (Fig. 5-2).

As dispersal rates are inherently difficult to measure, a surrogate for these was adopted by studying three different groups that differ in their dispersal mode: (1) "active" dispersers – chironomids; and (2) passive dispersers - submerged and floating-leaved macrophytes (henceforth referred to as macrophytes); and bryozoans, molluscs and cladocerans (henceforth referred to as invertebrates). Although chironomids are commonly classified as passive dispersers (Armitage et al. 1997), their weak flight can nevertheless effect a mean dispersal distance of around 500 m (Armitage et al. 1995, Delettre and Morvan 2008), and they can actively fly into a position where wind currents can then passively disperse them over longer distances (Nielsen and Nielsen 1962, Davies 1967, Armitage et al. 1995, Delettre and Morvan 2008). Furthermore, first-instar larvae of Orthocladiinae and Chironominae are vigorous swimmers and disperse from the site of hatching (Armitage et al. 1995). The combined effects of planktonic and adult activities are predicted to confer greater dispersal than that achieved by the passively dispersing macrophytes and invertebrates examined in this study.

Table 5-1. Mean average values of environmental data from Castle Lough, Cornabrass Lough, Head Lough, Killymackan Lough and the Upper Lough Erne (Trannish) at 2006-2007 (Goldsmith et al. 2008).

LAKE	Core Code	TP (ug/L)	TN (mg/L)	Chlorophyll-a (ug/L)	Cond (uS/cm)	Area (Ha)	Water Depth (cm)
Castle Lough	NCAS1	29	1,03	4,2	302	13	450
Cornabrass Lough	CBRAS1	96	1,05	5,3	353	18	430
Killymackan Lough	KILL2	111	0,80	17,4	248	19,2	170
Lough Head	NHEAD	383	1,79	9,0	327	31	85
ULE-T	ULE2	68	-	5.8	-	80	860

To characterise temporal changes in abundances for the three groups (macrophytes, invertebrates and chironomids), single sediment cores from each lake (NCAS1 for Castle Lough, CBRAS1 for Cornabrass Lough, KILL2 for Killymackan Lough, HEAD1 for Head Lough and ULET2 for the main ULE) were collected in June 2008 using a wide-bore (14.8 cm) "Big-Ben" piston corer (Patmore et al. in prep). Cores were collected from similar water depths (~150 cm) and extruded in the field at 1-cm intervals. Lithostratigraphic changes for the core sequences were measured and recorded in the field.

Chronologies for each sediment core were established by radiometric dating. Sediment samples from each core were analyzed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay in the Bloomsbury Environment Institute at University College London, using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. ^{210}Pb was determined via its gamma emissions at 46.5keV, and 226Ra by the 295keV and 352keV gamma rays emitted by its daughter isotope ^{214}Pb following storage for three weeks in sealed containers to allow radioactive equilibration. ^{137}CS and ^{241}Am were measured by their emissions at 662keV and 59.5keV. The absolute efficiencies of the detector were determined using calibrated sources and sediment samples of known activity (Appleby et al. 1986, 1992, Appleby 2001). Corrections were made for the effect of self-absorption of low energy gamma rays within the sample (Appleby et al. 1992). No attempt was made to date sediments beyond the range of the ^{210}Pb dating analyses as the focus of interest was the last 150 years. Dates were ascribed using the constant rate of supply (CRS) model (Appleby 2001).

Macrophyte composition was estimated using macrofossils; seeds, leaves, spines and a range of vegetative fragments (Birks 2001). Bryozoan composition was determined using statoblasts (dormant propagules) which have been shown to provide a reliable source of information on contemporary bryozoan abundances (Hartikainen et al. 2009). Cladoceran composition were determined using ephippial remains (Jeppesen et al. 2001) and molluscs from whole shells, shell-fragments and larvae (glochidia), respectively (Aldridge and Horne 1998, Ayres et al. 2008). Chironomid composition was estimated by counting larval head capsules which offer a consistent representation of extant larvae and are well-preserved in sediments (Brodersen and Lindegaard 1999).

Twenty 1-cm slices were sampled from cores NCAS1 and HEAD1, 16 from CBRAS1, 13 from KILL2 and 14 from ULET2. Each core was analysed at a resolution of 2-4 cm intervals for the top 30 cm (covering c. 150+ years, the key period of interest) and at 10 cm intervals below this. All samples were disaggregated in 10% potassium hydroxide (KOH) before sieving.

Macrofossil analyses were performed using an adaptation of standard methods (Birks 2001, Davidson et al. 2005). Three sieves of different mesh sizes (355 µm, 125 µm

and 90 µm) were used to separate the macrofossil and chironomid remains (Brooks et al. 2007). Due to the high volume of sediment retained in the 125 µm and 90 µm fractions, both samples were mixed after sieving to provide a total volume of 200 mL per 1-cm slice. Subsequently a subsample of 20 mL was analysed.

Chironomid head-capsules were picked simultaneously with other macrofossils and a minimum of 50 head capsules were enumerated in each sample (Heiri and Lotter 2001). Chironomid head-capsules were prepared using standard methods, mounted in Euparal and identified using Brooks et al. (2007). All macrofossil data were standardized as numbers of fossils per 100 cm^3 (raw data are provided in Appendix 1). The 20 mL subsamples obtained from the 125 µm and 90 µm sieves were standardized first up to a volume of 200 mL and then to 100 cm^3. Macrophyte and invertebrate macrofossils were identified by comparison with reference material held at the ECRC, UCL and the Natural History Museum, London and by using taxonomic keys (e.g. Birks 2001, Wood and Okamura 2005, Aldridge and Horne 1998, Preston 1995).

5.4.1 Data analysis

To visualize community trajectories within and among lakes, multidimensional scaling (NMDS) (Bray–Curtis metric) analysis was used for each group (macrophytes, invertebrates and chironomids) performed using the metaMDS algorithm in Rversion 2.13 for Macintosh (R Core Development Team 2011). Of many potential measures of dissimilarity, the Bray–Curtis metric has been shown to possess one of the strongest relationships between site dissimilarity and ecological distance (Faith et al. 1987), hence providing optimum ordinations for the NMDS technique. Consistent changes in the direction of trajectories of compositional change between NMDS plots for axes 1 and 2 were used to detect major phases of compositional change for each of the biological groups.

To quantify changes in compositional heterogeneity over time, a combination of Principal Curve (PC) analysis (pcurve in R; De'ath 1999), permutational analysis of homogeneity in multivariate dispersions (HMD; Anderson 2006, Anderson et al. 2006)and permutational multivariate analysis of variance (perMANOVA; Anderson 2001a) were used. PC analysis showed periods of high or low compositional variability over time and hence allowed detection of major phases of change.

perMANOVA and HMD were used to test the significance of compositional heterogeneity variability attributed to differences in species present and species relative abundances, respectively.

By using nonlinear regressions and smoothers the PC ordination method extracts one principal gradient from the data by passing it through the multivariate ordination space. The analysis provides a value for each sample location along the curve (lambda) that can be used as an indicator of variability over time when plotted against core depth. Major changes between lambda values were used to corroborate phases of compositional change observed in NMDS analysis. The test was calculated on Bray-Curtis dissimilarity data and each group (macrophytes, invertebrates and chironomids) was analysed separately. The starting point of the PC was defined by the first axis of a non-metric multidimensional scaling (NMDS) (Bray–Curtis metric). PCs were fitted using smoothing splines and the number of degrees of freedom of the smoothers was given by the median degrees of freedom of cross-validated fits to all species. Each fit used 10 iterations or ran to convergence, whichever occurred first (De'ath 1999).

perMANOVA is a non-parametric method for multivariate analysis of variance that compares variability of dissimilarity distances within groups versus variability among different groups (i.e. variation over time in the type of species), using the ratio of the *F*-statistic through permutational tests (Anderson 2001a, 2001b). Here, larger values of *F* reflect higher compositional differences between groups. Due to varying sedimentation rates among cores, permutation comparisons were made with strata (i.e. permutations were nested within each core under the reduced model using 4999 permutations). Species dissimilarities were calculated using the Bray-Curtis dissimilarity index. The magnitude of change in compositional heterogeneity attributed to types of species present (species sorting) through time within and between the lakes was calculated as the *F* statistic ratio attributed to each time period. Metacommunity theory predicts higher differences between sites under species sorting processes (Loreau and Mouquet 1999, Cadotte 2006). Consequently, higher values of *F* values were considered to be a reflection of species sorting processes. Owing to analytical requirements for equal numbers of samples for perMANOVA analysis, a set of 4 representative sediment samples per compositional phase (detected

by NMDS and PC analysis) were used. Due to observed low variation for HEAD1 in NDMS and PC analysis and the lack of confinable radiometric dates, the HEAD1 core was excluded from all perMANOVA analyses. The perMANOVA analyses were conducted using perMANOVA software version 6 (Anderson 2005).

To quantify the variation in community structure that was attributed to changes in relative abundances, the mean distances to group centroid were calculated using HMD analysis (Betadisper in R). Each group corresponded to the three delineated compositional phases identified by PC and NMDS analysis and all sediment samples corresponding to each phase were used. Each time fraction was treated as an independent group and species dissimilarities were calculated using a Bray-Curtis index of dissimilarity in a principal coordinate analysis (PCO) analysis (Anderson 2006). To test if the variance between groups was significant, distances of group members to the group centroid were subject to pairwise comparisons using random permutation of the residuals, with strata within each core, under the reduced model (number of permutations = 4999) as recommended by Anderson (2005). The analysis generates a permutation distribution of F under the Null hypothesis of no difference in dispersion between groups (i.e. no differences in β-diversity). The expectation here is that groups presenting greater multivariate dispersion have a heterogeneous species composition and are thus associated with lower nutrient values (see Chapter 3, Donohue et al. 2009). Due to observed low variation in species turnover for HEAD1 in NDMS and PC analysis and the lack of confinable radiometric dates, HEAD1 core was excluded from all HMD analyses.

5.5 Results

5.5.1 Core chronologies and sedimentation rates

Radiometric chronologies for Cores NCAS1, CBRAS1, HEAD1 and KILL2 are given in Fig. 3. Final ^{210}Pb dates were calculated using the CRS model for all cores. For Core NCAS1 (Castle Lough, Fig. 5-3a) the model placed the 1963 fallout maximum of the atmospheric testing of nuclear weapons at 11 cm c. and c. 1900 at 20 cm, respectively. Sedimentation rates based on the revised ^{210}Pb dates exhibited a fairly

stable pattern with a mean of 0.032 g cm^{-2} yr^{-1} from the c. 1880s to the c. 1980s but an increase in the last decade at 0.05 g cm^{-2} yr^{-1}. For Core CBRAS1 (Fig. 5-3b), c. 1963 was placed just above 11.5 cm and 1900 at around 20 cm. Sediment accumulation rates calculated from unsupported ^{210}Pb indicate a relatively uniform rate for the first half of the 20th century with a mean of 0.022 g cm^{-2} yr^{-1}, and a steady increase over the last 20 years up to 0.102 g cm^{-2} yr^{-1} in the present day. The dating model for Core KILL2 (Fig. 5-3c) places 1963 at c. 16 cm and 1900 at c. 25 cm. Sediment accumulation was relatively stable over the last 100 years, with a gradual increase up to the present day. There was a significant increase in sediment accumulation in the 1910s (23 cm) possibly caused by a sediment slumping event. The raw CRS dating model for HEAD1 (Head Lough, Fig. 5-3d) suggests that the 1986 layer is at 17.5 cm, which is close to a peak at 19.5 cm in the ^{137}Cs record. However, unsupported ^{210}Pb activities were low and the counting errors large, making the chronology of the core unreliable. Likewise ULET2 (Upper Lough Erne) presented very low activities of unsupported ^{210}Pb and dates could not be easily ascribed for the core.

5.5.2 Within-lake trajectories of change and compositional heterogeneity

NMDS and PC analyses provided evidence for a strong temporal species sorting and a concomitant homogenization of communities over time in all five cores (Fig. 5-4 and 5-5). Both analyses revealed three evident phases of change as indicated by changes in lambda values (PC analysis, Fig. 5-4) and changes in the direction of NMDS axis 1 and/or axis 2 (Fig. 5-5) as follows:

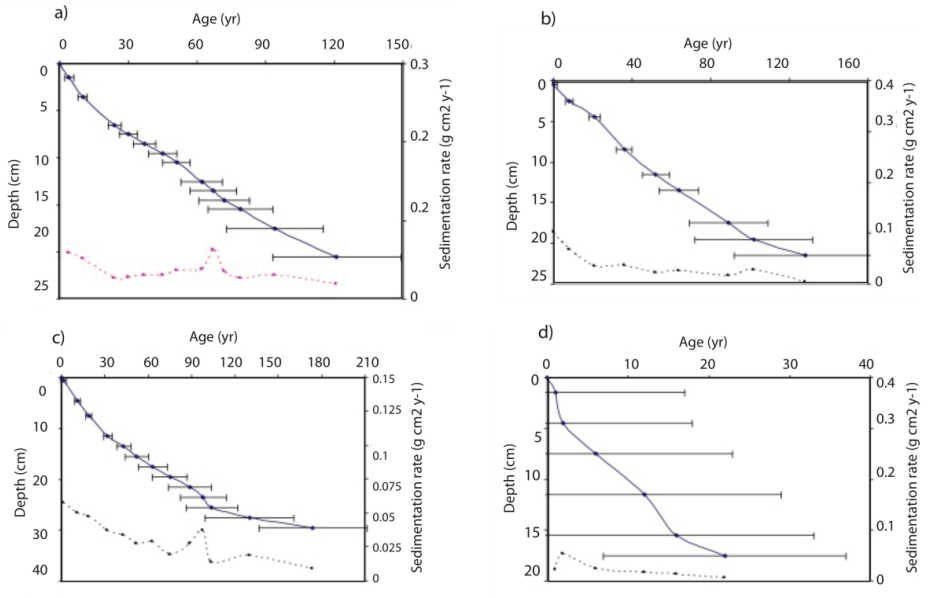

Figure 5-3. Radiometric chronology of cores NCAS1, CBRAS1, KILL2 and HEAD1 taken from Castle Lough, Cornabrass Lough, Killymackan Lough and Lough Head showing the CRS model ^{210}Pb dates and sedimentation rates.Solid line is for age, dash line for sedimentation rate. a) NCAS1; b) CBRAS1; c) KILL2; d) HEAD1.

Phase 1 - a constant phase of heterogeneous assemblages within lakes exhibited by most cores (except Lough Head) prior to c. 1900; Phase 2 - a transitional phase with compositional heterogeneity values declining gradually from c. 1950-1900; Phase 3 - a relatively constant phase of homogenous assemblages within lakes since the 1950s.

PC analysis on macrophytes explained between 62-87% of the macrophyte variation for all cores (Fig. 5-4a). This analysis showed that in cores NCAS1, ULET2, and CBRAS1 there was a high but constant variation of macrophyte communities between samples during Phase 1 (c. pre-1900). Over this period PC lambda values ranged between 2-4 among the 4 cores. In KILL2, variation was also steady but lambda values were lower than those observed for the other cores (range = 1.2-1.7). By contrast, in core HEAD1, there was little variation (lambda range = 0-0.06) at 70-90 cm and an increase in lambda values (~ 2.0) at 49-59 cm. In NMDS analysis Phase 1 samples were observed at the right side of the multidimensional space in all five cores and trajectories of change were determined along the second NMDS axis (Fig. 5-5).

PC analysis indicated that variation in macrophyte communities for Phase 2 (c. 1950-1900) gradually declined towards low lambda values of around 1 in cores NCAS1, ULET2 and CBRAS1 (Fig. 5-4a), In core KILL2 macrophyte community variability increased with lambdavarying between 2.4-2.7. The HEAD1 core presented low

levels of macrophyte variation (lambda range 0.7-0.2). NMDS analysis showed that Phase 2 samples were clustered in the middle of multivariate space and trajectories in community change were determined by NMDS axis 1 (Fig. 5-5).

Phase 3 (c. present day- 1950) in PC analysis was characterised by a relatively constant and low variation (lambda range = 0.3-0) in macrophyte community assemblages among all five cores (Fig. 5-4a). Sediment samples from this phase were observed on the left side of the NMDS plot (Fig. 5-5), where the trajectory of change was determined by NMDS axis 2.

PC analysis on invertebrate remains explained around 90% of community variation among all five cores (Fig. 5-4b). In Phase 1 the NCAS1, ULET2, KILL2 and HEAD1 cores showed a similar trend to the macrophytes with lambda values ranging from 1.7-3.2 in NCAS1, KILL2 and HEAD1 and from 3.5-5.2 in ULET2. In contrast, the CBRAS1 core showed lower (lambda range 1.2-0.6) and more constant variation among samples. NMDS plots showed that sediment samples for Phase 1 were located on the left side of the multidimensional space and trajectories of community change were determined by NMDS axis 2 (Fig. 5-6).

In Phase 2, PC analysis showed an increase in community variation in cores NCAS1 and CBRAS1 (lambda range 1.4-2.9). KILL2 and ULET2 cores showed a gradual decline in lambda values while there was little variation in HEAD1 (lambda range 0.6-0.3). This phase is represented in the middle of the NMDS plots, where trajectory of community change was determined by NMDS axis 1 (Fig. 5-6).

Phase 3 was characterised in PC analysis by near constant and low lambda values (range 0.1-0) in cores NCAS1, CBRAS1 and HEAD1 (Fig. 5-4b). Lambda values in KILL2 were also low (range 1.0-0) but gradually declined over time. In contrast, lambda values in core ULET2 were higher and increased gradually from 1.2-2.15. Samples from Phase 3 are located towards the right side of the NMDS plots and changes in trajectory were along NMDS axis 2 (Fig. 5-6).

PC analysis of the chironomid data explained between 50-89% of community variation in the five cores (Fig. 5-4c). During Phase 1 community variation was constant and higher than those values observed for the other two phases Lambda values ranged between 0.6-1.4 in cores NCAS1, KILL2 and HEAD1, from 2.1-2.7 in

ULET2 and from 1.0-1.8 in CBRAS1. Phase 3 samples in the NMDS plots were again located towards the right side of the NMDS plot, although its separation from other phases was less clear for the NCAS1, CBRAS1 and HEAD1 cores (Fig. 7). The trajectory of change was mostly along NMDS axis 2.

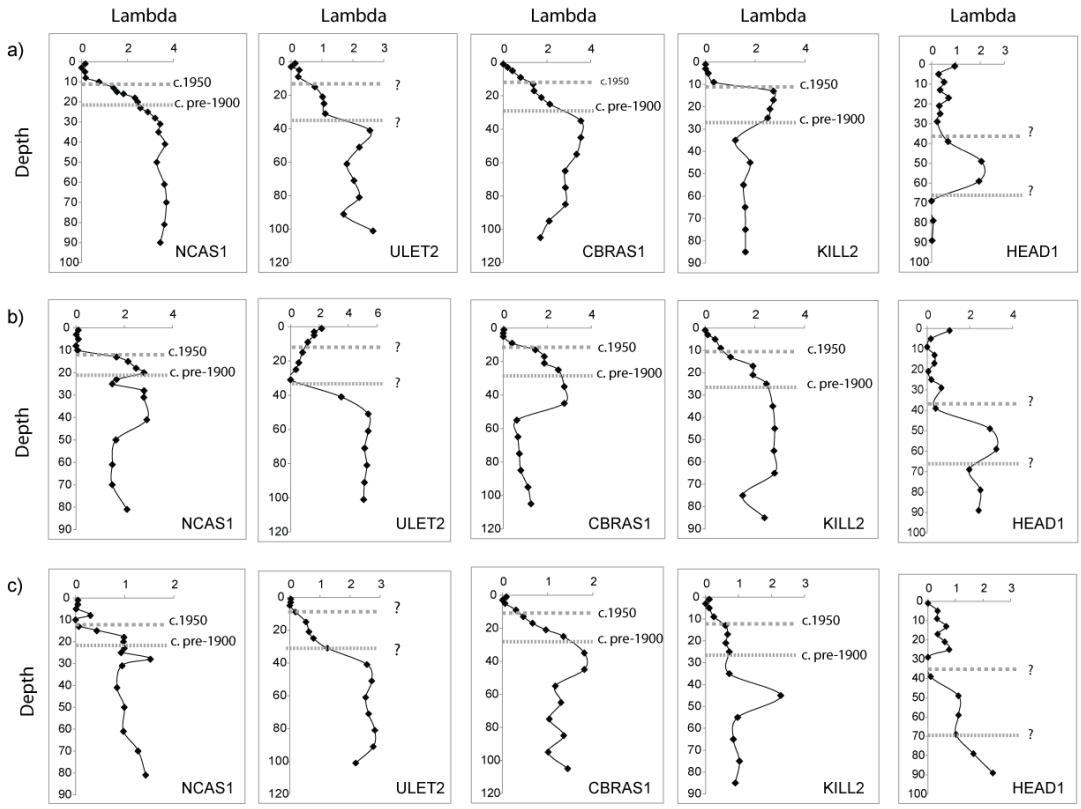

Figure 5-4. Principal curve lambda values against core depth (compositional variability increase with lambda values). a) Macrophytes b) Invertebrates; c) Chironomids.

Phase 2 in the PC analysis was characterised by a gradual decline in lambda values (range 0.9-0.2) among NCAS1, ULET2, CBRAS1 and KILL2. Core HEAD1 was characterised by a constant lambda value of 0.6 (Fig. 5-4c). NMDS analysis showed that Phase 2 samples were generally distributed around the middle of the NMDS plots with the trajectory of community change determined by NMDS axis 1 (Fig. 5-7).

PC analysis of Phase 3 resulted in low and stable lambda values (range 0.3-0.0) in all five cores (Fig. 5-4c). Samples of Phase 3 were distributed towards the left side of the NMDS plots for cores NCAS1, ULET2 and KILL2. Samples for CBRAS1 and HEAD1 in this phase were distributed in the middle of the NMDS plot (Fig. 5-7). The trajectory of change was determined by a combination of both NMDS axes.

5.5.3 Macrofossil representation

Macrofossil analysis for all cores revealed a total of 32 plant, 15 invertebrate and 77 chironomid macrofossil types (Figs. 5-8, 5-9, 5-10) (Appendix 1). All five cores illustrated broadly parallel stratigraphic changes linked to the relatively distinct phases identified by PC and NMDS analyses. In Phase 1 (pre-1900), macrophytes were well represented by bryophytes (including *Sphagnum* spp.), *Isoetes lacustris*, *Lobelia dortmanna*, *Callitriche* sp., *Chara* spp., *Nitella* spp., *Myriophyllum* sp. *(*probably *M. alterniflorum)*, *Najas flexilis*, *Stratiotes aloides*, *Potamogeton obtusifolius/fresii*, *Potamogeton praelongus/lucens*. There were also relatively large abundances of the bryozoans (*Plumatella fruticosa*, *Paludicella articulata*, *Cristatella mucedo*, *Plumatella* spp.) and a predominance of the chironomid taxa *Glyptotendipes severini*, *Phaenopsectra flavipes*, *Monodiamesinae*, *Orthocladius consobrinus*, *Protanypus*, *Pseudochironomus*, *Stempellina*, *Cladopelma lateralis*, *Microtendipes pedellus*, and *Dicrotendipes*. Other chironomid taxa also occurred in moderate numbers including, *Ablabesmyia*, *Procladius*, *Chironomus plumosus*, *Polypedilum nubeculosom*, *Tanytarsus pallidicornis*, *Tanytarsus mendax* and *Cladotanytarsus mancus*.

In Phase 2 (c. 1900-1950) remains of the macrophytes *I. lacustris*, *L. dortmanna* and *N. flexilis* declined, while Nymphaeaceae, *Myriophyllum spicatum*, *S. aloides*, *Lemna trisulca*, *L. minor* and *Chara* spp. and *Nitella* spp. increased. The bryozoans *P. fruticosa* and *P. articulata* declined, while *C. mucedo* and *Plumatella* spp., increased along with the cladocerans *Daphnia* spp.,(includes *D. hyaline*, *D. longispina* and *D. pulex)* and *Ceriodaphnia* sp., and the molluscs *Bithynia tentaculata*, *Pisidium* spp., and other snails (largely planorbid taxa). The chironomid taxa *P. flavipes*, *Monodiamesinae*, *O. consobrinus*, *Protanypus* and *Pseudochironomus* strongly declined or disappeared from the fossil record while other taxa like *Microchironomus*, *C. plumosus*, *C. lacophila*, *Dicrotendipes*, *Procladius*, *T. mendax*, *T. lugens*, *C. mancus*, *Cricotopus* agg., and *Endochironomus albipennis* increased.

In Phase 3 (c. 1950-present day), bryophyte remains strongly declined in abundance along with the macrophyte taxa *I. lacustris*, *L. dortmanna*, *Callitriche* sp., *Myriophyllum* sp.and *N. flexilis*, while Nymphaeaceae, *L. trisulca*, L. *minor* and *Ceratophyllum demersum* became abundant. The mollusc *B. tentaculata*, *Pisidium*

spp., other snails (largely planorbids), *Dreissena polymorpha* and *Anodonta cygnea* became especially abundant as did bryozoans belonging to the genus *Plumatella* (excluding *P. fruticosa*). The majority of chironomid taxa described in Phase 2 increased in abundance along with *Chironomus anthracinus* and *Psetrocladius*.

5.5.4 Among lake trajectories of change and compositional heterogeneity

Multivariate macrophyte community trajectories were similar for cores HEAD1, ULET2, CBRAS1 and KILL2 (Fig. 5-11a). With time ULET2, CBRAS1 and KILL2 converged towards a new similar condition with similar trajectory length, while NCAS1 showed a different trajectory and rather shorter length of change with current communities being somewhat different to the other lakes and more similar to Phase 1 and 2 communities of the other cores. However, the most recent sample for core NCAS1 indicated a similar trajectory of change along NMDS axis 2 (Fig. 5-11a). Although contemporary assemblages of ULET2 were distributed close to those of KILL2 and CBRAS1, contemporary samples were associated with a gradient of change that was slightly shorter indicating a closer relationship to previous Phase 2 communities in CBRAS1 and KILL2 (Fig 5-11a). On the other hand, HEAD1 showed a much more constant pattern with Phase 1 samples more closely related to Phase 2 communities of ULET2 and CBRAS1. Contemporary assemblages for HEAD1 were located at a similar position on NMDS axis 2 to those of ULET2, KILL2 and CBRAS1, but the trajectory of change on axis 1 was opposite to that of the latter cores.

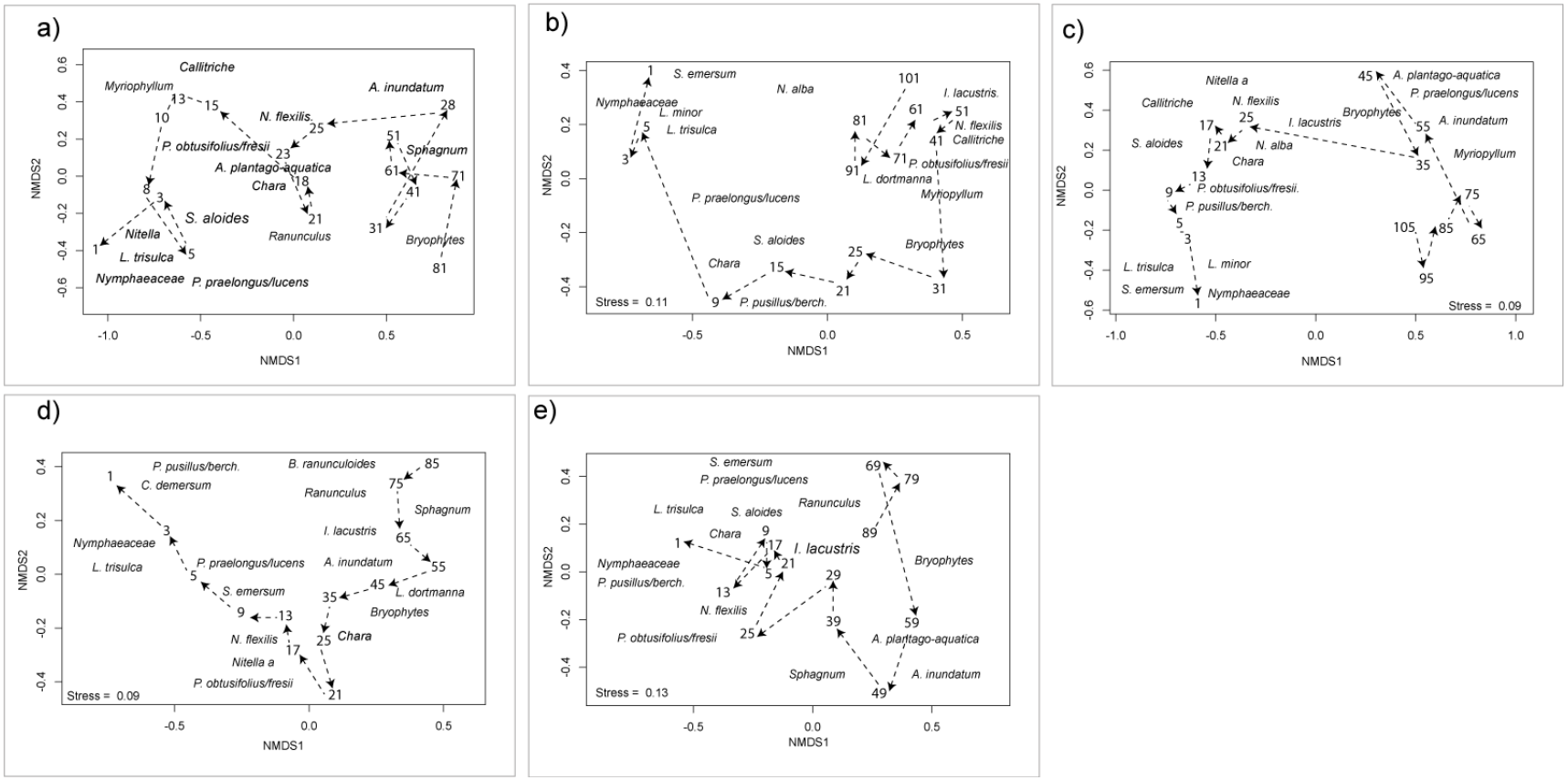

Figure 5-5. Nonmetric multidimensional scaling (NMDS) plot of macrophyte community turnover within each lake. a) Castle Lough; b) Upper Lough Erne; c) Cornabrass Lough; d) Killymackan Lough; e) Lough Head. Trajectory of change is indicated by an arrow. Dominant species for each sample are indicated. Numbers indicate sediment core depth (cm).

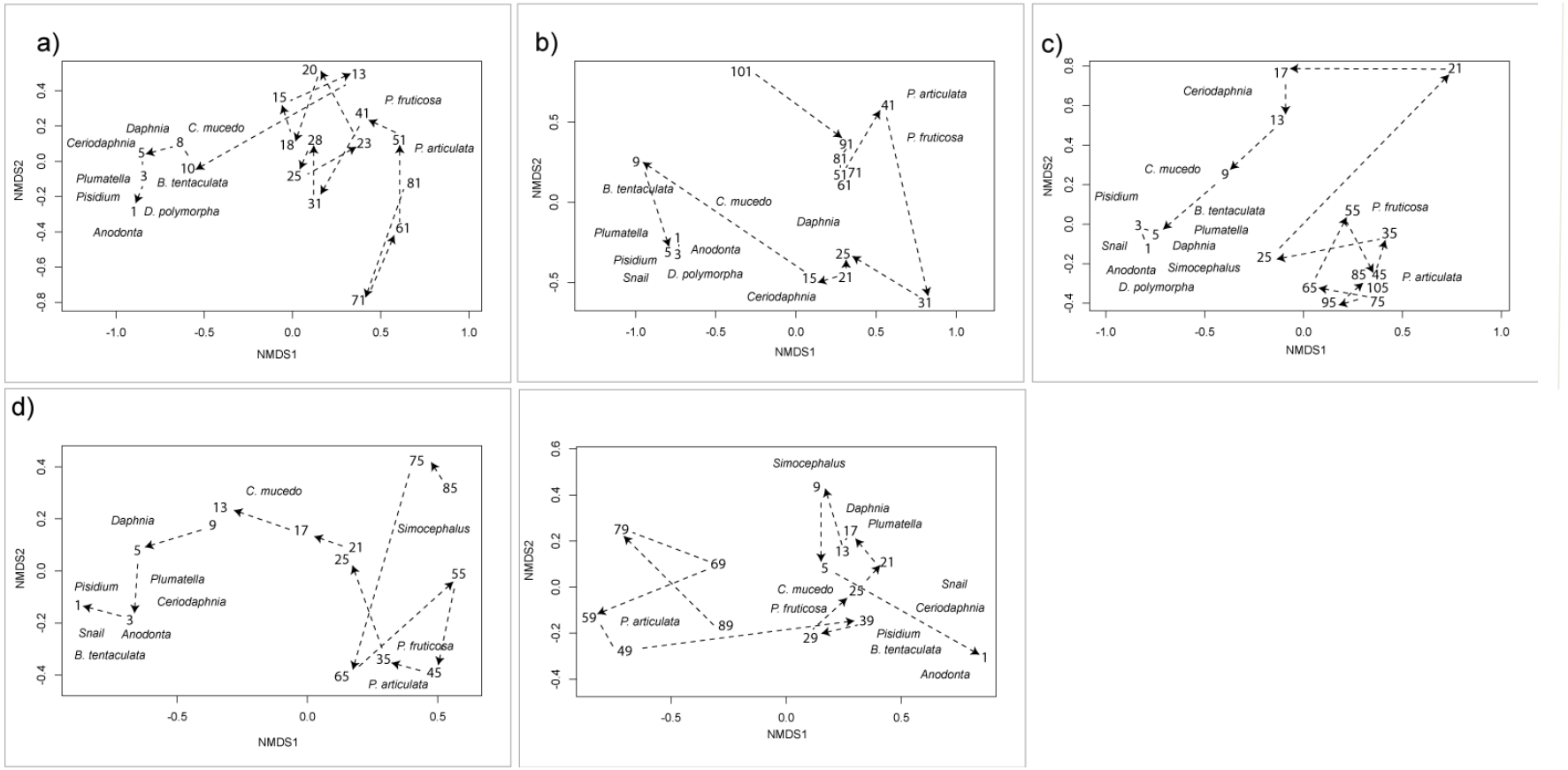

Figure 5-6. Nonmetric multidimensional scaling (NMDS) plot of invertebrate community turnover within each lake. a)Castle Lough; b) Upper Lough Erne; c) Cornabrass Lough; d) Killymackan Lough; e) Lough Head. Trajectory of change is indicated by an arrow. Dominant species for each sample are indicated.

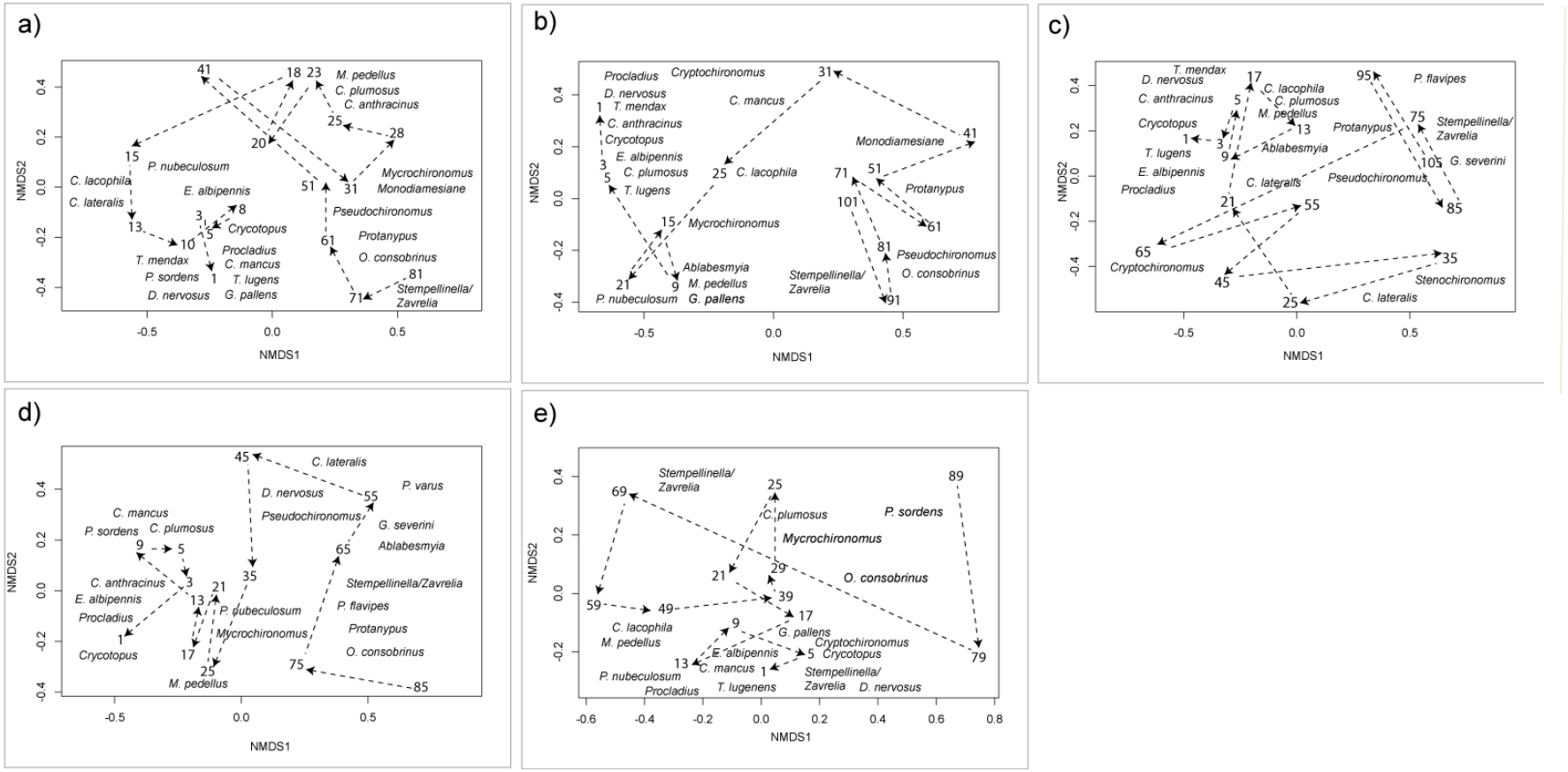

Figure 5-7. Nonmetric multidimensional scaling (NMDS) plot of chironomid community turnover within each lake. a) Castle Lough; b) Upper Lough Erne; c) Cornabrass Lough; d) Killymackan Lough; e) Lough Head. Trajectory of change is indicated by an arrow. Dominant species for each sample are indicated.

Multivariate invertebrate community trajectories showed that in Phase 1 cores NCAS1, CBRAS1, KILL2 and HEAD1 had a similar composition and generally converged towards a similar community assemblage over time (Fig. 5-11b). For ULET2 Phase 1 assemblages followed a slightly different track but rapidly became similar in composition to the HEAD1 samples. In Phase 2 ULET2 assemblages converged close to those in CBRAS1 and KILL2.

The multivariate trajectory of chironomids showed that in NHEAD, NCAS1 CBRAS1 and ULET2 assemblages were closely related in Phase 1 (Fig. 5-11c). However, KILL2 was different with Phase 1 assemblages being closely related to Phase 2 assemblages in CBRAS1 and Phase 3 assemblages in ULET2. Nonetheless, with time, all cores converged towards a generally similar assemblage.

Compositional heterogeneity varied substantially within (perMANOVA: $P< 0.01$ for all cases) and among (perMANOVA: $P< 0.001$ for all cases) lakes over time (Table 5-2 and 5-3). Within lake variation attributed to the type of species present (F statistic) between the three compositional phases was lowest for macrophyte assemblages in NCAS1 ($F = 7.88$), followed by those in ULET2 ($F = 10.99$), KILL2 ($F = 12.80$) and CBRAS1 ($F = 13.50$). For invertebrates, CBRAS1 ($F = 4.35$) presented the lowest variation, followed by NCAS1 ($F = 6.22$), ULET2 ($F = 9.44$) and KILL2 ($F = 19.27$).

The macrophyte compositional average dissimilarity between phases declined over time among all cores and CBRAS1 had the lowest proportion of variation (11.98) and KILL2 the highest (25.74). The invertebrate compositional average dissimilarity between phases declined for NCAS1 and CBRAS1 with a proportion of change of 0.35 for CBRAS1 and 0.30 for NCAS1 (Table 5-2). By contrast in ULET2 the average dissimilarity increased over time. For chironomids, compositional average dissimilarities declined over time for NCAS1, CBRAS1 and KILL2, while average dissimilarities for ULET2 increased (Table 5-3). Within the chironomids, NCAS1 had the lowest proportion of compositional change over time (7.63), followed by KILL2 (27.03) and CBRAS1 (50.93) respectively.

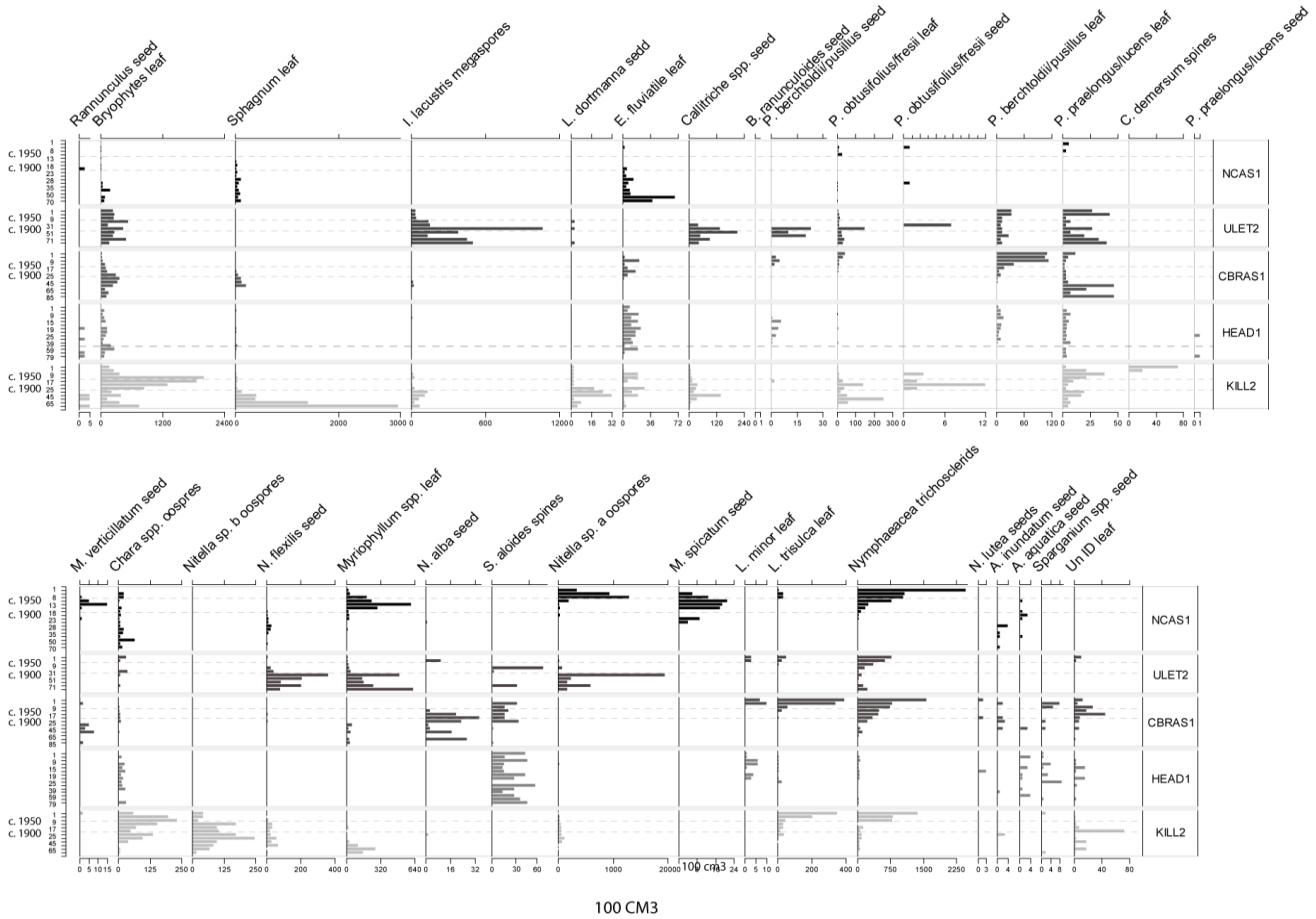

Figure 5-8. Stratigraphic summary of plant-macrofossils of NCAS1, ULET2, CBRAS1, KILL2 and HEAD1 cores. Sediment samples were amalgamated over three periods of approximately 50 years.

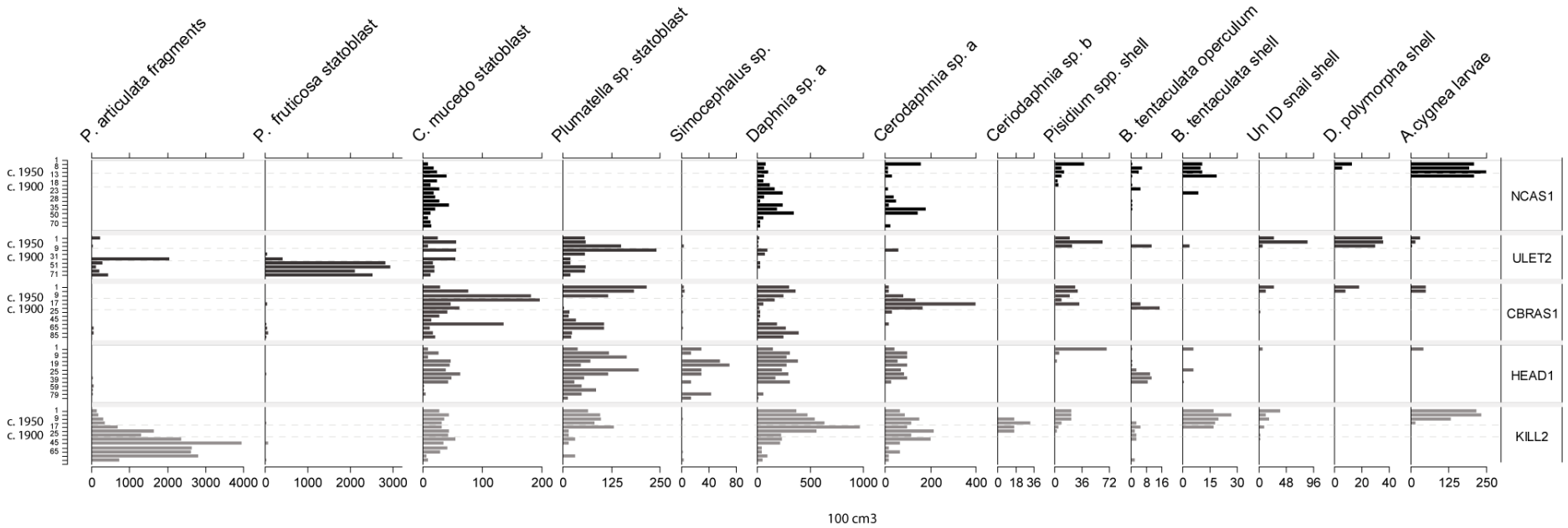

Figure 5-9. Stratigraphic summary of invertebrate macrofossils of NCAS1, ULET2, CBRAS1, KILL2 and HEAD1 cores. Sediment samples were amalgamated over three periods of approximately 50 years.

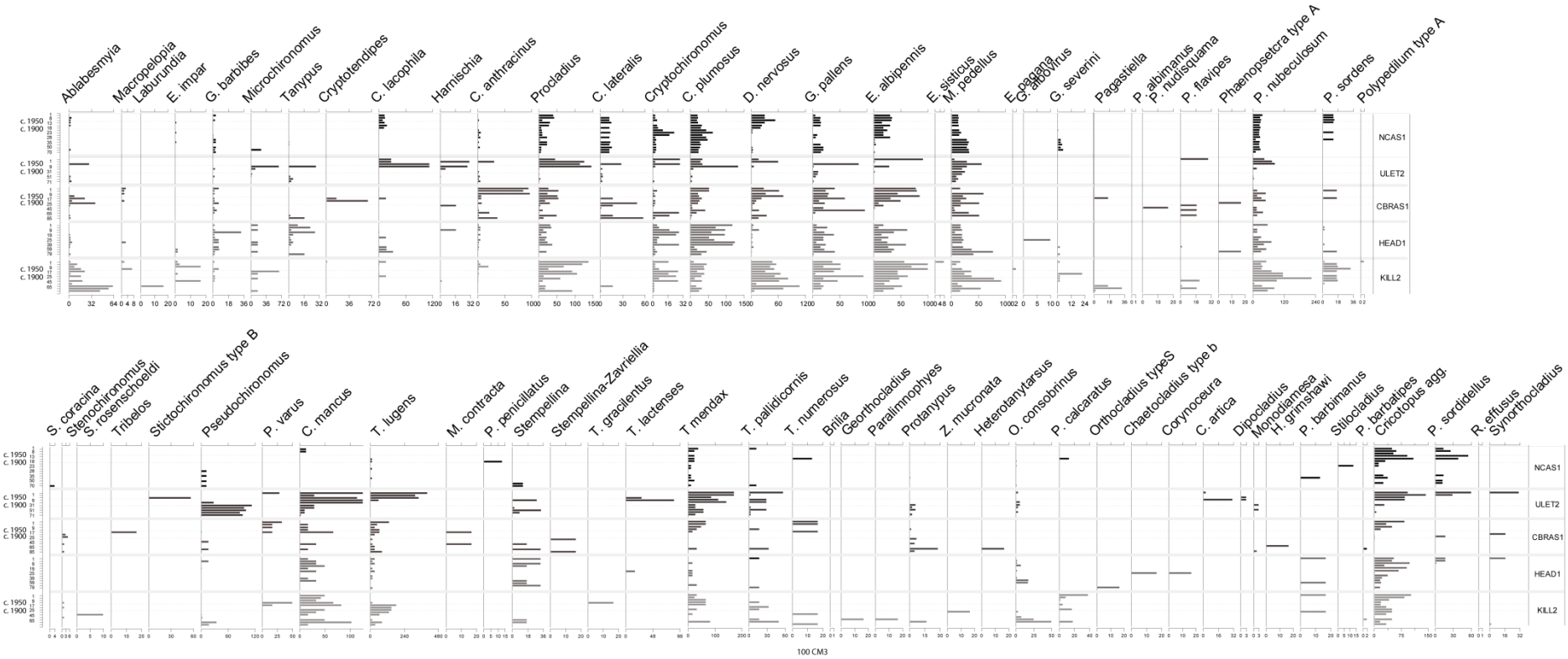

Figure 5-10. Stratigraphic summary of chironomid macrofossils of NCAS1, ULET2, CBRAS1, KILL2 and HEAD1 cores. Sediment samples were amalgamated over three periods of approximately 50 years.

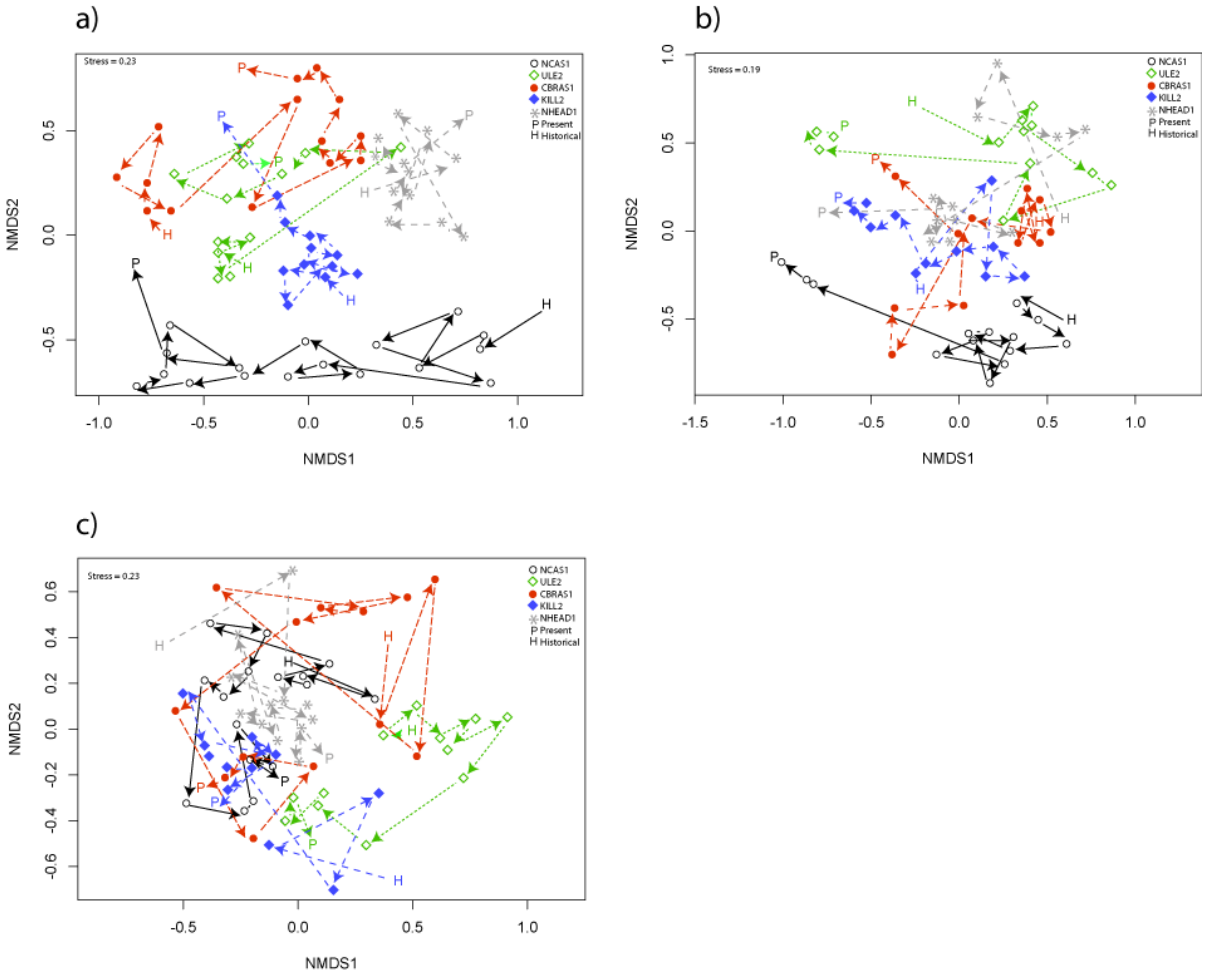

Figure 5-11. Nonmetric multidimensional scaling (NMDS) plot of community turnover among lakes. a) macrophytes; b) Invertebrates; c) Chironomids; Trajectory of change is indicated by an arrow. The most recent sediment sample from each core is indicated by P and the oldest one by and H.

The variation attributed to species sorting (*F* statistic) among the lakes increased over time for macrophytes (*F* = 6.68 for Phase 1 and *F* = 13. 87 for Phase 3) and invertebrates (*F* = 3.18 for Phase 1 and *F* = 6. 30 for Phase 3) but declined (*F* = 4.55 for Phase 1 and *F* = 3. 55 for Phase 3) for chironomids (Tables 5-2, 5-3, 5-4). Pairwise comparisons between lakes indicated five significant cases for macrophytes (*P*< 0.05 for all cases) and four for invertebrates and chironomids (P < 0.05) respectively in Phase 1 (Table 5-2 and 5-3). In Phase 2 two cases were significant for macrophytes (P = 0.03) and all six for invertebrates and chironomids (P < 0.05 for all cases) (Table 5-2 and 5-3). In Phase 3 all six pairwise comparison were significant for macrophytes (P < 0.05 for all cases), with four significant for invertebrates (P < 0.05 for all cases) and three for chironomids (P < 0.05 for all cases) (Table 5-2 and 5-3).

HMD analysis showed that within-lake variation in compositional heterogeneity attributed to relative abundance decreased for all three groups (Table 5-4). The within-lake proportion of change in macrophyte compositional heterogeneity variation over time was lowest for NCAS1 and ULET2 (0.11) followed by CBRAS1 (0.16) and highest for KILL2 (0.25) (Table 5-4). For invertebrates NCAS1 presented the highest variation over time (0.24) followed by CBRAS1 (0.20), KILL2 (0.04) and ULET2 (-0.08). For chironomids, ULET2 had the lowest variation (0.03), followed by NCAS1 (0.12), KILL2 (0.18) and CBRAS1 (0.26) (Table 5-4). Pairwise comparisons between time periods within each lake showed significant differences of macrophyte and chironomid assemblages for all sites between Phase 1 and Phase 3 (HMD: $P < 0.05$ in all cases). For invertebrates these differences were only evident in NCAS1 and CBRAS1 (Table 5-4).

HMD pairwise comparisons between sites revealed three significant differences for macrophytes and chironomids (NCAS1 vs. CBRAS1, ULET2 vs. CBRAS1 and ULET2 vs. KILL2; $P < 0.05$ for all cases) and one for invertebrates (NCAS1 vs. KILL2, $P = 0.034$) in Phase 1 (Table 5-4). In Phase 2there was only one significant difference for macrophytes (NCAS1 vs. CBRAS1, $P = 0.03$) and chironomids (CBRAS1 vs. KILL2, $P = 0.05$), but none were significant for invertebrates. In Phase 3 there were no significant differences for macrophytes and invertebrates and only one significant difference for invertebrates (NCAS1 vs. ULET2, $P = 0.046$) (Table 5-4).

Table 5-2. Results of perMANOVA analyses examining within and among-lake macrophyte, invertebrate and chironomid compositional heterogeneity changes at three periods of time (present-1950, 1950-1900, pre-1900) that correspond to three major compositional phases of species turnover.

	Macrophytes								Invertebrates								Chironomids							
Within-lake variation	NCAS1		ULET2		CBRAS1		KILL2		NCAS1		ULET2		CBRAS1		KILL2		NCAS1		ULET2		CBRAS1		KILL2	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
	7,88	0.0004	11,0	0.0004	13,16	0.0004	12,80	0.0004	6,22	0.0026	9,44	0.0004	4,35	0.0042	19,27	0.0004	3,3983	0.0032	13,58	0.0004	2,96	0.001	2,80	0.0004
	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*
Present-1950 vs. 1950-1900	2,70	0,033	2,77	0,033	3,61	0,033	5,27	0,033	4,02	0,033	2,35	0,03	2,68	0,033	3,24	0,033	1,6	0,062	2,1	0,033	1,9	0,0332	2,2	0,033
Present-1950 vs. pre-1900	3,72	0,030	4,38	0,030	4,40	0,030	3,43	0,030	2,71	0,030	3,24	0,03	2,13	0,030	7,81	0,030	2,8	0,0296	5,3	0,030	2,2	0,0296	1,6	0,030
1950-1900 vs. pre-1900	2,04	0,028	2,81	0,028	2,77	0,028	2,75	0,028	1,07	0,333	3,40	0,03	1,62	0,089	2,66	0,028	1,3	0,2014	3,6	0,028	1,2	NS	1,5	0,028
Average dissimilarity																								
c. Present-1950	38,5		21,8		23,4		22,6		20,1			44,3		21,4	22,1		27,2		31,4		22,9		35,3	
c. 1950-1900	54,7		32,8		28,5		25,8		34,8			41,5		57,3	32,6		46,2		41,8		56,6		34,9	
c. pre-1900	51,2		33,8		43,0		48,4		50,5			43,9		56,6	12,9		34,8		29,0		73,8		62,3	
Propotion of change (pre-1900 - present-1950)	12,7		12,0		19,6		25,8		30,3			-0,5		35,2	-9,2		7,6		-2,4		50,9		27,1	
Among-lake variation	pre-1900		1950-1900		present-1950				pre-1900		1950-1900		present-1950				pre-1900		1950-1900		present-1950			
	F	*P*	*F*	*P*	*F*	*P*			*F*	*P*	*F*	*P*	*F*	*P*										
	6,68	0.0002	4,58	0.0002	13,88	0.0002			3,18	0.0046	9,239	0.0002	6,30	0.0004			4,51	0.0004	5,44	0.0002	3,5538	0.003		
pairwise comparisons	t	*P*	t	*P*	t	*P*			t	*P*	t	*P*	t	*P*			t	*P*	t	*P*	t	*P*		
NCAS1 vs. ULET2	3,61	0.033	2,08	NS	4,62	0.033			2,26	0.033	2,67	0.033	2,5	NS			4,40	0.033	2,85	0.033	2,34	NS		
NCAS1 vs. CBRAS1	1,87	NS	2,42	0.029	2,37	0.029			1,92	0.029	2,43	0.029	4,1	0.029			2,31	0.029	1,66	0.029	2,47	0.029		
NVAS1 vs. KILL2	2,56	0.028	2,85	0.028	2,51	0.028			2,69	0.028	4,47	0.028	3,7	0.028			1,46	0.028	2,85	0.028	1,93	0.028		
ULET2 vs. CBRAS1	3,06	0.033	1,66	NS	5,75	0.033			1,09	NS	2,15	0.033	1,8	NS			1,19	NS	2,24	0.033	1,42	NS		
ULET2 vs. KILL2	2,31	0.026	1,45	NS	4,67	0.026			1,41	NS	4,03	0.026	2,1	0.026			2,51	0.026	2,79	0.026	1,83	0.026		
CBRAS1 vs. KILL2	1,98	0.030	2,35	NS	2,26	0.030			1,71	NS	2,93	0.030	1,9	0.030			1,63	NS	1,75	0.030	1,39	NS		
Total number of sig. cases		5		2		6				3		6		4				4		6		3		

Table 5-3. Results of homogeneity multivariate dispersion (HMD) analyses examining within and among-lake macrophyte, invertebrate and chironomid compositional heterogeneity changes at three interval of time (present-1950, 1950-1900, pre-1900) that correspond to three major compostional phases of species turnover.

	Macrophytes					Invertebrates					Chironomids				
Mean distance to centroid															
Period	NCAS1	ULET2	CBRAS1	KILL2	Avg.	NCAS1	ULET2	CBRAS1	KILL2	Avg.	NCAS1	ULET2	CBRAS1	KILL2	Avg.
c. Present-1950	0,22	0,13	0,19	0,13	0,17	0,11	0,27	0,11	0,13	0,15	0,17	0,18	0,18	0,20	0,18
c. 1950-1900	0,33	0,2	0,17	0,16	0,22	0,22	0,24	0,35	0,19	0,25	0,27	0,27	0,34	0,21	0,27
c. pre-1900	0,33	0,24	0,35	0,38	0,33	0,35	0,18	0,31	0,17	0,25	0,29	0,21	0,44	0,38	0,33
Propotion of change (pre-1900 - present-1950)	0,11	0,11	0,16	0,25		0,24	-0,08	0,20	0,04		0,12	0,03	0,26	0,18	

Among-lake pairwise comparisons	Macrophytes			Invertebrates			Chironomids		
	pre-1900	1950-1900	present-1950	pre-1900	1950-1900	present-1950	pre-1900	1950-1900	present-1950
	P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
NCAS1 vs. ULET2	NS	NS	NS	NS	NS	0.046*	NS	NS	NS
NCAS1 vs. CBRAS1	NS	NS	NS	NS	NS	NS	0.01	NS	NS
NVAS1 vs. KILL2	NS	0.03	NS	0.034	NS	NS	NS	NS	NS
ULET2 vs. CBRAS1	0.01	NS	NS	NS	NS	NS	0.001	NS	NS
ULET2 vs. KILL2	0.007	NS	NS	NS	NS	NS	0.036	NS	NS
CBRAS1 vs. KILL2	NS	NS	NS	NS	NS	NS	NS	0.05*	NS

Within-lake pairwise comparisons	Macrophytes				Invertebrates				Chironomids			
	NCAS1	ULET2	CBRAS1	KILL2	NCAS1	ULET2	CBRAS1	KILL2	NCAS1	ULET2	CBRAS1	KILL2
	P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
Present day-1950 vs. 1950-19	NS	NS	NS	NS	NS	NS	0.022	NS	0.047	NS	0.028	NS
Present day-1950 vs. pre-190(	0.004	0.004	0.003	0.006	0.002	NS	0.037	NS	0.025	NS	0.001	0.038
1950-1900 vs. pre-1900	NS	NS	0.047	0.011	0.027	NS	NS	NS	NS	NS	NS	0.025

5.6 Discussion

5.6.1 Phase changes and probable causes

Ordination revealed two major points of compositional change that divided assemblages from all three groups into three distinct phases. According to the radiometric dating models of NCAS1, KILL2 and CBRAS1, the first period of change corresponds roughly to the end of the 19th century and beginning of the 20th century (c. 1900) (Figs. 5-5, 5-6, 5-7). Based on historical records and previous research this period of change may be ascribed to two probable causes. First, around 1880-1890 there was a major hydrological disturbance caused by the first major drainage scheme in the ULE system (Price 1890). During this period, the plant-macrofossil record shows high abundances of *A. inundatum*, *A. plantago-aquatica,L. dortmanna* and bryophytes. These species can grow fully submerged but are more commonly associated with lake shorelines that present some degree of water level fluctuation (Sculthorpe 1967). Second, during the late 1800s and early 1900s, there was a gradual infrastructure development of water supply, storm drains and sanitary networks in nearby towns, which likely accelerated eutrophication (Battarbee 1986). The strong decline following this period of the plants *I. lacustris* and *L. dortmanna*, the chironomid taxa *Monodiamesinae*, *O. consobrinus* and *Protanypu*s and the bryozoan *P. fruticosa* is a typical response to eutrophication. It is likely therefore that compositional change in the late 1800s can be attributed to the joint interaction of changing hydrological conditions and eutrophication.

PC and NMDS analysis revealed a second less marked period of compositional change that, according to the dating model of NCAS1, CBRAS1 and KILL2 cores, corresponds to the 1950s-1960s. This coincides with: (1) a second attempt at water-level regulation (Erne Drainage and Development Act, Northern Ireland) in the early 1950s; and (2) an expanding urban population, the introduction of synthetic detergents and further development of sewage systems in the region (Battarbee 1986). Over this time period *A. inundatum* remains declined, along with those of *Myriophyllum* and *Nitella* species. A further change in this period was a marked increase in relative abundances of fine-leaved

Potamogeton(includes *P. berchtoldii/pusillus* and *P. obtusifolius*) and floating-leaved macrophyte species (includes *L. trisulca* and Nymphaeaceae). These changes suggest more stable hydrological conditions prevailed and a further acceleration of nutrient-enrichment (Davidson et al. 2005). The expansion of macrophyte-associated chironomid taxa, like *Dicrotendipes, Polypedilum, E. albipennis* and *Cricotopus,* and the expansion of molluscs and *Plumatella* spp. (excluding *P. fruticosa*) gives further support to an increase in the abundance of taller, canopy-forming macrophyte species and progression of eutrophication (Brodersen et al. 2001, Hartikainen et al. 2009).

5.6.2 Local vs. regional processes

This study provides strong support for both local and regional drivers of community change. This is manifested by an apparent combination of species-sorting and mass-effects. Thus, sedimentary records for all three biological groups (macrophytes, invertebrates and chironomids) suggest that species have sorted over time from those communities associated to low productivity environment (Phase 1) to those communities associated with nutrient-rich conditions in the present day (Phase 3) (Fig. 5-4, Fig. 5-8) (Table 5-1). *Isoetes-Lobelia-Callitriche* dominance along with high numbers of *N. flexilis* and *Myriophyllum* leaf remains in the older sediments suggests a community associated with low nutrient conditions (Spence 1967, Carpenter and Titus 1984, Arts 2002, Sand-Jensen et al. 2008, Salgado et al. 2010). Likewise, chironomids such as *P. flavipes*, *Monodiamesinae*, *Stempellina*, *Pseudochironomus, O. consobrinus*, *Protanypus*, *C. laricomalis, Cryptotendipes*, *C. intersectus* and *C. trifasciatus* have all been reported to inhabit low nutrient environments (Brodersen and Lindegaard 1999, Armitage 1995, Kansanen, 1985, Brundin 1949, Brodin 1982, Brodin 1986, Pinder and Reiss 1983, Brooks et al. 2007). Additional support for this idea comes from the occurrence of the bryozoan species *P. fruticosa* and *P. articulata* both of which are noted to occur in oligotrophic conditions (Økland and Økland 2000, Wood and Okamura 2005).

The gradual increase in representation of *Chara* spp., *Nitella* spp., *P. berchtoldii/pusillus, C. demersum* and floating-leaved species like *L. trisulca*, *L. minor* and Nymphaeaceae and the decline of *Isoetes-Lobelia-Callitriche* suggests a profound change in the ULE system and a transition to a more nutrient-rich environment during Phase 3 (e.g. Arts

2002, Smolders et al. 2003, Davidson et al. 2005, Sand-Jensen et al. 2008, Salgado et al. 2010). These changes were accompanied by a strong decline in abundances of *P. articulata* and *P. fruticosa* statoblasts and an increase in the abundance of statoblasts belonging to other species within the genus *Plumatella*. Hartikainen et al. (2009) have shown that *Plumatella* statoblast abundances are positively correlated with high nutrient concentrations. The increase in relative abundance of other chironomid taxa (*C. plumosus, C. anthracinus, Cryptochironomus, Polypedilum, Harnischia, T. mendax, T. pallidicornis, Cladotanytarsus mancus, Cricotopus* and *Tanypus*) along with an abrupt decline in the above described oligo-mestrophic chironomid taxa brings further evidence of a change towards a more nutrient-rich environment.

Further support for a joint interaction between eutrophication and connectivity over time comes from the trajectories of change for each lake that show similar patterns of convergence in multidimensional space (Fig. 5-11). This clustering, independent of local nutrient concentrations, is expected if both eutrophication and connectivity (dispersal) are jointly influencing compositional changes over time (Fig. 5-1c). The influence of dispersal is supported by several sources of information. A strong indication is simply the surprisingly high diversity of macrophytes despite nutrient concentrations that might be anticipated to result in much lower species diversity (Table 5-1). Thus there is a striking lack of disappearance of taxa over time and a persistence of macrophytes poorly adapted to enrichment e.g. *S. aloides, P. praelongus/lucens,* and *Myriophyllum* spp. (Arts 2002, Smolders et al. 2003, Davidson et al. 2005, Sand-Jensen et al. 2008, Salgado et al. 2010) (Chapter 3, Goldsmith et al. 2008).

A comparison of historical eutrophication patterns between the ULE system and the Norfolk Broads, eastern England, is also revealing. Previous authors have suggested a historical (pre-1900) resemblance between the aquatic flora of the Broads and that found in the fenland lakes of Northern Ireland (Small, 1931; Forbes, 2000). Despite similar contemporary nutrient levels and histories of eutrophication the above-mentioned macrophyte species have disappeared from nearly every lake in the Norfolk Broads (Ayres et al. 2008, Madgwick et al. 2011). The notable difference in contemporary macrophyte assemblages between these two systems may be attributed to dispersal. In

particular, the ULE system offers: (1) a higher degree of hydrological connectedness between lakes; and (2) the presence of a "mothership" lake (ULE) that is linked to almost all sites. The high degree of connectivity in the ULE system is achieved by the presence of rivers, streams, agricultural channels and flood events, which connect satellite lakes to the main ULE (Fig. 5-2). Furthermore, the ULE has been shown to sustain high macrophyte species richness due to its complex and large size (Chapter 3). These two characteristics (high diversity, high connectivity) may allow the satellite lakes and the ULE to act both as a refuge and as a source of propagules for a diversity of species. Thus, species poorly adapted to eutrophic conditions, such as *S. aloides*, *Myriophyllum* spp. and *P. praelongus/lucens,* may persist longer and have a reduced risk of extinction in ULE system due to high swapping of propagules between water bodies than in the less connected landscape of the Norfolk Broads.

Further evidence for the importance of dispersal and connectivity in the ULE system in maintaining biodiversity is provided by the responses of actively and passively dispersing taxa. Passively dispersing freshwater organisms rely on water flow (drift), animal vectors and wind for dispersal, while actively dispersing organisms are able to achieve dispersal themselves (e.g. via flight or swimming) (Bilton et al. 2001, Cáceres and D. Soluk 2002, Bohonak and Jenkins 2003, Figuerola 2005). In this study both macrophytes and invertebrates represented passively dispersing taxa. These two groups have presented diverse contemporary assemblages and exhibited little extinction over time. However, chironomids have lower species turnover and their community variation was mostly attributed to changes in relative abundance (Fig. 11c). The trajectories of change in multivariate space indicated that the two passively dispersing groups have greater temporal turnover than the more actively dispersing chironomids (Fig. 5-11). This result is gained by including in the study groups having different modes of dispersal and provides important support for the significance of dispersal and addresses predictions 2ii and 2iii posed in the introduction (Fig. 5-1).

5.6.3 Variation in change between sites

The macrophyte record revealed that, although there was a similar convergence in community composition in most lakes, the sequence of events in NCAS1 core was

somewhat different. This difference could be attributed to the fact that currently Castle Lough has moderate nutrient concentrations (TP 30 μg L^{-1}) in contrast to the high levels (TP > 70μg L^{-1}) in the other lakes, and hence its macrophyte communities are likely to show a reduced gradient of change (Fig. 5-1). Abundant remains of *Myriophyllum*, *Callitriche* and *S. aloides* in recent samples supports this conclusion. Furthermore, although this lake is directly connected to the main ULE through the River Finn, it is located in the most southern part of the ULE system which is characterised by more sheltered habitats. These differences could lead to communities typical of a more isolated water body.

The macrophyte record in core HEAD1 also differed from the other lake records. Although assemblages were compositionally similar to the other lakes, it was characterized by a reduced gradient of change. Currently this lake has the highest annual average of TP (398 μg L^{-1}) of the ULE system (Goldsmith et al. 2008) and hence it was expected to present a longer gradient in the trajectory of compositional change (Table 5-1, Fig. 5-1). This lack of variability could be ascribed to high sedimentation rates (Fig. 5-3) as suggested by the dating model. As a consequence, the samples may represent a relatively short period of time. However, as observed for Castle Lough, this different pattern was only observed for macrophytes. Patterns of change shown by invertebrates and chironomids were more similar to those in other sites. This suggests, as indicated by previous studies (e.g. Davidson et al. 2011), that changes in aquatic vegetation may precede those shown by invertebrates. However, another explanation could be high dispersal. Lough Head is not directly connected to the main ULE but is located in an area that is highly prone to flooding (Fig. 5-1) (www.dardni.gov.uk), and this relative position may therefore have prevented species sorting and extinctions through constant propagule inputs (Shmida and Wilson 1985). Unfortunately, the lack of robust dates precludes any attempt to test this idea.

5.6.4 Variation in compositional heterogeneity

The variation in compositional heterogeneity of the biological assemblages could have three causes: (1) a within-lake variation in the total number of individuals (relative

abundances); (2) a within-lake variation in the total number of species (α-diversity); and/or (3) a within-lake change in the identity of species present (Warwick and Clarke 1993). In the ULE system variability of compositional heterogeneity over time was primarily attributed to variation in the identity of species present and to a lesser extent, to changes in the relative abundances of species within assemblages with two distinctive patterns (Tables 5-2 and 5-3): First HMD analyses showed that with increasing eutrophication, within-lake assemblages of macrophytes, invertebrates and chironomids became significantly more homogenous (reduction in mean distance to centroid) (Table 5-3); and, second, perMANOVA analyses showed that differences between lakes (regional β-diversity) attributed to the within-lake variation of types of species present increased as eutrophication progressed (greater *F* statistic) (Table 5-2). These results were obtained from independent analyses of assemblages of three taxonomic biological groups within and between lakes suggesting that this is a consistent pattern, which occurs in lakes communities at both local and regional scales.

Although compositional heterogeneity of biotic assemblages between sites has been correlated positively with productivity (Chase and Leibold 2002), recent studies have demonstrated that, following eutrophication, several biological groups including macrophytes (Chapter 3), benthic invertebrates (Donohue et al. 2009) and zooplankton (Chase 2007), show a similar trend of compositional homogenisation with eutrophication at the local and regional scales. Two possible mechanisms have been suggested to explain this homogenising trend: (1) a decrease in habitat and trophic heterogeneity due to a reduction in macrophyte structure and a greater reliance on open-water productivity (Donohue et. al 2009); and (2) increasing stress through changes in environmental conditions, which could occur independently of alterations in habitat heterogeneity and which are driven by niche selection resulting in the exclusion of poorly competitive taxa (Loreau 2000, Chase et al. 2007, Donohue et al. 2009). The data indicate that, for the ULE system, both mechanisms probably interacted over time promoting a shift from a dynamic phase where local communities varied constantly in composition (c. pre-1900) to a transitional phase where local communities gradually decline in compositional

variability (c. 1950-1900) to a subsequently constant phase where local communities varied little in composition (c. present day-1950).

In the ULE system pre-1900 hydrological conditions were unstable characterised by stochastic water-level changes between summer and winter and concurrent flood events (Price 1890, Cunningham 1992). Previous studies have shown that recurrent flood events can reset macrophyte communities from year to year, both in terms of species relative abundances and richness, by removing plant stands and by homogenising communities through a high flux of propagules (Sousa et al. 2011, Ward 1998, Amoros and Bornette 2002). Long-term studies on terrestrial fire-prone plant communities have also illustrated that stochastic environmental fluctuations associated with recurrent fire events maintain stable communities at the metacommunity scale but results in highly unstable communities at the local scale (Thuiller et al. 2007). Therefore, it is likely that concurrent and stochastic hydrological disturbances in the ULE system for pre-1900 promoted the observed regionally dynamic phase of within-lake heterogeneous communities that ultimately changed and began to converge following dredging works in the 1890s and the onset and progression of eutrophication.

The engineering work caused water levels in the main Lough to drop by around 1.5 meters, causing less extensive variation in water levels and flood events (Cunningham 1992). This hydrological modification combined with an early nutrient enrichment of nutrients would have created a new set of more stable environmental conditions that changed gradually over time (especially eutrophication) allowing species to sort according to their environmental optima (Leibold and Norberg 2004). Further water level disturbance in the 1950s and the intensification of eutrophication would have reduced the frequency and extent of floods, and hence dispersal rates, promoting stronger species sorting in each lake with a concomitant homogenisation of assemblages (Leibold and Norberg 2004). If true, these alternative phases of change in compositional heterogeneity suggest that from a decadal to centennial scale, shifts between alternative community compositional phases occur gradually over time as suggested by Sayer et al. (2010).

The perMANOVA analyses revealed two other key aspects in the variation of compositional heterogeneity between passive and active dispersers. First, the variance

attributed to species sorting (*F* statistic) for macrophyte and invertebrate assemblages increased approximately two-fold while little variation and a slight decrease over time was observed for chironomid assemblage structure (Table 5-2). This pattern concurs with the initial predictions (2ii and 2iii) and the observed trajectories of change in the NMDS multivariate space (Fig. 5-11) bringing new evidence of the effects of for dispersal in compositional heterogeneity over time.

Second, the regional variability of within-lake variation (β-diversity) in species showed an inverse pattern between macrophyte and both chironomid and invertebrate assemblages (Table 5-2). Macrophyte β-diversity was highest for Phase 1 (c. pre-1900) and Phase 3 (c. present day-1950), while for chironomid and invertebrate assemblage β-diversity was highest for Phase 2 (c. 1950-1900). According to the mean distance to centroid and average dissimilarity values, macrophyte assemblages were highly heterogeneous during Phase 1 and homogenous during Phase 3. This trend concurs with contemporary studies (Chapter 3) showing that, in the ULE system, macrophyte β-diversity was highest at both high and low compositional levels of heterogeneity, and lowest at intermediate levels of compositional heterogeneity. Assessing the significance of the trend for the present study it is however impossible due to the limited number of comparisons. Due to the significant role of macrophytes in structuring invertebrate and chironomid species assemblages in the ULE system (Chapter 2), it is likely that differences in β-diversity between macrophytes and the two faunal groups may be attributed to an intermediate disturbance in habitat structure effect (Connell 1978). Within this framework, habitat structure homogenisation or large increases in habitat heterogeneity may lead to specific niche specialisation and hence a homogenisation of invertebrate and chironomid assemblages between sites. However a larger set of lakes is needed to confirm this pattern.

5.6.5 Implications for conservation

The evidence raised in this study from sediment samples gives support for the idea that despite a history of eutrophication, in the present day there are surprisingly high levels of diversity in the ULE system that are maintained by dispersal (Chapter 3). Nonetheless,

the observed temporal homogenisation of assemblages mediated by an increase in few species dominance and the increased regional β-diversity over time indicates that this may be a misleading scenario and that the system is on the verge of change. By studying changes in species dominance over time, the study in Chapter 4 indicates that that in metacommunity landscapes changes in dominance might occur more rapidly than changes in species richness. Hence, much stronger efforts should be made to the understanding of the effects of eutrophication in effecting compositional homogeneity in the region. Contemporary analysis of species occurrence turnover (Chapter 2) and on variability in compositional heterogeneity of assemblages (Chapter 3) suggest that the effect of eutrophication in structuring biological assemblages is becoming more pronounced even over a period of 2 years (from 2007 to 2009). Consequently, diversity levels can be expected to drop and with this a new more homogenous local and regional phase of compositional variability will result. These trends raise the possibility that the ULE system is exhibiting a time lag in its response to eutrophication that has been mediated by the co-influence of high hydrological connectedness. Time lags in responses to environmental change have been described previously for marine systems. For instance, O'dea et al. (2007) showed that, after the isolation of the Caribbean Ocean from the Eastern Pacific Ocean by uplift of the Panamanian Isthmus, extinction did not occur simultaneously but there was a lag in the extinction rates (especially in molluscs and corals) attributed to the co-influence of other variables that were not included in the study. If this applies to the ULE system, much stronger efforts should be made to abate eutrophication in the region.

5.6.6 Constraints and caveats

There are caveats to the use of sediment core records to infer temporal changes in species composition. Specifically, although all five lakes showed a similar trend of change, radiometric dating for cores ULET2 and HEAD1 was precluded. This limits inferences on the possible drivers of change over time and thus comparisons across lakes. Fortunately, the phases of compositional change from Castle Lough, Killymackan Lough and Cornabrass Lough were well-defined and similar, thus adding confidence to interpretations of the history of community change in the ULE system. Moreover, the

degree and change in species assemblages observed in ULET2 for macrophytes, chironomids and invertebrates concur with a previous diatoms-based study in the ULE that had a successful radiometric dating (Battarbee 1986). On the other hand, interpretations for Lough Head were more problematic as macrophyte assemblages show a more uniform composition over time. However, chironomid and invertebrate assemblages provide again support for inferences as they showed similar trends to the other lakes.

Another limitation is the lack of data on historical environmental changes, other than eutrophication and connectedness, which may have played a role in structuring communities over space and time. For example, changing inputs of dissolved organic carbon (DOC), have been reported to provide a degree of protection against some of the effects of eutrophication (Girvan and Foy 2006) and are known to have affected softwater macrophyte abundances in upland lakes of Fermanagh, Northern Ireland (McElarney et al. 2010). Although influence of DOC change on the study lakes is currently unknown, its importance, along with other environmental variables, in structuring present day macrophyte, chironomid and invertebrate communities in ULE was minor.

Since the end of the 1990s, *D. polymorpha* has invaded much of the ULE system and has been inferred to have displaced other native mussel species, created shifts in water clarity and altering ULE freshwater communities (Rosell et al. 1999, Minchin et al. 2003). This species acts as an ecosystem engineer that modifies the physical environment by increasing light penetration, thus improving conditions for macrophyte assemblages (Higgins and Vander Zanden 2010). However, the evidence from the present study indicates that major compositional changes started long before *D. polymorpha* invasion and no major signs of change were detected in the macrophyte data post-1990s. Field observations during contemporary macrophyte surveys in the study lakes also suggested that abundances of *D. polymorpha* were low (J. Salgado, pers. obs.), suggesting only minor influence at present.

5.7 Conclusions

By using a multi-proxy multi-lake palaeolimnological approach and testing a series of predictions regarding the influence of eutrophication and connectivity in structuring active and passive dispersing organisms over time (Fig. 5-1), this study reveals key interconnected aspects on the ecological history of the ULE system. For instance, the sediment record indicated two major points of compositional change that divided the target biological assemblages into three distinct phases, which corresponded to c. pre-1900, c. 1950-1900 and present-day-1950. The combined evidence of macrophyte, chironomid and invertebrate macrofossils indicated that these phases of change were attributed to a progressive increase in eutrophication since the early 1900s and to two hydrological dredging schemes that occurred at the end of the 1800s and 1950s.

Closely associated therewith is the long-term development of passively and actively dispersing organisms that reflected that both eutrophication and connectivity influenced community structure trajectory of change (prediction iii; Fig. 5-1c). Detected differences in length of trajectories were relatively similar between lakes and local diversity of recent (c. present day-1950) sediment samples reflected the presence of a few competitive dominants such as floating-leaved macrophyte species and other less adapted species like broad-leaved *Potamogeton* and *Myriophyllum*.

In addition, this study supports previous research (e.g. Donahue et al. 2009, Chapters 3 and 4) that has found eutrophication to decrease the within-lake compositional heterogeneity of organisms and brings further evidence on its homogenisation effects over time. Moreover, it reveals that regional β-diversity attributed to the within-lake variation of types of species increased as eutrophication progresses. This pattern has been detected on contemporary macrophyte assemblages (Chapter 3) and attributed to species-sorting processes. Finally, the data provides new support on the influence of connectivity and eutrophication in structuring within-lake compositional heterogeneity by showing a stronger change in temporal β-diversity (attributed to the within-lake variation in species identities) in the passive dispersing organisms (macrophytes and invertebrates) than in

the actively dispersing chironomids. This trend supports the initial predictions 2ii and 2iii (Fig. 5-1d).

6 Chapter 6 – Summary, conclusions and future directions

6.1 Introduction

The primary focus of the research contained in this thesis was to investigate the relative importance of eutrophication and connectivity (dispersal) in structuring macrophyte and invertebrate communities in the Upper Lough Erne system, Northern Ireland. Chapters 2-5 presented analyses of the biological groups representative of the benthic communities in a set of shallow lakes across both spatial and temporal scales. Key findings are summarised below. The chapter concludes with considerations for management and future research directions.

6.2 Summary

6.2.1 Spatial contemporary dynamics

The first part of the thesis focused on whether contemporary biological communities are influenced by both eutrophication and connectivity processes and if there are any geographically predictable patterns between community similarity and environmental or spatial gradients.

CHAPTER 2 –This chapter assessed the relative importance of eutrophication and connectedness (dispersal) in structuring actively dispersing (chironomids) and passively dispersing (macrophytes and filter-feeding invertebrates) organisms in a set of 20 satellite shallow lakes. Using macrophyte, invertebrate and chironomid relative abundances, lake environmental variables (water chemistry and physical parameters) and dispersal predictors (overland and watercourse distances between lakes), the study demonstrated that eutrophication, lake surface area and lake maximum water depth play a significant

role in structuring contemporary communities and that the relative importance of spatial predictors (overland and watercourse distances) varied according to dispersal mode of the organism. Submerged macrophyte distributions were explained by both overland and watercourse distances, while watercourse distances best predicted invertebrate distributions and overland distances best predicted chironomid distributions. There was no spatial autocorrelation between community similarity and environmental or spatial gradients, implying that the main Upper Lough Erne mediates extensive dispersal. This study also provided evidence that metacommunity structure varied between sampling years from a combined species-sorting and mass-effect perspective to a species-sorting perspective.

CHAPTER 3 – This study further explored the effects of eutrophication and connectivity in structuring contemporary macrophyte species diversity and compositional heterogeneity within and between the Upper Lough Erne (ULE) and a set of 20 well-connected shallow satellite lakes. The results indicated that despite high nutrient levels most study sites are characterized by high macrophyte α-diversity, a trend attributed to the hydrological connectedness of the system. Local (within-lake) variation in macrophyte assemblages was reflected by differences in relative abundances and composition. Total nitrogen, total phosphorus, chlorophyll-a, surface area, water depth and α-diversity emerged as the most significant variables explaining within-lake macrophyte compositional heterogeneity at the regional scale. Within-lake heterogeneity was related inversely to nutrient enrichment (as indicated by measurements of total phosphorus, total nitrogen and chlorophyll-a). Nutrient-rich lakes had more homogenous macrophyte assemblages than lakes with lower nutrient levels. Larger lakes were characterized by more heterogeneous and diverse macrophyte assemblages. Homogenous lakes were mostly associated with higher levels of chlorophyll-a, low α-diversity and relatively small and shallow. Low chlorophyll-a, high α-diversity, large surface area and deeper waters generally characterized highly heterogeneous lakes. Differences in within-lake compositional heterogeneity in the ULE system (regional β-diversity) varied in a U-shaped relationship, where regional β-diversity was minimized at intermediate levels of within-lake compositional heterogeneity.

6.2.2 Temporal dynamics

The second part of this study was to understand how patterns of species turnover, diversity and compositional heterogeneity developed within and between lakes over time.

CHAPTER 4 – This chapter focused on the long-term effects of nutrient enrichment on species turnover and community compositional heterogeneity, and the potential mechanisms allowing coexistence of submerged macrophytes, invertebrates and chironomids from three areas of Castle Lough. More specifically, this study tested: (1) whether nutrient enrichment promotes local dominance by some species and reduces compositional heterogeneity between sub-localities; and (2) whether the same metacommunity dynamics that affect diversity at the lake-landscape scale occur at the within-lake scale (i.e. an existence of a continuum of "sub-metacommunities"). Temporal assembly dynamics showed that communities in each lake area changed from c. pre-1900 being heterogeneous (even) to being more homogenous (dominated by a few species) in the present day. This change was accompanied by an increase in temporal β-diversity and little extinction over time. These trends are consistent with transitions that would be expected as a result of dispersal and advancing eutrophication. Spatial assembly dynamics revealed that c. pre- 1900 differences between areas (spatial β-diversity) were low and increased over time being highest from c. 1950 to present. This trend supports the notion of a continuum of "sub-metacommunities" where species sorting processes also occur at the within-lake scale of small and shallow vegetated lakes. Changes in dominance occurred more rapidly than changes in species richness and there is evidence that source-sink dynamics have allowed persistence of species that are poorly adapted to enrichment.

CHAPTER 5 – By using a multi-proxy, multi-lake palaeoecological approach, this final chapter addressed how species turnover and compositional heterogeneity developed through time between five lakes in response to advancing eutrophication and hydrological change. This study demonstrated that the Upper Lough Erne system is now far from its preindustrial oligotrophic-mesotrophic ecological condition. Three relatively distinct phases that corresponded to c. pre-1900 (oligo-mesotrophic assemblages), to c. 1950-1900 (meso-eutrophic assemblages) and to c. present-day-1950 (eutrophic

assemblages) were inferred from the long-term dynamics of passively (macrophytes and invertebrates) and actively (chironomids**)** dispersing organisms in the cores. These phases reflected a progressive increase in eutrophication since the early 1900s and to two hydrological dredging schemes that occurred at the end of the 1800s and 1950s. The data also revealed that within-lake compositional heterogeneity declined with eutrophication, while regional β-diversity attributable to within-lake variation in the identity of species increased. These findings accord well with previous studies that have found a decrease in the compositional variability of organisms within and between eutrophic lakes and bring new evidence of the homogenising effects of eutrophication at the local and regional scale. By incorporating metacommunity theory, this study also provides evidence that hydrological connectedness has buffered the effects of eutrophication and maintained local diversity over time via species re-introductions.

6.3 Conclusions

By undertaking comparative analyses over spatial and temporal scales for three groups of organisms, which differ in their dispersal modes from a set of shallow lakes in the ULE system, this thesis demonstrates that eutrophication and connectivity play fundamental and complex roles in determining community structure. The incorporation of a metacommunity theory perspective has been particularly effective in identifying key drivers of the changing ecology of the ULE system. Thus, despite eutrophication, the high connectedness of the system is helping to maintain surprisingly high levels of local diversity. Although, dispersal rates were not quantified per se, the co-occurrence of species less tolerant to high nutrient conditions at most sites and the relatively greater representation of actively dispersing organisms agree with previous theoretical and experimental work that demonstrates the importance of intermediate dispersal rates on species richness and abundance patterns. In addition, variability in compositional heterogeneity of contemporary macrophyte assemblages revealed a significant negative association with nutrient concentrations. This trend was supported by the sedimentary data from multiple lakes, which collectively revealed a homogenisation of within-lake

aquatic assemblages as eutrophication advanced through time. Closely associated therewith was an increase in the within-lake variability of species composition between lakes (β-diversity) as eutrophication progressed. Furthermore, the study gained evidence that lake surface area and water depth were positively associated with macrophyte species diversity and assemblage variability. This finding suggests that the main ULE plays a vital role in maintaining species diversity of all groups by acting as both a refuge and source of colonists within the system.

There are two main caveats for using the palaeoecological records to infer changes in species composition in this study. First, some macrophyte species like *U. vulgaris, S. sagittifolia* and *E. canadensis* are poorly preserved in the fossil record. The second is the lack of radiometric dating for the main ULE and Lough Head. Fortunately, the sedimentary records contained many of the modern predominant taxa that are required to quantify major transitions in community structure through time (Heino et al 2010; Allen et al 2011). Furthermore, trends of community change observed in the sedimentary data were consistent among the three biological groups, the five lakes for which palaeo-records were examined and the 20 study lakes for which contemporary assemblages were studied. These features indicate that the conclusions of the study appear to be robust and demonstrate that palaeoecological studies can provide a unique opportunity to track the development and responses of communities over multiple decades. This time frame is commonly neglected in metacommunity studies but can be essential to improve understanding of the mechanisms that drive community assembly.

6.4 Management implications

As a result of an increase in nutrient loading over the last century there has been a dramatic decline in the ecological integrity of most temperate shallow lakes (Roelofs 2002). As this process continues, plantless lakes or lakes with mono-specific macrophyte stands are becoming more and more common and macrophyte-diverse lakes are a rare exception. This study illustrates that the ULE system is one of those rare remaining

hydrological systems with wonderfully diverse macrophyte assemblages in most of its associated lakes. Nonetheless, reductions in the number of species, the homogenisation of communities through time, the variability in the identities of species between lakes and the significant negative trend observed between within-lake compositional heterogeneity and nutrient concentration all provide evidence that the system may be on the verge of major change. This is strongly supported by the palaeolimnological data, which revealed that in spite of being characterised by currently diverse communities, the ULE system is a long way from its pre-industrial ecological condition.

It is common practice to focus management actions on the effects of environmental change (e.g. eutrophication) and loss or gain of species richness (Hillebrand et al. 2008). However, concentrating exclusively on species richness and the effects of eutrophication may limit a full understanding of the structure and function of well-connected freshwater landscapes. Evidence from this study stressed the need to integrate other aspects such as connectivity, surface area and other attributes of diversity like species evenness. Hydrological connectedness is a key geomorphological feature in the ULE system. Despite nutrient-enrichment connectedness has helped to maintain high levels of diversity in most lakes as a result of dispersal. In addition, sedimentary data have demonstrated that changes in species evenness or dominance are likely to occur more rapidly than changes in species richness. Consequently, is imperative for the conservation and management of the system to acknowledge that species richness and evenness can respond in different ways to human impacts. The results also indicate that the main ULE maintains diversity by acting as a species refuge and source of colonists within the system. Hence, management and restoration strategies must pay special attention on the main ULE.

6.5 Future directions

Using contemporary and palaeolimnological techniques to characterise the abundances of different biological groups represents a novel way to understand the mechanisms of

community assembly in well-connected systems (metacommunities) at both the spatial and temporal scales. In particular, the inclusion of a temporal scale (decadal to centennial) provides better inferences than the great majority of metacommunity studies that incorporate only a spatial perspective. Temporal studies also reveal how the relative importance of regional and historical processes can change substantially over time. Below I elaborate on future directions for research that would further improve understanding of the dynamics of the ULE system and how it is assembled.

Although a substantial number of lakes were sampled by both contemporary surveys and palaeolimnological analyses, a larger data set that incorporates a greater gradient in connectivity and environmental heterogeneity would be of great interest with regard to firmly substantiating the inferences I have made on the basis of the studies conducted so far. The current study was supported by a large data set of macrophyte surveys and environmental variables obtained from ENSIS ltda., and Goldsmith et al. (2008). A subset of lakes from these databases was incorporated in order to gain representation of enrichment gradient and different levels of connectivity. However, both datasets set (ENSIS and Goldsmith et al. 2008) comprised eutrophic to hypertrophic lakes and all lakes had some degree of connectivity to the main ULE. Incorporating a set of lakes that are not affected (or are less affected) by eutrophication or completely isolated is desirable to fully contrast the effects of eutrophication and connectivity in the system.

Closely associated with the above would be an expansion of contemporary surveys into new sites along with further palaeolimnological analyses in order to better characterise rates of homogenisation of biological assemblages due to eutrophication. This poorly studied area for shallow lakes and riverine systems requires much further attention. Surveying a larger set of lakes would be time-consuming and expensive but a potentially cheaper and quicker approach that emerged from this study would be to focus on samples from the surface and bottom of cores to establish long-term changes from a larger set of lakes (Smol 2000). Given the fact that the sedimentary data revealed that overall, the largest differences in compositional heterogeneity, were observed between pre-1900 and present day (Chapters 4 and 5), using such a top-bottom approach might be a reliable method to establish homogenisation effects and rates.

Finally, it would be highly relevant to characterise actual dispersal rates. In this study, dispersal rate was inferred indirectly by degree of connectivity (using spatial and watercourse distances), spatial variability in species abundance and composition and assignment of taxa to modes of dispersal. Although watercourse distance was used in this study to infer dispersal rates, direction of water flow was not. This key aspect could be incorporated in future to obtain a more accurate picture of dispersal routes. Dispersal rates and directions are inherently difficult to measure in practice but mesocosms experiments between lakes that are directly connected can provide a direct approximation for some taxa (e.g. Cottenie and De Meestre 2004). Other approaches include measures of gene flow and mark-recapture experiments. No single approach is likely to be applicable to all taxa of interest and it would be necessary to identify focal taxa for such investigation since studying everything would be unrealistic. Such key taxa might include the bryozoan *Cristatella mucedo* and cladoceran species within the genus *Daphnia*. These two groups are relatively easy to sample and have been previously analysed for gene flow and mark-recapture experiments for other temperate lake systems (De meester 1996, Freeland et al. 2001, Charalambidou et al. 2003, Cottenie and De Meestre 2004).

References

Abernethy, V. J., Sabbatini, M. R., and K. J. Murphy. 1996. Response of *Elodea canadensis* Michx. and *Myriophyllum spicatum* L. to shade, cutting and competition in experimental culture. Hydrobiologia 340:219–224.

Abernethy, V.J. and N.J. Willby. 1999. Changes along a disturbance gradient in the density and composition of propagule banks in floodplain aquatic habitats. Plant Ecology140, Number 2, 177-190

Aldridge, D. C., and D. C. Horne. 1998. Fossil glochidia (Bivalvia, Unionidae): identification and value in palaeoenvironmental reconstructions. Journal of Micropalaeontology 17:179-182.

Allen, M. R., Vandyke, J. N., and C. E. Cáceres. 2011. Metacommunity assembly and sorting in newly formed lake communities. Ecology 92: 269–275.

Amarasekare, P., and R. M. Nisbet. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist 158:572–584.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6:1109–1122

Amoros, C., and G. Bornette. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshwater Biology 47: 761–776.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Anderson, M. J. 2005. PERMANOVA. Permutational multivariate analysis of variance: a computer program. Department of Statistics, University of Auckland, Auckland, Australia.

Anderson, M. 2006. Distance Based Tests for Homogeneity of Multivariate Dispersions. Biometrics 62:245–253.

Anderson, M., Ellingsen, K., and B. McArdle. 2006. Multivariate dispersion as a measure of β diversity. Ecology Letters 9:683–693.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N.

J. B., Stegen, J. C. and N. G. Swenson, 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14: 19–28.

Appleby, P. G. 2001. Chronostratigraphic techniques in recent sediments. In W M Last and J P Smol (eds.) Tracking Environmental Change Using Lake Sediments. Vol. 1: Basin Analysis, Coring, and Chronological Techniques. Kluwer Academic Publishers, Dordrecht. Pp171-203.

Appleby, P. G., Richardson, N., Nolan, P. J. 1992. Self-absorption corrections for well-type germanium detectors. Nuclear Instruments and Methods B 71: 228-233.

Appleby, P. G., Nolan, P. J., Gifford, D. W., Godfrey, M. J, Oldfield, F., Anderson, N. J., and R. W. Battarbee.1986. ^{210}Pb dating by low background gamma counting. Hydrobiologia 141: 21-27.

Armitage, P. D., Cranston, P. S., and L. C. V. Pinder. 1995. The chironomidae. The Biology and ecology of non-biting midges. Chapman and Hall, London.

Arts, G. 2002. Deterioration of atlantic soft water macrophyte communities by acidification, eutrophication and alkalinisation. Aquatic Botany 73:373–393.

Ayres, K., Sayer, C. D., Perrow, M., and E. Skeate. 2008. The contribution of palaeolimnology to shallow lake management: an example from Upton Great Broad, Norfolk, UK. Biodiversity and Conservation 17:2153–2168.

Barko, J. W., Hardin, D. G., and M. S. Matthews. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. Canadian Journal of Botany 60:877-887.

Barko, J., and R. Smart. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. The Journal of Ecology 71:161–175.

Barko, J., and R. Smart. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. Ecology 67:1328–1340.

Barrat-Segretain, M. H. 1996. Strategies of reproduction, dispersion, and competition in river plants: A review. Vegetatio 123:13-37.

Barrat-Segretain, M.H., and C. Amoros. 1996. Recolonization of cleared riverine macrophyte patches: importance of the border effect. Journal of Vegetation Science 7:769–776.

Barrat-Segretain M.H., Bornette ,G., and A. Hering-Vilas-Boas. 1998. Comparative

abilities of vegetative regeneration among aquatic plants growing in disturbed habitats. Aquatic Botany 60:201–211.

Bastviken, D. T. E., Caraco, N. F., and J. J. Cole. 1998. Experimental measurements of zebra mussel (*Dreissena polymorpha*) impacts on phytoplankton community composition. Freshwater Biology 39:375–386.

Battarbee, R. 1986. The Eutrophication of Lough Erne inferred from changes in the diatom assemblages of ^{210}Pb- and ^{37}Cs dated sediment cores. Proceedings of the Royal Irish Academy B: Biological, Geological, and Chemical Science 86B:141–168.

Beisner, B., Peres-Neto, P., Lindström, E., Barnett, A., and M. Longhi. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87:2985–2991.

Bilton, D., Freeland, J., and B. Okamura. 2001. Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics 32:159–181.

Birks, H. H. 2001. Plant macrofossils. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments, vol 3: terrestrial, algal and siliceous indicators. Kluwer, Dordecht, pp 49–74.

Birks, H. H. 1973. Modern macrofossil assemblages in lake sediments in Minnesota. In: Birks H.J.B. & West R.G. (eds), Quaternary Plant Ecology. Blackwell Scientific Publi- cations, Oxford, pp. 173–189.

Blackburn, T.M., Cassey, P., and K. J. Gaston. 2006. Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. Journal of Animal Ecology 75:1426–1439.

Bohonak, A. J., and D. G. Jenkins. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates.Ecology Letters 6:783–796.

Borcard, D., and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153:51–68.

Borcard, D., Legendre, P., and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045–1055.

Bornette, G., Amoros, C., and N. Lamouroux. 1998. Aquatic plant diversity in riverine

wetlands: the role of connectivity. Freshwater Biology 39:267–283.

Bornette, G., Piégay, H., Citterio, A., Amoros, C. and V. Godreau. 2001. Aquatic plant diversity in four river floodplains: a comparison at two hierarchical levels. Biodiversity and Conservation 10:1683-1701.

Bradshaw, A. 1965. Evolutionary significance of phenotyipc plasticity in plants. Advances in Genetics 13:115-151.

Brauman, K. A., Daily, G. C., Duarte, T. K., and H. A. Mooney. 2007. The nature and value of ecosystem services: an overview highlighting hydrologic services. Annual Review of Environment Resources 32:67–98.

Brauns, M., Garcia, X. F., Pusch, M. T., and N. Walz. 2007. Eulittoral macroinvertebrate communities of lowland lakes: discrimination among trophic states. Freshwater Biology 52:1022–1032.

Brodersen, K., and C. Lindegaard. 1999. Classification, assessment and trophic reconstruction of Danish lakes using chironomids. Freshwater Biology 42:143–157.

Brodersen, K., Odgaard, B., Vestergaard, O., and N. J. Anderson. 2001. Chironomid stratigraphy in the shallow and eutrophic Lake Sobygaard, Denmark: chironomid-macrophyte co-occurrence. Freshwater Biology 46:253–267.

Brodin, Y. W. 1986. The postglacial history of Lake Flarken, Southern Sweden, interpreted from subfossil insect remains. Internationale Revue der Gesamten Hydrobiologie 71: 371–432.

Brodin, Y. W. 1982. Palaeoecological studies of the recent development of the lake of Lake Växjösjön. IV Interpretation of the eutrophication process through the analysis of subfossil chironomids. Archiv für Hidrobiologie 93:313-136.

Brooks, S. J., Heiri, O., and P. G. Langdon. 2007. The identification and use of palaearctic chironomidae larvae in palaeoecology. Technical guide No. 10. Quaternary Research Association, London.

Brown, B., and C. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology 79:571–580.

Brundin, L. 1949. Chironomiden una andere Bodentiere der sudschwedischen Urgebirgseen. Ein betrgag zur Kenntnis der bodenfaunistischen Charakterzuge schwedischer oligotropher Seen. Report of the Institute of Freshwater Research,

Drottingholm 30:1-914.

Burks, R., and E. Jeppesen. 2001. Littoral zone structures as *Daphnia* refugia against fish predators. Limnology and Oceanography 46: 230-237.

Bushnell, J. H. 1966. Environmental relations of Michigan Ectoprocta, and dynamics of natural populations of *Plumatella repens*. Ecological Monographs 36:95–123.

Cáceres, C. E., and D. Soluk. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131:402–408.

Cadotte, M. W. and T. Fukami. 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. Ecology Letters 8:548–557.

Cadotte, M. 2006a. Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. Ecology 87:1008–1016.

Cadotte, M. 2006b. Dispersal and Species Diversity: A Meta-Analysis. The American Naturalist 167 6:913-924.

Canfield, D. E. Jr., Shireman, J., Colle, D. E., Haller, W. T., Watkins, C. E. II, and M.J. Maceina. 1984. Prediction of chlorophyll a concentrations in Florida lakes: importance of aquatic macrophytes. Canadian Journal of Fisheries and Aquatic Science 41:497-501.

Capers, R., Selsky, R., and G. Bugbee. 2010. The relative importance of local conditions and regional processes in structuring aquatic plant communities. Freshwater Biology 55:952–966.

Caraco, N. F., Cole, J. J., Raymond, P. A., Strayer, D. L, Pace, M. L., Findlay, S. E. G., and D. T. Fischer. 1997. Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. Ecology 78:588–602.

Carpenter, S., and J. E. Titus. 1984. Composition and spatial heterogeneity of submersed vegetation in a softwater lake in Wisconsin. Plant Ecology 57:153-165.

Chalcraft, D. R., Cox, S. B., Clark, C., Cleland, E. E., Suding, K. N., Weiher, E. and D. Pennington. 2008. Scale-dependent responses of plant biodiversity to nitrogen enrichment. Ecology 89:2165–2171.

Chapman, M. G., Underwood, A. J., and G. A. Skilleter. 1995. Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage at two control locations. Journal of Experimental Marine Biology and Ecology

189:103–122.

Charalambidou, I., and L. Santamaría. 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. Acta Oecologica 23:165–176.

Charalambidou, I., Santamaría, L., and J. Figuerola. 2003. How far can the freshwater bryozoan *Cristatella mucedo* disperse in duck guts? Archiv für Hydrobiologie 157:547–554.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity–biodiversity relationship. Nature 416: 427–430.

Chase, J. 2003. Community assembly: when should history matter? Oecologia 136:489–498.

Chase, J. M., Amarasekare, P., Cottenie, K., Gonzalez, A., Holt, R. D., Holyoak, M., Hoopes, M. F., Leibold, M. A., Loreau, M., Mouquet, N., Shurin, J. B. and D. Tilman. 2005. Competing theories for competitive metacommunities. Metacommunities: Spatial Dynamics and Ecological Communities (eds M. Holyoak, M.A. Leibold & R.D. Holt). pp. 335–354, University of Chicago Press, Chicago and London.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences (USA) 104:17430–17434.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Conley, D. J., Paerl, H. W., Howarth, R. W. Boesch, D. F., Seitzinger, S. P., Havens, K. E., Lancelot, C., and Likens, G. E. 2009. Controlling Eutrophication: Nitrogen and Phosphorus. Science 323:1014-1015.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302–1310.

Connor, E. F., and E. D. McCoy. 1979. Statistics and biology of the species–area relationship. American Naturalist 113: 791–833.

Cook, C. D. K. 1987. Dispersion in aquatic and amphibious vascular plants, pp 179-190. In: Crawford, R. M. M. (ed.) Plant life in aquatic and amphibious habitats. Special Publication British Ecological Society, No. 5. Blackwell Scientific Publications, Oxford, England.

Cottenie, K., Nuytten, N., Michels, E., and L. De Meester. 2001. Zooplankton community structure and environmental conditions in a set of interconnected ponds. Hydrobiologia 442:339–350.

Cottenie, K., Michels, E., Nuytten, N., and L. De Meester. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. Ecology 84:991–1000.

Cottenie, K., and L. De Meester. 2004. Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. Ecology 85:114–119.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Crump, B., Adams, H., Hobbie, J., and G. Kling. 2007. Biogeography of bacterioplankton in lakes and streams of an arctic tundra catchment. Ecology 88:1365–1378.

Cunningham, J. B. 1992. The conflict surrounding the drainage of the River Erne 1881-1890. Clogher Record 14:78–103.

Davidson, T. A., Sayer, C. D., Bennion, H., David, C., Rose, N., and M. Wade. 2005. A 250 year comparison of historical, macrofossil and pollen records of aquatic plants in a shallow lake. Freshwater Biology 50:1671–1686.

Davidson, T. A., Sayer, C. D., Langdon, P. G., Burgess, A., and M. Jackson. 2010. Inferring past zooplanktivorous fish and macrophyte density in a shallow lake: application of a new regression tree model. Freshwater Biology 55:584–599.

Davidson, T. A., Bennion, H., Jeppesen, E., Clarke, G. H., Sayer, C. D., Morley, D., Odgaard, B. V., Rasmussen, P., Rawcliffe, R. and J., Salgado.2011. The role of cladocerans in tracking long-term change in shallow lake trophic status. Hydrobiologia 676:299-315.

Davies, B. R. 1974. The planktonic activity of larval Chironomidae in Loch Leven, Kinross. Proceedings of the Royal Society of Edinbrurgh B 74:241-258.

Davies, B. R. 1976. The dispersal of chironomidae larvae; A review. Journal of the Entomological Society of South Africa 39:39-62.

Davis, F. 1985. Historical changes in submerged macrophyte communities of upper Chesapeake Bay. Ecology 66:981-993.

Dawson, E. H. 1988. Water flow and the vegetation of running water, pp 283-309. In:

Symoens, J. J. (ed.) Vegetation of inland waters. Kluwer Academic Publishers, Dordrecht, The Netherlands.

De'ath, G. 1999. Principal curves: a new technique for indirect and direct gradient analysis. Ecology 80:2237–2253.

Declerck, S., Vanderstukken, M., Pals, A., Muylaert, K., and L. de Meester. 2007. Plankton biodiversity along a gradient of productivity and its mediation by macrophytes. Ecology 88: 2199–2210.

De Haas, E. M., Wagner, C., Koelmans, A. A., Kraak, M. H. S., and W. Admiraal. 2006. Habitat selection by chironomid larvae: fast growth requires fast food. Journal of Animal Ecology 75:148–155.

Delettre, Y. R., and N. Morvan. 2008. Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. Freshwater Biology 44:399–411.

De Meester, L. 1996. Local genetic differentiation and adaptation in freshwater zooplankton populations: patterns and processes. Ecoscience 3:385–399.

De Meester, L., Gómez, A., Okamura, B., and K. Schwenk. 2002. The monopolization hypothesis and the dispersal–gene flow paradox in aquatic organisms. Acta Oecologica 23:121–135.

Dieffenbacher-Krall, A., and W. Halteman. 2000. The relationship of modern plant remains to water depth in alkaline lakes in New England, USA. Journal of Paleolimnology 24:213-229.

Donohue, I., Jackson, A. L., Pusch, M. T., and K. Irvine. 2009. Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. Ecology 90: 3470–3477.

Engelhardt, K. A. M., and J. A. Kadlec. 2001a. Species traits, species richness and the resilience of wetlands after disturbance. Journal of Aquatic Plant Management 39:36–39.

Engelhardt, K. A. M., and M. E. Ritchie. 2001b. Effects of macrophyte species richness on wetland ecosystem functioning and services. Nature 411:687–689.

European Parliament. 2000. Directive 2000/60/EC of the European Parliament, establishing a framework for community action in the field of water policy. Official Journal of the European Communities 327:1–72.

Faith, D. P., Minchin, P. R., and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57–68.

Figuerola, J. 2005. Invertebrate eggs can fly: evidence of waterfowl-mediated gene flow in aquatic invertebrates. American Naturalist 165:274–280.

Figuerola, J., and A. Green. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshwater Biology 47:483–494.

Forbes, A. E., and J. M. Chase. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96:433–440.

Freeland, J., Romualdi, C., and B. Okamura. 2000. Gene flow and genetic diversity: a comparison of freshwater bryozoan populations in Europe and North America Heredity 85:498–508.

Freeland, J., Noble, L., and B. Okamura. 2000. Genetic consequences of the metapopulation biology of a facultatively sexual freshwater invertebrate. Journal of Evolutionary Biology 13:383-395.

Fukami, T. 2004. Assembly history interacts with ecosystem size to influence species diversity. Ecology 85:3234–3242.

Fukami, T., and P. Morin. 2003. Productivity–biodiversity relationships depend on the history of community assembly. Nature 424:423–426.

Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M. and J. H. Lawton. 2000. Abundance-occupancy relationships. Journal of Applied Ecology 37:39–59.

Gibson, C., Wu, Y., Smith, S., and S. Wolfe-Murphy. 1995. Synoptic limnology of a diverse geological region: catchment and water chemistry. Hydrobiologia 306:213–227.

Gilpin, M. E., and I. A. Hanski. 1991. Metapopulation dynamics: Empirical and theoretical investigations. Academic.

Girvan, J., and R. H. Foy. 2006. Trophic stability in an Irish mesotrophic lake: Lough Melvin. Aquatic Conservation 16:623–636.

Goldsmith, B., Davidson, T. A., Burgess, A., Hughes, M., Madgwick, G., Rawcliffe, R., Rippey, B., and J. Tyler. 2008. Site condition assessments of standing water features in SACS and ASSIS: Northern Ireland. Final Report to the Northern Ireland

Environment Agency. ENSIS Ltd. Environmental Change Research Centre:1–954.

Gomez, A., Carvalho, G.R., and Lunt, D.H. 2000. Phylogeography and regional endemism of a passively dispersing zooplankter: mitochondrial DNA variation in rotifer resting egg banks. Proceedings of the Royal Society London B 267:2189–2197.

Grasmück, N., Haury, J., Léglize, L. and S. Muller. 1995. Assessment of the bio-indicator capacity of aquatic macrophytes using multivariate analysis. Hydrobiologia 300:115–122.

Green, A. J., Figuerola, J., and M. I. Sánchez. 2002. Implications of waterbird ecology for the dispersal of aquatic organisms. Acta Oecologica 23:177–189.

Grime, J. P., Hodgson, J. G., and R. Hunt. (1988) Comparative plant ecology. A functional approach to common British species. Unwin Hyman, London.

Hamilton, A. L. 1965. An analysis of freshwater benthic community with speciesl refernce to the Chironomidae. PhD. Thesis, University of British Columbia.

Hannon, G., and M. Gaillard. 1997. The plant-macrofossil record of past lake-level changes. Journal of Paleolimnology 18:15-28.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, New York, New York, USA.

Hartikainen, H., Johnes, P., Moncrieff, C., and B. Okamura. 2009. Bryozoan populations reflect nutrient enrichment and productivity gradients in rivers. Freshwater Biology 54:2320–2334.

Havel, J., and J. Shurin. 2004. Mechanisms, effects, and scales of dispersal in freshwater zooplankton. Limnology and Oceanography 49:1229–1238.

Heegaard, E. 2004. Trends in aquatic macrophyte species turnover in Northern Ireland — which factors determine the spatial distribution of local species turnover? Global Ecology and Biogeography 13:397–408.

Heiri, O., and A. F. Lotter. 2001. Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. Journal of Paleolimnology 26:343-350.

Higgins, S. N., and M. J. Vander Zanden. 2010. What a difference a species makes: a meta–analysis of dreissenid mussel impacts on freshwater ecosystems. Ecological

Monographs 80:179–196.

Hill, S., Sayer, C. D., Hammond, P., Rimmer, V., Davidson, T. A., Hoare, D., Burgess, A., and B. Okamura. 2007. Are rare species rare or just overlooked? Assessing the distribution of the freshwater bryozoan, *Lophopus crystallinus*. Biological Conservation 135:223–234.

Hillebrand, H., Bennett, D. M., and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89:1510–1520.

Holyoak, M., Leibold, M. A., and R. D. Holt, editors. 2005. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Hoopes, M. F., Holt, R. D., and M. Holyoak. 2005. The effects of spatial processes on two species interactions. Pages 35–67 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Horgan, M. J., and E. L. Mills. 1997. Clearance rates and filtering activity of zebra mussel (*Dreissena polymorpha*): implications for freshwater lakes. Canadian Journal of Fisheries and Aquatic Sciences 54:249-255.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography, Princeton University Press.

Hutchinson, G. E., 1975. Limnological Botany. Wiley, New York 660 pp.

Jankowski, T., and D. Straile. 2003. A comparison of egg-bank and long-term plankton dynamics of two Daphnia species, D. hyalina and D. galeata: Potentials and limits of reconstruction. Limnology and Oceanography 48:1948–1955.

Jenkins, D. G., and A. L. Buikema, Jr. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. Ecological Monographs 68:421–443.

Jeppesen E., Søndergaard Ma., Søndergaard Mo., and K., Christoffersen (Eds).1998. The Structuring Role of Submerged Macrophytes in Lakes. Ecological Studies 131. Springer-Verlag, New York.

Jeppesen, E., Peder Jensen, J., Sondergaard, M., Lauridsen, T., and Landkildehus, F.

2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology 45:201-218.

Jeppesen, E., Leavitt, P., De Meester, L., and J. Jensen. 2001. Functional ecology and palaeolimnology: using cladoceran remains to reconstruct anthropogenic impact. Trends in Ecology and Evolution 16:191–198.

Johnson, L. E., and J. T. Carlton. 1996. Post-Establishment Spread in Large-Scale Invasions: Dispersal Mechanisms of the Zebra Mussel *Dreissena Polymorpha*. Ecology 77: 1686-1690.

Joint Nature Conservation Committee (JNCC). 2005. Common Standards Monitoring Guidance for Standing Waters. JNCC Report, JNCC, Peterborough.

Johnes, P. J., and A. L. Heathwaite. 1992. A procedure for the simultaneous determination of total nitrogen and total phosphorus in freshwater samples using persulphate microwave digestion. Water Research 10:1281–1287.

Jones, J. I., Li, W., and S. C. Maberly.2003. Area, altitude and aquatic plant diversity. Ecography 26:411–420.

Junk, W. J., Bayley, P. B., and R. E. Sparks. 1989. The flood-pulse concept in river-flood plains systems. Canadian Special Publications of Fisheries and Aquatic Sciences 106:110–127.

Kansanen, P. H. 1985. Assesment of pollution history from recent sediemnts in lake Vanajavesi, southern Finland. II. Changes in Chironomidae, Chaoboraidae and Ceratopogonidae (Diptera) fauana. Annales Zoologici Fennici 22:57-90.

Keddy, E. A. 1976. Lakes as islands: the distributional ecology of two aquatic plants, *Lemna minor* L. and *Lemna trisulca* L. Ecology 57:353-359.

Kennison, G. C. B., Dunsford D. S., and J. Schutten. 1998. Stable or changing lakes? A classification of aquatic macrophyte assemblages from a eutrophic shallow lake system in the United Kingdom. Aquatic Conservation: Marine and Freshwater Ecosystems 8:669–684.

Klaus, V. H., Sintermann, J., Kleinebecker, T., and N. Hölzel. 2011. Sedimentation-induced eutrophication in large river floodplains – An obstacle to restoration?. Biological Conservation 144:451–458.

Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in

metacommunities of Sarracenia purpurea inquilines. The American Naturalist 162:165–171.

Koleff, P., Gaston, K. J., and J. J. Lennon. 2003. Measuring β-diversity for presence absence data. Journal of Animal Ecology 72:367-382.

Korhonen, J. J., Soininen, J., and H. Hillebrand. 2010. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. Ecology 91:508–517.

Langdon, P. G., Ruiz, Z., Wynne, S., Sayer, C. D., and T. A. Davidson. 2010. Ecological influences on larval chironomid communities in shallow lakes: implications for palaeolimnological interpretations. Freshwater Biology 55:531–545.

Lauridsen, T. L., Jensen, J. P., Jeppesen, E., and M. Søndergaard. 2003. Response of submerged macrophytes in Danish lakes to nutrient loading reductions and biomanipulation. Hydrobiologia 505-509:641–649.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos 84:177–192.

Legendre P., and M. J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80:107–138.

Legendre, P., and L. Legendre. 1998. Numerical Ecology, 2nd edn. Elsevier, Amsterdam.

Legendre, P., and E. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.

Legendre, P., Borcard, D., and P. R. Peres-Neto. 2005. Analyzing β diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75:435–450.

Legendre, P., Cáceres M., and D. Borcard. 2010. Community surveys through space and time: testing the space-time interaction in the absence of replication. Ecology 91:262–272.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J., Hoopes, M., Holt, R., Shurin, J., Law, R., and D. Tilman. 2004. The metacommunity concept: a framework for multiscale community ecology. Ecology Letters 7:601–613.

Leibold, M. A, and J. Norberg. 2004. Biodiversity in metacommunities: Plankton as complex adaptive systems? Limnology and Oceanography 49:1278–1289.

Logue, J. B., Mouquet, N., Peter, H., Hillebrand, H., and The Metacommunity Working

Group. 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends in Ecology and Evolution Volume 26:482-491.

Lomolino, M. V. 2000. Ecology's most general, yet protean pattern: the species–area relationship. Journal of Biogeography 27:17–26.

Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. American Naturalist 154:427–440.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Macchiusi, F., and Baker, R. L. 1992. Effects of predators and food availability on activity and growth of *Chironomus tentans* (Chironomidae, Diptera). Freshwater Biology, 28:207–216.

Madgwick, G., Emson, D., Sayer, C. D., Willby, N. J., Rose, N. L., Jackson, M. J., and A. Kelly. 2011.Centennial-scale changes to the aquatic vegetation structure of a shallow eutrophic lake and implications for restoration. Freshwater Biology 56:2620–2636.

Mathers, R., De Carlos, M., Crowley, K., and D. Ó Teangana. 2002. A Review of the Potential Effect of Irish Hydroelectric Installations on Atlantic Salmon (*Salmo salar* L.) Populations, with Particular Reference to the River Erne. Biology and Environment: Proceedings of the Royal Irish Academy 102:69–79.

Matias, M. G., Underwood, A. J., Hochuli, D. F., and R. A. Coleman. 2010. Independent effects of patch size and structural complexity on diversity of benthic macroinvertebrates. Ecology 91:1908–1915.

McDonald, R. 2004. Invasive Species in Ireland:1–152.

McElarney, Y. R., Rasmussen, P., Foy, R. H., and N. J., Anderson. 2010. Response of aquatic macrophytes in Northern Irish softwater lakes to forestry management; eutrophication and dissolved organic carbon. Aquatic Botany 93:227–236.

McGowan, S., Leavitt, P., Hall, R., Anderson, J. N., Jeppesen, E., and B. Odgaard. 2005. Controls of algal abundance and community composition during ecosystem state change. Ecology 86:2200–2211.

Mesters, C. M. L. 1995. Shifts in macrophyte species composition as a result of

eutrophication and pollution in Dutch transboundary streams over the past decades. Journal of Aquatic Ecosystem Health 4:295–305.

Middelboe, A. L., and S. Markager. 1997. Depth limits and minimum light requirements of freshwater macrophytes. Freshwater Biology 37: 553–568.

Minchin, D., Maguire, C., and R. Rosell. 2003. The Zebra Mussel (*Dreissena polymorpha* Pallas) invades Ireland: Human mediated vectors and the potential for rapid intranational dispersal. Biology and Environment: Proceedings of the Royal Irish Academy 103B:23–30.

Moore, J. W. 1980. Factors influencing the composition, structure and density of a population of benthic invertebrates. Archiv fur Hydrobiologie 88: 202-218.

Moss, B., Madgwick, J., and G. Phillips. 1996. A guide to the restoration of nutrient enriched shallow lakes. Broads Authority, Environment Agency and EU life programme, Norwich.

Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: the regional similarity hypothesis. American Naturalist 159:420–426.

Mouquet, N., and M. Loreau. 2003. Community patterns in source-sink metacommunities. American Naturalist: 544–557.

Nichols, S. A., and B. H. Shaw. 1986 Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum, Potamogeton crispus* and *Elodea canadensis*. Hydrobiologia 131:3–21.

Nielsen, H. T., and E. T. Nielsen. 1962. Swarming of mosquitoes. Laboratory experiments under control conditions. Entomologica Experimentalis et Applicata (Amsterdam) 5:14-39.

O'Dea, A., Jackson, J. B. C., Fortunato, H. J., Smith, T., D'Croz, L., Johnson, K. G., and J. A. Todd. 2007. Environmental change preceded Caribbean extinction by 2 million years. Proceedings of the Natural American Science March 104: 5501–5506.

Okamura, B. 1996. Occurrence, prevalence, and effects of the myxozoan Tetracapsula bryozoides Canning, Okamura and Curry, 1996, parasitic in the freshwater bryozoan Cristatella mucedo Cuvier (Bryozoa, Phylactolaemata). Fol Parasitol. 43: 262-266.

Okamura, B. 2000. Metapopulation biology of freshwater bryozoans, p. 316-320. In A. H. Cubilla and J.B.C. Jackson [eds.]. Proceedings of the 11th International

Bryozoology Association Conference. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.

Okamura, B., and R. Freeland, 2002. Gene flow and the evolutionary ecology of passively dispersing aquatic invertebrates. Dispersal ecology pp: 194-216. ed. Bullock, J. M., Kenward, R. E., and R. S., Halis. British Ecological Society.

Okamura, B., Ayres, K., Salgado, J., Davidson, T. A.,Shaw, R. F.,Stephens, T., Hoare, D., and C. D. Sayer.Subm. Propagules in sediments provide evidence for metapopulation dynamics in a freshwater bryozoan. Aquatic ecology: 1-25.

Økland, K., and J. Økland. 2000. Freshwater bryozoans (Bryozoa) of Norway: Distribution and ecology of *Cristatella mucedo* and *Paludicella articulata*. Hydrobiologia 421:1–24.

Oliver, D. 1971. Life history of the Chironomidae. Annual Review of Entomology 16: 211-230.

Paillex, A., Dolédec, S., Castella, E., and S. Mérigoux. 2009. Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. Journal of Applied Ecology 46:250–258.

Peres-Neto, P. R., Legendre, P., Dray, S., and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87:2614–2625.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. American Naturalist 100:33–46.

Pinder, L. C. V., and F. Reiss. 1983. The larvae of Chironominae (Diptera: Chironomidae) of the Holartic region. Keys and diagnoses. Entomologica Scandinavica Supplement 19:293-435.

Pinel-Alloul, B., Niyonsenga, T., and P. Legendre. 1995. Spatial and environmental components of freshwater zooplankton structure. Ecoscience 2:1–19.

Preston, C. D., and J. M. Croft. 1997. Aquatic Plants in Britain and Ireland. Harley Books, London.

Preston, C. D. 1995. Pondweeds of Great Britain and Ireland.Botanical Society of the British Isles.

Price, J. 1890. Lough Erne Drainage. Minutes of Proceedings of the Institution of Civil

Engineers C1:73–94.

Pringle, C. M. 2001. Hydrologic connectivity and the management of biological reserves: a global perspective. Ecological Applications 11:981-99.

R Core Development Team. 2009. R 2.9.2. R project for Statistical Computing, Vienna, Austria. hwww.r-project.com

Rasmussen, P., and N. J., Anderson. 2005. Natural and anthropogenic forcing of aquatic macrophyte development in a shallow Danish lake during the last 7000 years. Journal of Biogeography 32:1993–2005.

Rasmussen, J. B. 1985. Effects of density and microdetritus enrichment on the growth of chironomid larvae in a small pond. Canadian Journal of Fisheries and Aquatic Sciences 42:1418–1422.

Rasmussen, J. B. 1984. Comparison of gut contents and assimilation efficiency of fourth instar larvae of two coexisting chironomids, *Chironomus riparius* and *Glyptotendipes paripes* (Edwards). Canadian Journal of Zoology62:1022–1026.

Ricciardi, A., Neves, R., and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology 67:613-619.

Riis, T., and K. Sand-Jensen. 2001. Historical changes in species composition and richness accompanying perturbation and eutrophication of Danish lowland streams over 100 years. Freshwater Biology 46:269–280.

Robach F., Eglin, I., and M. Tremolieres. 1997. Species richness of aquatic macrophytes in former channels connected to a river: a comparison between two aluvial hydrosystems differing in their regime and regulation. Global Ecology and Biogeography Letters 6:267–274.

Roelofs, J. 2002. Soft-water macrophytes and ecosystems: why are they so vulnerable to environmental changes? Introduction. Aquatic Botany 73:285–286.

Rosell, R.S., Maguire, C. M., and T. K. McCarthy,. 1999. First reported settlement of zebra mussels *Dreissena polymorpha* in the Erne system, co. Fermanagh, Northern Ireland. Biology and Environment: Proceedings of The Royal Irish Academy 98b:191-193.

Rosenberg, D. M., Berkes, F., Bodaly, R. A., Hecky, R. E., Kelly, C. A., and J. W. M.

Rudd. 1997. Large-scale impacts of hydroelectric development. Environmental Reviews 5:27–54.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press.

Rørslett, B. 1991. Principal determinants of aquatic macrophyte richness in northern European lakes. Aquatic Botany 39: 173–193.

Salgado, J., Sayer, C. D., Carvalho, L., Davidson, T. A., and I. Gunn. 2010. Assessing aquatic macrophyte community change through the integration of palaeolimnological and historical data at Loch Leven, Scotland. Journal of Paleolimnology 43:191–204.

Salo J., Kalliola R., Hakkinen I., Makinen Y., Niemela P., Puhakka M., and P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322:254–258.

Sand-Jensen, K., Pedersen, N. L., Thorsgaard, I., Moeslund, B., Borum, J., and K. P. Brodersen. 2008. 100 years of vegetation decline and recovery in Lake Fure, Denmark. Journal of Ecology 96:260–271.

Santamaría, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. Acta Oecologica 23:137–154.

Sayer, C. D., Roberts, N., Sadler, J., David, C., and P. Wade. 1999. Biodiversity Changes in a shallow Lake Ecosytem: A Multi-Proxy Palaeolimnological Analysis. Journal of Biogeography 26:97–114.

Sayer, C. D., Davidson, T. A., and J. I. Jones. 2010a. Seasonal dynamics of macrophytes and phytoplankton in shallow lakes: a eutrophication-driven pathway from plants to plankton? Freshwater Biology 55:500–513.

Sayer, C. D., Burgess, A. Kari, K. Davidson, T. A., Peglar, S., Yang, H., and N. Rose. 2010b. Long-term dynamics of submerged macrophytes and algae in a small and shallow, eutrophic lake: implications for the stability of macrophyte-dominance. Freshwater Biology 55:565–583.

Sculthorpe, C. D. 1967. The biology of aquatic plants. Edward Arnold Ltd., London.

Schindler, D. W. 1974. Eutrophication and Recovery in Experimental Lakes: Implications for Lake Management. Science 184: 897-899.

Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography 12:1–20.

Shurin, J. B. 2000. Dispersal limitation, invasion resistance and the structure of pond zooplankton communities. Ecology 81:3074–3086.

Shurin, J. B., Havel, J. E., Leibold, M. A., and B. Pinel-Alloul. 2000. Local and regional zooplankton species richness: a scale-independent test for saturation. Ecology 81:3062–3073.

Shurin, J.B., Amarasekare, P., Chase, J. M., Holt, R. D., Hoopes, M. and M. A. Leibold. 2003. Alternative stable states and regional community structure. Journal of Theoretical Biology 227:359–368.

Smith, M. D., Wilcox, J. C., Kelly, T., and A. K. Knapp. 2004. Dominance not richness determines invasibility of tallgrass prairie. Oikos 106:253–262.

Smith, R., Jordan, C., and J. Annett. 2005. A phosphorus budget for Northern Ireland: inputs to inland and coastal waters. Journal of Hydrology 304:193–202.

Smolders, A., Lamers, L., Hartog, C., and J. Roelofs. 2003. Mechanisms involved in the decline of *Stratiotes aloides* L. in the Netherlands: sulphate as a key variable. Hydrobiologia 506:603–610.

Smolders, A., Lucassen, E., and J. Roelofs. 2002. The isoetid environment: biogeochemistry and threats. Aquatic Botany 73:325–350.

Smolders, A., and J. Roelofs. 1996. The roles of internal iron hydroxide precipitation, sulphide toxicity and oxidizing ability in the survival of *Stratiotes aloides* roots at different iron concentrations in sediment pore water. New Phytologist 133:253–260.

Søndergaard, M., Johansson, L., Lauridsen, T. Jørgensen, T., Liboriussen, L., and E. Jeppesen. 2010. Submerged macrophytes as indicators of the ecological quality of lakes. Freshwater Biology 55:893–908.

Sousa, W. T. Z., Thomaz, S. M., and, K. J. Murphy. 2011. Drivers of aquatic macrophyte community structure in a Neotropical riverine lake. Acta Oecologica 37:462-475.

Spence, D. H. N., 1982. The zonation of plants in freshwater lakes. Advances in Ecological Research 12:37-126.

Spence, D. H. N. 1967. Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. The Journal of Ecology 55:147–

170.

Stansfield, J., Perrow, M., Tench, L., Jowitt, A., and A. Taylor. 1997. Submerged macrophytes as refuges for grazing Cladocera against fish predation: Observations on seasonal changes in relation to macrophyte cover and predation pressure. Hydrobiologia 342:229–240.

Steiner, C. F., Long, Z. T., Krumins, J. A., and P. J. Morin. 2006. Population and community resilience in multitrophic communities. Ecology 87:996–1007.

Stokstad, E. 2009. On the Origin of Ecological Structure. Science 2:33-35.

Strayer, D., Caraco, N., Cole, J., and S. Findlay. 1999. Transformation of freshwater ecosystems by bivalves. BioScience.

Strayer, D. L. 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55:152–174.

Talling, J. F., and Driver. 1961. Some problems in the estimation of chlorophyll-a in phytoplankton. Pages 142–146 in M. S. Doty, editor. Proceedings Conf. Primary Production Measurement Marine Freshwater, University of Hawaii. U.S. Energy Commission Publication TID 7633.

Tessier, A. J., Leibold, M. A., and J. Tsao. 2000. A fundamental trade-off in resource exploitation by *Daphnia* and consequences to plankton communities. Ecology 81: 826-841.

Thomas, J. D. 1987. An evaluation of ther interactions between freshwater pulmonate snalis hosts of human schistosomes and macrophytes. Philosophical Transactions of the Royal Society of London, B 135:75–125.

Thomas, J. D., Nwanko, D., and P. Sterry. 1985. The Feeding strategies of Juvenile and adult *Biomphalaria glabrata* (Say) under simulated natural conditions and their relevance to ccological theory and snail control. Proceedings of the Royal Society of London Series B-Biological Sciences 226:177–209.

Thomaz, S. M., Bini, L. M., and R. L., Bozelli. 2007. Floods increase similarity among aquatic habitats in riverfloodplain systems. Hydrobiologia 579:1-13.

Thuiller, W., Slingsby, J. , Privett, S., and R. Cowling. 2007. Stochastic species turnover and stable coexistence in a species-rich, fire-prone plant community. PloS One 9:e938.

Timms, R., and B. Moss. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnology and Oceanography 29:472-486.

Tockner, K., and J. A. Standford. 2002. Riverine flood plains: present state and future. Trends in the Environment and Conservation 29: 308–330.

Tockner, K., Bunn, S. E., Gordon, C., Naiman, R.J., Quinn, G. P., and J. A., Stanford. 2008. Floodplains: critically threatened ecosystems. In: Polunin, N. (Ed.), Future of Aquatic Ecosystems. Cambridge University Press, Cambridge, pp. 45–61.

Tuomisto, H., and K. Ruokolainen. 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. Ecology 87:2697–2708.

Tuomisto, H. 2010a. A diversity of β diversities: straightening up a concept gone awry. Part 1. Defining β diversity as a function of α and γ diversity. Ecography 33: 2–22.

Tuomisto, H. 2010b. A diversity of β diversities: straightening up a concept gone awry. Part 2. Quantifying β diversity and related phenomena. Ecography 33:23–45.

Underwood, A. J. 1990. Experiments in ecology and management – their logics, functions and interpretations. Australian Journal of Ecology 15: 365–358.

Underwood, A. J. 1991. Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. Australian Journal of Marine and Freshwater Reserach 42: 569–587.

Underwood, G., Thomas, J. D., and J. Baker. 1992. An experimental investigation of interactions in snail-macrophyte-epiphyte systems. Oecologia 91:587–595.

Underwood, A. J. 1994. On Beyond BACI: Sampling Designs that Might Reliably Detect Environmental Disturbances. Ecological Applications 4:3–15.

Underwood, A.J., Chapman, M. G., and S.D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology 250:97–115.

Urban, M. C., and L. De Meester. 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. Proceedings of the Royal Society B: Biological Sciences 276:4129–4138.

Van Diggelen, Middleton, R., Bakker, B., Grootjans, J., and A. M. Wassen. 2006. Fens and floodplains of the temperate zone: present status, threats, conservation and

restoration. Applied Vegetation Science 9:157–162.

Verberk, W. C. E. P., van der Velde, G., and H. Esselink. 2010. Explaining abundance–occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. Journal of Animal Ecology 79:589–601.

Vernon, J.G., Okamura, B., Jones, C. S., and L. R. Noble. 1996.Temporal patterns of clonality and parasitism in a population of freshwater bryozoans. Proceeding of the Royal Society Series B. 263: 1313-1318

Vestergaard, O., and K. Sand-Jensen. 2000. Aquatic macrophyte richness in Danish lakes in relation to alkalinity, transparency, and lake area. Canadian Journal of Fisheries and Aquatic Sciences 57:2022–2031.

Walshe, B. 1951. The feeding habits of certain chironomid larvae (subfamily Tendipedinae). Proceedings of the Zoological Society of London121: 63-79.

Ward, J. V. 1998. Riverine landscapes, biodiversity patterns, disturbance regimes, and aquatic conservation. Biology and Conservation 83:269–278.

Ward, J. V., Tockner K., and F, Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management 15:125–139.

Warwick, R. M., and K. R. Clarke. 1993. Increased variability as a symptom of stress in marine communities. Journal of Experimental Marine Biology and Ecology 172:215–226.

Warwick, R. M., Clarke, K. R. and Suharsono .1990. A statistical analysis of coral community responses to the 1982-83 El Niño in the Thousand Islands, Indonesia. Coral Reefs 8:171–179.

Wetzel, R. G., and G. E. Likens. 1991. Limnological analysis. Springer-Verlag, New York, New York, USA.

Wilsey, B. J., and H. W. Polley. 2002. Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. Ecology Letters 5:676–684.

Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30:279–338.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

Whittaker, R. J., Willis, K. J., and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28: 453–470.

Wilson, D. S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73: 1984-2000.

Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K. De Vos, P., Verstraete, W., and N. Boon. 2009. Initial community evenness favours functionality under selective stress. Nature 458: 623-626.

Wood, T.S., and B. Okamura. 2005. A new key to the freshwater bryozoans of Britain, Ireland and continental Europe, with notes on their ecology. The Freshwater Biological Association, Ambleside.

Wood, T.S., Anurakpongsatorn, P., Chaichana, R., Mahujchariyawong, J., and T. Satapanajaru. 2005. Predation on freshwater bryozoans by the apple snail, *Pomacea canaliculata*, Ampulariidae, an invasive species in Southeast Asia: a summary report. Denisia 16: 283-286.

Zale, A., and R. Neves. 1982. Fish hosts of four species of lampsiline mussels (Mollusca; Unionidae) in Big Moccasin Creek, Virginia. Canadian Journal of Zoology 11:1535–2542.

Zhao, Y., Sayer, C.D., Birks, H., Hughes, M., and S., Peglar. 2006. Spatial representation of aquatic vegetation by macrofossils and pollen in a small and shallow lake. Journal of Paleolimnology 35:335–350.

Appendix 1

Results of perMANOVA analysis and post-hoc pairwise comparisons on Period 1 (2006-2007) macrophyte data. Significant values (under $P \leq 0.01$) are showed. (NS) Not significant comparisons. Group number corresponds to each study lake (see Table 3-3).

Source	df	SS	MS	F	P(perm)	P(MC)
Lo	20	474188.4444	23709.4222	7.2669	0.0010	0.0010
Residual	819	2672104.4078	3262.6427			
Total	839	3146292.8522				

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Pair-wise a posteriori comparisons

Groups	t	P_perm	P_MC	#unique vals
(1, 2)	3.2760	0.0010	0.0010	1000
(1, 3)	2.2198	0.0030	0.0110	999
(1, 4)	1.4743	NS	NS	1000
(1, 5)	1.7170	NS	NS	1000
(1, 6)	2.7289	0.0010	0.0010	1000
(1, 7)	1.4590	NS	NS	999
(1, 8)	1.2787	NS	NS	998
(1, 9)	1.2327	NS	NS	1000
(1,10)	1.4903	NS	NS	1000
(1,11)	4.6364	0.0010	0.0010	997
(1,12)	2.2835	0.0040	0.0020	999
(1,13)	1.4062	NS	NS	999
(1,14)	2.0737	0.0070	0.0020	1000
(1,15)	2.9376	0.0010	0.0010	999
(1,16)	2.1884	0.0020	0.0030	998
(1,17)	1.9159	0.0080	0.0170	1000

(1,18)	1.7005	NS	NS	999
(1,19)	2.8622	0.0010	0.0010	998
(1,20)	1.6620	NS	NS	998
(1,21)	2.2354	0.0020	0.0030	998
(2, 3)	2.9727	0.0010	0.0010	997
(2, 4)	3.2900	0.0010	0.0010	1000
(2, 5)	3.5162	0.0010	0.0010	998
(2, 6)	1.9949	0.0030	0.0040	1000
(2, 7)	2.6093	0.0010	0.0010	1000
(2, 8)	2.8509	0.0010	0.0010	1000
(2, 9)	2.8265	0.0010	0.0010	999
(2,10)	4.4117	0.0010	0.0010	1000
(2,11)	5.3307	0.0010	0.0010	999
(2,12)	3.1929	0.0010	0.0010	999
(2,13)	3.5858	0.0010	0.0010	998
(2,14)	2.4100	0.0010	0.0010	999
(2,15)	3.4659	0.0010	0.0010	999
(2,16)	2.6210	0.0010	0.0010	999
(2,17)	2.9568	0.0010	0.0010	1000
(2,18)	3.2305	0.0010	0.0010	1000
(2,19)	3.2543	0.0010	0.0010	1000
(2,20)	3.0994	0.0010	0.0010	1000
(2,21)	2.4686	0.0010	0.0010	999
(3, 4)	1.8414	NS	NS	1000
(3, 5)	2.3742	0.0050	0.0060	998
(3, 6)	2.0951	0.0100	0.0070	999
(3, 7)	2.2699	0.0050	0.0020	1000
(3, 8)	2.2112	0.0030	0.0060	999
(3, 9)	2.0209	NS	NS	1000
(3,10)	3.1875	0.0010	0.0010	1000
(3,11)	4.8739	0.0010	0.0010	998
(3,12)	1.5241	NS	NS	999
(3,13)	2.5903	0.0010	0.0010	1000
(3,14)	1.1921	NS	NS	1000

(3,15)	2.5434	0.0010	0.0010	999
(3,16)	2.6935	0.0010	0.0010	1000
(3,17)	2.7184	0.0010	0.0020	999
(3,18)	2.5139	0.0030	0.0010	998
(3,19)	3.0349	0.0010	0.0010	999
(3,20)	2.5128	0.0010	0.0010	999
(3,21)	1.8333	NS	NS	999
(4, 5)	2.3410	0.0070	0.0050	998
(4, 6)	2.6710	0.0010	0.0020	1000
(4, 7)	1.6193	NS	NS	1000
(4, 8)	1.6462	NS	NS	999
(4, 9)	1.6265	NS	NS	997
(4,10)	2.5680	0.0020	0.0020	1000
(4,11)	4.6835	0.0010	0.0010	1000
(4,12)	1.4790	NS	NS	1000
(4,13)	2.3841	0.0030	0.0020	999
(4,14)	1.7406	NS	NS	999
(4,15)	2.4438	0.0040	0.0030	1000
(4,16)	2.7059	0.0010	0.0010	998
(4,17)	1.7484	NS	NS	999
(4,18)	1.9873	0.0100	0.0120	999
(4,19)	2.8144	0.0010	0.0010	998
(4,20)	1.8590	NS	NS	1000
(4,21)	1.8687	0.0110	0.0110	999
(5, 6)	2.9532	0.0010	0.0010	1000
(5, 7)	2.2766	0.0070	0.0040	999
(5, 8)	2.3336	0.0060	0.0040	1000
(5, 9)	1.9108	NS	NS	1000
(5,10)	2.1077	NS	NS	998
(5,11)	5.2248	0.0010	0.0010	999
(5,12)	2.6277	0.0020	0.0010	998
(5,13)	2.0986	0.0100	0.0150	999
(5,14)	2.3103	0.0060	0.0060	998
(5,15)	3.7263	0.0010	0.0010	999

(5,16)	2.7764	0.0010	0.0010	999
(5,17)	3.0013	0.0010	0.0020	1000
(5,18)	2.5621	0.0020	0.0010	1000
(5,19)	3.4586	0.0010	0.0010	997
(5,20)	2.5218	0.0020	0.0030	998
(5,21)	2.4969	0.0010	0.0010	999
(6, 7)	2.0547	NS	NS	998
(6, 8)	2.5938	0.0010	0.0020	999
(6, 9)	2.2058	0.0080	0.0040	998
(6,10)	3.8885	0.0010	0.0010	998
(6,11)	5.1106	0.0010	0.0010	999
(6,12)	2.5796	0.0010	0.0010	998
(6,13)	3.1120	0.0010	0.0010	1000
(6,14)	1.9204	0.0080	0.0110	998
(6,15)	2.9930	0.0010	0.0010	998
(6,16)	1.8143	NS	NS	999
(6,17)	2.7772	0.0010	0.0010	998
(6,18)	3.0194	0.0010	0.0010	1000
(6,19)	3.2669	0.0010	0.0010	998
(6,20)	2.7756	0.0010	0.0010	999
(6,21)	1.9572	0.0070	0.0070	1000
(7, 8)	1.7315	NS	NS	998
(7, 9)	1.3950	NS	NS	998
(7,10)	2.5107	0.0050	0.0030	999
(7,11)	4.4638	0.0010	0.0010	999
(7,12)	2.0305	0.0100	0.0080	998
(7,13)	2.3348	0.0030	0.0020	1000
(7,14)	1.7995	NS	NS	999
(7,15)	2.7310	0.0010	0.0010	1000
(7,16)	2.0793	0.0100	0.0030	999
(7,17)	1.6077	NS	NS	999
(7,18)	1.7429	NS	NS	1000
(7,19)	2.4014	0.0010	0.0010	999
(7,20)	1.4413	NS	NS	999

(7,21)	1.6119	NS	NS	999
(8, 9)	1.2769	NS	NS	1000
(8,10)	2.5650	0.0020	0.0020	999
(8,11)	4.4111	0.0010	0.0010	998
(8,12)	2.3919	0.0010	0.0040	998
(8,13)	1.9094	0.0100	0.0160	1000
(8,14)	2.0481	0.0040	0.0080	1000
(8,15)	2.5286	0.0010	0.0020	999
(8,16)	2.3739	0.0020	0.0020	999
(8,17)	2.4106	0.0020	0.0010	999
(8,18)	1.9710	0.0070	0.0090	998
(8,19)	2.4364	0.0010	0.0010	1000
(8,20)	1.8729	0.0050	0.0100	1000
(8,21)	2.1545	0.0020	0.0010	1000
(9,10)	2.3401	0.0050	0.0020	998
(9,11)	4.5933	0.0010	0.0010	1000
(9,12)	2.2408	0.0050	0.0030	997
(9,13)	1.9695	0.0070	0.0070	999
(9,14)	1.8533	NS	NS	999
(9,15)	2.8759	0.0010	0.0010	999
(9,16)	2.2811	0.0010	0.0040	999
(9,17)	2.1330	0.0040	0.0060	997
(9,18)	2.1001	0.0030	0.0030	999
(9,19)	2.4113	0.0010	0.0010	998
(9,20)	1.9140	0.0060	0.0070	997
(9,21)	1.8740	NS	0.0100	996
(10,11)	5.5072	0.0010	0.0010	1000
(10,12)	3.3304	0.0010	0.0010	997
(10,13)	1.9249	NS	NS	1000
(10,14)	3.1282	0.0010	0.0010	999
(10,15)	4.0457	0.0010	0.0010	999
(10,16)	3.0918	0.0010	0.0010	1000
(10,17)	3.1111	0.0010	0.0010	1000
(10,18)	2.2092	0.0020	0.0040	1000

(10,19)	3.6497	0.0010	0.0010	997
(10,20)	2.2553	0.0030	0.0040	998
(10,21)	3.2811	0.0010	0.0010	1000
(11,12)	4.7313	0.0010	0.0010	999
(11,13)	3.7844	0.0010	0.0010	998
(11,14)	4.5762	0.0010	0.0010	1000
(11,15)	4.6684	0.0010	0.0010	999
(11,16)	4.9575	0.0010	0.0010	997
(11,17)	4.5736	0.0010	0.0010	1000
(11,18)	3.9580	0.0010	0.0010	999
(11,19)	3.8652	0.0010	0.0010	1000
(11,20)	4.2142	0.0010	0.0010	998
(11,21)	4.4110	0.0010	0.0010	999
(12,13)	2.8325	0.0010	0.0010	1000
(12,14)	1.4794	NS	NS	997
(12,15)	2.6822	0.0010	0.0010	1000
(12,16)	2.8109	0.0010	0.0010	999
(12,17)	2.1722	0.0020	0.0040	998
(12,18)	2.4929	0.0020	0.0020	999
(12,19)	3.0077	0.0010	0.0010	1000
(12,20)	2.4136	0.0010	0.0010	997
(12,21)	1.5929	NS	NS	999
(13,14)	2.4799	0.0020	0.0020	1000
(13,15)	3.3002	0.0010	0.0010	998
(13,16)	2.5041	0.0010	0.0010	1000
(13,17)	2.7028	0.0010	0.0010	998
(13,18)	1.7228	NS	NS	1000
(13,19)	2.8961	0.0010	0.0010	998
(13,20)	2.0779	0.0020	0.0020	999
(13,21)	2.6336	0.0010	0.0010	998
(14,15)	2.4244	0.0010	0.0010	998
(14,16)	2.4998	0.0010	0.0010	999
(14,17)	2.2496	0.0010	0.0030	998
(14,18)	2.1272	0.0020	0.0040	999

(14,19)	2.5555	0.0010	0.0010	999
(14,20)	2.2473	0.0010	0.0010	999
(14,21)	1.4472	NS	NS	1000
(15,16)	3.3790	0.0010	0.0010	998
(15,17)	2.8547	0.0010	0.0010	1000
(15,18)	2.8632	0.0010	0.0010	1000
(15,19)	3.0118	0.0010	0.0010	998
(15,20)	2.7415	0.0010	0.0010	1000
(15,21)	2.6895	0.0010	0.0010	998
(16,17)	2.6746	0.0010	0.0010	1000
(16,18)	2.4453	0.0010	0.0010	998
(16,19)	3.3397	0.0010	0.0010	998
(16,20)	2.4177	0.0010	0.0010	999
(16,21)	2.4023	0.0020	0.0010	1000
(17,18)	2.1999	0.0020	0.0050	999
(17,19)	2.8451	0.0010	0.0010	1000
(17,20)	1.9202	0.0050	0.0100	1000
(17,21)	1.8656	0.0060	0.0020	999
(18,19)	2.2375	0.0010	0.0030	1000
(18,20)	1.0792	NS	NS	1000
(18,21)	2.2354	0.0030	0.0020	998
(19,20)	2.1605	0.0010	0.0010	999
(19,21)	2.2700	0.0010	0.0010	1000
(20,21)	1.8645	0.0030	0.0040	999

Results of perMANOVA analysis and post-hoc pairwise comparisons on Period 2 (2008-2009) macrophyte data . Significant values (under $P \leq 0.01$) are showed. (NS) Not significant comparisons. Group number corresponds to each study lake (Table 3-3).

Source	df	SS	MS	F	P(perm)	P(MC)
Lo	14	438780.0881	31341.4349	9.1549	0.0010	0.0010
Residual	435	1489210.4694	3423.4723			
Total	449	1927990.5574				

Pair-wise a posteriori comparisons

Groups	t	P_perm	P_MC	#unique vals
(1, 2)	2.6238	0.0010	0.0010	999
(1, 3)	2.9563	0.0010	0.0010	998
(1, 4)	2.8530	0.0010	0.0010	1000
(1, 5)	1.8188	0.0020	0.0040	998
(1, 6)	3.1700	0.0010	0.0010	1000
(1, 7)	3.7729	0.0010	0.0010	1000
(1, 8)	5.4894	0.0010	0.0010	998
(1, 9)	3.2992	0.0010	0.0010	998
(1,10)	2.8654	0.0010	0.0010	1000
(1,11)	2.7857	0.0010	0.0010	996
(1,12)	3.3128	0.0010	0.0010	996
(1,13)	1.9355	0.0010	0.0010	998
(1,14)	2.3450	0.0010	0.0010	999
(1,15)	1.8213	0.0010	0.0020	998
(2, 3)	1.5611	NS	NS	998
(2, 4)	3.2591	0.0010	0.0010	998
(2, 5)	1.5846	NS	NS	999
(2, 6)	1.3460	NS	NS	999
(2, 7)	1.9188	NS	NS	997
(2, 8)	4.9668	0.0010	0.0010	996
(2, 9)	3.0146	0.0010	0.0010	997
(2,10)	1.8992	0.0030	0.0040	999
(2,11)	3.1490	0.0010	0.0010	999
(2,12)	1.3048	NS	NS	999
(2,13)	2.2335	0.0010	0.0010	998
(2,14)	1.9257	0.0020	0.0030	999
(2,15)	2.0543	0.0010	0.0010	999
(3, 4)	3.8621	0.0010	0.0010	999
(3, 5)	1.8325	0.0110	0.0100	998
(3, 6)	1.7135	NS	NS	998
(3, 7)	1.2380	NS	NS	1000

(3, 8)	5.6492	0.0010	0.0010	1000
(3, 9)	3.8144	0.0010	0.0010	999
(3,10)	2.9834	0.0010	0.0010	999
(3,11)	3.4553	0.0010	0.0010	1000
(3,12)	1.8745	0.0110	0.0170	998
(3,13)	2.7675	0.0010	0.0010	999
(3,14)	2.5719	0.0010	0.0010	999
(3,15)	2.7259	0.0010	0.0010	1000
(4, 5)	2.8523	0.0010	0.0010	1000
(4, 6)	3.8550	0.0010	0.0010	1000
(4, 7)	4.7141	0.0010	0.0010	998
(4, 8)	5.3882	0.0010	0.0010	1000
(4, 9)	3.1826	0.0010	0.0010	1000
(4,10)	3.0300	0.0010	0.0010	998
(4,11)	1.6009	NS	NS	998
(4,12)	3.7530	0.0010	0.0010	999
(4,13)	2.3556	0.0010	0.0010	1000
(4,14)	2.8615	0.0010	0.0010	998
(4,15)	2.2936	0.0010	0.0010	999
(5, 6)	1.9683	0.0090	0.0110	1000
(5, 7)	2.4902	0.0030	0.0010	999
(5, 8)	4.9757	0.0010	0.0010	998
(5, 9)	3.1519	0.0010	0.0010	998
(5,10)	2.4280	0.0010	0.0010	996
(5,11)	2.5835	0.0010	0.0010	995
(5,12)	2.2312	0.0010	0.0030	996
(5,13)	1.9347	0.0010	0.0010	995
(5,14)	1.8666	0.0020	0.0010	1000
(5,15)	1.7441	0.0010	0.0030	1000
(6, 7)	1.7498	NS	NS	1000
(6, 8)	5.6727	0.0010	0.0010	998
(6, 9)	3.9835	0.0010	0.0010	999
(6,10)	2.9638	0.0010	0.0010	1000
(6,11)	3.4862	0.0010	0.0010	997

(6,12)	1.8854	0.0130	0.0110	999
(6,13)	2.9201	0.0010	0.0010	998
(6,14)	2.2876	0.0010	0.0030	1000
(6,15)	2.8881	0.0010	0.0010	1000
(7, 8)	6.6308	0.0010	0.0010	1000
(7, 9)	4.6575	0.0010	0.0010	998
(7,10)	3.6069	0.0010	0.0010	1000
(7,11)	4.2605	0.0010	0.0010	996
(7,12)	1.8687	NS	NS	1000
(7,13)	3.5692	0.0010	0.0010	1000
(7,14)	3.1752	0.0010	0.0010	1000
(7,15)	3.5009	0.0010	0.0010	999
(8, 9)	4.7447	0.0010	0.0010	997
(8,10)	4.9120	0.0010	0.0010	999
(8,11)	5.1967	0.0010	0.0010	998
(8,12)	5.4450	0.0010	0.0010	998
(8,13)	3.7957	0.0010	0.0010	997
(8,14)	4.3716	0.0010	0.0010	1000
(8,15)	4.3315	0.0010	0.0010	999
(9,10)	2.6304	0.0010	0.0010	998
(9,11)	3.6009	0.0010	0.0010	999
(9,12)	3.5582	0.0010	0.0010	996
(9,13)	2.2231	0.0010	0.0010	998
(9,14)	2.6195	0.0010	0.0010	999
(9,15)	2.2339	0.0010	0.0010	1000
(10,11)	3.0850	0.0010	0.0010	1000
(10,12)	2.5481	0.0010	0.0010	999
(10,13)	2.0892	0.0010	0.0010	998
(10,14)	2.2111	0.0010	0.0010	1000
(10,15)	1.7464	0.0010	0.0010	999
(11,12)	3.6388	0.0010	0.0010	1000
(11,13)	2.2881	0.0010	0.0010	999
(11,14)	2.7080	0.0010	0.0010	999
(11,15)	2.4545	0.0010	0.0010	998

(12,13)	2.7645	0.0010	0.0010	998
(12,14)	2.3518	0.0010	0.0010	998
(12,15)	2.7280	0.0010	0.0010	999
(13,14)	1.4451	0.0090	0.0100	1000
(13,15)	1.2594	NS	NS	1000
(14,15)	1.8562	0.0010	0.0010	998
