Aquatic macroinvertebrate biodiversity of lowland rural and urban ponds in Leicestershire

by

Matthew Hill

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CERTIFICATE OF ORIGINALITY

This is to certify that I am responsible for the work submitted in this thesis, that the original work is my own except as specified in acknowledgements or in footnotes, and that neither the thesis nor the original work contained therein has been submitted to this or any other institution for a degree.

MATTHEW HILL

Abstract

Ponds are common and abundant features in nearly all landscapes typical of European lowland landscapes yet research on freshwater biodiversity has traditionally focussed on larger waterbodies such as lakes and rivers. This has led to an increased need to understand and quantify the biodiversity associated with pond habitats to better inform the active conservation and management of these small waterbodies. This thesis examines the aquatic macroinvertebrate biodiversity (alpha, beta and gamma) and conservation value of 95 ponds in Leicestershire, UK, across a variety of urban and rural landscape types and at a range of spatial scales. In addition, the relative importance of local (physicochemical and biological) and spatial (connectivity) variables in structuring macroinvertebrate communities within ponds is investigated. At a regional scale, the greatest macroinvertebrate biodiversity and conservation value was recorded within meadow ponds compared to urban, agricultural and forest ponds. Spatially, ponds were highly physically and biologically heterogeneous. Temporally (seasonally), invertebrate communities were most dissimilar in meadow and agricultural ponds but assemblages were similar in urban and forest ponds. In urban landscapes, park ponds supported a greater diversity of invertebrates than 'other' urban or garden ponds and typically had a greater conservation value. Garden ponds were the most taxon poor of those investigated. Perennial floodplain meadow ponds supported a greater biodiversity of invertebrates compared to ephemeral meadow ponds although conservation value was similar. Despite regular inundation from the River Soar, ephemeral ponds supported distinct communities compared to perennial meadow ponds. Aquatic macrophytes supported a higher diversity of taxa than other pond mesohabitats across all landscapes studied. Physicochemical factors were identified to be the dominant influence on macroinvertebrate assemblages although, a combination of local and spatial factors best explained the variation in community composition at a regional scale and for meadow ponds. Spatial factors were not identified to significantly influence urban pond communities. This study highlights the ecological importance and conservation value of ponds in rural and anthropogenically disturbed landscapes. Recognition of the significant contribution of ponds to freshwater biodiversity at regional and landscape scales is important for future conservation of pond habitats and will help focus and direct conservation strategies to where they are needed most.

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Table of Contents

List of Tables

List of Figures

List of Equations

Chapter 1. Introduction

1.1 Pond habitats

Ponds are defined as small water bodies between 1 m^2 and 2 ha in area which normally hold water for at least 4 months of the year (Pond Conservation Group, 1993) and includes both anthropogenic and naturally formed ponds (Biggs *et al.,* 2005). Ponds can form through natural processes such as land subsidence, depressions left from uprooting following tree fall (Wood *et al.,* 2003) and glacial and river action (Gee *et al.,* 1997; Oertli *et al.,* 2005). Most ponds primarily rely on precipitation to fill their basin (Brönmark and Hansson, 2005) although groundwater fed ponds also occur widely. Natural ponds occur in a variety of shapes and sizes, are usually shallow (0.5 m-2 m), frequently short lived (less than 100 years) and often accumulate sediment over decades or centuries until the basin has been filled (Biggs *et al.,* 1994a). In lowland landscapes many ponds are anthropogenically excavated (Biggs *et al.,* 1994b; Wood *et al.,* 2003), historically constructed to water livestock (Moss, 1998), for ornamental purposes, protection against fire, fish aquaculture, industrial processes (e.g., woollen industry) or to collect storm water runoff (Oertli *et al.,* 2005). Lentic water bodies are located in nearly all environments (Wood *et al.,* 2003) and there are estimated to be 304 million lakes and ponds globally, (Downing *et al.,* 2006) comprising 3.7% of the non-glaciated land surface area (Verpoorter *et al.,* 2014). Ponds often occur in networks or clusters in natural and anthropogenic landscapes (pondscapes) (Nicolet *et al.,* 2007). Many ponds today are created in urban landscapes for recreational purposes or as part of a 'wildlife garden' (Davies *et al.,* 2009b; Hassall, 2014). Anthropogenic ponds essentially provide a natural environment and habitat (Biggs *et al.,* 1994a) and are utilised by a wide range of flora and fauna (Davies *et al.,* 2009b).

Ephemeral ponds are small lentic water bodies that experience a recurrent dry phase (hydroperiodicity) which can vary widely in length and can be either predictable or unpredictable (Williams, 1997). Ephemeral ponds are much more common in the UK than many assume. It has been estimated that up to 25% of UK lowland ponds may be ephemeral (Williams *et al.,* 2010) although they have historically been a neglected aquatic habitat in Britain (Schwartz and Jenkins, 2000; Nicolet *et al.,* 2004). There is a large spectrum of ephemeral ponds ranging from semi-permanent ponds which dry for a period of weeks to small puddles that remain wet for a matter of days (Collinson *et al.,* 1995). There are three key requirements for the development of ephemeral pond habitats; the availability of water, a land surface depression and a substratum of fine silt, clay or bedrock to retain water and regulate drainage (Williams *et al.,* 2001).

Ephemeral ponds are often shallow and have high surface area to volume ratios (Brönmark and Hansson, 2005). There is little or no net gain of sediment within ephemeral ponds as the sediment accumulated during the wet phase will typically be oxidised during the dry phase (Collinson *et al.,* 1995). Low sediment accumulation rates create a stable and self - sustaining habitat (Biggs *et al.,* 2001) which can persist for centuries or millennia (some ephemeral pingos (a periglacial landform) are estimated to be in excess of 8,000 years old) (Wood *et al.,* 2003). A pond's natural hydroseral succession is to proceed towards a more terrestrial environment (Williams, 1997). Organic sediment accumulation will eventually reach the pond surface; the pond will pass through a semi-permanent phase, eventually becoming ephemeral and ultimately terrestrial (Williams *et al.,* 2001). A demanding physical, chemical and biological environment occurs within ephemeral ponds which can influence the faunal community it supports (Bagella *et al.,* 2010). The key characteristic driving the harsh physicochemical environment is the cyclical drying and re-wetting of the pond basin (hydroperiodicity) (Vanschoenwinkel *et al.,* 2009; Williams, 1996). The fluctuating hydroperiod causes a reduction in habitat volume during drying, increased insolation and temperature, large fluctuations of pH and conductivity, and reduced dissolved oxygen concentrations (turbidity, nutrient levels and trophic processes will all be influenced by the physicochemical processes occurring within ephemeral ponds) (Williams, 1996; Williams, 2006).

Whilst interest and research on pond biodiversity has increased more recently (Oertli *et al*., 2009; Céréghino *et al.,* 2014), ephemeral and urban ponds remain some of the most poorly studied waterbodies scientifically. Ponds are common and abundant features in the urban landscape (there are estimated to be between 2.5 - 3.5 million garden ponds in the United Kingdom (Davies *et al.,* 2009b)), many have been anthropogenically built for a variety of purposes including; flood reduction, water treatment, public amenity and to promote urban biodiversity (Williams *et al.,* 2013; Briers, 2014; Hassall, 2014). Whilst the significant cultural and aesthetic value that urban ponds provide to members of the public is widely acknowledged (Lundy and Wade, 2011), the wider conservation value in anthropogenically dominated landscapes is poorly quantified. Previous research has highlighted urban ponds' considerable contribution to biodiversity (Gledhill *et al.,* 2008; Hassall, 2014; Hassall and Anderson, 2015) whilst other studies have suggested that urban ponds are often ecologically poor and currently of little value to aquatic conservation (Noble and Hassall, 2014).

1.2 Biodiversity

Multiple definitions of the term biodiversity have led to considerable confusion as to what it actually means (Hamilton, 2005). At its broadest, biodiversity can be simply referred to as the number of taxa within a defined geographic range (Begon *et al.,* 1996). However, this is an oversimplified representation relying solely on the number of taxa. A more robust, multi-faceted definition of biodiversity was detailed in the Convention of Biological Diversity definition of terms: "'biological diversity" means the variability among living organisms from all sources including, *inter alia,* terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems' (United Nations, 1992: 3). The three fundamental levels of biodiversity are included within the United Nation's definition above: genetic, organismal and ecosystem diversity (Noss, 1990; Gaston and Spicer, 2009).

Quantification of biodiversity can be divided into alpha (α), beta (β) and gamma (γ) diversity (Sepkoski, 1988). Alpha diversity represents the biotic diversity within an individual (local) sample site and is often measured using alpha diversity indices such as the Shannon Wiener diversity index and Fisher's alpha (Magurran, 2004). Beta-diversity characterises the spatial and/or temporal distribution and variation of ecological communities between individual sites within a given area (Whittaker, 1960; Wilson and Shmida, 1984; Anderson *et al.,* 2006; Tuomisto, 2010). Lastly, gamma diversity is the overall biodiversity across the whole study region (often at landscape or regional scales); a product of alpha- and beta- diversity (Arellano and Halffter, 2003).

Ponds may be useful agents to test ecological theory, such as island biogeography theory (MacArthur and Wilson, 1967) as they can be viewed as isolated islands of suitable habitat surrounded by a matrix of unsuitable habitat (Blaustein and Schwartz, 2001; Rundle *et al.,* 2002). This ecological theory is one of the most widely known and accepted species distribution concepts (Gravel *et al.,* 2011). Island biogeography theory suggests that species richness is in dynamic equilibrium depending on immigration and extinction of flora and fauna at a site, which is influenced by the size of the island and its proximity to the 'mainland' or other islands (McArthur and Wilson, 1967). Smaller, isolated islands are predicted to have lower species richness than a larger sized island on or proximal to the mainland as smaller, isolated islands are more prone to stochastic extinction and have diminished recolonization/immigration rates (Scheffer *et al.,* 2006). Species richness is expected to increase as the available area of habitat and proximity to other habitats increases because there is greater niche habitat availability, increased species interactions and lower extinction rates (Begon *et al.,* 1996; Holden, 2008).

Closely related to the theory of island biogeography is the concept of connectivity. Landscape connectivity can be defined as "the degree to which the landscape impedes or facilitates movement along resource patches" (Taylor *et al.,* 1993: 571) and incorporates two key components; 1) structural connectivity - the spatial connectivity (physical arrangement/structure) of habitats types in the landscape and; 2) functional connectivity – the actual movement of taxa (behavioural response of taxa to the physical arrangement of the landscape) through the landscape (Goodwin, 2003; Crooks and Sanjayan, 2006; Ribeiro *et al.,* 2011). Fragmentation is one of the key contemporary drivers of biodiversity loss (Ray *et al.,* 2002), thus maintaining landscape connectivity is pivotal for biodiversity conservation (Crooks and Sanjayan, 2006). Connectivity has been shown to influence taxonomic distribution/composition by facilitating the colonization and dispersal of organisms (McArthur and Wilson, 1967; Moilanen and Nieminen, 2002; Jeffries, 2005). Structural connectivity is very often used in biodiversity and conservation research as it is relatively easy to measure using Geographical Information systems (GIS) (Taylor *et al.,* 2006) whereas assessing and quantifying functional connectivity can be extremely difficult (Ribeiro *et al.,* 2011). However, basing biodiversity and conservation research and management strategies on structural connectivity can be misleading as it can generalize the response of organisms (Ribeiro *et al.,* 2011; Tischendorf and Fahrig, 2000). Functional connectivity can provide a means to analyse an individual organisms'/populations' behavioural response to the structural habitat and the different scales of connectivity that may be present within the habitat (Tischendorf and Fahrig, 2000).

1.2.1 Biodiversity loss

Global and local biodiversity loss is being significantly driven by anthropogenic transformations of the natural landscape (Pereira *et al.,* 2012). It is estimated that between 39 - 50% of the earth's surface has been modified or degraded (Vitousek *et al.,* 1997). Row crop and pasture occupy approximately 40% (Foley *et al.,* 2005) and urban landscapes currently cover <3% of the of the earth's surface (Grimm *et al.,* 2008). Urbanised land is projected to increase up to 185% from current levels by 2030 (Seto *et al.,* 2012). Wholesale changes to the earth's surface have increased the fragmentation and isolation of the natural landscapes subsequently leading to reduced biodiversity (Fahrig, 2003). Both large-scale land cover alterations and an increasing mobility of humans have resulted in the homogenization of the earth's fauna and flora in many anthropogenic regions (McKinney, 2006). In addition, anthropogenically induced climate change can cause geographical range changes and altitudinal shifts in floral and faunal distribution, contributing to biotic homogenization particularly in biodiversity hotspots (Thuiller, 2007; Rosset *et al.,* 2010). Human introductions (accidental and deliberate) of non-native taxa have promoted the proliferation of generalist, opportunistic species at the expense of specialized, sensitive taxa in many instances. Species extinctions are occurring at rates of up to 1000 times that of the natural background rate (Millennium Ecosystem Assessment, 2005). Over-exploitation of natural resources (biotic and abiotic) and the modification of biogeochemical cycles have contributed to the homogenization and reduction of biodiversity (Millennium Ecosystem Assessment, 2005; Pereira *et al.,* 2012; Isbell *et al.,* 2013). Water quality of freshwater habitats (and consequently biodiversity) has often been degraded within non-natural landscapes as agricultural run-off and industrial/urban pollution can increase nutrient (phosphorus and nitrogen) concentrations and pollutants such as heavy metals within the water (Foley *et al.,* 2005; Dudgeon *et al.,* 2006).

Although the detrimental impacts of land cover change are well documented, the needs of humans are consistently being met at the expense of species heterogeneity, biogeochemical cycles and ecosystem function (Millennium Ecosystem Assessment 2005). Biodiversity conservation currently relies on designated protected areas (hotspots) (Mcdonald *et al.,* 2008) however; increasing anthropogenic land cover is projected to threaten the flora and fauna within many of these protected areas

(Guneralp and Seto, 2013). Ecological conservation cannot (and should not) depend exclusively on protected areas (Chester and Robson, 2013), and biodiversity conservation should be opportunistically increased wherever possible. Biodiversity conservation needs to be integrated further into urban landscapes and as a result research is required to quantify areas of considerable biodiversity and conservation value within anthropogenic landscapes (Chester and Robson, 2013; Goertzen and Suhling, 2013).

1.3 Context for thesis

Quantifying the invertebrate biodiversity of ephemeral and perennial ponds at multiple spatial and temporal scales is vital to inform future freshwater conservation and management strategies, and will provide a greater understanding of the dynamic invertebrate communities within pond landscapes. However, there is a paucity of research on the ecology of pond ecosystems in the UK and across Europe, as historic research effort has primarily focused on rivers and lakes (Miracle *et al.,* 2010). Research on the biodiversity of ephemeral ponds 'lags at least 50 years behind that of better known water body types' (Williams *et al.,* 2001: 7) and urban ponds have also been very poorly studied due to their small size and the often misplaced assumption that they are of poor biodiversity value. These research gaps have recently been recognised and highlighted within the scientific literature (Gledhill *et al.,* 2008; Chester and Robson, 2013; Hassall, 2014). There have been few studies into pond landscapes (pondscapes) and how their connectivity or isolation may influence biodiversity. As a result, further research is required to quantify macroinvertebrate biodiversity, understand the ecological processes operating within ponds at local and regional scales and determine their contribution to the conservation and enhancement of freshwater biodiversity in semi-natural and anthropogenic landscapes.

1.4 Aims and research objectives

This thesis aims to quantify the aquatic macroinvertebrate diversity, abundance and conservation value of ponds within a range of land cover types typical of a lowland landscape in Leicestershire, UK. There is an increasing acknowledgment of the need to clarify the current status of pond biodiversity and their contribution to local and regional freshwater biodiversity, especially in landscapes that have been heavily influenced by anthropogenic processes. In light of the knowledge gaps highlighted above, this thesis will particularly focus on pond types that have received little research attention historically: ephemeral and urban ponds.

Specifically, the thesis research addressed the following objectives;

1. To quantify pond macroinvertebrate biodiversity and conservation value at a regional scale within a range of landscapes in Leicestershire, UK (Chapter 4).
2. To examine the seasonal variability of aquatic macroinvertebrate communities associated with ponds (Chapters 4, 5 & 6).
3. To characterise aquatic macroinvertebrate biodiversity within a range of ponds (garden, 'other' urban and park) in the urban landscape (Chapter 5).
4. To quantify the macroinvertebrate biodiversity of perennial and ephemeral ponds in two floodplain meadow landscapes of the lower River Soar floodplain, UK (Chapter 6).
5. To examine the physicochemical, biological and spatial (connectivity) characteristics influencing macroinvertebrate community composition within ponds at a range of spatial scales (Chapter 7).

1.5 Thesis structure

The structure and subsequent progression of the research is outlined in Figure 1.1. Chapter 2 presents a detailed review of the existing published literature examining the macroinvertebrate biodiversity and ecological importance of ephemeral and perennial ponds and identifies a number of research gaps within the literature. The local (physicochemical and biological) and spatial (connectivity) environmental variables influencing macroinvertebrate communities and metacommunities supported by pond landscapes are discussed. This chapter also highlights the conservation and management strategies in place to protect, maintain and enhance macroinvertebrate biodiversity of ponds habitats. The methodological framework and techniques utilised in this thesis are outlined in Chapter 3. Standard field and laboratory techniques and the statistical analyses used to address the research aims and objectives (Chapter 1.4) are presented. Wherever possible the techniques employed follow standard procedures enabling comparisons to be made with existing literature. Chapter 4 will address the regional macroinvertebrate biodiversity within ponds across a range of landscapes (meadow, agricultural, forest and urban) in Leicestershire, UK. A selection of alpha

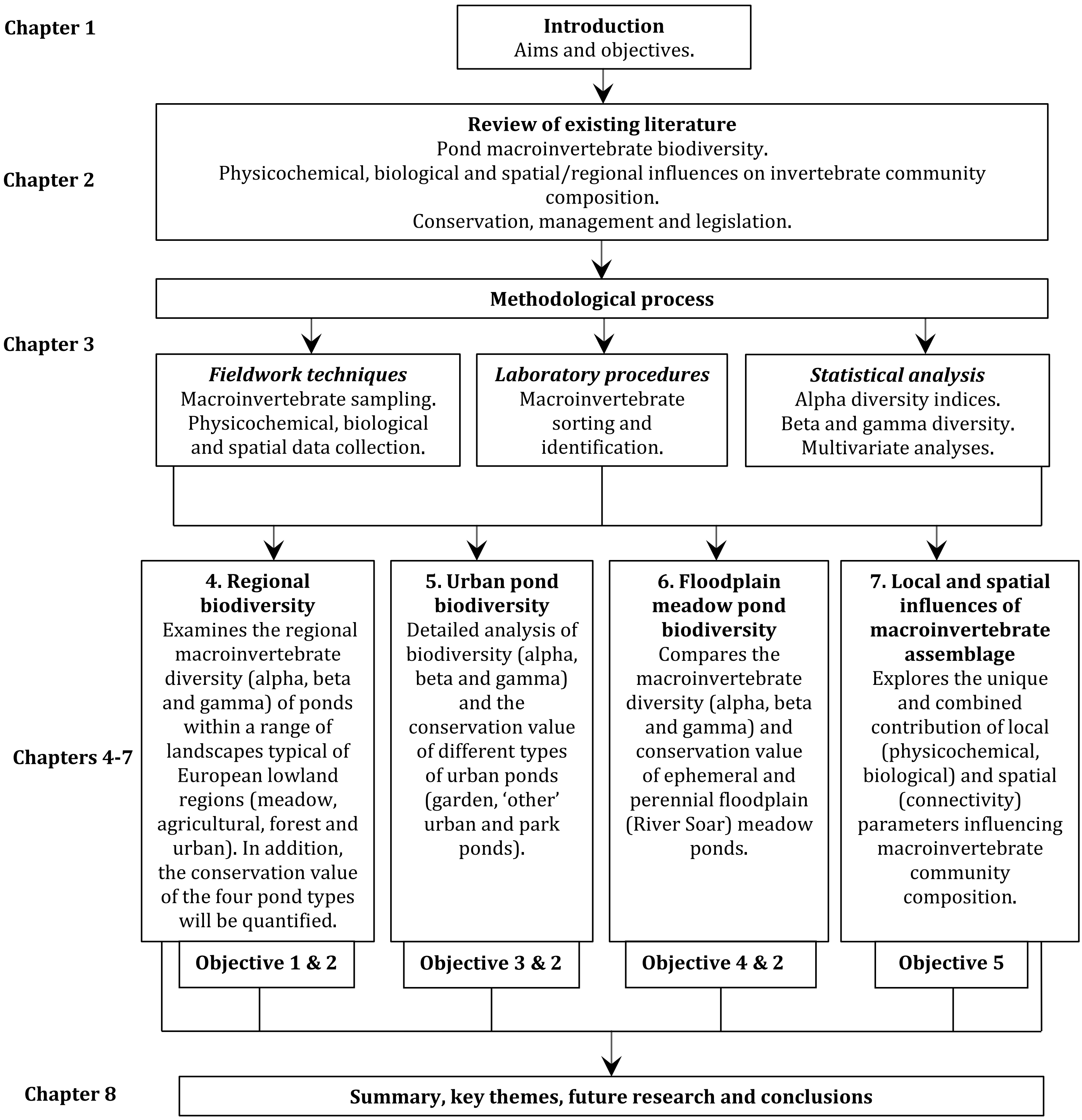

Figure 1.1 – Thesis structure. Objectives addressed relate to thesis objectives listed in Chapter 1.4.

diversity indices will be used to summarize the biodiversity recorded within the different pond types at mesohabitat and total pond scales. In addition, alpha diversity indices will summarize the seasonal (spring, summer and autumn) aquatic macroinvertebrate diversity. The distribution and variance (beta-diversity) of invertebrate communities within and between pond types will be determined, and their relative conservation value will be quantified. Macroinvertebrate biodiversity within urban pond habitats will be presented in Chapter 5. Alpha diversity indices will be used to reveal patterns in biodiversity associated with three urban pond types (garden, 'other' urban and park) and beta-diversity will be evaluated to characterize the compositional heterogeneity within and between the urban pond types. Urban pond conservation value (using the Community Conservation Index) will be measured. Chapter 6 will examine the biodiversity associated with ephemeral and perennial ponds in two floodplain (River Soar) meadow landscapes. Alpha, beta and gamma diversity and the proportion of predators/non-predators and actively/passively dispersing macroinvertebrates will be addressed. Additionally, ephemeral and perennial floodplain meadow pond conservation value will be examined. The influence of physicochemical, biological and spatial parameters on the invertebrate community assemblage within the different land covers will be quantified in Chapter 7. Multivariate analysis will be employed to assess the unique and combined contribution of environmental factors influencing macroinvertebrate community composition within a range of pond types (all ponds in the study region, urban ponds, meadow ponds and ephemeral ponds). In addition, the relationship between macroinvertebrate community dissimilarity and geographic distance will be investigated. Chapter 8 will provide a summary of the key findings, consider the key themes (scale, conservation, management implications) arising throughout the thesis and provide suggestions for areas of future research.

Chapter 2. Pond Macroinvertebrate Biodiversity

2.1 Introduction

This chapter aims to provide a comprehensive review of the existing literature in relation to the biodiversity of macroinvertebrate communities within pond ecosystems. This chapter aims to outline and discuss three key areas of pond biodiversity research;

1. Aquatic macroinvertebrate biodiversity and the ecological importance of rural and urban pond habitats;
2. Abiotic and biotic influences on macroinvertebrate distribution and community composition;
3. Threats to pond biodiversity and the conservation and management of perennial and ephemeral ponds.

2.2 Pond or (shallow) lake: what's the difference?

Ponds are defined as small, natural or anthropogenic water bodies between 1 m^2 and 2 ha in area which normally holds water for at least 4 months of the year (Pond Conservation Group, 1993). This definition incorporates both perennial ponds which hold water all year round and ephemeral ponds which have a recurrent dry/desiccation phase of varying length (Williams *et al.,* 1997; Nicolet *et al.,* 2004). However, the distinction between large lakes and smaller lakes/larger perennial ponds is not always clear as the size of lentic freshwater bodies represents a gradient and 'comprises an environmental continuum without any clear delimitation' (Søndergaard *et al.,* 2005: 144). Notwithstanding, Søndergaard *et al.* (2005) has suggested that there are several factors that can separate larger lakes from smaller lakes/ponds;

i) Ponds/smaller lakes often have a much greater littoral zone and closer contact with the surrounding terrestrial habitat which can result in a greater interaction between aquatic and terrestrial biota and matter (Søndergaard *et al.,* 2005);

ii) Smaller lakes and ponds typically have much smaller catchments than lakes (Davies *et al.,* 2008a) resulting in more isolated and insular freshwater habitats compared to larger lakes with greater catchment areas and riverine inflows (Søndergaard *et al.,* 2005);

iii) Vertebrate predators (fish) are typically less well supported in ponds (Søndergaard *et al.,* 2005);

iv) In the absence of fish, macroinvertebrate predation is likely to increase in importance in smaller lakes and ponds, with predatory invertebrates potentially taking over the role of fish (Søndergaard *et al.,* 2005; Cobbaert *et al.,* 2010);

v) Smaller lakes and ponds are typically much shallower and are protected from the wind which can enable submerged and floating macrophytes to cover large proportions of the pond surface area (Søndergaard *et al.,* 2005);

vi) Ponds/smaller lakes have a more heterogeneous habitat and physicochemical environment (e.g., greater littoral zone compared to lakes - increased structural complexity) which can provide a range of habitat niches for fauna to colonize (Williams *et al.,* 2003). In addition, smaller lakes and ponds have relatively stagnant surface water compared to larger lakes which is favoured by certain freshwater taxa (Søndergaard *et al.,* 2005) and;

vii) Ponds and smaller lakes are almost always polymictic, with increased benthic-pelagic coupling and a significantly greater influence and impact on water column nutrients from the sediment compared to larger lakes (Søndergaard *et al.,* 2005).

The oxic and polymictic nature of ponds and smaller lakes, comprising well-mixed water columns (with similar temperature throughout the water column) and an often intense interaction between sediments and the nutrients in the water column (Søndergaard *et al.,* 2005), contrasts with deeper, larger lakes. These are typically holomictic and the flora and fauna is limited by seasonal thermal stratification (Søndergaard *et al.,* 2003; 2005; Brönmark and Hansson, 2005). In larger lakes, wind induced turbulence is an important feature mixing the water column (Berman and Shteinman, 1998; Kann and Welch, 2005). The shallowness of ponds can enable a much greater littoral zone to develop (the whole pond may be covered by aquatic macrophytes), whereas in larger and deeper lakes the hypolimnion (profundal) is typically free of aquatic macrophytes (Brönmark and Hansson, 2005). Natural fish populations are typically limited in both abundance and diversity in ponds and their influence on the functioning and structure of ponds is reduced compared to larger lakes (De Meester *et al.,* 2005). However, many anthropogenically created ponds and shallow lakes are stocked with fish for angling or ornamental purposes (Wood *et al.,* 2001; Hassall, 2014) and fish have been demonstrated to influence invertebrate composition (Wood *et al.,* 2001; Schilling *et al.,* 2009; Beresford and Jones, 2010; Chaichana *et al.,* 2011) and cause trophic cascades (Nyström *et al.,* 2001; Knight *et al.,* 2005) in both lakes and ponds. The smaller catchment area of ponds compared to larger lakes can enable quite different environmental conditions to develop (reflecting local microsite conditions (Scheffer *et al.,* 2006)) even in ponds that are in close geographical proximity to each other (Williams *et al.,* 2003; Davies *et al.,* 2008b). This high physicochemical heterogeneity provides a wide range of environmental conditions for flora and fauna to colonize and at a regional scale ponds have been demonstrated to support greater aquatic macrophyte and macroinvertebrate diversity than lakes (Williams *et al.,* 2003; Biggs *et al.,* 2005).

The distinction between shallow lakes and ponds can be particularly difficult as a number of similarities can be drawn between the structure and function of ponds and shallow lakes. Europe's most important piece of water legislation, the Water Framework Directive (WFD), does not include ponds (Miracle *et al.,* 2010). Indeed, Søndergaard *et al.* (2005) distinguished larger lakes from smaller lakes and ponds, but did not separate smaller/shallow lakes from ponds, highlighting the many characteristics that ponds and shallow lakes share. Similar to ponds, shallow lakes are typically oxic, polymictic and do not often stratify stably in the summer (Scheffer, 2004). Nutrients in the water column of shallow lakes and ponds are heavily influenced by sediment-water interactions (Scheffer, 2004; Brönmark and Hansson, 2005; Søndergaard *et al.,* 2003*;* 2005). Both ponds and shallow lakes demonstrate benthic-pelagic coupling (although it is likely to be greater in shallow lakes) and can be heavily influenced by aquatic macrophytes (Scheffer, 2004; Brönmark and Hansson, 2005; Scheffer and van Nes, 2007). Both are shallow (<3 m) which can allow light to penetrate to the bottom sediments, although shallow lake surface areas can reach 100 km^2 (Scheffer, 2004). It can be particularly difficult to delimit the surface area where a pond ends and a shallow lake starts as the [environmental] transition zone between the two is gradual (De Meester *et al*., 2005).

Although the theory of multiple stable states has been traditionally associated with shallow lakes, given the largely artificial separation between shallow lakes and larger ponds, larger ponds can also be characterised by alternative (multiple) stable states (Cottenie *et al.*, 2001; Ruggiero *et al.,* 2003). In the oligotrophic state, shallow lakes/larger ponds are characterised by clear water, a low biomass of phytoplankton, low nutrient cycling between sediments and water (low nitrogen (N) and phosphorus (P) concentrations), well established macrophyte beds and greater abundances of piscivorous fish (Cottenie *et al.,* 2001; Dent *et al.,* 2002). Macrophyte beds can stabilise sediments, reducing sediment re-suspension and nutrient availability, and provide refuge for zooplankton from predation which may increase phytoplankton grazing resulting in the maintainence of an oligotrophic clear water state (Jeppesen *et al.,* 1998). There is a positive feedback; greater abundance of macrophytes increases water clarity, allowing light to penetrate to the bottom and stabilising the bottom sediments, both of which maintain and enhance macrophyte growth (Dent *et al.,* 2002). In the turbid state, shallow lakes are characterised by high N and P concentrations, a high phytoplankton biomass, rapid recycling of nutrients between sediments and water, reduced aquatic macrophyte beds (reduced water column light) and higher abundances of zooplanktivorous fish (Scheffer, 2001; Dent *et al.,* 2002). The transition from an oligotrophic (clear water) stable state to a turbid state can be caused by an increased input of N and P (e.g., agricultural runoff), damage to macrophyte beds (e.g., in a storm) or an increase in density of planktivorous fish (Blindow *et al.,* 1993; Dent *et al.,* 2002). Where macrophytes are damaged there will be a greater effect of wind and waves, re-suspending unstable sediment (increasing cycling of N and P and increasing turbidity) and reducing the grazing of phytoplankton through loss of zooplankton refuge (Dent *et al.,* 2002). Planktivorous fish preferentially prey on larger sized zooplankton (which are very effective grazers of plankton) thus enabling phytoplankton to reach a high biomass and an increase in turbidity (Dent *et al.,* 2002).

However, a number of differences can be identified between shallow lakes and ponds (Table 2.1). Processes at the shoreline, such as nutrient interception, bank erosion and shading, are likely to have a greater influence in ponds than shallow lakes as ponds have much larger perimeter to surface area ratios (Fairchild *et al.,* 2005). As surface area increases, wind-induced turbulence is likely to become more important in mixing the water column and driving sediment re-suspension in shallow lakes (De Meester *et al.,* 2005; Chung *et al.,* 2009; Søndergaard *et al.,* 1992). Whilst wind is a primary control of mixing depth in larger shallow lakes, ponds are often protected from wind action (by surrounding vegetation). Fairchild *et al.,* (2005), in a study of ponds in Pennsylvania, USA, suggest that light penetration may be the key driver of mixing depth in smaller ponds. Stratification in eutrophic ponds with minimal light penetration (high turbidity) is more plausible than eutrophic shallow lakes of a similar depth as the larger area of shallow lakes increases the influence of wind in mixing the water (Fairchild *et al.,* 2005). Indeed the shallow mixing depth in many of these US eutrophic ponds (with reduced light penetration) was associated with seasonal stratification of the water column, with a near anoxic hypolimnion (Fairchild *et al.,* 2005). In addition, smaller, natural lentic habitats such as ponds will typically support smaller and often unstable populations of fish (benthivorous/planktivorous) which have been demonstrated to be an important influence on N and P concentrations in the water column by re-suspension of nutrients through disturbance of bottom sediments when feeding (Jeppesen *et al.,*1997), predation on pelagic zooplankton (reducing grazing on phytoplankton) and also play an important role in structuring aquatic macrophytes in larger shallow lakes (Jeppesen *et al.,* 1997*;* Scheffer, 2004; De Meester *et al.,* 2005).

In this study, it was decided to follow the generally accepted definition of 2 ha for a pond (all 95 sites studied were below this) to separate ponds from shallow lakes, as both an opperational and functional demarcation. This is supported in the present study as there were no examples of ponds exhibiting classic characteristics of alternative stable states (no turbid ponds: given the small area of many ponds they are likely to switch between states and different years may result in different conditions), although it should be noted that De Meester *et al.* (2005) argue that this definition may be counterproductive to research on the functioning and structure of both shallow lakes and ponds.

Table 2.1 - Functional and structural differences between shallow lakes and perennial pond systems

Feature	Shallow Lake	Pond
Surface area	Surface area greater than 2 ha (can reach 100 km^2; Scheffer, 2004).	Surface area less than 2 ha.
Depth	<3 m	<<3 m
Wind mixing	Wind plays an important role in mixing water and can drive sediment re-suspension.	Often wind-protected and have low/minimal wave heights. Does not rely on wind to mix water column. Light penetration may be key driver of mixing in ponds.
Submerged Macrophytes	Submerged macrophytes often absent from the middle of shallow lakes (if turbid).	Submerged and floating macrophytes can encroach and cover entire pond basin.
Fish	Fish (piscivorous, planktivorous and benthivorous) play an important role in the functioning and structure of shallow lakes. Can determine lake state by influencing N and P concentrations in the water column (sediment resuspension) and the structure of aquatic macrophytes.	Lower density, abundance and stability of natural fish populations. Less influence in the functioning of a pond, although can reduce invertebrate diversity within ponds. However (mainly benthivorous) fish are often added to ponds for angling/aesthetic purposes.
Importance of pelagic habitat	Likely to be strong benthic-pelagic coupling.	Likely to be a reduced importance of benthic pelagic coupling (reduced pelagic area/number of pelagic taxa).
Extreme events	Larger shallow lakes more resilient to extreme events and sudden stochastic change.	Smaller ponds are more susceptible to extreme events (e.g., fish introduction, pollution, land use change) and sudden stochastic events.

2.3 Macroinvertebrate biodiversity within pond habitats

Biodiversity is one of the key criteria for the conservation of ponds (Boix *et al.,* 2008; Sayer, 2014). A common misconception is that ponds are ecologically unimportant because they are relatively small, common and abundant landscape features (Wood *et al.,* 2003). Despite their small size, pond habitats contribute significantly (at a regional and local scale) to aquatic macroinvertebrate biodiversity (Biggs *et al.,* 2005; Céréghino *et al.,* 2014). The following section reviews the available literature on macroinvertebrate biodiversity associated with ponds located in a range of rural and urban landscapes. This in itself represents only a fraction of the overall biological diversity present within ponds. Aquatic macrophytes (Williams *et al.,* 1998; Jeffries, 2008; Hassall *et al.,* 2012), algae (Asencio, 2014), and Zooplankton (Rundle *et al.,* 2002; Cottenie *et al.,* 2003; Drenner *et al.,* 2009) are also very well represented within ponds and all six species of native UK amphibians (including the protected Great Crested Newt (*Triturus cristatus*) and the Natterjack Toad (*Epidalea calamita*)) utilise ponds (Boothby, 1997b; O'Brien, 2014; Peterman *et al.,* 2014). In addition, the following section outlines the ecological importance of ponds to freshwater biodiversity.

2.3.1 Agricultural ponds

Ponds are small and numerous in agricultural landscapes, covering an area of 77,000 km^2 globally and in temperate locations such as the UK they constitute about 3-4% of the agricultural environment (Downing *et al.,* 2006). Agricultural ponds were traditionally created to water livestock, for irrigation (Declerck *et al.,* 2006) and fish aquaculture (Downing *et al.,* 2006). Within many UK counties such as Cheshire and Norfolk land owners and farm owners are vitally important for the continued survival of pondscapes as the majority of ponds are located in agricultural settings (Boothby *et al.,* 1995a; Sayer *et al.,* 2012).

Ponds in agricultural landscapes significantly contribute to regional biodiversity and can have high conservation value, often harbouring rare and endangered species (Søndergaard *et al.,* 2005; Declerck *et al.,* 2006; Fuentes-Rodríguez, 2013; Usio *et al.,* 2013). Farm ponds in the Astarac region (SW France) supported a total of 52 macroinvertebrate taxa and made a greater contribution to the richness of Coleoptera, Odonata and Heteroptera than rivers in the study area (Céréghino *et al.,* 2008a). In the same region (Astarac: SW France), Ruggiero *et al.* (2008) recorded 23 Odonata species from 37 agricultural ponds which encompassed a third of the regional Odonata species pool in SW France. Although some individual agricultural ponds in the Astarac region were species poor, they still contributed to the overall regional/pondscape diversity (Céréghino *et al.,* 2008a). Agricultural ponds in Norfolk, UK, supported 57 taxa, and evidence suggested the careful management of farm ponds elevated the invertebrate biodiversity at both an alpha (individual) and gamma (regional) scale (Sayer *et al.,* 2012). In addition, a total of 76 freshwater beetle taxa (one third of the national species pool) were recorded from 54 ponds in intensively farmed regions in Ireland (Gioria *et al.,* 2011).

Integrated Constructed Wetlands (ICW) are man-made wetlands (a series of interconnected ponds containing emergent and submerged plants) built to treat agricultural wastewater (Becerra-Jurado *et al.,* 2010). They can ensure that ponds remain in agricultural landscapes and have been recorded to contribute significantly to freshwater biodiversity; total macroinvertebrate diversity in the last ponds of an ICW series (116 taxa) in Ireland was comparable to total diversity in natural ponds (129 taxa), although the ICW pond at the beginning of the series supported limited invertebrate biodiversity compared to the others (Becerra-Jurado *et al.,* 2010).

2.3.2 Forest ponds

The creation of ponds was historically actively encouraged in forested areas by the Forestry Commission in the UK (Jeffries, 1991). Their creation increased the biodiversity and habitat diversity within many Forestry Commission plantations. However, no rare or endangered species were recorded from 49 perennial forest ponds studied throughout Scotland, but a diverse community of macroinvertebrate taxa, especially species of Hemiptera, Coleoptera and Odonata was observed (Jeffries, 1991). Tree debris in ponds can provide attachment sites and egg laying sites for sponges and snails, smaller debris is often used by Trichoptera to build cases and leaf litter provides a rich source of food for many detritivorous macroinvertebrate taxa (e.g., Asellidae and some Gastropoda) and can facilitate high secondary production (Oertli *et al.,* 1993; Biggs *et al.,* 1994b). Ponds located within woodlands are often ephemeral, providing habitat for rare and endemic species (Brooks, 2000; Armitage *et al.,* 2012) and can act as refugia for macroinvertebrate taxa even when surrounded by industrial, urban landscapes (Spyra and Krodkiewska, 2013). Forest ponds are commonly shaded which has been attributed to reduced macrophyte and macroinvertebrate richness in agricultural areas (Sayer *et al.,* 2012); although forested ponds are just as likely to support uncommon and rare macroinvertebrate taxa (e.g., *Agabus striolatus*: Coleoptera) as other pond types (Biggs *et al.,* 1994a; Biggs *et al.,* 1994b).

2.3.3 Urban ponds

Between 2000 and 2010 the urban landscape in the United Kingdom increased in area by 141,000 hectares (Khan, 2013) and over 60% of the population now resides in urban regions (Pateman, 2011). The density of urban areas is also increasing in many UK cities often at the expense of green spaces (Dallimer *et al.,* 2011). Urban and garden ponds are likely to play an increasingly important role in supporting and contributing to urban biodiversity and mitigating against urban biodiversity loss (Colding *et al.,* 2009; Hassall and Anderson, 2015). An average of 28 and a total of 119 aquatic macroinvertebrate taxa were recorded from 37 ponds in the town of Halton, UK, however, this was lower than the wider landscape in the north west of England (Gledhill *et al.,* 2008). The same study indicated that invertebrate biodiversity was higher in ponds in new town developments, where there was a higher density of ponds, than urban ponds in established, old urban areas (Gledhill *et al.,* 2008). Common macroinvertebrate species can colonize even the most degraded urban ponds (Wood *et al.,* 2003). Storm water retention ponds and urban drainage systems at a landscape-scale can make a significant contribution to the regional freshwater biodiversity and support aquatic invertebrate communities of high conservation value (Scher and Thiery, 2005; Le Viol *et al.,* 2009; Vermonden *et al.,* 2009; Briers, 2014; Hassall, 2014). Six storm water retention ponds along the A7 and A54 roads in SW France supported 29 species of Odonata (Scher and Thiery, 2005). Within 4 sustainable urban drainage system (SUDS) sites in Dunfermline, Scotland a total of 66 taxa were recorded (Briers, 2014). However, urban ponds can also be of very poor ecological quality, often supporting lower biodiversity than ponds in the wider landscape (Noble and Hassall, 2014). Urban ponds in Liverpool were observed to have considerably lower macroinvertebrate species richness than rural ponds, supporting an average of 7 taxa, although substantial heterogeneity was displayed among the urban ponds, with one pond supporting 19 macroinvertebrate taxa (Gledhill *et al.,* 2005). School ponds provide an important resource for educational study and raise awareness of the wider societal value of wildlife and ponds even when biodiversity is relatively low (Braund, 1997). However, a pond next to a school was unlikely to result in an increase in regional diversity, although they could make and important contribution to the wider pond network (Braund, 1997).

The UK government has encouraged wildlife gardening to increase the suitability of household gardens for wildlife in an attempt to combat pressures associated with urbanization (Davies *et al.,* 2009b). Between 2.5 and 3.5 million garden ponds exist in the UK covering an area of around 349 ha (Davies *et al.,* 2009b). Garden ponds are often frequented by amphibians (Baker *et al.,* 2011; Hassall, 2014) but previous studies have recorded relatively limited invertebrate diversity in garden ponds. In Brighton, wildlife ponds harboured an average of only 4 macroinvertebrate taxa, the most common were *Gammarus pulex* (Amphipoda: Gammaridae), *Culex spp.* larvae (Diptera: Culicidae) and pulmonate snails and the least common were Odonata (Wong and Young, 1997). In Sheffield, 19 small experimental garden ponds remained healthy throughout the study period and supported a limited range of macroinvertebrate taxa including Diptera, (e.g., Chironomidae and Culicidae), *Asellus aquaticus* (Isopoda: Asellidae), Coleoptera, and aquatic snails (Gaston *et al.,* 2005a). Garden pond creation may offset pond loss in the wider landscape but they are unlikely to encompass the diversity of pond types and habitats in the wider landscape (Gaston *et al.,* 2005a). Urban and garden ponds may contribute to and augment regional and urban species richness (Gaston *et al.,* 2005b; Hassall and Anderson, 2015), act as refugia for aquatic taxa in urban spaces and as stepping stones between surface waters in the wider landscape (Gledhill *et al.,* 2008).

2.3.4 New ponds

New ponds provide high quality habitat for freshwater ecology, often supporting high macroinvertebrate biodiversity and are important to the wider conservation and enhancement of freshwater biodiversity (Williams *et al.,* 2008). They typically have different physicochemical conditions (often dynamic) compared to older ponds, less vegetation, dominated by inorganic substances and during their early years support few top predators (Williams *et al.,* 2008). New ponds usually have lower nutrient levels than older ponds and less contaminants in the sediments. This creates opportunities for the rapid colonization of taxa and the development of a wide range of macrophyte and macroinvertebrate communities (Gee *et al.,* 1997; Williams *et al.,* 2008). New ponds are often rapidly colonized by Coleoptera because of their ability to fly (Davy-Bowker, 2002). They may support assemblages of macroinvertebrate species not found in older ponds at a later stage of succession including *Ischnura pumilio* (Zygoptera: Coenagrionidae) and *Helophorus longitarsis* (Coleoptera: Helophoridae) (Williams *et al.,* 2008) and may become as species rich as old ponds in around 10-12 years (Williams *et al.,* 1997). Rapid colonization of macroinvertebrate taxa and macrophytes within new ponds may be the result of an adaptation to the physicochemical conditions within the new pond (Williams *et al.,* 2008).

A study of a new pond network in Pinkhill Meadow, Oxfordshire, recorded higher species richness than in other new ponds in the UK (Williams *et al.,* 2008). Usually, species richness within new ponds is the result of a bottom up effect produced by the environmental conditions during pond creation or stochastic processes influencing colonization and dispersal (Williams *et al.,* 2008). However, the rapid colonization of Pinkhill Meadow ponds was hypothesised to be the result of the high connectivity to the surrounding aquatic environment (Williams *et al.,* 2008). A total of 8 invertebrate species (all Coleoptera) listed as nationally scarce and 13 uncommon species were recorded from the Pinkhill Meadow new ponds and the site was colonized by 20% of UK aquatic plant and macroinvertebrate species during the 7 year study period (FBA, 1999; Williams *et al.,* 2008).

2.3.5 Ephemeral ponds

Ephemeral ponds are small lentic water bodies that experience a recurrent desiccation phase which can vary widely in length (Williams, 1997). As a result of the extreme physicochemical demands (caused by the cyclical drying and re-wetting of the pond basin - hydroperiodicity) on flora and fauna, "constraint" and "restriction" are common misconceptions regarding ephemeral pond biodiversity (Williams, 1996). Adaptation to the demanding conditions within ephemeral ponds has enabled a relatively diverse and unique ecology to inhabit them (Williams, 2006). Macroinvertebrates are the largest group recorded in ephemeral ponds (Zacharias *et al.,* 2007), although microcrustacea are also very well represented (Khalaf and MacDonald, 1975). Williams (1997) has suggested there are two principle components to macroinvertebrate communities within ephemeral ponds. The first are invertebrates recorded in both ephemeral and perennial ponds, such as Odonata, Coleoptera and Diptera (Williams, 1997; Nicolet *et al.,* 2004). Many are ecological generalists and have the required prerequisite characteristics to survive in ephemeral ponds (Wiggins *et al.,* 1980). Although Nicolet *et al.* (2004) argues that macroinvertebrate species typical of perennial ponds, but supported within ephemeral ponds, may be the result of a long hydroperiod, chance (stochastic processes) or connectivity to adjacent permanent water bodies. The second component of ephemeral macroinvertebrate communities are species only found within ephemeral ponds (ephemeral pond specialists - those that have developed strategies and adaptations to survive the demanding conditions) (Williams, 1997). This often results in communities supported within ephemeral ponds differing considerably compared to perennial ponds (Collinson *et al.,* 1995; Stenert and Maltchik, 2007).

Components of the macroinvertebrate community supported within ephemeral ponds can be further classified into four groups (Wiggins *et al.,* 1980). The classification is representative of ephemeral vernal ponds (dry from July through to spring; having a dry phase of 8 - 9 months) and autumnal pond communities (retain water in the autumn and have a dry phase of 3 months) in the USA (Wiggins *et al.,* 1980). The classification has significant relevance for temperate ephemeral pond communities such as those found in the UK as they follow a similar cycle to autumnal ponds (after Wiggins *et al.,* 1980);

- Group 1 - Year round residents, which cannot disperse actively, adapting to the dry period by burrowing into the sediment or producing desiccation resistant/diapausing eggs including; Hirudinea, Oligochaeta and Gastropoda (Wiggins *et al.,* 1980).
- Group 2 - Invertebrates that colonize during the spring as they require water for oviposition and aestivate overwinter in the dry basin as eggs or larvae. They are capable of dispersal and include species of Coleoptera, Diptera and some Trichoptera such as Polycentropodidae (Wiggins *et al.,* 1980).
- Group 3 - Taxa that tend to colonize the pond after it has dried, oviposit in the dry basin and overwinter as eggs (Wiggins *et al.,* 1980). This group includes some species of the Trichoptera Limnephilidae and Diptera families Culicidae, Chironomidae and Chaoboridae that will disperse when they emerge as adults.
- Group 4 - Taxa colonize ephemeral ponds in spring, as oviposition relies on water, and often spend the dry phase in proximal permanent waterbodies. Species of Coleoptera and Hemiptera (most are predators) employ a strategy of avoidance and migration rather than tolerance (Wiggins *et al.,* 1980).

The demanding ephemeral pond physicochemical environment has generated specific floral and faunal adaptations allowing taxa to become highly specialized and take advantage of the seasonality in resource availability (Williams *et al.,* 1999) (Table 2.2). The adaptations can be placed into three categories (Williams, 1997);

1) Physical tolerance - desiccation resistant/diapausing eggs, aestivation and flexible life cycles which corresponds to dry periods (Table 2.2). The Gastropoda *Anisus leucostoma,* and Odonata species *Aeshna juncea and Libellula quadrimaculata* exhibit a diapause state during dry periods (Nicolet *et al.,* 2004). A number of invertebrate taxa lay eggs with variable diapause characteristics (bet hedging): some hatch after the initial inundation, but some will only respond to a later inundation to raise the chance of maintaining a successful population within the ephemeral pond (Simovich and Hathaway, 1997; Williams, 2006). Diapause can be maintained across many time scales, from for one season, to years or even decades (Hairston, 1996).

2) Life history traits - ephemeral pond organisms often demonstrate *r*-selected traits (an evolutionary strategy employed by organisms to maintain populations, especially in frequently disturbed and unsuitable environments (Holden, 2008)) including rapid growth, short life cycle, opportunistic/generalised feeding, small size, large number of offspring and large dispersal potential (Table 2.2). Most life history adaptations are influenced by internal factors (e.g., physiology, behaviour and morphology) and external factors (e.g., water loss, temperature, photoperiod) (Williams, 1997).

3) Migration - Active dispersal: the movement/migration of species (often insects with flight) between habitats (Williams, 1997) (Table 2.2). Can also occur in non-flying fauna such as leeches which can crawl short distances between ponds (Williams, 1997). Passive dispersal: use of vector species (water fowl, mammals and larger insects) or the wind by taxa that cannot disperse themselves (Williams, 1997; Cáceres and Soluk, 2002). There is likely to be a large stochastic element in the colonization and distribution of invertebrates in ephemeral ponds, especially from passive dispersal because of the spatially and temporally variable nature of dispersal (Jeffries, 1989; Graham, 2002).

Basing ephemeral pond macroinvertebrate diversity solely on their aquatic diversity can inhibit the wider understanding of the total floral and faunal diversity and conservation value of ephemeral ponds (Drake, 2001). The dry phase fauna may present a significant component of the overall richness and there may be a danger of underestimating the total diversity by not incorporating the terrestrial biota (Collinson *et al.,* 1995). For example, a rich diversity of ground/rove beetles including rare taxa (e.g., *Calodera uliginosa* and a single *Calodera rufescens*) is known to be supported by ephemeral ponds in Loughborough Big Meadow, Leicestershire (Lott, 2001).

Table 2.2 - Summary of selected literature relating to the adaptive strategies of inverebrate taxa in ephemeral pond environments

Location	**Taxon**	**Adaptation**	**Author/s**
Does not state	Flatworm	Flatworms fragment as pond water level recedes and each fragment is contained within a hard mucus cyst. A young worm develops in the cyst during the dry period and hatches as pond fills.	Brönmark & Hansson, 2005
USA	Gastropoda	To survive desiccation some snails form a protective epiphragm of mucus across the shell opening.	Williams, 1987
S. California, USA	*Branchinecta sandiegonensis, Streptocephalus woottoni* (Branchiopoda: Anostraca)	Bet-hedging; produce egg cysts which will not hatch immediately upon inundation, but have different emergence rates to maintain a viable population. Can survive for up to 8 years within a cyst bank.	Simovich & Hathaway, 1997 Belk, 1998
Ruiru, Kenya	*Streptocephalus vitreus* (Branchiopoda: Anostraca)	Fast hatching eggs, laid near the pond edge ensuring the pond is nearly full when hatching. Rapid rate of growth to maturity and becomes sexually mature before full growth. Lays drought resistant eggs that are able to survive the terrestrial phase.	Hildrew, 1985
USA, UK, AUS	*Chirocephalus diaphanous*	Dispersal in the stomach of wildfowl and by the wind.	Williams, 1997
Arid/semi-arid regions	(Branchiopoda: Anostraca)	In periods of diminutive oxygen Anostraca swim near air-water interface to obtain available oxygen.	Lahr, 1997
Drakensberg and Botswana	*Branchipodopsis Spp.* (Branchiopoda: Anostraca)	Early maturation (4-5days), frequent/daily production of resting eggs, bet hedging and production of eggs with different dispersal potential. Resistant to low conductivity.	Brendonck *et al.,* 2000
New Mexico and Arizona, USA	*Eulimnadia texana* (Branchiopoda: Spinicaudata)	High growth rate.	Marcus & Weeks, 1997
E. Victoria, Australia	Cladocera (*Saycia cooki)*	Produces a large number of desiccation resistant ephippial eggs and reaches peak abundance early in pool cycle (wet phase).	Morton & Bayly, 1977.
Everglades Park, USA	Copepoda	Lays diapause or resting eggs which can remain dormant for months/years. Only pond inundation will terminate diapause.	Bruno *et al.,* 2001; Frisch, 2002
Namibia (Semi-Desert)	Libellulidae (*Sympetrum fonscolombii, Pantala flavescens)*	Greater activity (more encounters with prey) and therefore higher capture rates and growth rates than Libellulidae in permanent waters.	Johansson & Suhling, 2004
Does not state	Hemiptera	Active migration. Colonize ephemeral ponds in spring and oviposit. Juveniles have a rapid growth rate and metamorphose before the pond dries. Disperse as adults to proximal ponds.	Brönmark & Hansson, 2005
Lizard Peninsula, UK	Coleoptera, microcrustacea	Coleopteran richness was greater in more permanent, larger ponds suggesting that there was a non-random process of colonization, selecting sites of greatest suitability. Microcrustacea were more prevalent in ephemeral ponds as they were often outcompeted in perennial ponds. Microcrustacea distribution was driven by stochastic passive dispersal and their adaptive abilities to withstand desiccation.	Rundle *et al.,* 2002
Cheshire, UK	Dytiscidae (*e.g., Dytiscus marginalis, Agabus bipustulatus)*	Active dispersal: colonize ephemeral ponds during spring, migrate to permanent ponds during terrestrial phase, or reside in damp pond basin.	Davy-Bowker, 2002
n/a	Coleoptera	Active dispersal: use polarized light as a factor to detect a pond and identify a suitable habitat.	Schwind, 1995
Ontario, Canada	Chironomidae	Active migration. Chironomidae, which oviposit in water, were attracted to ephemeral tanks which were dark and contained leafy detrital matter. Mosquito oviposition habitat seeking behaviours are based on significant knowledge of chemical and occasionally physical stimuli.	Williams *et al.,* 2007

2.3.6 Temporal biodiversity and succession

There is typically a rapid successional/cyclical development each time an ephemeral pond dries or fills (Wilbur, 1997). Initially periphyton and phytoplankton grow, the first fauna to appear in the spring tend to be detritivorous (Wiggins *et al.,* 1980) feeding on the remaining allochthonous litter from the previous terrestrial phase. Pioneer communities colonize including Ostracoda, Copepoda and other microcrustacea (Jeffries, 2011). Ephemeral pond communities are dominated by microcrustacea during early successional stages (Williams *et al.,* 2007) as they emerge from diapause eggs and other *in situ* desiccation-avoidance mechanisms. Productivity will initially be high as nutrient-rich runoff water enters the pond, decomposition during the dry phase creates a large availability of detrital matter, and competition and predation are low (Batzner and Wissinger, 1996). Pioneer communities support the later colonizing predators (insects) which become dominant and can ameliorate the high levels of pioneer competition allowing species to complete the aquatic stage of their life cycle before the pond dries (Wilbur, 1997). However, in some cases intra-/inter- specific competition can reach such levels that species will not be able to complete their life cycles (Wilbur, 1997).

Seasonal drying in ephemeral ponds causes an exponential decline in the numbers of aquatic invertebrate species, which have either migrated away or are in diapause/aestivate life stages. After the dry phase there is a re-setting of the succession process and a rapid re-appearance of invertebrates via both re-emergence and re-colonization processes. This highlights the importance of the connectedness of a pondscape because many taxa will reside in permanent ponds during the dry phase (Jeffries, 2011).

Over a period of 10 years, ephemeral ponds in Northumberland, UK, displayed significant temporal heterogeneity of macroinvertebrate communities driven by occasional key events (e.g., exceptional wet or dry phases), management and their historical legacy. Specifically, ephemeral pond invertebrate communities partially reflected the communities that preceded them (Jeffries, 2011). Similarly, macroinvertebrate biodiversity was recorded to increase temporally (over a 10 year study period) within ephemeral and perennial ponds in Cheshire, UK (Hassall *et al.,* 2012). Macroinvertebrate diversity increased at an alpha scale (from 30 to 40 species) and gamma scale (from 181 to 209 species) between 1995/1996 and 2006 (Hassall *et* *al.,* 2012). The increase in gamma diversity has been attributed to the colonization by mobile species such as Coleoptera and Odonata from proximal ponds (Hassall *et al.,* 2012). In contrast to Jeffries (2011), there was a reduction in temporal beta-diversity indicating that invertebrate community composition between the ponds was becoming more similar over time (Hassall *et al.,* 2012).

2.4 Regional context: pond biodiversity in the East Midlands, UK

There has been an increasing volume of published research on perennial and ephemeral pond biodiversity (Oertli *et al.,* 2009) in both northern (Jeffries, 1991; Boothby *et al.,* 1995a; Guest, 1997; Jeffries, 2011; Hassall *et al.,* 2012) and southern UK (Rundle *et al.,* 2002; Williams *et al.,* 2003; Bilton *et al.,* 2009; Armitage *et al.,* 2012; Sayer *et al.,* 2012). However, there is a relative paucity of research undertaken into pond biodiversity within Midlands regions. A historic survey on the biodiversity of Charnwood field ponds recorded 207 species including 93 riparian Coleoptera, 70 aquatic Coleoptera, 19 water insects, 10 snails, 5 leeches and a single native white clawed crayfish (Lott, 1999, *unpublished data*). Eleven nationally scarce aquatic Coleoptera species were recorded including; *Cercyon convexiusculus, Haliplus heydeni, Hydraena testacea* and *Ilybius fenestratus* (Lott, 1999, *unpublished data*). At least one Red Data Book species was recorded from 26 of the 30 pond sites. High beta-diversities were recorded in the field ponds especially for snails and riparian Coleoptera. Charnwood field ponds represent valuable habitat for macroinvertebrates, specifically riparian Coleoptera (such as rove beetles) which contribute to the diversity and conservation value within field pond landscapes (Lott, 1999 *unpublished data*).

Beresford and Wade (1982) noted Loughborough field ponds had declined by 60% between 1934 and 1979 as a result of mismanagement or infilling by farm owners. Of the remaining 370 ponds, 50% were suffering from gradual or rapid infilling. There were over 77 floral species recorded in the Loughborough field ponds but the total number of floral species was lower than for 1900 when a total of 87 species were recorded (Beresford and Wade, 1982).

2.5 Ecological importance of ponds

Ponds have been observed to support a greater macroinvertebrate species diversity and number of rare and endemic species than other freshwater habitats in the UK (Williams *et al.,* 2003; Davies *et al.,* 2008b). At an individual (alpha, α) scale the richest ponds have a similar number of taxa to adjacent rivers (rivers are typically species rich but relatively uniform), but taxon poor ponds were among the most species deprived, highlighting the considerable heterogeneity in individual pond species richness (Williams *et al.,* 2003). However, at a regional scale (gamma, γ) ponds have a significantly greater macroinvertebrate and macrophyte diversity than rivers, streams, and lakes and support a greater abundance of rare species than the other waterbody types in the UK (Williams *et al.,* 2003; Biggs *et al.,* 2005; Biggs *et al.,* 2007) and Europe (Davies *et al.,* 2008b). Biggs *et al.* (2005) recorded 377 invertebrate species from 617 rivers but 413 invertebrate species from only 200 ponds (including double the number of Red Data Book species). The high variance of pond physicochemical conditions (even when ponds are in close proximity) ensures a variety of habitats/niches are available for colonization and the increased influence of stochastic process on smaller water bodies contributes to the high inter-patch species heterogeneity (beta-diversity) and regional diversity (Williams *et al.,* 2003; Davies *et al.,* 2008b; Zealand and Jeffries, 2009). This heterogeneity suggests several small ponds are likely to hold a greater biodiversity than a single large pond (Oertli *et al.,* 2002). As a result of the significant contribution of ponds to freshwater biodiversity (Hassall, 2014; Sayer, 2014), many ponds could be viewed as biodiversity hotspots within the landscape (Céréghino *et al.,* 2014).

Ponds often provide suitable habitat and can support high diversities of littoral and also pelagic macroinvertebrate taxa (Wood *et al.,* 2001; Williams *et al.,* 2003). The shallow nature and small size of ponds typically creates a large littoral zone providing a wide heterogeneity of habitat for littoral species and the lower densities of vertebrate predators that typically occur in ponds (low predation pressure in the pelagic zone) facilitate a diverse pelagic community (Wood *et al.,* 2001; Søndergaard *et al*., 2005). However, ponds anthropogenically stocked with fish (for ornamental or angling purposes) have been demonstrated to be dominated by burrowing taxa such as Chironomidae and to support lower invertebrate diversities than unstocked ponds (Wood *et al.,* 2001).

There are over 400 species of aquatic plant that have been recorded in ponds (Duigan and Jones, 1997). A total of 150 of the 280 wetland invertebrates within the red data book utilise ponds as habitats (Drake, 1995) and 31 of the 42 freshwater invertebrate species, excluding Diptera, categorised as endangered in the red data book list are associated with ponds (Gee *et al.,* 1994). Of the 38 freshwater and brackish water organisms protected under Section 5 and 8 of the Wildlife and Countryside Act 1981, 23 utilise pond habitats (Wood *et al.,* 2003) including the Glutinous snail *Myxas glutinosa* (Gastropoda: Lymnaeidae) (Williams *et al.,* 1998). Ponds are associated with over 100 UK Biodiversity Action Plan priority species (Freshwater Habitats Trust, 2014).

Ponds in NW England have been found to be of significant biodiversity value (Boothby, 1997b; Hassall *et al.,* 2012). A total of 492 ponds were examined and 13% were reported to support 40 or more macroinvertebrate species, 3% supported 50 or more invertebrate species and 32% contained at least one species on the JNCC scarcity index (Boothby, 1997b). Several Odonata species of special conservation interest were recorded in ball clay ponds, Dorset (Friday, 1988b) and 5 coleopteran species with IUCN Red list status were recorded from agricultural ponds in Ireland (Gioria *et al.,* 2010).

Ratcliffe (1977), in the Nature Conservation Review, described ephemeral ponds as an unimportant environment. Recent publications on ephemeral ponds have challenged this statement. Even though ephemeral ponds typically support a lower diversity of aquatic invertebrate taxa than other water body types (Williams, 1996; Nicolet, 2001; Della Bella *et al.,* 2005; Stenert and Maltchik, 2007) because of their demanding physicochemical environment, they are sites of high ecological importance (high conservation value) supporting a comparable, and often greater diversity of rare and endemic macroinvertebrate taxa than perennial waterbodies (Bratton, 1990; Simovich, 1998; Blaustein and Schwartz, 2001; Nicolet *et al.,* 2004; Della Bella *et al.,* 2005; Céréghino *et al.,* 2008b; Díaz-Paniagua *et al.,* 2010).

Uncommon flora and invertebrate species were recorded in 82% of the 70 ephemeral ponds surveyed throughout the UK and one quarter held at least one invertebrate from the red data book species list (Nicolet, 2001). In the same study 17% of invertebrates recorded from ephemeral ponds were nationally scarce and 6% were red data book species (Nicolet, 2001). This was higher than the number of nationally scarce or red data book species recorded from rivers or perennial ponds (Nicolet, 2001). A similar study of 71 ephemeral ponds in semi-natural landscapes in England and Wales found that 75% supported at least one uncommon and/or one nationally scarce macroinvertebrate species (Nicolet *et al.,* 2004). A total of 9 nationally scarce invertebrate species were recorded from 12 ephemeral tyre rut ponds in Southern England (Armitage at al., 2012). Two species of freshwater invertebrate protected under Section 5 and 8 of the Wildlife and Countryside Act 1981, are reliant on ephemeral ponds for their long term survival; *Triops cancriformis* (tadpole shrimp, Notostraca: Triopsidae), found in only 10 locations in past 200 years and currently found in 2 sites in UK, and *Chirocephalus diaphanus* (fairy shrimp, Anostraca: Chirocephalidae), the UK's only known anostracan, has been recorded from only 12 sites in England (Williams, 1997).

In Oxfordshire, perennial ponds supported a greater diversity of macroinvertebrate taxa than ephemeral ponds however, 4 of the 5 ponds studied with the highest rarity scores were ephemeral (Collinson *et al.,* 1995). Ephemeral ponds are associated with the Zygoptera, *Lestes dryas,* the Coleoptera *Dryops similaris, Haliplus furcatus, Helophorus strigifrons, Graptodytes flavipes* and the Gastropoda *Lymnaea glabra,* all of which are on the Red Data Book list (Collinson *et al.,* 1995). One of the UK's rarest plants, *Carex vulpina* (Cyperaceae) was recorded only within ephemeral ponds from a large-scale study of 377 perennial and ephemeral ponds throughout the UK (Williams *et al.,* 1998). At least one nationally rare macroinvertebrate species was recorded from 75% of ephemeral ponds in the New Forest and Lizard Peninsula, UK, which were dominated by Chironomidae and Coleoptera (Bilton *et al.,* 2009). This included *Agabus labiatus* which can utilise the specialist environment as it has a short larval stage and can survive the dry phase in *in situ* (Bilton *et al.,* 2009). In the same ponds in the New Forest and Lizard Peninsula, a total of 68 species of Coleoptera were recorded, 24 of which were of conservation interest (Gutierrez-Estrada and Bilton, 2010).

2.6 Local (physicochemical/biological) and spatial (connectivity/ dispersal) parameters influencing macroinvertebrate communities within ponds

A wide range of physicochemical and biological variables can influence the composition and richness of macroinvertebrate communities within pond habitats. Environmental parameters can be divided into two categories (Vanschoenwinkel *et al.,* 2007; Waterkeyn *et al.,* 2008):

I. **Local** - pond size, age, depth, macrophyte cover/diversity, predation, water chemistry, habitat diversity, shading, turbidity and hydroperiodicity;
II. **Spatial/regional** - connectivity and dispersal.

Pond size has been reported to be a key influence on macroinvertebrate composition within ponds, (Brönmark 1985; Nilsson and Svensson, 1995; Biggs *et al.,* 2005; Stenert and Maltchik, 2007; Ruggiero *et al.,* 2008; Shieh and Chi, 2010) as a greater surface water area can allow larger populations to develop and reduce the chance of extinction (Shieh and Chi, 2010). However, some studies found that pond size has relatively little influence on community composition (Scheffer *et al.,* 2006; Nakanishi *et al.,* 2014). In Switzerland, Oertli *et al.* (2002) demonstrated that the influence of pond size can vary depending on the macroinvertebrate group; Odonata had a relatively strong correlation with pond size, whilst Coleoptera, Sphaeriidae and overall faunal richness displayed a weak association with pond size. In the same study, an agglomeration of smaller ponds was recorded to support greater species richness and conservation value than a larger pond of an equivalent surface area (but larger ponds did support species not recorded from smaller ponds) (Oertli *et al.,* 2002).

At a landscape-scale, older ponds appeared to support a greater diversity of species (especially Coleoptera) and number of rare species (Fairchild *et al.,* 2000). However, pond age does not appear to be as important as other variables (Miguel-Chinchilla *et al.,* 2014). This is probably because new ponds are often located proximal to other waterbodies (higher connectivity), which can facilitate a rapid colonization (Gee *et al.* 1997; Williams *et al.,* 2008). Additionally, disturbances, such as drought or stocking with fish (Grayson, 1992), may reduce the influence of pond age.

Macroinvertebrate richness in ball clay ponds in Purbeck were largely influenced by pH; Mollusca and Ephemeroptera were absent and Chironomidae and Trichoptera richness greatly decreased when pH was below 5.5 (Friday, 1987). Environmental variables influencing pond biodiversity varied between alpine and lowland ponds in Switzerland (Hinden *et al.,* 2005). pH increased in importance with altitude, conductivity negatively influenced lowland pond communities but had a positive association with alpine biodiversity; and pond area influenced lowland pond community composition but was insignificant in alpine ponds (Hinden *et al.,* 2005). Fish predation and macrophyte cover were also reported to be important determinants of invertebrate assemblage in alpine ponds (Hinden *et al.,* 2005).

Macrophytes within ponds can increase the dissolved oxygen in the water column, habitat diversity, available food, oviposition sites and can provide protection from predators (Bazzanti *et al.,* 2010; Fontanarrosa *et al.*, 2013). Invertebrate species richness within perennial and ephemeral ponds has been recorded to be highest in macrophyte beds compared to other mesohabitats (Della Bella *et al.,* 2005; Bazzanti *et al.,* 2010). Pond margins had the greatest diversity of fauna in Welsh ponds as there was a high density of flora but an increasing number of riparian trees around the pond margin reduced the number of Odonata, Ephemeroptera and Trichoptera (Gee *et al.,* 1997). Ponds shaded by trees have typically been associated with a lower biodiversity however, they are also likely to support uncommon species and the decaying wood/leaves provide resources for many Diptera larvae (Biggs *et al.,* 1994a). The influence of macrophytes can be sub-divided into emergent and submerged macrophytes as different invertebrate assemblages have been associated with the two macrophyte types (Parsons and Matthews, 1995).

Fish predation has been identified to significantly reduce invertebrate richness and abundance (Diehl, 1992; Fairchild *et al.,* 2000; Angélibert *et al.,* 2004; Chaichana *et al.,* 2011) although trout (low densities) did not appear to impact invertebrate abundance in Welsh ponds (Gee, 1997). Invertebrate densities in submerged macrophyte beds were not influenced by fish indicating that macrophytes can act as refugia for invertebrate taxa (Gilinsky, 1984; Diehl, 1992). Within fishless ponds, Dytiscidae, Hemiptera and Odonata are top predators and can influence community structure by reducing macroinvertebrate richness and abundance at both local and metacommunity scales (Cadotte *et al.,* 2006; Turner and Chislock, 2007; Cobbaert *et al.,* 2010).

Spatial parameters such as pond connectedness and pond density can influence the structure of macroinvertebrate communities (Cottenie *et al.,* 2003; Briers and Biggs, 2005; Oertli *et al.,* 2005; Vanschoenwinkel *et al.,* 2007; Gledhill *et al.,* 2008). In a connected pondscape, ponds often support a greater diversity of macroinvertebrates compared to more isolated ponds as there is greater opportunity for active and passive dispersal and colonization of invertebrate taxa (e.g., snails can be carried by vector species to nearby ponds) (Brönmark, 1985; Williams *et al.,* 2008). Stochastic events often related to dispersal can be important in explaining the heterogeneous macroinvertebrate assemblages that occur in environmentally similar ponds (De Meester *et al.,* 2005; Verdonschot *et al.,* 2011). Pond biodiversity has been found to be higher in NW England than elsewhere in the UK potentially because this region has a much higher density pondscape (Gledhill *et al.,* 2008). Alongside pond density, macrophyte richness may also have been influential in urban ponds as the greatest vegetation richness was correlated with the highest macroinvertebrate richness (Gledhill *et al.,* 2008).

The National Pond Survey (a study of 200 ponds) reported pH, connectedness, size and macrophyte cover to be the key environmental drivers determining species richness and rarity (Biggs *et al.,* 2005). Jeffries (1991) expressed the relative importance of environmental variables on macroinvertebrate communities in a hierarchical model with biogeographic region providing the context and background for ecological communities. Next, three variables dominated and drove community composition: acidity, physicochemical stability and basin topography. At the lowest level are other environmental parameters (e.g., salinity and biotic interactions) which may influence individual ponds and impose further community variation (Jeffries, 1991). A summary of the environmental parameters influencing perennial pond macroinvertebrate community composition and species richness is presented in Table 2.3.

The nature of the hydroperiod (length and frequency of the wet phase) dominates floral and faunal community composition within ephemeral ponds (Brönmark and Hansson, 2005; Jeffries, 2011; Moraes *et al.,* 2014) both directly and indirectly (changes to water chemistry and physical environment) (Fairchild, *et al.,* 2003). Permanence was the key determinant of species richness and the presence of predators, rather than pond area, within ephemeral ponds on the Lizard Peninsula, UK (Bilton *et al.,* 2001). Hydroperiod and pond size were the key variables determining invertebrate community structure (combined they explained 47% of the variation in abundance and 59% of species richness) in 36 rock pools in South Africa (Vanschoenwinkel *et al.,* 2009). In the same study, hydroperiod was recorded to have a greater effect on passive dispersers than active dispersers; passively dispersing taxa often survive the dry phase in situ and have to face the consequences of desiccation whilst active dispersers can migrate as the pond

Table 2.3 - Summary of selected literature relating to the key environmental variables influencing macroinvertebrate assemblage and taxon richness within perennial ponds

Location	Pond Type	Influential Environmental Variable	Author/s
Cheshire, UK	Agricultural	Ponds with a perennial hydroperiod and less shading demonstrated increased invertebrate diversity. Fish predation caused a decline in Coleoptera richness but an increase in Odonata diversity. Oligotrophic and eutrophic (phosphorous) ponds were associated with low macrophyte and invertebrate richness.	Hassall *et al.,* 2011
Szczecin Hills, Poland	Agricultural	At a regional scale, pond size was the key variable determining macrophyte species richness. At the local scale, pond size and isolation influenced macrophyte diversity. Increasing pond isolation and a smaller pond size were associated with low macrophyte species richness.	Bosiacka & Pienkowski, 2012
SE Ireland	Wastewater treatment	Differences between macroinvertebrate assemblages in constructed and natural ponds used for wastewater treatment were driven by: connectivity, pH and vegetation structure.	Becerra-Jurado *et al.,* 2009
Geneva, Switzerland	Forest	Substrate preferences were exhibited by zoobenthos species. Temporal variation in zoobenthos species was caused by the reproduction effect (large abundances of new-borns).	Oertli, 1995
Alberta, Canada	Woodland/ wetland	Dytiscidae decreased predatory macroinvertebrate (Zygoptera and *Chaoborus*) and gastropod abundance but not species richness. Dytiscidae predation initiated two trophic cascades; 1) decreased snail abundance leading to an increase in periphyton biomass (up to 6 times greater than Dytiscidae free ponds) and; 2) an increase in cladoceran (*Daphnia*) biomass through predation on cladoceran predators.	Cobbaert *et al.,* 2010
London, UK	Urban	Cadmium (occurs from abrasion of vehicle tyres and enters pond habitats via runoff) was correlated with decreased rotifer species assemblage. Zinc, lead, pH and macrophyte cover all may have a role in determining rotifer composition.	Langley *et al.,* 1995
Western Taiwan	School pond	Pond size and depth, altitude, sediment depth and the Anuran *Bufo melanostictus* (Common Asian Toad) were the key variables influencing macroinvertebrate communities. Active dispersers were most associated with pond size whilst passive dispersers were associated with pond depth and sediment depth.	Shieh & Chi, 2010
Bookham Common, Surrey, UK	Field	Smaller ponds supported greater macroinvertebrate diversity (50 species) than the larger pond (43 species). This may be the result of a high density of fish and few macrophyte species in the larger pond, decreasing the availability of protection and food for macroinvertebrate taxa. Faunal similarities were shown between the two ponds as a result of the colonization from the nearby stream.	Kett & Kirk, 1994
New York, USA	Field	Macrophytes contribute significantly to macroinvertebrate abundance. Within vegetated mesohabitats macroinvertebrate abundance was many times higher than in non-vegetated mesohabitats. A total of 60% of macroinvertebrate species recorded were present on only 3 macrophyte species.	Krull, 1970
Sweden	Does not state	Predation. Rainbow Trout (*Oncorhynchus mykiss*) depressed benthic macroinvertebrate abundance. Signal crayfish (*Pacifastacus leniusculus*) deleteriously impacted snail abundance.	Nyström *et al.,* 2001

dries and re-colonize quickly as the pond fills to exploit the resources (Vanschoenwinkel *et al.,* 2009). Macroinvertebrate richness and abundance increased in accordance with increasing hydroperiod length in ephemeral ponds in New Hampshire, USA (Tarr *et al.,* 2005). Increased hydroperiod length can increase the time available for colonization, enabling more of the regional fauna to colonize ephemeral pond habitats (Schnieder and Frost, 1996).

Although the drying of ponds may be a routine hazard that many species have adapted to, the persistence and composition of macroinvertebrate communities may be influenced by other processes such as predation, locating a mate and other physicochemical and spatial parameters as well as hydroperiodicity (Jeffries, 1994; Spencer *et al.,* 1999). Figures 2.1 and 2.2 summarize the abiotic and biotic variables influencing ephemeral pond invertebrate communities. The physicochemical conditions of ephemeral ponds can be divided into two phases; *stable-* physicochemical conditions that occur during the highest water volume (often in winter months) and; *unstable-* extreme physicochemical conditions (see Chapter 1.1 and Williams, 1996) which occur as water volume declines (in the summer months) and when the basin is initially inundated after the dry phase (Khalaf and MacDonald, 1975). Ephemeral ponds near Rome were identified to be influenced significantly by dissolved oxygen, depth, pond size and macrophyte richness as well as hydroperiod length (Della Bella *et al.,* 2005). Physicochemistry (Nicolet *et al.,* 2004; Bilton *et al.,* 2009; Gutierrez-Estrada and Bilton, 2010), substratum preferences (Fairchild *et al.,* 2003) and pond area (Spencer *et al.,* 1999; Kiflawi *et al.,* 2003; Studinski and Grubbs, 2007) have been recorded to significantly influence ephemeral pond communities. Ephemeral ponds can support invertebrate taxa and larger open-water invertebrates which are outcompeted or cannot survive in permanent ponds (De Meester *et al.,* 2005), as there is often 'lower predation pressure' caused by the lack of vertebrate predators (fish) within ephemeral ponds (Brönmark and Hansson, 2005: 60). Invertebrate (Coleoptera, Notonectidae) and amphibian predation can be an important aspect regulating fishless ephemeral pond communities (Larson, 1990; Herwig and Schindler, 1996; Jeffries, 1996; Schnieder and Frost, 1996; Blaustein 1998; Bilton *et al.,* 2001; Brendonck *et al.,* 2002). In addition, the seasonal influx of aerial colonizers and phenological changes to competition and predation are other biotic stresses shaping invertebrate communities within ephemeral ponds (Brendonck *et al.,* 2002).

Island biogeography theory (MacArthur and Wilson, 1967) may be useful for the prediction and modelling of macroinvertebrate distribution in perennial and ephemeral ponds as they act as aquatic isolated islands in an environment of unsuitable terrestrial land (Ripley and Simovich, 2009) and may explain differences in distribution that cannot be explained by the hydroperiod (Wilcox, 2001). It was possible to predict 62% of species richness in ephemeral ponds in the Lower Galilee, Israel, using an island biogeography model (Kiflawi *et al.,* 2003). Using island biogeography to predict species richness in ephemeral ponds can be complicated by: life history adaptations to cope with the complex environment (Angeler and Alvarez-Cobelas, 2005); the continual state of non-equilibrium caused by drying (Wilbur, 1997) and fluctuating pond size during the study period (Ripley and Simovich, 2009). Additional literature relating to the key abiotic and biotic variables influencing ephemeral pond communities is summarised in Table 2.4.

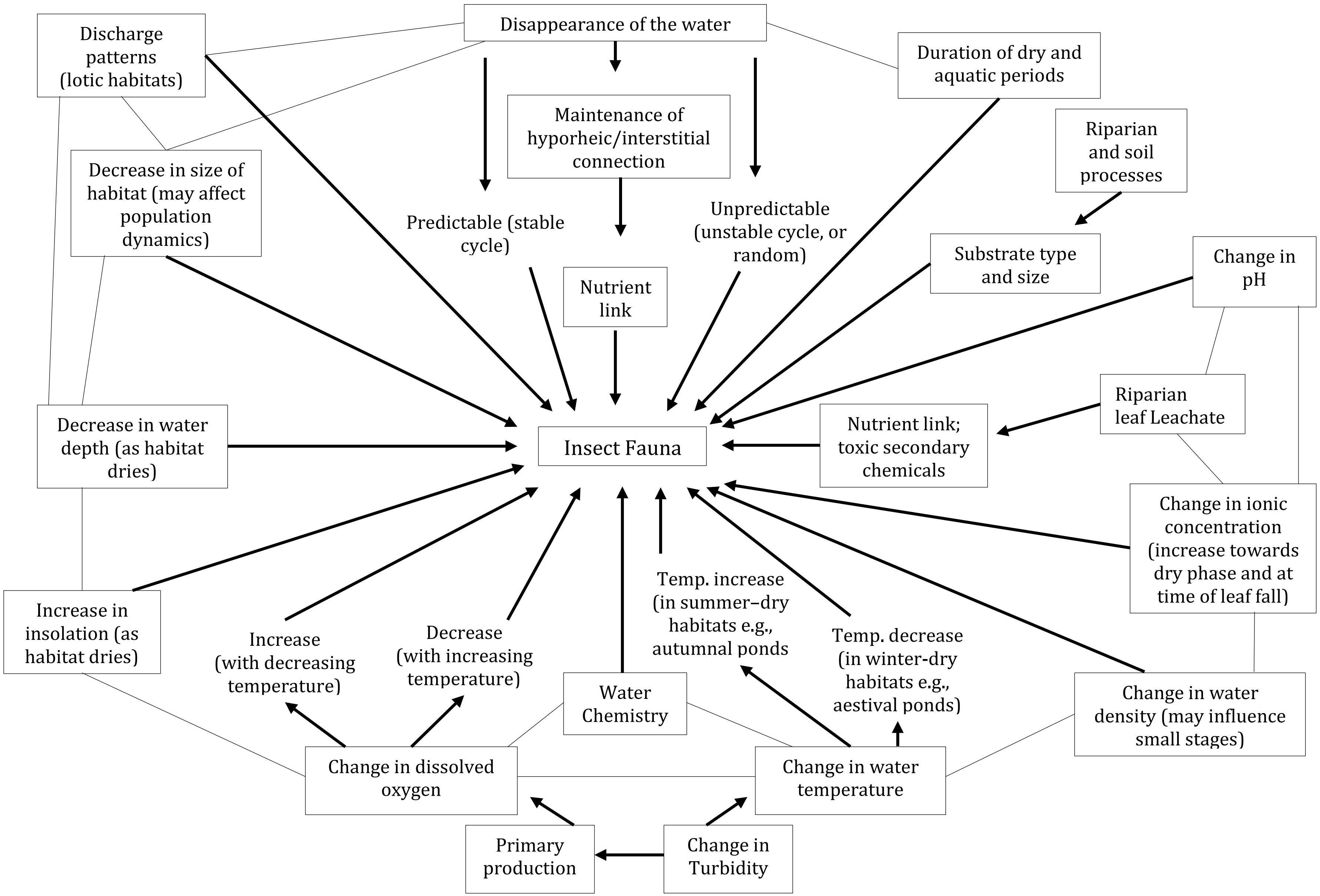

Figure 2.1 - Physical and chemical characteristics of ephemeral ponds which influence macroinvertebrate fauna (Williams, 1996: 636)

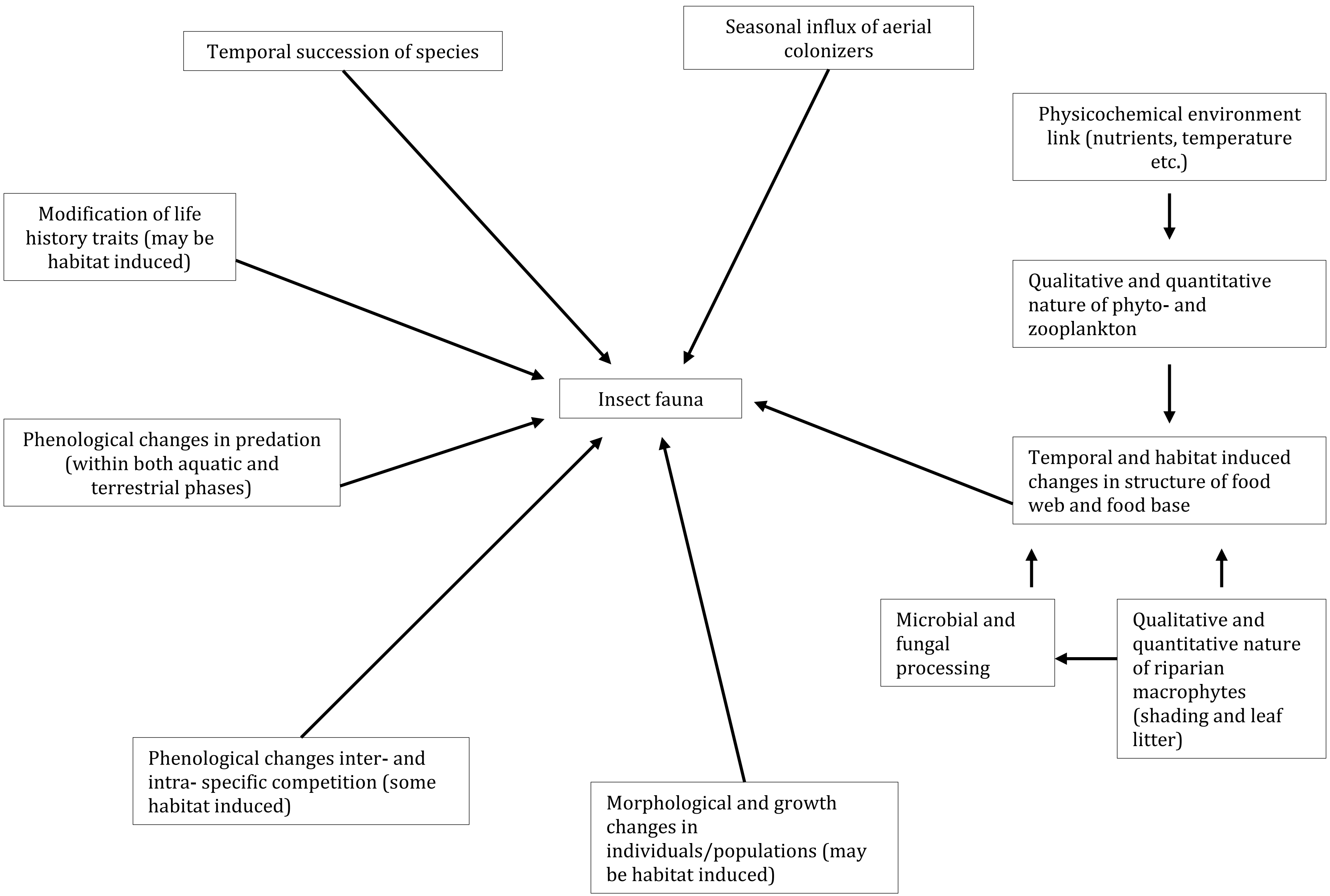

Figure 2.2- Biological characteristics influencing macroinvertebrate taxa in ephemeral ponds (Williams, 1996: 637)

Table 2.4 - Summary of selected literature relating to the key environmental variables influencing macroinvertebrate assemblage and richness in ephemeral ponds

Location	**Pond Type**	**Hydroperiod Length**	**Influential Environmental Variable**	**Author/s**
Camargue Region (S. France)	Mediterranean	5-9 months	Hydroperiod and salinity accounted for approximately 50% of the variation in macroinvertebrate assemblage. Secondary variables influencing communities were: fish predation, macrophyte cover, pH, phosphorus, pond area and max depth.	Waterkeyn *et al.,* 2008
Espolla Pond, NE Iberian Peninsula	Mediterranean	3-100 days	Hydroperiod and flooded area influenced macroinvertebrate community assemblage.	Boix *et al.,* 2001
Donana National Park, SW Spain	Mediterranean	0.4-8.9 months in dry year 4.2-12 months in wet year	Macroinvertebrate community assemblages differed with changing hydroperiod. A shorter hydroperiod decreased aquatic time available for invertebrates concentrating the biological processes into a shorter time frame, altering community composition. High species richness in the ponds was the result of high connectivity.	Florencio *et al.,* 2009
Rome, Italy	Mediterranean	Filled in late autumn dried by late spring	Species richness corresponds to hydroperiod, pond area and pH.	Bazzanti *et al.,* 1996
Rome, Italy	Mediterranean	Does not state	Hydroperiod was the key determinant of macroinvertebrate richness. Macrophyte cover also influenced species richness (food and mesohabitat) but pond area was recorded to be insignificant.	Bazzanti *et al.,* 2003
Mt. Kabul, Israel	Mediterranean	50-165 days	Hydroperiod was the key determinant of cladoceran and Ostracoda species richness. Sediment depth was also influential. Surface area was recorded to have no significant influence.	Eitam *et al.,* 2004
Sardinia	Mediterranean	5-7 months	Hydroperiod and connectivity influenced crustacean composition, but grazing was the most important influence on macrophyte assemblage. Altitude and pond surface area also influenced macrophyte and crustacean assemblage. In addition, increased floral diversity was correlated with increased crustacean diversity (refuge and trophic resources).	Bagella *et al.,* 2010
New Hampshire, USA	Wetland	Short (<4 months), intermediate (>4 months), permanent	A longer hydroperiod increased macroinvertebrate richness and abundance. Higher temperature, dissolved oxygen and fish predation also influenced invertebrate richness and abundance.	Tarr *et al.,* 2005
Mississippi River, St Charles Missouri, USA	Floodplain wetland	Variable	Hydroperiod. Predation was lower in ponds with a shorter hydroperiod as the ponds tended to be free of fish, whilst predation was higher in more permanent ephemeral ponds. Macroinvertebrate richness and abundance decreased as pond duration increased as a result of amplified predation.	Corti *et al.,* 1997
Sacramento, USA	Wetland	1-6 months	Hydroperiod (pond area and depth) was the key determinant of crustacean species richness.	King *et al.,* 1996
S. California, USA	Ephemeral wetland	Did not measure	Hydroperiod. The longer the hydroperiod the greater the cumulative crustacean species richness. Although, it was suggested that pond depth was a better predictor of absolute species richness than pond permanence.	Ripley & Simovich, 2009
Cedra Valley, N Apennines, Italy	Alpine	59-159 wet days	Hydroperiod determined zooplankton species richness. Hydro-chemical variables such as pH could have also influenced zooplankton diversity.	Tavernini *et al.,* 2005

Ontario	Snow Melt	34 and 98 days	Hydroperiod was the key determinant of Ciliate abundance and richness. pH was also demonstrated to be important.	Andrushchyshyn *et al.,* 2003
Jamaica	Rock pools	Dried at least once during the study	Invertebrate richness and abundance were influenced by hydroperiod. Shorter pond duration caused a more unpredictable, less diverse invertebrate community. Desiccation frequency was also observed to be influential on species diversity and abundance.	Therriault & Kolasa, 2001
Massachusetts, USA	Forest	300 days and <250 days	Hydroperiod. There was an increase in diversity of benthic invertebrate taxa with increasing hydroperiod length. Chironomidae dominated ponds with a shorter hydroperiod.	Brooks, 2000.
Texas, USA	Grassland	Dried at least once during the study	Predation. Microcrustacea in ephemeral ponds were larger than those in perennial ponds as fish (absent from ephemeral ponds) are size selective predators and preferentially ate the larger microcrustacea. Macroinvertebrate predators consume smaller microcrustacea allowing larger individuals to survive in fishless ephemeral ponds.	Drenner *et al.,* 2009
Ohio, USA	Perennial/ Ephemeral	20 of 61 ponds dried for part of study	Hydroperiod, predation and pond depth were correlated with Physidae composition. Conductivity and pH were not considered important influences of species composition.	Turner & Montgomery, 2009
Wupatki National Monument, Arizona, USA	Ephemeral	Does not state	Distance from permanent waters influenced taxon richness (further away less species, nearer more species). Frequency of disturbance impacted ephemeral pool community structure. Pond size and pond age were not recorded to be significant.	Graham, 2002
Ohio, USA	Nature Reserve	Dry by July and August	Temperature, depth and dissolved oxygen could explain snail abundance and density. Depth and dissolved oxygen were positively correlated with Zygoptera nymphs. Biotic and abiotic factors explained <37% of within pond distribution suggesting that there were a range of other factors could influence invertebrate distribution.	Smith *et al.,* 2003

2.6.1 Metacommunity dynamics

Pond community structure and floral and faunal distribution can be explained using the metacommunity concept. A metacommunity can be defined as 'a set of local communities that are linked by dispersal of multiple potentially interacting species' (Leibold *et al.,* 2004: 602). There is a network of local communities in which species interactions occur and affect colonization and extinction (Leibold *et al.,* 2004). Metacommunity theory is often based upon three hierarchical levels; the microsite which consists of an individual species, which are nested within localities (patches) which contain local communities and the communities are connected to, and interact with other communities which form a region (Leibold *et al.,* 2004). Metacommunities can be modelled simplistically into 4 paradigms (Leibold *et al.,* 2004);

I. **Patch dynamic paradigm** - assumption that there are numerous homogenous patches in which the driving factor is a trade-off between competitive ability and dispersal.
II. **Species sorting paradigm** - patches are heterogeneous and species interactions are driven by abiotic factors. The same species are found in heterogeneous patches through their ability to specialize to the abiotic niches.
III. **Mass effects paradigm** - dispersal affects local communities. Different patches have different conditions at a given time, dispersal of individuals between patches is common, creating source-sink relationships. Local extinctions are prevented by dispersal from patches where they are good competitors.
IV. **The neutral paradigm** - assumes species are similar in the patches and are influenced by a random change (stochastic processes) in compositional space.

Pond metacommunities can be structured by both local and regional factors. Dispersal can be considered a homogenizing process reducing the differences between ponds (mass effects) but it is the local variation in environmental characteristics (species sorting) of the ponds which can regulate pond communities even when there are high dispersal rates and maintain pond heterogeneity (Cottenie *et al.,* 2003; Cottenie and De Meester, 2004). Studies have shown macroinvertebrate species composition to be dominated by local environmental factors (selective removal of unfit taxa), suggesting a strong species sorting, but a combination of local and regional factors (connectivity/dispersal: mass effects) best explains the variation in macroinvertebrate community composition (Cottenie *et al.,* 2003; Vanschoenwinkel *et al.,* 2007). Regional factors such as high dispersal rates and source/sink dynamics (mass effects) enable a constant colonization of macroinvertebrate taxa and their persistence within the metacommunity (Cottenie *et al.*, 2003; Urban, 2004; Vanschoenwinkel *et al.,* 2007). However, Cadotte *et al.* (2006) noted dispersal was beneficial to species richness at the local scale, but had little effect on species richness at the regional level as the negative impact of predation was demonstrated to be much stronger than the positive regional impact of dispersal.

The dispersal mechanism of macroinvertebrate species may affect the mechanisms fundamental to metacommunity structure (Vanschoenwinkel *et al.,* 2007; Van De Meutter *et al.,* 2007). Mass effects were greatest in passive dispersers in a pond metacommunity studied by Van De Meutter *et al.* (2007). Invertebrate species that rely on passive dispersal were more similar in ponds directly connected to source ponds (mass effects) than indirectly connected, and adjacent ponds can buffer dispersal to more distant ponds (Van De Meutter *et al.,* 2007). Actively dispersing invertebrates showed no metacommunity pattern, suggesting intense active dispersal can cause some homogenization of the metacommunity (Van De Meutter *et al.,* 2007). Pond isolation was deleterious for Odonata species richness as fewer species colonized sites further away from the source; the behavioural dispersal limitation exhibited by Odonata can act as a filter and influence community structure (McCauley, 2006). In pools in Scotland, physicochemistry could not explain the differences in macroinvertebrate fauna between ponds (Jeffries, 1989). However, the irregular nature (chance) of colonization by some taxa such as Zygoptera and Ceratopogonidae was noted to be important (Jeffries, 1989).

2.7 Threats to pond numbers and macroinvertebrate biodiversity

An intensification of farming techniques poses a significant threat to flora and fauna inhabiting ponds in agricultural landscapes. Many have been polluted by diffuse nutrient loading from chemical and organic fertilizer and pesticide contamination (Brönmark and Hansson, 2002; Biggs *et al.,* 2007), or are lost as a result of infilling or land drainage leading to an increase in the fragmentation of pond habitats (Boothby *et al.,* 1995b; Boothby and Hull, 1997; Moss, 1998; Davies *et al.,* 2009a). Low species richness and no aquatic Coleoptera were recorded from ponds in Brown Moss Nature

Reserve, Shropshire, because the ponds were highly eutrophic as a result of excessive nutrient loading from the surrounding intensively fertilised agricultural land and housing developments (Chaichana *et al.,* 2011).

The urbanising landscape is a contemporary pressure causing a decline in pond numbers (Hassall, 2014). Industrialization within developed/developing countries has increased the pollution of pond environments from point sources such as heavy metals and industrial wastes, (Hunt and Corr, 1997; Brönmark and Hansson, 2002; Camponelli *et al.,* 2009; Bhat *et al.,* 2013; Vincent and Kirkwood, 2014). Detrimental anthropogenic effects may be exacerbated as ponds cannot dilute, store or transfer pollution like rivers and lakes with outlets (Biggs *et al.,* 2005). Reduced connectivity and isolation of ponds in urban areas is threatening their biodiversity, especially species reliant on the terrestrial matrix, and is influencing dispersal potential (Cushman, 2006). Pond isolation can increase local extinction rates and regional losses of flora and fauna (Boothby *et al.,* 1995a).

Ephemeral ponds are one of the waterbodies under the greatest threat in the UK because their small size, shallow basin and distinctive hydrology make them fragile systems susceptible to damage from anthropogenic processes (Collinson *et al.,* 1995; Williams *et al.,* 1999). Urban developments, surface drainage, nitrogen and phosphorus enrichment, infilling from agriculture (Rhazi *et al.,* 2001), pollution, raising water levels through the mistaken belief that the pond is drying out (Biggs *et al.,* 2001) and deforestation have resulted in the degradation and loss of many ephemeral ponds (Zacharias *et al.,* 2007). Thousands of Scottish ephemeral ponds were lost largely as a result of land drainage (Maitland, 1999). Lowering the water table under the facade of land improvement has caused the extinction of *Coenagrion armatum* (Zygoptera: Coenagrionidae) and the near extinction of *Lestes dryas* (Zygoptera: Lestidae) in the UK (Williams, 1997). The lack of awareness and the value placed on aesthetic beauty in society have increased pressures on ephemeral ponds. They are widely considered to be unattractive and uninteresting during the dry phase because they are a muddy depression often overgrown with weeds. Perennial ponds are considered more attractive and consequently ephemeral ponds are often deepened and have their macrophytes removed, essentially making them permanent (Bratton 1990; Biggs *et al.,* 1994a; Biggs *et al.,* 2001).

Anthropogenically driven climate change threatens ephemeral and perennial pond biodiversity in temperate regions (Zacharias *et al.,* 2007; Matthews, 2010; Rosset *et al.,* 2010; Rosset and Oertli, 2011). Precipitation fluctuations will affect the thermal mass, increasing mean annual pond water temperature, reducing dissolved oxygen and affecting the pond community composition (Matthews, 2010). Ponds may act as refuges and stepping stones in the northward and altitudinal shift of species (Oertli *et al.,* 2009). Hence, a species altitudinal shift as a result of climate warming could increase alpine pond taxonomic richness, but concurrently lead to the extinction of cold stenothermal species unable migrate any higher (Oertli *et al.,* 2008; Rosset *et al.,* 2010 Rosset and Oertli, 2011). The invasion of exotic species presents an additional risk to the heterogeneity of pond biodiversity (Brönmark and Hansson, 2002).

2.7.1 Pond loss

At a European scale pond numbers have declined between 40% and 90% since the late 1800s (Hull, 1997). UK pond numbers were estimated to be at a peak in 1880, following the Acts of Enclosure from 1750-1820 (causing many fields to have fixed boundaries: hedges, ditches or walls) which resulted in many ponds being created in the enclosed fields to water livestock (Oldham and Swan, 1997). However, ponds have declined significantly since 1880 when it was estimated 800,000 ponds existed in the UK (from a survey of Ordnance Survey maps) or 14 in every square mile (Rackham, 1986). This is likely to be a large underestimation as the survey was biased towards larger ponds and did not include ephemeral or garden ponds (Wood *et al.,* 2003). By 1920 the number of ponds had declined to around 340,000 (Rackham, 1986). Pond loss accelerated during and after the Second World War as land drainage and urbanisation intensified (Oldham and Swan, 1997). The Lowland Pond Survey 1996 (Williams *et al.,* 1998) estimated UK pond numbers to be only 228,900. Between 1984 and 1990 the loss of small ponds in the UK was estimated to be between 4-9% (Williams, 2006). Documented pond loss in different UK regions is presented in Table 2.5.

However, pond loss appears to have stabilized and pond abundance in lowland areas of the UK increased by 6% from 1990-1998 (Haines-Young *et al.,* 2000) and approximately 1.4% per annum between 1998 and 2007 (Williams *et al.,* 2010). The number of UK lowland ponds in 2007 was estimated to be 478,000 although, 80% were considered to be in poor quality in England and Wales (Williams *et al.,* 2010).

Table 2.5 - Estimated pond loss from different regions of the UK (Wood et al., 2003: 213)

Area	**Period**	**Loss (%)**	**Annual Loss (%)**	**Change in number of ponds (n)**	**Land Use**	**Source**
Huddersfield	1985-1997	31	2.6	60 to 42	Urban/industrial	Wood *et al.,* 2001
North Leicestershire	1934-1979	60	1.33	958-370	Mostly pasture	Beresford & Wade, 1982
Bedfordshire	1910-1981	82	1.15	Not quoted	Intensive arable	Beresford & Wade, 1982
Sussex	1977-1996	21	1.1	33 to 26	Pasture (dew ponds)	Beebee, 1997
London Region	1870-1984	Up to 90	0.79	Up to 16,000 to 1600	Mixed	Langton, 1985
Hertfordshire	1881-1981	50	0.5	Not quoted	Mixed	Green, 1989
Huntingdonshire (Cambs.)	1890-1980	56	0.68	Not quoted	Mixed	Beresford & Wade, 1982
Cheshire	1870-1993	61	0.5	41,564 to 16,728	Rural and urban	Boothby & Hull, 1997
Essex (selected areas)	1870-1989	55-69	0.46-0.58	1366 to between 616 to 423	Mixed	Heath & Whitehead, 1997
Cambridgeshire	1840/90-1990	68	0.45-0.68	Not quoted	Intensive arable	Jeffries & Mills, 1997
Leicestershire	1840/90-1991	60	0.40-0.60	Not quoted	Intensive arable	Jeffries & Mills, 1997
Durham	1840/90-1992	41	0.27-0.41	Not quoted	Arable and pasture	Jeffries & Mills, 1997
Clwyd	1840/90-1993	32	0.21-0.32	Not quoted	Arable and pasture	Jeffries & Mills, 1997
Midlothian	1840/90-1994	23	0.15-0.23	Not quoted	Arable and pasture	Jeffries & Mills, 1997
Edinburgh	1840/90-1995	6	0.04-0.06	Not quoted	Urban	Jeffries & Mills, 1997
England and Wales	1880-1920	57.5	1.41	800,000 to 340,000	Mixed	Rackham, 1986
Britain	1990-1996	7.4	1.23	230,600 to 228,900	Mixed-lowland ponds	Williams *et al.,* 1998
Great Britain	1900-1990	75	0.78	1,189,200 to 297,300	Mixed	Bailey-Watts *et al.,* 2000

2.8 Pond conservation and management

> 'Conservation entails careful management of the pond environment to limit loss or devaluation and, where appropriate, ensure the long term preservation of the pond resource', (Boothby, 1999: 71)

Traditionally, conservation and management effort of UK aquatic systems has been directed towards rivers and lakes however, public awareness and concern for pond biodiversity has increased (Everand, 1999; Nicolet *et al.,* 2007; Oertli *et al.,* 2009) because of the increasing abundance of ponds that are in nature reserves, or pond warden schemes which have been initiated (Wood *et al.,* 2003). Internationally, the number of indexed publications focusing on the topic 'pond' after 2001 was about 10% higher than before 2001 and at a European scale it was 40% higher after 2001 than before (Oertli *et al.,* 2009). When the words 'pond' and 'biodiversity' were analysed (using ISI Web of Knowledge data base), the number of publications were 7 times higher in 2008 than 2000 illustrating the substantial rise in interest in pond biodiversity (Oertli *et al.,* 2009). Notwithstanding, when comparing the volume of pond research alongside stream, river and lake publications, publications considering ponds constituted less than 10% of the total (Oertli *et al.,* 2009).

Boothby *et al.* (1999) suggests that pond conservation at the landscape-scale has 4 key themes;

1) Taking stock - increase understanding and knowledge of pond resources at difference scales, identify knowledge gaps and utilise the identified resources to their greatest effect.
2) Valuing pond resources - determining the overall value of the pond resource and incorporating acceptable levels of change based on the value given.
3) Stewardship of the resource - ensure the safe guarding of the pond environment through policies, planning and promoting responsible stewardship through the highest standards of management.
4) Access and awareness - promote and facilitate access to pond landscape and raise awareness of the pond environment and its value.

The Million Ponds Project is a 50 year landscape biodiversity initiative which aims to create an extensive network of clean ponds and return UK pond numbers to one million (pre-industrial revolution estimate) (Freshwater Habitats Trust, 2014). Co-ordinated by the charity Freshwater Habitats Trust, the Million Ponds Project is a partnership of land owners, charities and public bodies. A key feature of the 500,000 ponds which will be created (there is estimated to be approximately 500,000 ponds currently in existence in the UK (Williams *et al.,* 2010)) is that they have excellent water quality as over 80% of currently existing ponds are degraded (Freshwater Habitats Trust, 2014). Phase 1 of the project (2008-2012) incorporated the creation of at least 5,000 ponds, 1,023 of which focus specifically on supporting Biodiversity Action Plan (BAP) species (Freshwater Habitats Trust, 2014). Phase 2 (2012-2020) is a seven year project which will ensure that 90% of priority ponds are of a good condition (Freshwater Habitats Trust, 2014).

Intervention is also required to mitigate the impact of urbanisation and land use intensification, otherwise pond degradation will increase, fragmentation will be exacerbated and there could be severe consequences for the flora and fauna reliant on ponds and their terrestrial matrix (Oertli *et al.,* 2005). Carefully planned restoration and management of the existing pond resource provides another pond biodiversity conservation strategy alongside the development of new ponds (Duigan and Jones, 1997; Gee *et al.,* 1997; Sayer *et al*., 2012; Sayer, 2014). Active pond management is relatively cheap and may create a culture of care and pride towards small waterbodies, especially in agricultural landscapes where the development of new ponds may be unsuitable (Sayer *et al.,* 2012; Sayer *et al.,* 2013). Pond biodiversity conservation may be best served by a combination of pond management and the creation of new ponds, which will greatly increase the numbers of high quality pond habitats, provide a range of pond types and successional stages suitable for a wide range of flora and fauna (Sayer *et al.,* 2013; Freshwater Habitats Trust, 2014; Sayer, 2014).

There have been advances in the monitoring of ponds. The National Pond Monitoring Network (NPMN) was set up in 2004, developing an inventory of ponds and facilitating the identification of pond locations on a UK base map. This can be used to highlight important pond localities which should be considered by Natural England under the provision of the EU Water Framework Directive (Biggs *et al.,* 2005). The NPMN will be the key mechanism monitoring pond Priority Habitat sites (BRIG, 2008). Bottom-up approaches such as pond warden schemes are considered one of the best ways for pond management and conservation to progress (Boothby *et al.,* 1995a). Pond warden schemes incorporate an individual or group of community volunteers (pond wardens) to monitor and manage the ponds within their parish (Jeffreys and Rooney, 1997) which could improve the ecological quality of many degraded ponds at a national scale. The schemes have been set up across the UK; in Derby, over 60% of the ponds in the city have been assigned a pond warden and are regularly monitored and surveyed (DCPWA, 2014). Pond Wardens ensure the conservation and maintenance of ponds and raise awareness of the importance of ponds by communicating with schools, local businesses and communities (Jeffreys and Rooney, 1997). In addition, the Open Air Laboratories (OPAL) network is a UK initiative led by Imperial College London to involve members of the public of all ages in nature monitoring and conservation (OPAL, 2014a). This citizen science initiative provides all the information and documents required (downloadable from OPAL's website) to take a wide range of biodiversity surveys, including a pond survey, and an online form to submit the results (OPAL, 2014b). Through actively involving the public in biodiversity monitoring the health of many more ponds can be determined providing a greater understanding of the state of UK freshwater/terrestrial habitats and can raise awareness of current biodiversity and environmental issues (OPAL, 2014c).

Using surrogate or indicator taxa, the conservation value and biological quality of numerous ponds within a pondscape can be assessed quickly and efficiently (Green, 1989; Briers and Biggs, 2003; Bilton *et al.,* 2006). In an Oxfordshire pondscape, Coenagrionidae and Limnephilidae richness best represented the overall species richness of the pond; based on their taxonomic diversity they expressed over 95% of the total site richness (Briers and Biggs, 2003). However, indicator taxa may be location/region specific as good indicator taxa in one area may not be as appropriate in other locations (Briers and Biggs, 2003). The predictive system for multimetrics (PSYM) which compares predicted macrophyte and invertebrate species (using environmental data to predict which invertebrates and macrophytes should be in the pond if it was un-degraded) with the actual plant and invertebrate species recorded in the pond to give a single value of ecological quality was developed to permit a rapid assessment of the biological quality of ponds (Biggs *et al*., 2000; Biggs *et al.,* 2005).

There remains relatively little information for ephemeral pond management and conservation (Biggs *et al.,* 2001). Adequate management of these systems will only become a reality if ephemeral ponds are recognised as a valuable environment for rare flora and fauna (Williams, 1997; Biggs *et al.,* 2001). The value of ephemeral ponds needs to be disseminated to the public to increase public knowledge and their status (Williams, 2006; Zacharias *et al.,* 2007). Regional and national biodiversity assessment and monitoring should consider ephemeral ponds to encompass the whole range of aquatic environments (Nicolet *et al.,* 2004).

2.8.1 Legislation

At an international scale, the most powerful piece of water legislation in Europe, the Water Framework Directive (WFD), offers little benefit or protection to ponds because it will only protect water bodies over 50 hectares in size (Nicolet *et al.,* 2007; Miracle *et al.,* 2010; Chaichana *et al.,* 2011). However, the EU Habitats Directive (Europe's primary nature conservation legislation), provides some legislative protection to a number of specific pond types including Turloughs (Gwendolin and Kenneth, 2009) and Mediterranean temporary ponds (Beja and Alcazar, 2003; Della Bella *et al.,* 2005; Nicolet *et al.,* 2007; Céréghino *et al.,* 2008b) and also provides protection to a small number of species associated with ponds (e.g., the Great Crested Newt (*Triturus cristatus*)) (EC, 1992).

Pond biodiversity and conservation value has begun to be acknowledged at a national level as ponds were incorporated into the UK Biodiversity Action Plan (BAP), becoming a priority habitat in 2007 (BRIG, 2008; Gledhill *et al.,* 2008). The Biodiversity Action Plan provides detailed conservation strategies and action plans to those landscapes (priority habitats) and their biodiversity (priority species) considered at risk. To qualify as a BAP Priority Pond Habitat, certain criteria need to be met including: supporting a BAP priority species, 3 nationally scarce invertebrate species, >50 aquatic invertebrate species and/or record a PSYM score of >75% (BRIG, 2008). It is estimated that 20% of UK ponds meet the BAP criteria (Williams *et al.,* 2010). The UK wide BAP partnership has now been replaced by the UK Post-2010 Biodiversity Framework (covers the period 2011-2020), which focuses biodiversity strategies at a country level (JNCC and DEFRA, 2012; JNCC, 2013; Natural England, 2014b). There are separate Habitats of Principle Importance (HPI; habitats considered to require action and conservation effort) and Species of Principle Importance (SPI; species under threat and requiring conservation effort) for England, Scotland, Wales and Northern Ireland. The priority habitats included in the England HPI (including ponds) are the same as those previously under the UK BAP (BRIG, 2008) and the England SPI are those species identified under the BAP as requiring conservation action in England (Natural England, 2014a). Ponds which qualify as a Priority Habitat under the UK Post-2010 Biodiversity Framework Pond Priority Habitat criteria, which uses the same criteria as the UK BAP, will receive some legislative and policy protection through the Biodiversity Duty under the Natural Environment and Rural Communities Act 2006 and an increased consideration for their conservation by government bodies and policy makers (Williams *et al.,* 2010).

Pond conservation currently relies on the designation of individual sites for conservation based on their significant biodiversity or the occurrence of rare taxa (Priority Species or taxa under the Wildlife and Countryside Act 1981). However, given the significant contribution ponds make at a regional scale and the temporal variability of individual pond sites (a rare species that is present in one year may not be in subsequent years), a number of studies have suggested that pond conservation will be most beneficial at the landscape-scale conserving the pondscape (Hassall *et al.,* 2012; Sayer, 2014). The agri-environment schemes could support/enhance pond landscape conservation through the provision of financial incentives to farmers to adopt environmentally sensitive farming methods to preserve biodiversity, including lentic aquatic fauna (Davies *et al.,* 2009a). Currently any farmer can apply for the environmental stewardship initiative although, Davies *et al.* (2009a) argues the resources would be better targeted on agricultural areas of high biodiversity value, which if taking this approach could protect 90% of species concerned. Ponds were identified to be particularly good habitats to protect as they support a significant proportion of the biodiversity, including rare species and were relatively small and cost effective (Davies *et al.,* 2009a).

Ponds can receive some legislative protection indirectly. Ponds located on land which is protected through various policies and legislation (SSSI, nature reserves and ancient monuments) will be protected (Everand, 1999; Marshall *et al.,* 1999). If species documented by the Wildlife and Countryside Act 1981 are recorded within pond environments they will be protected (as a SSSI) as the species habitat must not be damaged (Marshall *et al.,* 1999).

The European Pond Conservation Network (EPCN) was set up to combat the lack of initiatives in place to protect ponds, as well as to strengthen existing activities and ensure a rigorous scientific and practical basis for pond conservation (Nicolet *et al.,* 2007). The EPCN aims to raise awareness and broadcast to the public the importance of conservation and attractiveness of ponds, exchange pond information between researchers and managers, guide policies and promote effective pond conservation (Oertli *et al.,* 2005; Nicolet *et al.,* 2007). A key function of EPCN is to disseminate and communicate to 'stakeholders' (land owners, pond managers, politicians) scientific knowledge and management successes (Oertli *et al.,* 2009: 2).

2.9 Summary

This chapter has provided a review of the biodiversity within ponds, the local and spatial environmental parameters influencing invertebrate community composition and has outlined the current position of pond conservation. Historically, freshwater research has focussed on larger water bodies (lakes and rivers) although, interest in pond biodiversity has greatly increased, demonstrated by the 7 fold increase in scientific publications between 2000 and 2008 (Oertli *et al*., 2009). Macroinvertebrate communities present in ponds are determined by a complex interaction of multiple local (physicochemical and biological) and spatial (connectivity) processes. Despite their small size, ponds support a substantial diversity of macroinvertebrate taxa (including rare and endemic taxa) and often have high conservation value (Davies *et al.,* 2008b) across a wide range of land cover types. Yet, their high ecological value has not been widely recognised at a policy level and as a result ponds receive little legislative conservation protection compared to lakes and rivers. However, the inclusion of ponds within the BAP process (now the Post-2010 Biodiversity Framework) and agri-environment scheme offers some protection to the pond resource and the biodiversity it supports. The following chapter outlines the methodological processes utilised in this thesis.

Chapter 3. Methodology

3.1 Introduction

This chapter outlines the methodological approaches adopted and used in this thesis. A comprehensive methodological framework is presented which considers the spatial and temporal dynamism of pond landscapes and how this influences macroinvertebrate biodiversity. The methodological techniques utilised in the field in this thesis are primarily applicable to the study of lentic water bodies (see Biggs *et al.,* 1998) although many are common across freshwater and aquatic sciences. This chapter aims to;

I. Present the selection procedure used to determine pond study sites and their location within Leicestershire, UK;
II. Outline the fieldwork techniques (macroinvertebrate sampling and environmental data collection) and laboratory processes (macroinvertebrate sorting and identification) employed;
III. Summarize the statistical techniques employed in this thesis to characterise and quantify the spatial and seasonal alpha, beta and gamma diversity of macroinvertebrate taxa within ponds across a range of land cover types, assess the local and regional pond conservation value and examine the influence of environmental parameters on invertebrate community structure and composition within pond habitats.

The fieldwork techniques and methods support the thesis aims and objectives (Chapter 1.4) and provide the basis for undertaking the detailed descriptive and statistical analysis outlined in subsequent chapters.

3.2 Site selection

Loughborough is located in Charnwood Borough, Leicestershire, UK. Loughborough is the largest urban area (population of approx. 60,000) in Leicestershire, outside the city of Leicester. Its varying land use supports a wide range of ponds from urban, park and garden ponds to rural floodplain meadow and agricultural ponds in the surrounding landscape. Loughborough has increased in size and population since the industrial revolution and as a result sections of the River Soar near Loughborough has been channelized and navigable canals run parallel to the River Soar (LRWT, 2011a) to reduce flood risk and ensure safe passage of boat traffic. The River Soar rises in the south of Leicestershire, and following the confluence of approximately six tributaries increases in size from a small headwater stream to a navigable channel as it flows through Loughborough and continues northward until its confluence with the River Trent in Nottinghamshire (LRWT, 2011a). The River Soar has a history of regular flooding and has resulted in numerous small ephemeral floodwater ponds on its floodplain. Although more common in the past, parts of the floodplain are still regularly inundated, such as Loughborough Big Meadow and Cossington Meadow Nature Reserve (LRWT, 2014a; LRWT, 2014b). This natural flooding allows the gradual refilling of ephemeral and perennial meadow ponds and ensures the meadows remain "moist" all year round (LRWT, 2011b).

In total, 95 ponds were selected for investigation within Charnwood Borough, which encompass and provide a representative coverage of a European lowland landscape (Figure 3.1; see Appendix 1 for full list of sites). Ephemeral and perennial ponds were identified within a wide variety of landscapes from local rural (agricultural areas, forests, and floodplain meadows on the River Soar floodplain) and urban environments (gardens, urban areas/parks, Loughborough University campus, schools and a golf course) (Figure 3.2; 3.3). Sites were initially selected by viewing an Ordnance Survey map (1:25,000) and Google earth and selecting appropriate sample sites. Prior to site visits, contact was made with Charnwood Borough Council and Leicestershire County Council for the location of ponds in Charnwood Borough. Thirty perennial (24) and ephemeral (6) ponds located within Charnwood Borough had previously been surveyed in a study conducted by Dr Derek Lott (1999), some of which were used in this thesis. Leicestershire and Rutland Wildlife Trust granted permission to access and sample ponds in Loughborough Big Meadow (9) and Cossington Meadow Nature Reserve (25). Loughborough University's biodiversity co-ordinator and the supervisory team helped with the identification of pond sites on Loughborough University campus (14). Contact was made with a number of local primary and secondary schools (4) in the study area enquiring if it was possible to sample ponds located on their grounds. Permission was obtained to sample garden ponds (13) based on an email correspondence sent to all Loughborough University staff and students within the Department of Geography.

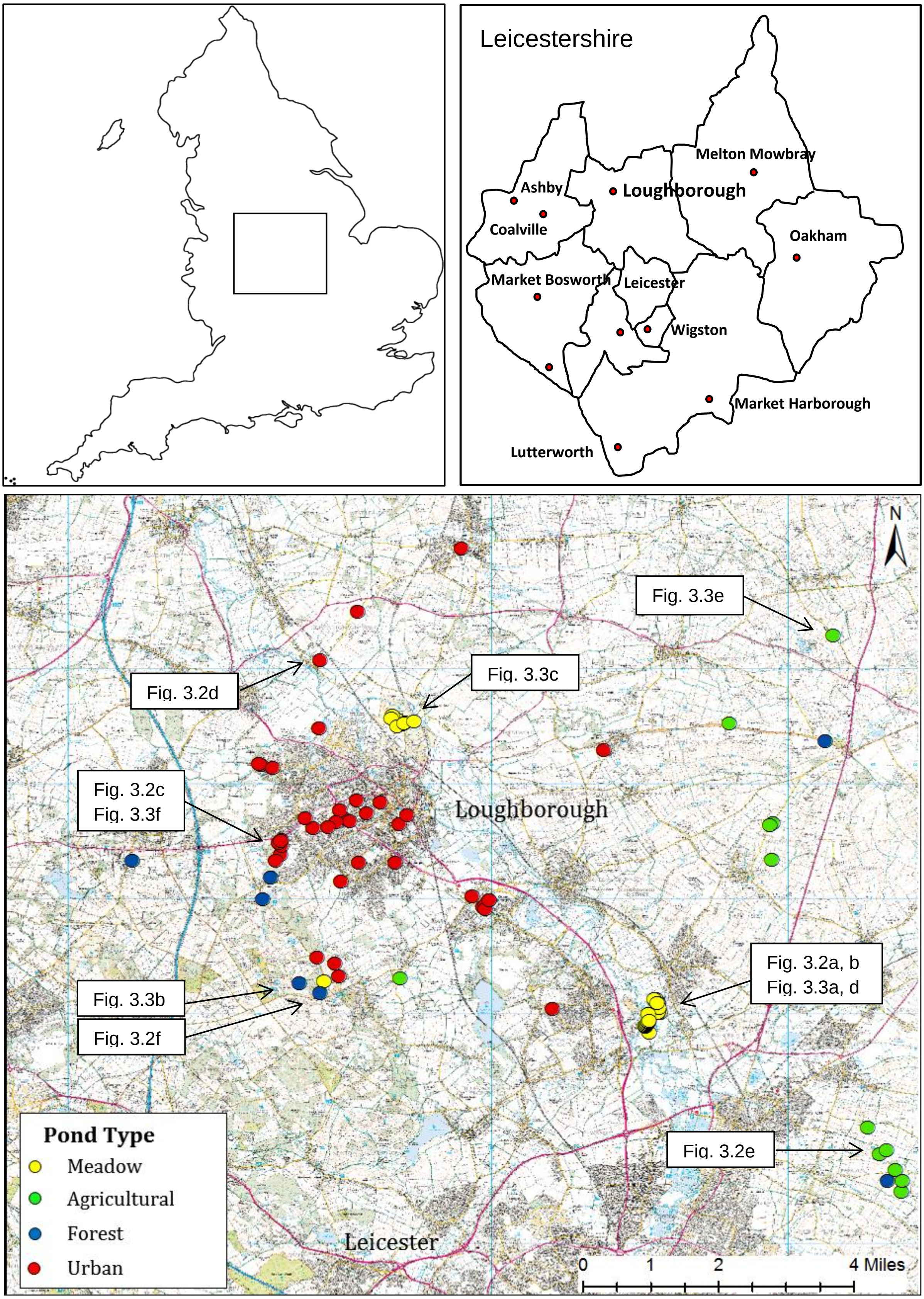

Figure 3.1 - Location of the 95 pond sites selected for analysis within Leicestershire and the River Soar valley. Ponds have been grouped according to their type.

Figure 3.2 - Perennial pond sites within; (a) meadow (M2) (b) meadow (M12) (c) urban (UP5) (d) garden (UP30) (e) agricultural (AP3) and (f) forest landscapes (FP5). Photographs: M. Hill. See Figure 3.1 for pond locations. See also Appendix 1 for site details and Appendix 2 for additional sample site photographs.

Figure 3.3 - Ephemeral pond sites within; (a) meadow (M9) (b) forest (FP6) (c) meadow (M29): (d) meadow (M10) (e) agricultural (AP10) and (f) urban landscapes (UP4). Photographs: M. Hill. See Figure 3.1 for pond locations. See also Appendix 1 for site details and Appendix 2 for additional sample site photographs.

During field visits all ponds identified were geo-referenced using a Garmin etrex H handheld GPS and a photograph was taken to identify each sample site and as an aid in the future analysis of the pond. The location of ponds used in this thesis are presented in Figure 3.1; grid references collected from individual pond locations were digitized and converted to a point on an Ordnance Survey 1: 25000 base map of the Loughborough district using an Arc Map Geographical Information System (GIS). Five ponds initially selected to be sampled were removed from the study because they were greater than 2 hectares and/or access was not granted by land owners for ponds located on agricultural and urban land.

3.3 Fieldwork techniques

The pond survey incorporated 95 pond sample sites encompassing 68 perennial and 27 ephemeral ponds in rural and urban environments that best represent the land cover types within Leicestershire. These comprised a total of 35 meadow ponds, 41 urban ponds, 12 agricultural ponds and 7 forest ponds which were selected to enable a comparison across landscape types. Each pond was sampled on three occasions corresponding to the spring (March), summer (June) and autumn (September) seasons during 2012 in order to characterise any temporal variability which may occur as a result of macroinvertebrate life cycles (Resh, 1979) and hydrological regimes (fluctuating water levels and drying).

3.3.1 Environmental parameters

Local environmental parameters (physicochemical and biological) were recorded at each pond site on a data recording sheet prior to macroinvertebrate sampling. The recording sheet used in this thesis is an adapted version of the recording sheet comprised for the National Pond Survey (Biggs *et al.,* 1998, see Appendix 3). At each pond site all waterbodies within the vicinity of each pond site were geo-referenced (based on observations at each site, ordnance survey maps, google earth and knowledge from local authoritative sources). A GIS data set of ponds and waterbodies within the study region was created using an Ordnance Survey map and the digitized geo-referenced pond sites and waterbodies (many of which were ephemeral or small perennial waterbodies that were not originally recorded on the Ordnance Survey map). GIS software (ArcMap 10.1) was used to determine the connectivity; number of waterbodies hydrologically connected to the pond sample sites and pond proximity; the number of waterbodies within 500m of each pond site (spatial variables) (Vanschoenwinkel *et al.,* 2007; Waterkeyn *et al.,* 2008). The abiotic variables measured at each sample pond and the equipment used is shown in Table 3.1.

Table 3.1 - Abiotic variables which will be measured and the equipment used

Environmental Variable	**Equipment**
Pond depth	Wading rod (ruler)
Pond area	Tape measure/OS map (GIS)
Permanence	Observation
Conductivity	Hanna HI 98311 digital meter
pH	Hanna HI 98127 digital meter
Dissolved oxygen	Hanna HI 9142 digital meter
Water temperature	Hanna HI98127/Hanna HI 98311
Hydroperiodicity (number of months pond basin was dry/wet)	Based on sampling and observations
Vegetation cover (visual estimation) % Surface area submerged macrophyte cover % Surface area emergent macrophyte cover % Surface area floating macrophyte cover % Surface area riparian vegetation around perimeter % Surface area covered by over-hanging trees	Based on observations
Water source	Based on observations
Successional stage	Based on observations
Pond substratum (% visual estimation)	Based on observations
Bank type	Based on observations
Presence of fish and wildfowl	Based on observations
Evidence of livestock grazing/grazing intensity	Based on observations
Management practices	Based on observations
Evidence of pollution	Based on observations
Surrounding landscape	Based on observations
Connectivity (no. of direct connections to other water bodies within 500m e.g., via floodwater, ditches or rivulets)	Observation/Ordnance Survey map/ Geographical Information Systems
Pond proximity (no. of water bodies within 500m of the focal pond (based on edge to edge distance))	Observations/Ordnance Survey map/ Geographical Information Systems

3.2 Macroinvertebrate sampling

The semi-quantitative sweep sampling technique was considered most appropriate for sampling macroinvertebrate communities within small lentic water bodies (García-Criado and Trigal, 2005). A standard aluminium frame pond net with a 250μm mesh size was used to sample macroinvertebrate taxa. The pond net is a widely used piece of sampling equipment by aquatic ecologists and has been demonstrated to be a highly effective sampling tool for pond environments (García-Criado and Trigal, 2005). The sweep net collects a high abundance and diversity of macroinvertebrates facilitating the detailed analysis of the community composition (Cheal *et al.,* 1993). In addition, it captures faster swimming and less frequently occurring taxa more effectively than other methods (Cheal *et al.,* 1993). To obtain a macroinvertebrate sample the net is held upright and swept through the water column for a pre-determined time period in accessible areas of the pond. During each sweep the substrate was gently disturbed to ensure both benthic and nektonic macroinvertebrates were sampled (Le Viol *et al.,* 2009). Amphibians or fish collected in the sample were recorded *in situ* before being released back into the pond.

The length of time the pond net sweep was undertaken was proportional to water surface area (Hinden *et al.,* 2005; Armitage *et al.,* 2012) (Table 3.2), up to a maximum of three minutes for larger ponds (Williams *et al.,* 2003; Gioria *et al.,* 2010). It should be noted that the three minutes refers to the period the net is in the water and does not include the transition between mesohabitats, or emptying the net to allow more of the sample to be collected (Biggs *et al.,* 1998). This sampling strategy was employed in order to obtain comprehensive macroinvertebrate samples from all sites and to ensure the small freshwater habitats/communities were not destroyed/degraded (Armitage *et al.,* 2012).

Table 3.2 - Allocated sampling time to area of the water surface

Area	**Sampling Length**
<10 m^2	30 seconds
10-20 m^2	1 minute
20-30 m^2	1.5 minutes
30-40 m^2	2 minutes
40-50 m^2	2.5 minutes
>50 m^2	3 minutes

A habitat dependent, time limited method was employed following the methodological guidelines of the National Pond Survey (Biggs *et al.,* 1998). An assessment of the pond was undertaken to identify discreet mesohabitats within the pond prior to sampling (Jeffries, 1991; Biggs *et al.,* 1998; Wood *et al.,* 2001). The sampling time attributed to each pond was divided equally between the mesohabitats (the number of mesohabitats typically varied from 1 to 5). Where the pond was dominated by one particular mesohabitat, or it broadly covered separate areas of the pond, the allocated sampling time was further sub-divided to represent this variability (Biggs *et al.,* 1998).

The length of time sweep sampling in individual ephemeral ponds varied for some ponds during the three surveys as the ephemeral pond surface area fluctuated seasonally (Table 3.2). A number of ponds were dry for one or two seasons and therefore aquatic invertebrate samples could not be collected during the dry phase. In addition, an inspection of any hard surfaces or larger substrates (e.g., rocks) for aquatic macroinvertebrates was undertaken for up to 60 seconds at each pond site.

3.4 Macroinvertebrate preservation, sorting and identification

Immediately after sampling, macroinvertebrate samples from each mesohabitat were preserved in separate, labelled zip lock bags containing 4% formaldehyde. The samples were stored in a laboratory refrigerator or a refrigerated cold room for subsequent sorting and identification.

Macroinvertebrate samples were processed individually. Samples were washed in a nest of sieves (2.5 mm-0.5 mm) to remove fine sediment (silt and clay) and detrital material, and then transferred into a white flat bottomed sorting tray, covered with water to reduce reflection from the light. Soft nose metal tweezers were used to remove macroinvertebrates from the white sorting tray into 70% industrial methylated spirit (IMS) within a pre-labelled sample tube. All samples were processed and identified by the same author throughout to reduce any operator bias. Taxa were identified under a Zeiss Stemi 1000 dissecting microscope with a Zeiss KL200 light source to species level wherever possible using the relevant biological identification keys including; Macan, 1977; Elliot and Mann, 1979; Hynes, 1984; Fres, 1985; Elliot *et al.,* 1988; Friday, 1988a; Savage, 1989; Smith, 1989; Gledhill *et al.,* 1993; Edington and Hildrew, 1995; Wallace *et al.,* 2003; Cham, 2009 and; Foster and Friday, 2011. Macroinvertebrates omitted from species-level identification were; Chironomidae, Ceratopogonidae, Chaoboridae, Chrysomelidae, Culicidae, Dicranota, Dixidae, Ephydridae, Empididae, Psychodidae, Simuliidae, Stratiomyidae, Syrphidae, Tipulidae, Oligochaeta, Physidae, Zonitidae, Pisidiidae, Argulidae, Taeniopterygidae, Collembola, Planariidae and Hydrachnidiae which were identified to the lowest possible taxonomic level.

3.5 Data analysis techniques

The following section outlines the principle data analysis techniques employed in this thesis. The data analysis techniques undertaken in this thesis facilitate the identification of spatial and seasonal patterns and relationships between the macroinvertebrate community, physicochemical characteristics and land cover types (Quinn and Keough, 2002). Macroinvertebrate taxa-abundance data and environmental data were prepared in Microsoft Excel and alpha diversity indices were calculated in Species Diversity and Richness IV program (SDI IV) (Pisces Conservation Ltd, 2008). Statistical data analysis was undertaken using Statistical Package for the Social Sciences (SPSS) (version 21, IBM Corporation, New York), Community Analysis Package 3.0 program (CAP) (Pisces Conservation Ltd, 2004), Plymouth Routines in Multivariate Ecological Research 6 (PRIMER 6) (Clarke and Gorley, 2006) and CANOCO (version 4.5, Wageningen UR, Wageningen). The data analysis techniques employed reflect the thesis aims and objectives to test the primary abiotic and macroinvertebrate data. Preliminary statistics incorporated all invertebrates sampled within this study but as a result of the very high abundances of meiofauna (microcrustacea - Ostracoda, Copepoda and Cladocera) these were removed from all subsequent statistical analysis.

One-way and nested Analysis of Variance (ANOVA) and post hoc tests

Analysis of the ecological dataset (raw data faunal counts and ecological indices) was undertaken using one-way Analysis of Variance (ANOVA) to identify any significant differences in a set of mean values between groups. A normal distribution in the data set is assumed by ANOVA which was inspected prior to analysis. Nested Analysis of Variance was undertaken to examine the differences between mesohabitats (nested within pond type) on a dependant variable and to examine the differences between seasons (nested within pond type) on a dependant variable. *Post hoc* Tukey (HSD)/Sidak tests were undertaken in SPSS (version 21) to determine which groups of means differed statistically from one another within the dataset. All results were considered statistically significant at $p<0.05$. Significant variations between groups for the one-way and nested ANOVA were displayed in tables and graphically (where appropriate) using error bar plots and box plots, prepared in SPSS (version 21) (George and Mallery, 2013).

Correlation Analysis

Pearson's Correlation coefficient and scatter plots were employed to assess the relationship between environmental parameters and the ecological data set. Pearson's correlation provides a measure of the correlation between two variables and the correlation coefficient (*r*) demonstrates the strength of the relationship (Townend, 2002). Correlation coefficient values close to +1 indicate that there is a strong positive correlation, values close to -1 indicate a strong negative correlation whilst values close to zero suggest there is no correlation/relationship between parameters (Townend, 2002). All correlative analysis was undertaken using SPSS (version 21). Visualisation of the relationships was aided by the addition of a line of best fit.

3.5.1 Alpha diversity

3.5.1.1 Alpha diversity indices

Alpha (α) diversity indices can express the richness and evenness of a macroinvertebrate community into a single statistic (Hurlbert, 1971; Magurran, 2004). Ecological alpha diversity indices were calculated (using Species Diversity and Richness IV program (SDI IV) (Pisces Conservation Ltd., 2008) in addition to the raw macroinvertebrate data (abundance and species number) to explore the differences in alpha (α) diversity of invertebrate communities within pond habitats. The alpha macroinvertebrate diversity indices derived for the pond sample sites were; Shannon Wiener diversity index (Equation 3.1), Berger-Parker Dominance index (Equation 3.2), Simpsons diversity index (Equation 3.3), Fisher's alpha (Equation 3.4), Margalef diversity (Equation 3.5) and McIntosh diversity (Equation 3.6) (formulas based on Magurran, 2004 and Shepherd, 2014). The Shannon Wiener diversity index uses species richness and relative abundance to calculate entropy, giving a measure of uncertainty in the distribution (Jost *et al.,* 2006). The Simpsons diversity index, first proposed by Simpson (1949), calculates the probability that two randomly selected individuals from a sample will belong to the same species by incorporating both the number of species and the species abundance (Magurran, 2004; Janauer *et al.,* 2010). Berger Parker Dominance index was derived by Berger and Parker (1970) and expresses 'the proportional abundance of the most abundant species' within a given sample (Magurran, 2004: 117; Vanschoenwinkel *et al.,* 2013). Developed by McIntosh (1967), the McIntosh diversity index expresses ecological assemblages as a point in S dimensional hypervolume (Magurran, 2004). At the origin of S dimensional hypervolume there is no diversity; the greater the communities Euclidean distance from the origin the greater the diversity (Magurran, 2004). Margalef diversity is a popular alpha diversity index and attempts to reduce the influence of sampling effects by dividing the species number by the total number of individuals (Gamito, 2010; Jocque and Field, 2014). These five ecological diversity indices can be described as non-parametric measures because no assumptions are made about the underlying distribution of the dataset (Magurran, 2004). In contrast, Fisher's α is a parametric measure and has an underlying assumption of a log series distribution of species abundance, although this is a robust measure and can be used when species abundances do not follow a log series distribution (Magurran, 2004).

$H' = -\sum P_i \ln P_i$

(where, P is the proportion of individuals in the *ith* species).

Equation 3.1- Shannon Wiener diversity index

$d = \frac{N_{max}}{N}$

(where, N is the total number of individuals in the sample and N_{max} is the number of individuals in the most abundance species).

Equation 3.2 - Berger Parker Dominance index

$D = 1/\sum P_i^2$

(where, p_i is the number of individuals in the ith species / total individuals in a sample)

Equation 3.3 - Simpsons Diversity index

$S = \alpha \ln \left(1 + \frac{N}{\alpha}\right)$

(where N is the total number of individuals, S is the number of species and α is the Fisher's alpha)

Equation 3.4 - Fisher's alpha

$D_{mg} = \frac{(s-1)}{\ln N}$

(where S is the number of species recorded and N is the total number of individuals)

Equation 3.5 - Margalef diversity index

$D = \frac{N-U}{N-\sqrt{N}}$

(Where n is the number of taxa in a sample and U is the distance (Euclidean) of the faunal community from its origin when plotted in S-dimensional hypervolume (see equation below) (Pisces Conservation Ltd, 2008)

$U = \sqrt{\sum n_i^2}$

(where n_i is the number of individuals in the ith species (Pisces Conservation Ltd, 2008))

Equation 3.6 - McIntosh diversity index

3.5.2 Beta-diversity

Beta-diversity indices can express the spatial and temporal distribution and heterogeneity of ecological communities between sample sites in a given area

(Anderson *et al.,* 2006; Hassall *et al.,* 2012; Usio *et al.,* 2013; Briers, 2014; Hamerlik *et al.,* 2014). Beta-diversity was employed in this thesis alongside alpha diversity to further examine spatial and seasonal aquatic macroinvertebrate community distribution and dissimilarity between pond sites. The beta-diversity metrics calculated in this thesis were Analysis of similarity (ANOSIM), Similarity percentage analysis (SIMPER), Jaccard's Coefficient of Similarity, Sørensen Similarity index and spatial dissimilarity in macroinvertebrate assemblages. Other measures of beta-diversity include Non-Metric Multidimensional Scaling (NMDS) which is described in Chapter 3.5.3.1.

3.5.2.1 Analysis of Similarity (ANOSIM)

Analysis of similarity (ANOSIM) was employed using PRIMER 6 to assess the variation in macroinvertebrate community assemblage between pond sites. The ranked significance of the similarity between sites was compared with the similarity that was generated by random chance. For each sample 1000 random permutations were tested (Clarke and Gorley, 2006).

3.5.2.2 Similarity Percentage Analysis (SIMPER)

To quantify which species contributed most to the similarity or dissimilarity between pond sites, SIMPER analysis was undertaken using PRIMER 6. SIMPER records and orders the contribution of each macroinvertebrate taxa to the similarity within groups or the dissimilarity between sample groups based on the Bray-Curtis method of dissimilarity (Clarke and Gorley, 2006). The average Bray-Curtis dissimilarity scores are calculated between all pairs of sample groups (e.g., all forest pond sites against all meadow pond sites and so on). The average Bray-Curtis dissimilarity between group 1 and 2 is then broken down into the individual contributions of macroinvertebrate taxa (often presented as a percentage) to the similarity and/or dissimilarity between the sample groups (Clarke and Gorley, 2006).

3.5.2.3 Jaccard's Coefficient of Similarity and Sørensen Similarity index

To examine the macroinvertebrate compositional heterogeneity between sites within a sample group (e.g., meadow ponds) and for all ponds across the region, Jaccard's Coefficient of Similarity and Sørensen's Similarity index were calculated (Equation 3.7 and 3.8) in Community and Analysis Package 3.0. These beta-diversity measures are the most widely used in ecology (Chao *et al.,* 2006). They are based on presence/absence data and 'quantify the shared range of each pair of species as a proportion of their combined range' (Barbosa *et al.,* 2012: 1395).

$$J = \frac{c}{a+b+c}$$

(where c is the number of species common to both samples, a is the number of species unique to one community and b is the number of species unique to the second community (Real and Vargas, 1996))

Equation 3.7 – Jaccard's Similarity Coefficient

$$\boldsymbol{QS} = \frac{2a}{2a+b+c}$$

(where a is the number of species common in both samples b is the number of species unique to sample 1 and c is the number of species unique to sample 2 (Wolda *et al.,* 1981; Chao *et al.,* 2006))

Equation 3.8 - Sørensen Similarity index

3.5.2.4 Spatial (distance) dissimilarity in macroinvertebrate assemblages

To examine the influence of spatial factors (geographic distance) on macroinvertebrate community structure, a Bray-Curtis dissimilarity matrix of the faunal communities at each pond site was constructed. The spatial configuration of the ponds sampled in this thesis was constructed in a distance matrix based on the nearest 'edge to edge distance (meters) of each possible pair of ponds' (Vanschoenwinkel *et al.,* 2007: 1259). In addition, an environmental distance (log transformed) matrix was constructed based on their Euclidean distance (Equation 3.9). The Bray-Curtis dissimilarity and environmental Euclidean matrices were calculated using PRIMER 6 (Clarke and Gorley, 2006). The relationship between the distance between each pair of ponds, macroinvertebrate community dissimilarity and environmental distance was assessed using the Relate (non-parametric mantel type test using Spearman's Rank correlation) function in PRIMER 6 (Clarke and Gorley, 2006).

$$D_1 = \sqrt{\sum_i (y_{i1} - y_{i2})^2}$$

Equation 3.9 - Euclidean distance (Clarke and Gorley, 2006: 45)

3.5.3 Ordination

Ordination methods, notably indirect/direct gradient analysis and non-metric multidimensional scaling (NMDS), can be used to analyse and summarize the biotic community patterns and structures and identify gradients in the taxon compositions within samples (Lepš and Šmilauer, 2003). Ordination analysis was undertaken using

CANOCO Version 4.5 (ter Braak and Šmilauer, 2002) and PRIMER 6 (Clarke and Gorley, 2006). Prior to any ordination analyses the species-abundance data was log transformed to reduce the influence of commonly occurring taxa. Down weighting of rare species was also applied to Detrended and Canonical Correspondence Analysis to reduce the influence of rare and less commonly occurring taxa. Due to natural seasonal variability in community composition, seasonal data from individual pond sites were combined and mean values of environmental parameters derived. Local and regional environmental parameters; pond surface area, depth, percentage emergent, submerged and floating macrophytes, percentage water surface and pond margin shaded, pond proximity, connectivity, dissolved oxygen, conductivity and fish presence were $\log_{10}$ transformed to reduce the influence of skew and eliminate their physical units (Legendre and Birks, 2012).

3.5.3.1 Non-metric multidimensional scaling (NMDS)

Non-metric multidimensional scaling (NMDS) is an ordination technique used to graphically represent the degree of (dis)similarity in individual sample communities of a data set. It is a robust procedure that can accurately represent among-sample relationships in a low dimensional picture (Clarke, 1993). For the purposes of this research NMDS was used to visualise the macroinvertebrate community (dis)similarity between pond sites and was performed in PRIMER 6. Species-abundance data was log (x+1) transformed prior to analysis. NMDS is an iterative procedure that maximises the rank order correlation between the dissimilarity among pond sample sites (dissimilarity matrix) and the distance in ordination space (in this thesis the Bray-Curtis Dissimilarity measure was used) (Clarke, 1993; Clarke and Gorley, 2006). Non-metric multidimensional scaling (NMDS) places those sites with similar ecological communities closer together along the ordination axes and those with less similar assemblages further apart. The iterative procedure refines the relative position of the sites along the ordination axes in an attempt to minimise the degree of 'stress' which measures the lack of fit or distortion between the dissimilarity matrix and the dissimilarity in the ordination space (Clarke, 1993; Lepš and Šmilauer, 2003). A stress level of ≤0.2 is seen as an appropriate fit and can provide and accurate visualisation of the (dis)similarity of sample plots within the ordination space (Clarke, 1993). In NMDS the number of axes is chosen *a priori* and should reflect the minimum stress (Lepš and Šmilauer, 2003).

3.5.3.2 Detrended Correspondence Analysis (DCA)

DCA is an indirect gradient analysis that uses ordination methods to calculate and present graphically the total heterogeneity (gradient length) in an ecological data set (Lepš and Šmilauer, 2003). There are two stages to a DCA; firstly ordination analysis is undertaken on ecological data and secondly, a comparison of the suggested gradients (ecological variability) with prior knowledge of environmental conditions is conducted (ter Braak, 1995; Lepš and Šmilauer, 2003). Detrended Correspondence Analysis was developed in an attempt to correct two key faults of Correspondence Analysis; 1) compression at the end of the axis (the edge effect) and; 2) the second axis's systematic relationship with the first axis (the arch effect) (ter Braak, 1995). Detrended Correspondence Analysis (DCA) was used in this thesis as an exploratory analysis of macroinvertebrate data to determine gradient lengths and the most appropriate constrained ordination method (Ryves *et al.,* 2002). Unimodal methods (CA/CCA) are most appropriate on data sets with a gradient length >4, whereas linear methods (PCA/RDA) are most suitable if the longest gradient length is <3 (Lepš and Šmilauer, 2003). Both unimodal and linear ordination methods work well on data sets with gradient length between 3 and 4 (Lepš and Šmilauer, 2003).

3.5.3.3 Canonical Correspondence Analysis (CCA)

Canonical Correspondence is a direct gradient analysis which aims to capture the variation in community assemblage that can be explained by measured local (physicochemical and biological) and spatial (pond proximity and connectivity) environmental factors (ter Braak, 1995; Lepš and Šmilauer, 2003). As a result CCA can be used to identify and visualise the environmental variables that are significantly influencing the variation in biotic community composition (ter Braak and Verdonschot, 1995). Individual taxa and faunal community plots are constrained within the multidimensional ordination space by the environmental variables included in the CCA (as linear combinations of the physicochemical variables). There has been concern about the use of environmental variables that are highly correlated (multicollinearity) to each another in ordination analysis (ter Braak, 1995). A Principle Components Analysis was undertaken on $\log_{10}$ transformed physicochemical data to identify the most important environmental variables (principle components) to be retained for ordination analysis and thus minimize multicollinearity (redundancy) (Monk *et al.,* 2007). The statistical significance of associations between each of the environmental variables and the canonical axes were determined using the forward selection procedure, employing a random Monte Carlo permutations test (999 random permutations) with Bonferroni correction. Only the environmental parameters significantly influencing the faunal distribution ($p<0.05$) were included in the final models.

3.5.3.4 Variance partitioning

Variance partitioning analysis was undertaken using CANOCO 4.5 on macroinvertebrate taxa-abundance data to examine the relative importance of different environmental parameters in structuring macroinvertebrate assemblages (Vanschoenwinkel *et al.,* 2007; Van de Gucht *et al.,* 2007). Only environmental parameters from the Canonical Correspondence Analysis (CCA) identified to influence macroinvertebrate community composition significantly were used in the variance partitioning analysis. The significant environmental variables were categorised into distinct environmental groups: physicochemical, biological and spatial. The total percentage of variance explained by the CCA was partitioned into unique contribution (percentage of variance explained by each individual group of environmental variables), common contributions (variation explained by a combination of groups of environmental variables) and residual variation (unexplainable variation) using partial CCA's (Borcard *et al.,* 1992; Lepš and Šmilauer, 2003; Vanschoenwinkel *et al.,* 2007). The variance partitioning was expressed graphically using a Venn diagram.

3.5.4 Conservation value

3.5.4.1 Community Conservation Index (CCI)

To further asses the conservation value of pond habitats the Community Conservation Index was calculated for each pond site (Chad and Extence, 2004; Rosset *et al.,* 2013; Armitage *et al.,* 2012). Conservation value is often based on the rarity status of individual species. Rather than classify conservation value in terms of individuals, the Community Conservation Index accounts for the overall macroinvertebrate community thus incorporating community richness as well as individual macroinvertebrate rarity into the conservation value (Chad and Extence, 2004).

Each macroinvertebrate taxa present within an individual pond are assigned a score based on the categories presented in Table 3.3. The conservation score assigned to each macroinvertebrate taxa was based on the conservation scores provided by Chad and Extence (2004) who determined conservation values for most macroinvertebrate taxa recorded in the UK (Armitage *et al.,* 2012, Appendix 4). The sum of the assigned macroinvertebrate conservation scores is divided by the total number of species in the sample to calculate the average conservation score for the pond (Chad and Extence, 2004). This is then multiplied by a community score to give the overall conservation value (Table 3.4; Equation 3.10). The community score allocated to each pond is determined by the rarest taxa (the greatest conservation score) in the sample (Table 3.4). Ponds which record a final score of 0-5 have low conservation value; >5-10 a moderate conservation value; >10-15 a fairly high conservation value; >15-20 a high conservation value and >20 a very high conservation value.

Table 3.3 - Individual conservation scores and terms for invertebrate species (Chad and Extence, 2004: 599)

Score	**Term**
10	RDB 1 (Endangered)
9	RDB 2 (Vulnerable)
8	RDB 3(Rare)
7	Notable (but not RDB status) or regionally very notable
6	Regionally notable
5	Local
4	Occasional - Species not in categories 10-5, which occur in up to 10%of all samples in similar habitats
3	Frequent - Species not in categories 10-5, which occur in 10-25% of all samples from similar habitats
2	Common – Species not in categories 10-5, which occur in 25-50% of all samples from similar habitats
1	Very common – Species not in categories 10-5, which occur in 50-100% of all samples from similar habitats

Table 3.4 - Community score categories (Chad and Extence, 2004: 602)

Community Score	**Term (Rarest Taxon Score)**
15	10
12	9
10	8
7	7
5	5 or 6
3	3 or 4
1	Scoring taxa absent

$$\textbf{CCI=} \frac{\Sigma CS}{\text{n}} \text{ x CoS}$$

(Where CS is the individual taxa conservation scores within the sample, n is the number of contributing species within the sample, CoS is the community score (derived from the highest taxa conservation score within the sample).

Equation 3.10 - Community Conservation Index (Chad and Extence, 2004: 601)

3.5.4.2 UK Post-2010 Biodiversity Framework (England) Pond Priority Habitat (PPH)

Becoming a Pond Priority habitat (PPH) under the UK Post-2010 Biodiversity Framework (previously the UK BAP) is the main process through which ponds in England can receive some form of conservation protection along with detailed conservation and management plans (Natural England, 2014a). As a result this method has become a key procedure to quantify a pond habitats conservation value in this thesis. In order to qualify as a PPH in England a pond is required to meet one or more of the following criteria (BRIG, 2008: 2):

1. Habitats of international importance (Annex 1 of the EU Habitats Directive)
2. Species of high conservation importance (Red Data Book species, UK BAP species, species protected under the Wildlife and Countryside Act 1981 Schedule 5 and 8, EU Habitats Directive Annex II species, a nationally scarce wetland plant or three nationally scarce aquatic invertebrate species)
3. Exceptional assemblages of key biotic groups (≥30 wetland plant species or ≥ 50 aquatic macroinvertebrate species)
4. Pond of high ecological quality (Predictive System for Mulitmetrics (PSYM) score of ≥ 75%)
5. Other important ponds (ponds recognised as important based on their rarity age or landscape context e.g., pingos and duneslack ponds)

The qualification criteria for Pond Priority Habitats in England under the UK Post-2010 Biodiversity Framework are the same as the criteria used for the UK Biodiversity Action Plan (which the Biodiversity Framework has replaced) (Natural England, 2014a; Natural England, 2014b). The ponds in this thesis were assessed against these criteria (BRIG, 2008: 2) to determine whether any of the ponds qualified as a Pond Priority Habitat (PPH) and as a result would receive consideration from policy makers within

Leicestershire. However, a complete examination of pond sites using the PPH criteria was not possible. The PSYM score could not be calculated as it requires the Freshwater Habitats Trust to undertake the analysis in their own software (it is not available to others) and was beyond the timescale of this thesis.

3.6 Summary

This chapter has outlined the fieldwork techniques, equipment used and statistical tests utilised to quantify the aquatic macroinvertebrate biodiversity and conservation value of ponds across a range of landscapes typical of European lowland landscapes. Detailed fieldwork strategies implemented to sample and collate the spatial and temporal (seasonal) variability of macroinvertebrate biodiversity and environmental variables within ponds across a range of land cover types were outlined. Analytical methods selected to examine the spatial/temporal alpha, beta and gamma biodiversity and conservation value across a variety of landscapes were described. In addition, statistical methods to assess environmental parameters which may influence invertebrate distribution and compositions were outlined.

Chapter 4. Regional macroinvertebrate biodiversity

4.1 Introduction

Historically, freshwater research and management practices have been focussed on larger water bodies such as rivers and lakes (Oertli *et al.,* 2009). However, there has been an increasing consideration of the biodiversity and conservation value of pond habitats. The number of peer reviewed scientific papers published per year examining pond biodiversity has tripled in the last decade (Céréghino *et al.,* 2014). Despite their small size, ponds represent a significant freshwater resource and have been recognised as harbouring substantial macroinvertebrate biodiversity, supporting common and rare/endemic species (Williams *et al.,* 2003; Biggs *et al.,* 2005). As a result, ponds typically have high conservation value and estimates suggest that up to 20% of all pond habitats may meet the requirements to become a Pond Priority Habitat (BRIG, 2008). The heterogeneity of physicochemical parameters displayed within ponds (even when in close proximity, individual ponds may display heterogeneous physicochemical conditions), provides a wide range of habitat niches for macroinvertebrate taxa to colonize resulting in high community heterogeneity and regional pond diversity (Davies *et al.,* 2008b). Landscape-scale studies have highlighted the considerable contribution ponds make to regional biodiversity (greater macroinvertebrate biodiversity than lakes, streams and rivers) although landscape-scale pond research has primarily focussed on agricultural landscapes (Williams *et al.,* 2003; Davies *et al.,* 2008b; Gioria *et al.,* 2010).

This chapter explores the macroinvertebrate biodiversity within ponds at three diversity scales (alpha, beta and gamma) within a variety of land covers across Leicestershire. Alpha diversity can be defined as the macroinvertebrate richness within a pond site or habitat. It is often measured using alpha diversity indices which incorporate the number of taxa and the dominance/evenness of different species within that community (Magurran, 2004). Although alpha diversity indices reduce large amounts of data and information into to a single value (Wolda, 1983) they are commonly used and provide an appropriate index to assess macroinvertebrate biodiversity within and between different landscapes. Beta (β) diversity is the measure of the variability in macroinvertebrate communities between individual sample/pond sites (Clergue *et al.,* 2005). Historically, beta-diversity has received considerably less research attention compared to alpha (local) diversity. However, interest in beta-diversity has greatly increased in the last decade as it can capture the dynamic spatial and temporal pattern of biodiversity, provide a direct link between local (alpha) and regional (gamma) scale diversity and can provide important information for the design and management of conservation areas (e.g., nature reserves/SSSI sites) (Anderson *et al.,* 2011; Al-Shami *et al.,* 2013; Heino *et al.,* 2015). Alpha diversity can be considered the "inventory" component of diversity, measuring the species composition of a single site, whilst beta-diversity is the "differentiation" component of diversity, determining the heterogeneity in community composition across a range of sites (McKnight *et al.,* 2007). Gamma (γ) diversity is the product of alpha- and beta- diversity and is the overall macroinvertebrate biodiversity within the entire study region.

4.1.1 Research/knowledge gaps

Pond research at larger scales has largely focussed on invertebrate diversity within a particular landscape (Williams *et al.,* 2003; Céréghino *et al.,* 2008a; Gledhill *et al.,* 2008; Usio *et al.,* 2013; Ilg and Oertli, 2014) although there have been a few national scale studies (Williams *et al.,* 1998; Nicolet *et al.,* 2004). There have been very few studies which have considered the regional macroinvertebrate biodiversity within ponds across a range of land cover types (urban, agricultural, meadow, forest) that typically cover lowland landscapes. In addition, there has been little research attention focused on macroinvertebrate biodiversity within the East Midlands of the UK despite the high occurrence of ponds. The importance of ponds to freshwater biodiversity is now being recognised (Biggs *et al.,* 2005) although, there is a need to consider pond biodiversity at larger scales and across a variety of landscape types, to provide a detailed assessment of the current biodiversity status within a region thereby helping to direct conservation and restoration strategies to pond landscapes where it is most urgently required and/or may be most beneficial.

4.1.2 Chapter aims and hypotheses

In order to address the research gaps identified above this chapter aims to characterise the local and regional macroinvertebrate biodiversity and conservation value within meadow, agricultural, forest and urban pond types in the East Midlands, UK (see Chapter 1.4: Objective 1). In addition, this chapter will assess the spatial and seasonal variation in macroinvertebrate community assemblage within and between the four pond types (see Chapter 1.4; Objective 2).

This chapter will test the following hypotheses;

H_1: Aquatic macroinvertebrate diversity will be greatest in meadow ponds and lowest in urban ponds;

H_2: Macroinvertebrate diversity will be highest in emergent and submerged macrophyte mesohabitats and lowest in open water mesohabitats;

H_3: There will be significant community heterogeneity between pond types;

H_4: Meadow, agricultural and forest ponds will have a higher conservation value than urban ponds.

The fieldwork and statistical analysis methods employed in this chapter are outlined in Chapter 3.

4.2 Results

Ponds within this large-scale regional study were located on four land cover types typical of a European lowland landscape; ponds located within natural floodplain meadows and lammas/wildflower meadows were defined as meadow ponds (35 ponds); agricultural ponds (12 ponds) were situated within a landscape that was intensely cultivated and dominated by one or two crops, notably rapeseed and wheat; forest ponds (7 ponds) were recorded within mixed woodland (oak, silver birch, alder and European ash) or Oak woodland; and urban ponds (41 ponds) were defined as lentic waterbodies located within a built environment. This includes ponds within domestic gardens, urban green space (such as parks) and in highly developed areas (industrial, roadside and city centre) such as storm water retention ponds.

4.2.1 Alpha and gamma diversity

A total of 185104 individuals were recorded (Table 4.1) during three sampling occasions (spring, summer and autumn) from 95 ponds in the town of Loughborough and the surrounding landscape. 45210 individuals were sampled during spring 2012, 46316 during summer 2012 and 93578 in autumn 2012. A total of 228 taxa were identified from the study region, representing 19 orders and 68 families. Meadow ponds supported a total of 175 macroinvertebrate taxa; 170 taxa were recorded within urban ponds; 126 taxa from agricultural ponds and 62 taxa from forest ponds. The largest numbers of taxa were recorded from the orders Coleoptera (75), Trichoptera (36), Hemiptera (32), Gastropoda (18) and Odonata (18). A full macroinvertebrate taxa list for each pond site is presented in Appendix 5. The invertebrate taxa most widely distributed across the pond sites were; Chironomidae (Diptera: 91 ponds); Oligochaeta (Annelida: 90 ponds); *Crangonyx pseudogracilis* (Amphipoda, Crustacea: 66 ponds), Tipulidae (Diptera: 64 ponds); *Asellus aquaticus* (Isopoda, Crustacea: 62 ponds) and *Cloeon dipterum* (Ephemeroptera, Insecta: 62 ponds).

Two species of non-native macroinvertebrate were recorded. *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca), a snail native to New Zealand introduced into the UK (as early as the mid-19th Century) most likely from Australia in ship's drinking water supplies (Ponder, 1988). *P. antipodarum* has become a widespread and common species in the United Kingdom (Macan, 1977) and has not been recorded to have had a significant negative impact on native biodiversity. *Crangonyx pseudogracilis* (Amphipoda, Crustacea) is native to North America (Conlan, 1994) and has become a common and widespread species in the United Kingdom since its introduction in the 1930s, inhabiting a wide range of freshwater systems (Gledhill *et al.,* 1993).

Table 4.1 - Summary of the macroinvertebrate families recorded and total abundance from the three sampling periods for all 95 ponds (see Appendix 5 for taxonomic details for each pond)

	Abundance		Abundance
Planariidae	127	Limnephilidae	780
Lymnaeidae	9816	Beraeidae	1
Physidae	6720	Molannidae	3
Planorbidae	11131	Leptoceridae	44
Bythniidae	154	Polycentropodidae	94
Hydrobiidae	1986	Hydropsychidae	10
Succineidae	4	Corixidae	24725
Ancylidae	61	Gerridae	329
Valvatidae	153	Hydrometridae	11
Zonitidae	187	Notonectidae	1211
Pisidiidae	1913	Naucoridae	89
Oligochaeta	9256	Nepidae	14
Erpobdellidae	917	Gyrinidae	17
Glossiphoniidae	1115	Noteridae	167
Piscicolidae	50	Dytiscidae	2773
Crangonyctidae	21005	Elminthidae	4
Gammaridae	1371	Hygrobiidae	17
Asellidae	15874	Haliplidae	521
Argulidae	2	Hydrophilidae	904
Hydrachnidiae	99	Scirtidae	548
Collembola	194	Ceratopogonidae	476
Nemouridae	2	Chaoboridae	7613
Taeniopterygidae	1	Chironomidae	38470
Baetidae	12524	Chrysomelidae	9
Caenidae	342	Culicidae	5720
Sialidae	22	Dicranota	1
Sisyridae	4	Dixidae	300
Pyralidae	712	Ephydridae	8
Platycnemididae	2	Empididae	3
Coenagrionidae	2970	Psychodidae	147
Lestidae	15	Simuliidae	5
Calopterygidae	3	Stratiomyidae	96
Aeshnidae	131	Syrphidae	1
Libellulidae	36	Tipulidae	1062
Phryganeidae	26	Diptera other	6

Normal distributions for taxon richness and invertebrate community abundance were inspected; community abundance was not normally distributed and was $\log_{10}$ transformed. Macroinvertebrate taxon richness varied substantially between pond sites, ranging from 2 taxa (within an urban pond) to 73 taxa (within a meadow pond). Mean invertebrate taxon richness across the region for the pond sites examined was 29 taxa. Invertebrate richness differed significantly between ponds located within the different landscapes in the study area (ANOVA $F_{3, 94}$=7.258; p<0.01) (Figure 4.1). The greatest invertebrate richness was recorded in meadow ponds (mean: 39.2 range: 5-73), the lowest richness was recorded from forest ponds (mean: 18.43 range: 10-27). Mean invertebrate taxon richness in agricultural ponds was 34.17 (range: 9-51) and 20.75 in urban ponds (range: 2-61) (Table 4.2). The *post hoc* Tukey test indicated taxon richness was significantly higher in meadow ponds than forest or urban ponds (Figure 4.1). Taxon richness in agricultural ponds was not significantly different compared to the other three pond types. Total macroinvertebrate community abundance did not differ significantly between the four pond types (ANOVA p>0.05), although high variability was recorded among the pond types (Appendix 5).

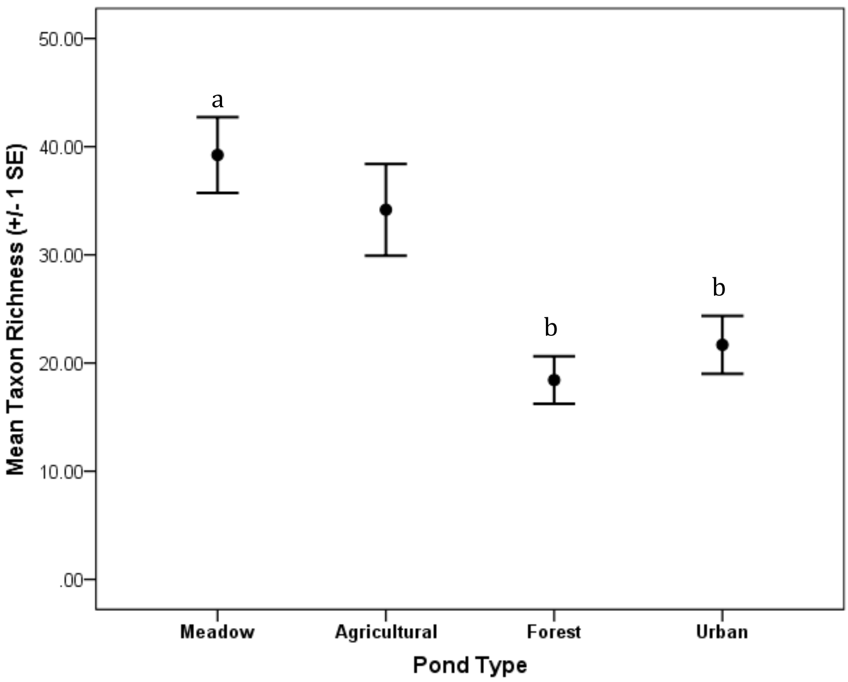

Figure 4.1 - Mean taxon richness (+/- 1 SE) within ponds in meadow, agricultural, forest and urban landscapes in Leicestershire. Pond types/groups that are significantly different in post hoc pairwise Tukey test are indicated with different letters (a or b).

One-way Analysis of Variance (ANOVA) revealed significant differences among ponds from meadow, agricultural, forest and urban landscapes for alpha diversity indices; Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha (Table 4.2).

Table 4.2 - One-way ANOVA between alpha diversity indices and pond type. Significant values ($p \leq 0.05$) are presented in bold.

Alpha Diversity Indices	F. Ratio	P. Value
Shannon Wiener diversity index	6.592	**0.000**
Simpsons diversity index	6.017	**0.001**
Margalef diversity index	8.208	**0.000**
McIntosh diversity index	3.857	**0.012**
Fisher's alpha	8.462	**0.000**
Berger Parker Dominance index	2.695	0.051

Meadow ponds had the highest diversity scores across all indices examined (Figure 4.2, Appendix 6), although there was some variability regarding the lowest diversity scores. The lowest Shannon Wiener diversity and McIntosh diversity index scores were recorded from urban ponds whilst Fisher's alpha and the Margalef diversity index indicated that forest ponds obtained the lowest diversity scores. *Post hoc* Tukey tests revealed Shannon Wiener diversity, Simpsons diversity, and McIntosh diversity indices to be significantly higher in meadow than urban ponds (ANOVA $p<0.05$) whereas the Margalef diversity and Fisher's alpha scores were recorded to be significantly higher in meadow ponds than both urban and forest ponds (ANOVA $p<0.05$).

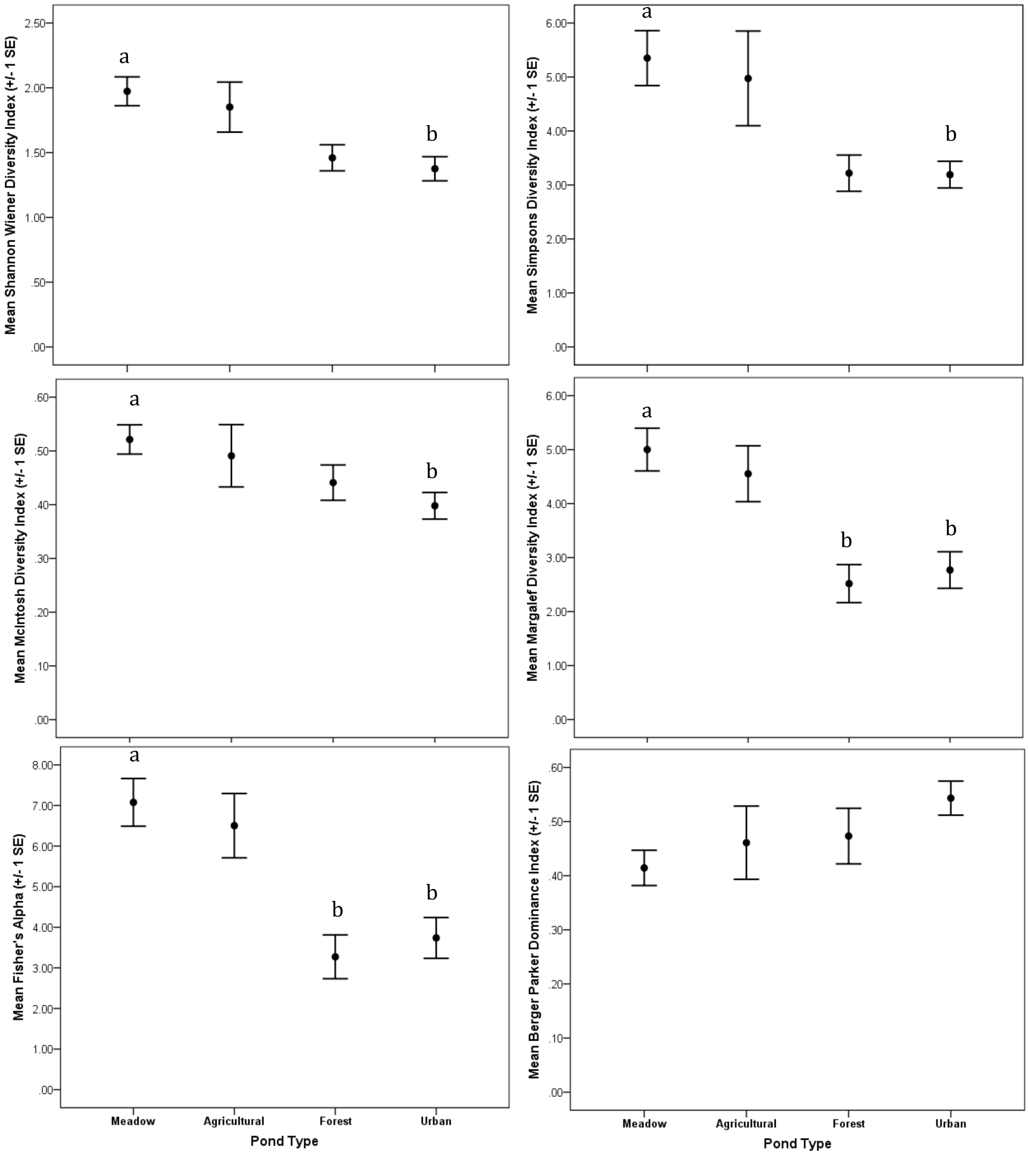

Figure 4.2 - Comparisons of mean Shannon Wiener diversity index, Simpsons diversity index, Fisher's alpha, McIntosh diversity index, Margalef diversity index and Berger Parker Dominance index between the four pond types. Pond types/groups that are significantly different in post hoc pairwise Tukey test are indicated with different letters (a or b).

4.2.2 Seasonal variation in macroinvertebrate diversity

A summary of invertebrate families sampled, the number of species in each family and their abundance in the spring, summer and autumn season samples is presented in Table 4.3. Of particular note is the higher abundance and numbers of taxa collected in the autumn season (total taxa: 174), compared to the spring (total taxa: 166) or summer seasons (total taxa: 154). This is most likely to be the result of an increase in active and passive dispersal/colonization activity during the summer months and the hatching of invertebrate taxa from eggs in the autumn. Macroinvertebrate families such as Coenagrionidae, Dytiscidae, Lymnaeidae, Hydrobiidae and Planorbidae demonstrated an increase in abundance across the seasons. In addition, Hemiptera, Coleoptera (particularly Dytiscidae) and Hirudinea recorded higher taxon richness in the autumn season. However, some families in the order Trichoptera (such as Limnephilidae and Leptoceridae) displayed large reductions in abundance and taxon richness in the autumn season. Invertebrate richness was recorded to be lowest during the summer season (Table 4.3). This was anticipated as some of the ephemeral ponds dried out during the sampling period and some aquatic insect families developed into adults and emerged for reproduction.

Table 4.3 - Summary of the macroinvertebrate families collected, the number of taxa and their abundance from the three sampling seasons: spring 2012, summer 2012 and autumn 2012.

	Taxa			Abundance		
	Spring	Summer	Autumn	Spring	Summer	Autumn
Planariidae	1	1	1	18	12	97
Lymnaeidae	4	4	3	1556	1557	6703
Physidae*	1	1	1	251	191	6278
Planorbidae	9	9	9	928	1564	8639
Bythniidae	1	1	1	12	28	114
Hydrobiidae	1	1	1	259	587	1140
Succineidae	0	1	1	0	2	2
Ancylidae	1	1	1	13	42	6
Valvatidae	1	2	2	4	42	107
Zonitidae*	1	1	1	45	98	44
Pisidiidae	1	1	1	1097	451	365
Oligochaeta*	1	1	1	3225	2865	3166
Erpobdellidae	2	2	2	308	171	438
Glossiphoniidae	4	3	5	465	114	536
Piscicolidae	1	0	1	19	0	31
Crangonyctidae	1	1	1	10259	4802	5944
Gammaridae	1	1	1	64	108	1199
Asellidae	2	2	2	6640	2277	6957
Argulidae*	0	1	1	0	1	1
Hydrachnidiae**	1	1	1	2	79	18
Collembola**	1	1	1	10	179	5
Nemouridae	2	0	0	2	0	0
Taeniopterygidae*	1	0	0	1	0	0
Baetidae	2	2	2	3790	5445	3289
Caenidae	2	3	1	18	260	64
Sialidae	1	0	1	10	0	12
Sisyridae*	0	0	1	0	0	4
Pyralidae	1	1	1	18	13	681
Platycnemididae	0	0	1	0	0	2
Coenagrionidae	6	5	6	209	290	2471
Lestidae	1	1	0	1	14	0
Calopterygidae	0	1	0	0	3	0
Aeshnidae	4	5	5	15	34	82
Libellulidae	1	2	2	2	9	25
Phryganeidae	1	1	2	1	1	24

	Taxa			Abundance		
	Spring	Summer	Autumn	Spring	Summer	Autumn
Limnephilidae	18	11	7	578	192	10
Beraeidae	0	1	0	0	1	0
Molannidae	1	1	0	1	2	0
Leptoceridae	2	4	0	2	35	7
Polycentropodidae	3	3	5	36	18	40
Hydropsychidae	1	1	1	1	1	8
Corixidae	19	16	18	1181	862	22682
Gerridae	0	3	3	0	17	312
Hydrometridae	0	0	1	0	0	11
Notonectidae	4	4	4	62	559	590
Naucoridae	1	1	2	4	8	77
Nepidae	0	1	2	0	2	12
Gyrinidae	1	1	1	1	15	1
Noteridae	1	1	1	3	96	68
Dytiscidae	20	17	29	528	862	1383
Elmidae	0	1	0	0	4	0
Hygrobiidae	0	1	1	0	3	14
Haliplidae	7	5	7	68	44	409
Hydrophilidae	18	12	17	157	443	304
Scirtidae	1	1	1	38	505	5
Ceratopogonidae*	1	1	1	66	131	279
Chaoboridae*	1	1	1	1560	790	5263
Chironomidae*	1	1	1	11031	15182	12257
Chrysomelidae*	1	1	1	1	7	1
Culicidae*	1	1	1	214	4637	869
Dicranota*	1	0	0	1	0	0
Dixidae*	1	1	1	12	18	270
Ephydridae*	0	1	1	0	1	7
Empididae*	1	0	1	1	0	2
Psychodidae*	1	1	1	36	96	15
Simuliidae*	1	1	1	1	1	3
Stratiomyidae*	1	1	1	27	56	13
Syrphidae*	0	0	1	0	0	1
Tipulidae*	1	1	1	357	486	219
Diptera Other	1	1	1	1	3	2

* Taxa identified to family level only

** Taxa identified to order level only

Nested ANOVA indicated a significant difference in macroinvertebrate community abundance (ANOVA $F_{2, 255}$=7.284; p<0.001) and taxon richness (ANOVA $F_{2, 255}$=9.760; p<0.001) between the three sampling seasons (spring, summer and autumn) (Figure 4.3). The *post hoc* Sidak test demonstrated that community abundance and taxon richness were significantly higher in the autumn season than the spring or summer seasons (p<0.001). 76% of the total macroinvertebrate taxon richness was represented in the autumn season. Community abundance increased seasonally in meadow, agricultural and forest ponds but among urban ponds, abundance decreased in the summer (Figure 4.3). In meadow and agricultural ponds, taxon richness was higher in the autumn than the spring and summer seasons, whilst invertebrate richness from forest and urban ponds was similar across all three sampling seasons (Figure 4.3).

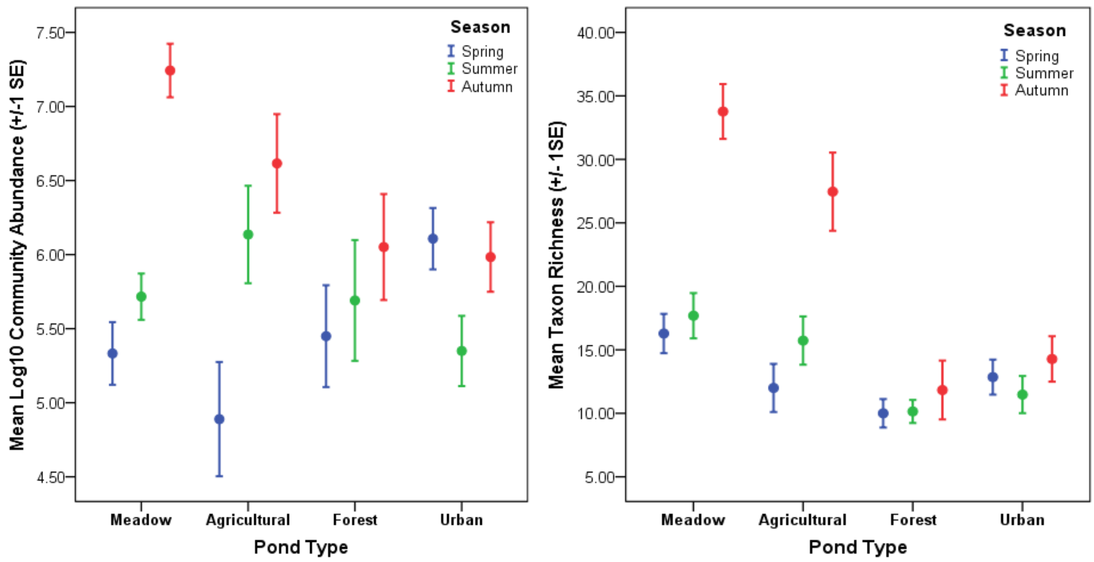

Figure 4.3 - Mean taxon richness and mean log_{10} community abundance in ponds between the spring, summer and autumn seasons

In addition, nested ANOVA identified a significant difference in alpha diversity indices between the three seasons (Table 4.4). *Post hoc* analysis showed that Shannon Wiener diversity index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha were significantly higher in the autumn season than the spring and summer seasons (Figure 4.4). Berger Parker Dominance was significantly lower in the autumn season compared to the spring and summer season.

The higher macroinvertebrate diversities recorded from agricultural and meadow ponds during the autumn season were driven by a large increase in macroinvertebrate taxa with high vagility. A greater number of taxa within the orders Coleoptera (greatest increase within the family Dytiscidae), Hemiptera and Odonata were recorded from the autumn season compared to the other seasons in meadow and agricultural ponds. Conversely, trichopteran (an actively dispersing invertebrate family) diversity was greatest in the spring and summer season compared to the autumn season.

Table 4.4 - Nested ANOVA between log_{10} community abundance, taxon richness and alpha diversity indices and season nested within pond type. Significant values ($p \leq 0.05$) are presented in bold.

		Pond Type (Season)
Log_{10} community abundance	*F.*	7.284
	P.	**0.000**
Taxon richness	*F.*	9.760
	P.	**0.000**
Shannon Wiener diversity index	*F.*	5.139
	P.	**0.000**
Berger Parker Dominance index	*F.*	3.236
	P.	**0.002**
Simpsons diversity index	*F.*	5.859
	P.	**0.000**
Margalef diversity index	*F.*	6.584
	P.	**0.000**
McIntosh diversity index	*F.*	3.492
	P.	**0.001**
Fisher's alpha	*F.*	4.750
	P.	**0.000**

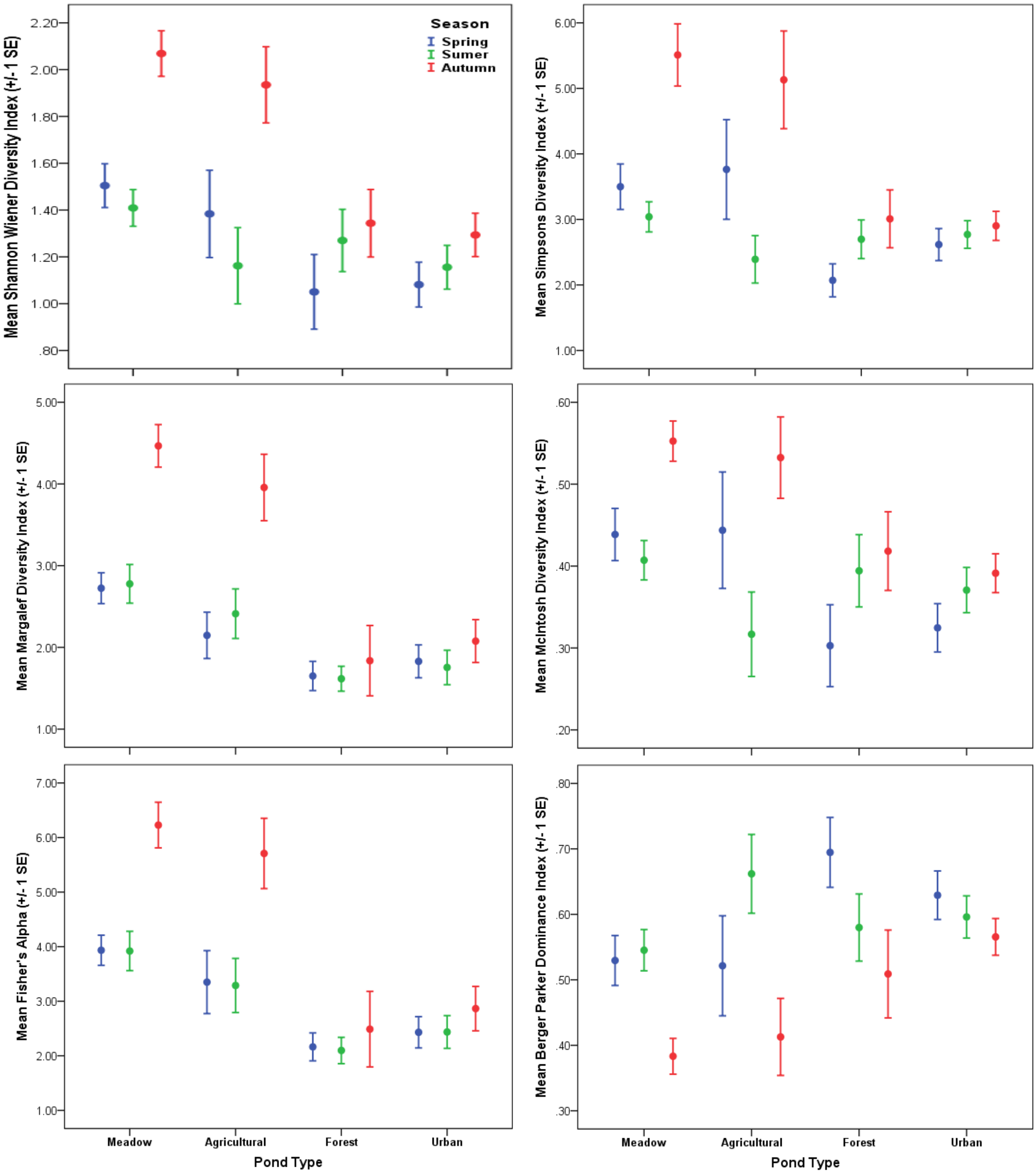

Figure 4.4 - Comparisons of mean Shannon Wiener diversity index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index, Fisher's alpha and Berger Parker Dominance index between the three sampling periods (spring, summer and autumn) within the four pond types

4.2.3 Mesohabitat macroinvertebrate diversity

Five mesohabitats were recorded within the ponds from the study area: open water (OW), emergent macrophytes (EM), submerged macrophytes (SM), floating macrophytes (FM) and overhanging vegetation (OHV). OW was the most extensive and frequently occurring mesohabitat occurring more than 180 times throughout the three sampling periods, SM was recorded 104 times, EM was recorded 85 times and FM and OHT was present 23 and 28 times respectively. All mesohabitats were present in agricultural and urban pond types but EM and FM were absent from forest ponds and FM was absent from meadow ponds.

Nested ANOVA was used to examine differences between pond mesohabitats. Nested ANOVA indicated that there was a significant difference in $\log_{10}$ community abundance, taxon richness, Shannon Wiener diversity index, Berger Parker Dominance index, Simpson diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha among the five mesohabitats (Table 4.5). *Post hoc* Sidak tests indicated EM and SM supported significantly higher taxon richness, Margalef diversity index and Fisher's alpha scores than OW, FM and OHV (Figure 4.5). EM was recorded to have significantly higher taxon richness, Margalef diversity index and Fisher's alpha than SM. Both EM and SM supported a significantly greater McIntosh diversity index than OW. Simpsons diversity index were significantly higher in EM than OW. The Berger Parker Dominance index was significantly higher in OW than EM and SM. The Shannon Wiener diversity index was significantly greater in EM than OW, FM and OHV whilst SM was significantly higher than OW and FM. Log_{10} community abundance did not differ significantly between the pond mesohabitats.

Emergent and submerged macrophytes supported the highest taxon richness, Fisher's alpha, Shannon Wiener diversity, Simpsons diversity, Margalef diversity and McIntosh diversity indices among meadow, agricultural and forest ponds. However, urban ponds displayed a different pattern; overhanging vegetation was identified to support similar alpha diversity indices to EM and SM (Figure 4.5). EM and SM recorded the lowest Berger Parker Dominance index scores among meadow, agricultural and forest ponds, but were identified to be among the highest in urban ponds (Figure 4.5).

Table 4.5 - Nested ANOVA between log_{10} community abundance, taxon richness and alpha diversity indices and mesohabitat nested within pond type. Significant values (p≤0.05) are presented in bold.

		Pond Type (Mesohabitat)
Log_{10} community abundance	*F.*	0.867
	P.	0.555
Taxon richness	*F.*	7.778
	P.	**0.000**
Shannon Wiener diversity index	*F.*	4.188
	P.	**0.000**
Berger Parker Dominance index	*F.*	3.067
	P.	**0.001**
Simpsons diversity index	*F.*	2.861
	P.	**0.001**
Margalef diversity index	*F.*	8.126
	P.	**0.000**
McIntosh diversity index	*F.*	2.989
	P.	**0.001**
Fisher's alpha	*F.*	7.329
	P.	**0.000**

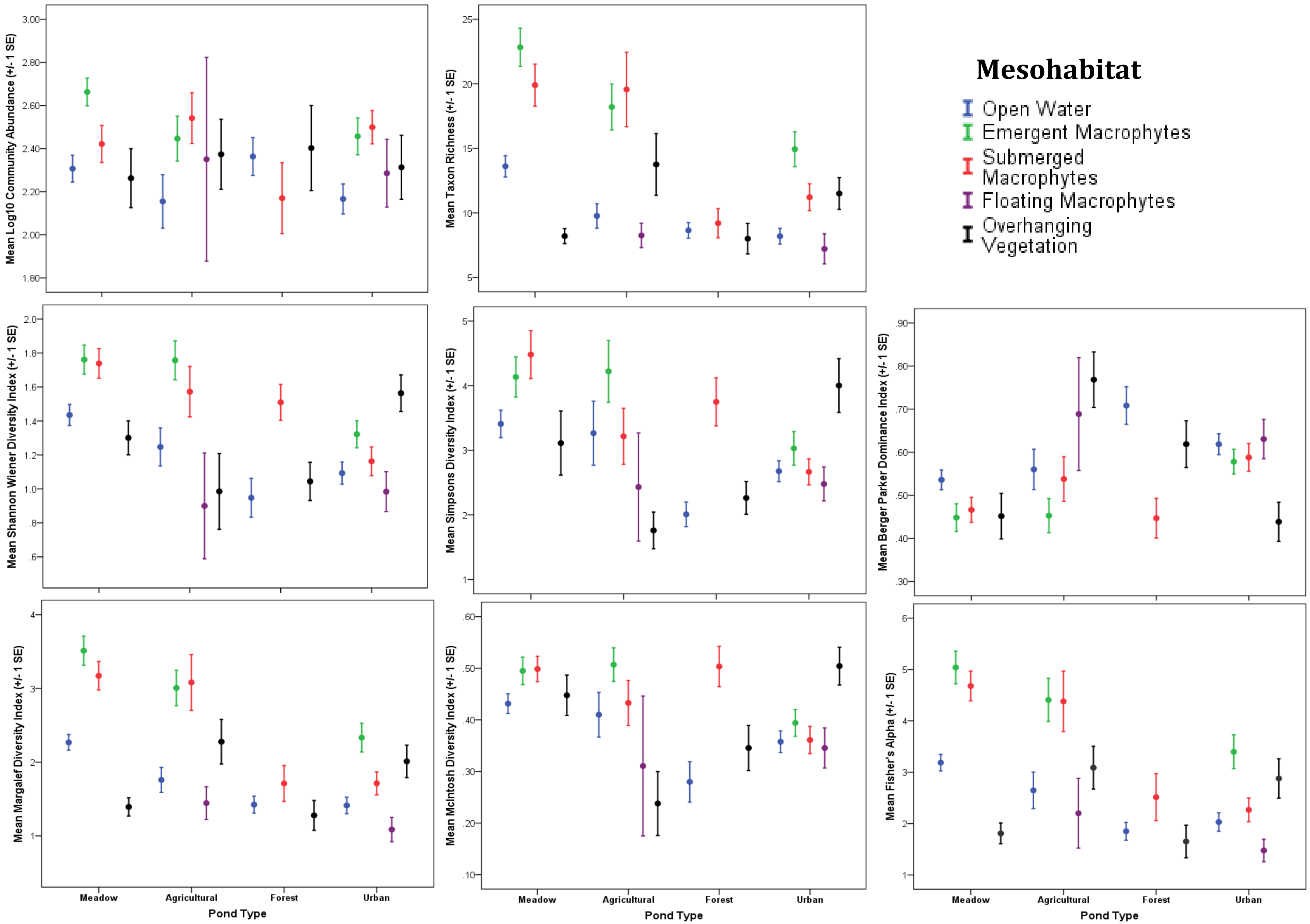

Figure 4.5 - Comparisons of mean $\log_{10}$ community abundance, taxon richness, Shannon Wiener diversity index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index, Fisher's alpha and Berger Parker Dominance index within the five mesohabitats in the four pond types.

4.2.4 Pond physicochemistry

A summary of the physicochemical variables measured during fieldwork for the study region and the four pond types is presented in Table 4.6. Seasonal data from individual pond sites were combined and mean values of environmental parameters derived. A full list of physicochemical parameters recorded at each pond site is presented in Appendix 7. Pond physicochemistry was tested for a normal distribution and area, depth, pond margin shaded, surface water shaded, submerged, emergent, and floating macrophytes were log_{10} transformed. Significant differences in pond margin/surface water shading, floating macrophytes, pH, conductivity, and fish presence between the pond types were recorded using one-way ANOVA (ANOVA $p<0.05$). Area, depth, emergent macrophytes, submerged macrophytes and dissolved oxygen were found to not differ significantly among pond types (ANOVA $p>0.05$). Ephemeral ponds were recorded from all four pond types. A total of 6 urban, 14 meadow, 4 forest and 3 agricultural ponds had an ephemeral hydrology and dried for a minimum of three months during the study period. *Post hoc* Tukey tests indicated that meadow ponds had significantly less water surface shaded by vegetation than forest and urban ponds. In addition, pond margin shaded by vegetation was significantly lower in meadow ponds than the other three pond types. pH was significantly lower in forest ponds than meadow and agricultural ponds and conductivity was significantly higher in agricultural ponds than the urban and forest ponds. The percentage of surface water covered by floating vegetation within urban and agricultural ponds was significantly greater than within meadow ponds.

The presence of fish varied significantly between the ponds types (ANOVA $F_{3, 94}=3.761$; $p<0.05$). The *post hoc* Tukey test indicated that the presence of fish was significantly greater among urban ponds than agricultural ponds. This is unsurprising as many urban ponds are specifically built to support fish communities (or often have fish deliberately added to them), especially ponds located within private gardens and urban green spaces.

Table 4.6 - Summary table of measured physicochemical variables; SWS - pond surface water shaded, PMS - pond margin shaded, EM - emergent macrophytes, SM - submerged macrophytes, FM - floating macrophytes, COND - conductivity, DO - dissolved oxygen. n = number of ponds.

		Area (m2)	Depth (cm)	SWS (%)	PMS (%)	EM (%)	SM (%)	FM (%)	pH	COND	DO (%)
Urban n = 41	**Mean**	780.3	67.5	17.5	28.9	23.0	21.1	15.8	7.8	501.3	71.2
	Std. Deviation	1929.5	65.7	28.5	33.8	29.3	23.5	26.0	0.6	280.3	25.6
	Standard Error	301.3	10.3	4.5	5.3	4.6	3.7	4.1	0.1	43.8	4
	Min	0.8	4	0	0	0	0	0	6.3	63.7	13.1
	Max	9309	>200	100	100	100	90	96.7	9.8	1322	118
Meadow n = 35	**Mean**	376.8	52.5	6.1	8.5	21.5	29.1	2.1	8	613.7	83.7
	Std. Deviation	911.3	38.6	19.7	22.9	25.8	26.8	5.9	0.7	299.6	19.2
	Standard Error	154	6.5	3.3	3.9	4.4	4.5	1	0.1	50.7	3.2
	Min	10.3	8	0	0	0	0	0	6.4	80	28.3
	Max	5256	>200	93.3	96.7	86.7	100	30.3	9.1	1494	119.5
Forest n = 7	**Mean**	182.5	52.4	44.7	56.6	15.4	15.2	8.1	7.2	352.2	61.6
	Std. Deviation	131.5	66.4	38.1	33.4	23.5	17.3	20.7	0.6	295.2	31.8
	Standard Error	49.7	25.1	14.4	12.6	8.9	6.5	7.8	0.2	111.6	12
	Min	88.6	13	4.3	5	0	0.3	0	6.2	104.3	29
	Max	472.7	>100	95	98.3	57.6	41.3	55	7.8	993	113.1
Agricultural n = 12	**Mean**	501.5	66.7	15.2	29	36.5	16.7	8.1	7.9	781.6	72.5
	Std. Deviation	1282.1	50.9	28.9	33.7	28.3	12.2	8.0	0.2	265.4	27.2
	Standard Error	307.1	17.7	8.3	9.7	8.2	3.5	2.3	0.1	76.6	7.9
	Min	24.3	12	0	0	5	0	0	7.6	476.3	26.5
	Max	4566	>100	100	100	86.7	37.3	28.3	8.3	1326.7	131.6
Region n = 95	**Mean**	552.4	60.7	15	23.4	23.6	23.1	9.2	7.8	567.2	75.3
	Std. Deviation	1457	54.9	27.8	32.6	27.6	23.6	19.3	0.6	302.9	24.7
	Standard Error	149.5	5.6	2.9	3.4	2.8	2.4	2	0.1	31.1	2.5
	Min	0.8	4	0	0	0	0	0	6.2	63.7	13.1
	Max	9309	>100	100	100	100	100	96.7	9.8	1494	131.6

4.2.5 Community heterogeneity

At a gamma (γ) scale, aquatic macroinvertebrate communities were significantly different (ANOSIM $p<0.01$). Pairwise tests identified a significant difference in macroinvertebrate community composition between meadow and urban ponds, agricultural and forest ponds and agricultural and urban ponds ($p<0.05$) (Table 4.7).

Table 4.7 - Analysis of similarity (ANOSIM) calculations between the four pond types (pairwise tests). Significant values (p≤0.05) are presented in bold.

Pairwise Tests		**P. Value**
1st Group	2nd Group	
Agricultural	Forest	**0.041**
Agricultural	Meadow	0.120
Agricultural	Urban	**0.012**
Forest	Meadow	0.097
Forest	Urban	0.626
Meadow	Urban	**0.001**

Both Jaccard's Coefficient of Similarity and the Sørensen Similarity index indicate that, across the study region, invertebrate communities supported by ponds were heterogeneous (Table 4.8). *Post hoc* Tukey tests demonstrated that urban ponds had significantly lower (ANOVA $p<0.05$) Jaccard's Coefficient of Similarity and Sørensen Similarity scores than meadow, agricultural and forest ponds. This suggests that there is a greater overlap of macroinvertebrate taxa within communities in meadow, agricultural and forest pond types (Table 4.8). Table 4.9 presents the top 4 taxa identified (and their percentage contribution) as contributing most substantively to the differences between the four pond types.

Table 4.8 - Mean Jaccard's Coefficient of Similarity and Sørensen Similarity index for the four pond types and the sample sites combined (region)

	Meadow Pond	**Agricultural Pond**	**Forest Pond**	**Urban Pond**	**Region**
Mean Jaccard's Coefficient of Similarity	0.24	0.26	0.26	0.18	0.19
Mean Sørensen Similarity index	0.37	0.40	0.41	0.30	0.30

Table 4.9 - Summary of top 4 aquatic macroinvertebrate taxa identified by SIMPER as most strongly influencing the between pond type dissimilarity. Their percentage contribution to between pond type dissimilarity is presented within the parenthesis. n = number of pond sites and j = total number of taxa. x/x represents the total number of taxa common between the pond types.

	Agricultural	**Forest**	**Meadow**	**Urban**
Agricultural	*n =12* *j = 126*	*F/A =49*	*M/A = 110*	*U/A = 101*
Forest	Culicidae (4.5) Chaoboridae (4.1) *A. aquaticus* (3.8) *C. dipterum* (3.6)	*n =7* *j = 62*	*M/F= 55*	*U/F = 59*
Meadow	Chaoboridae (3) Culicidae (2.7) *C. pseudogracilis* (2.6) *L. peregra* (2.6)	Oligochaeta (3.8) Culicidae (3.8) Chaoboridae (3.7) *A. aquaticus* (3.5)	*n = 35* *j = 175*	*U/M = 133*
Urban	*C. pseudogracilis* (3.9) Chaoboridae (3.8) *A. aquaticus* (3.7) Culicidae (3.6)	Culicidae (5.5) *A. aquaticus* (5.4) *C. pseudogracilis* (5.3) Chaoboridae (5.3)	*C. pseudogracilis* (3.6) *A. aquaticus* (3.5) Oligochaeta (3.3) Chironomidae (2.9)	*n =41* *j* = 170

A two-dimensional stress level of 0.21 was calculated by NMDS analysis suggesting a realistic visualisation of dissimilarity between macroinvertebrate assemblages recorded for the four pond types (Figure 4.6). The NMDS biplot demonstrated a relatively clear distinction between the invertebrate community assemblages in meadow ponds and urban ponds (Figure 4.6) which was also highlighted by ANOSIM (Table 4.4). Considerable overlap of urban pond sites with forest ponds was demonstrated in the biplot highlighting the similarity in macroinvertebrate community composition for these two pond types. This pattern was reinforced by ANOSIM which also recorded no significant difference between urban ponds and forest ponds macroinvertebrate assemblages (Table 4.4). Meadow and urban ponds were dispersed across the NMDS ordination space suggesting that within these pond types the invertebrate communities were heterogeneous (Figure 4.6). This was also corroborated by Jaccard's Coefficient of Similarity and Sørensen's Similarity index, which indicated significant heterogeneity of macroinvertebrate assemblages within urban pond sites (Table 4.5). In contrast, agricultural (except one site: AP9 (see Appendix 1)) and forest ponds formed relatively tight clusters suggesting that these pond types had relatively homogenous macroinvertebrate assemblages (Figure 4.6). A distinction between forest and agricultural ponds was revealed by the NMDS biplot indicating that the two pond types supported different invertebrates within their communities (Figure 4.6).

The NMDS plot revealed a clear separation between perennial and ephemeral ponds (Figure 4.6), indicating macroinvertebrate community assemblages in ephemeral and perennial ponds were heterogeneous. The majority of perennial ponds formed a large grouping towards the top of the second axis in the NMDS diagram (circled: 1), whereas ephemeral ponds were towards the bottom of the second axis (circled: 2) (Figure 4.6).

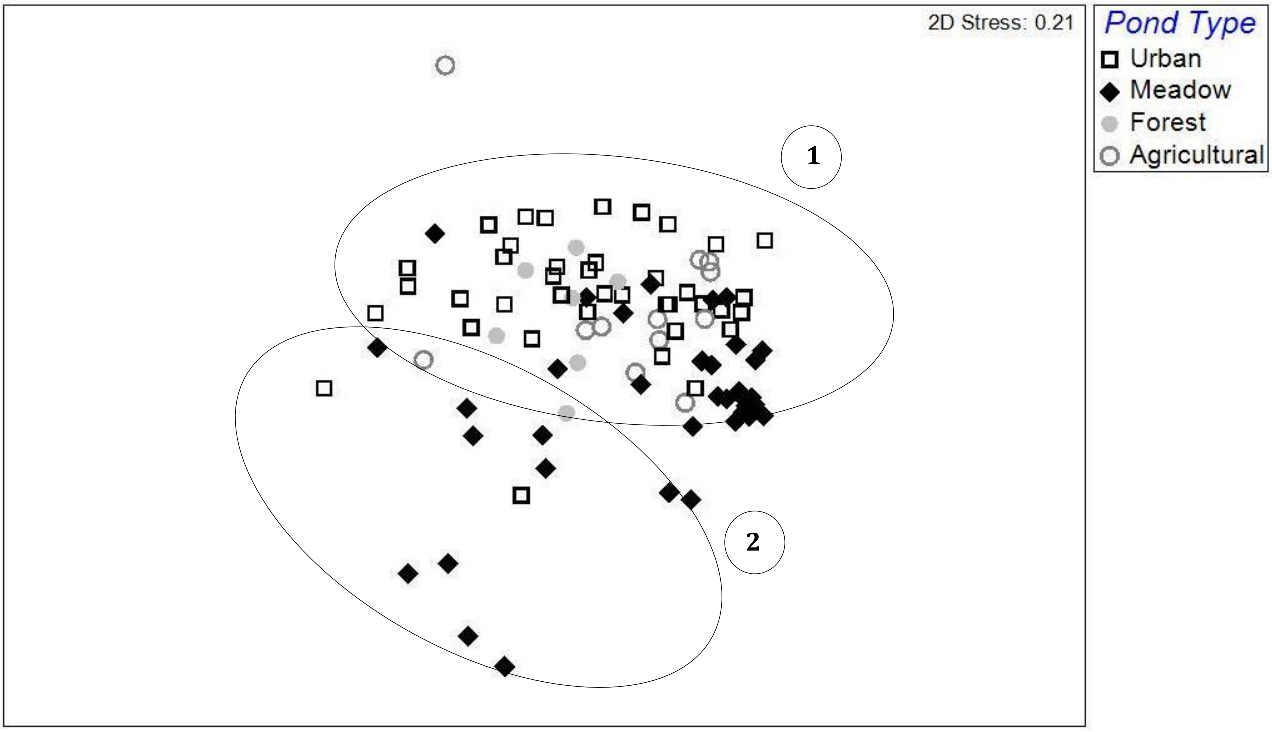

Figure 4.6 - Two dimensional NMDS biplot of dissimilarity (Bray-Curtis) of macroinvertebrate composition within pond sample sites (two-dimensional stress: 0.21). Ellipses display grouping of perennial ponds (top) and ephemeral ponds (bottom).

4.2.5.1 Seasonal community heterogeneity

When the macroinvertebrate community composition of the four pond types over the three sampling seasons (spring, summer and autumn) were examined using NMDS (four separate NMDS analyses (Figure 4.7)), a significant distinction between the autumn invertebrate assemblages and the other two seasons among meadow (ANOSIM $p<0.001$), and agricultural (ANOSIM $p<0.001$) pond types was displayed (Figure 4.7).

This suggests there was significant seasonal heterogeneity and turn-over in community composition in the macroinvertebrate assemblages within these two pond types. ANOSIM also indicated that there was a significant difference (ANOSIM $p<0.01$) in invertebrate community composition between spring and summer assemblages from meadow ponds whilst the spring and summer communities from the agricultural ponds were similar (ANOSIM $p>0.05$) and overlapped within the NMDS ordination (Figure 4.7). Meadow pond macroinvertebrate communities identified from the autumn sample were clustered towards the left of NMDS biplot whilst the spring and summer invertebrate communities were situated towards the right of the ordination space (Figure 4.7). The opposite pattern was demonstrated among agricultural ponds. The urban and forest pond macroinvertebrate communities from the spring, summer and autumn seasons overlapped within the NMDS ordination space (ANOSIM $p>0.05$) suggesting that the seasonal communities were similar in composition and there was little turnover in community composition during the three sampling periods.

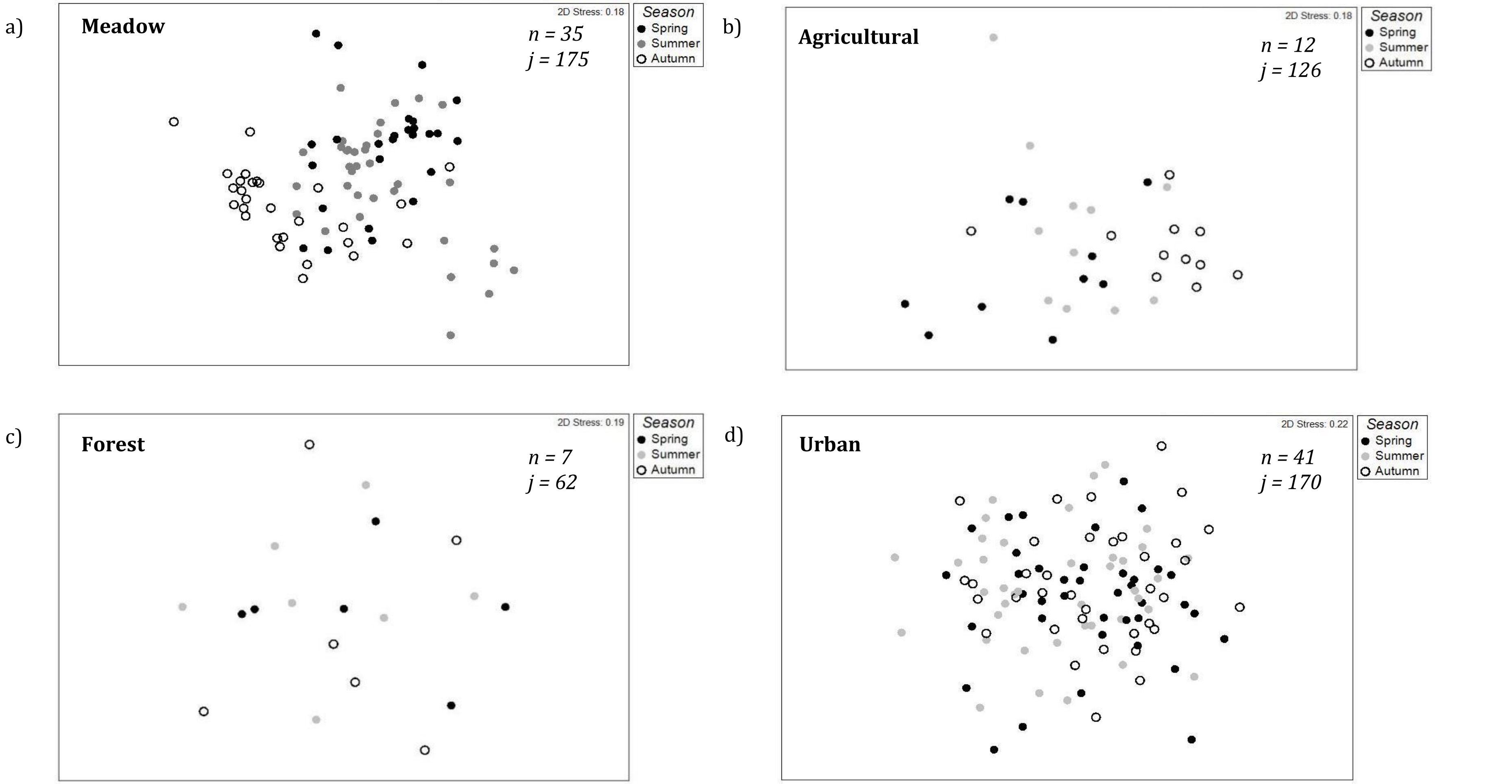

Figure 4.7 - Two dimensional NMDS plot of dissimilarity (Bray-Curtis) of seasonal (spring, summer and autumn) invertebrate communities within the four pond types; (a) meadow (b) agricultural (c) forest and (d) urban. n = number of pond sites and j = total number of taxa.

4.2.6 Conservation Value

There were 13 species of conservation interest recorded from the Leicestershire pond sites; 11 Coleoptera; 1 Gastropoda; 1 neuropteran and 1 Odonata (Table 4.10). A total of 23 ponds supported one or more invertebrate species with a conservation status (13 meadow ponds, 5 urban ponds, 4 agricultural ponds and 1 forest pond). A single agricultural pond supported 3 species with a conservation status. One meadow and one urban pond each supported two invertebrate species of conservation interest.

Table 4.10 - Macroinvertebrate species of conservation interest with their designations and location/s

Family	Species	Conservation Designation	Sample Location/s
Sisyridae	*Sisyra terminalis*	Nationally Notable	1 Agricultural Pond
Coenagrionidae	*Coenagrion pulchellum*	IUCN Lower Risk - Near Threatened	1 Urban Pond
Gyrinidae	*Gyrinus distinctus*	Nationally Scarce	1 Urban Pond
Dytiscidae	*Agabus conspersus*	Nationally Scarce Nationally Notable	1 Meadow Pond 1 Agricultural Pond
Dytiscidae	*Agabus uliginosus*	IUCN Lower Risk - Near Threatened Nationally Notable	1 Urban Pond
Dytiscidae	*Hygrotus nigrolineatus*	Nationally Scarce Nationally Notable	4 Meadow Ponds
Dytiscidae	*Ilybius subaeneus*	Nationally Scarce	1 Meadow Pond
Dytiscidae	*Rhantus frontalis*	Nationally Scarce Nationally Notable	6 Meadow Ponds 2 Agricultural Ponds
Hydrophilidae	*Berosus luridus*	IUCN Lower Risk - Near Threatened Nationally Notable	1 Meadow Pond
Hydrophilidae	*Helochares punctatus*	Nationally Scarce	1 Urban Pond
Hydrophilidae	*Helophorus dorsalis*	Nationally Scarce Nationally Notable	2 Agricultural Ponds 1 Meadow Pond
Hydrophilidae	*Helophorus strigifrons*	Nationally Scarce Nationally Notable	2 Urban Ponds 1 Forest Pond
Hydrophilidae	*Paracymus scutellaris*	Nationally Scarce	1 Meadow Pond

4.2.6.1 UK Post-2010 Biodiversity Framework (England) Pond Priority Habitat (PPH)

An assessment of pond sites using UK Post-2010 Biodiversity Framework Pond Priority habitat (PPH) criteria for England (previously the Biodiversity Action Plan Pond Priority Habitat (Natural England, 2014a)) was undertaken. A full calculation of ponds that could qualify as PPH was not possible to carry out as the Predictive System for Multimetrics (PSYM) score could not be obtained (see Biggs *et al.,* 2000). When considering all other criteria required to become a PPH site (see Methodology Chapter 3.5.4.2), a total of 16 ponds were identified as meeting these requirements (11 meadow ponds, 2 agricultural ponds, 3 urban ponds). A single agricultural pond qualified as a PPH as it supported three nationally scarce invertebrate species (*H. dorsalis, R. frontalis* and *A. conspersus*). A total of 15 ponds (11 meadow, 1 agricultural and 3 urban ponds) qualified based on their exceptional taxon richness, supporting >50 taxa. Regionally, 17% of the pond sites met the requirements to become a PPH.

4.2.6.2 Community Conservation Index (CCI)

The Community Conservation Index incorporates both the individual rarity of taxa (based on expert knowledge and legislative designations) and the overall community richness (Chad and Extence, 2004). The conservation score assigned to each invertebrate taxon was based on the macroinvertebrate conservation scores provided by Chad and Extence (2004) who derived conservation values for most UK macroinvertebrate taxa (Armitage *et al.,* 2012, Appendix 4). Across the region, 12 ponds supported invertebrate communities which had a high (total score >15-20: 6 meadow ponds, see Chapter 3.5.4.1 and Table 4.11) or very high conservation value (total score >20: 5 meadow ponds and 1 agricultural pond) (Table 4.11). No forest or urban ponds were calculated to have a high or very high conservation value when all sampling dates were considered. CCI scores were identified to be significantly different between the 4 pond types (ANOVA $F_{3, 94}$=12.05; p<0.001) when considering the entire data set. Meadow ponds had higher CCI scores than forest and urban pond types (ANOVA p<0.05). Meadow ponds were dominated by invertebrate communities with a fairly high (total score >10-15), high or very high conservation value whereas most urban and forest ponds had a low (total score 0-5) or moderate conservation value (total score >5-

10) (Table 4.11). The majority of agricultural ponds supported communities with a moderate or fairly high conservation value.

Published data of macroinvertebrate community assemblages from ponds is often based on a single season (summer) survey (Armitage *et al.,* 2012). In order to be comparable to this literature, CCI values were calculated for the spring, summer and autumn seasons. A total of 8 ponds in spring, 2 ponds in summer and 6 ponds in autumn had a high or very high conservation value (Table 4.11). Meadow ponds recorded significantly higher CCI scores than urban ponds in the spring season and was significantly higher than urban and forest ponds in the summer and autumn seasons (ANOVA $p<0.05$). No significant difference in the CCI scores was recorded between the spring, summer and autumn seasons (ANOVA $p>0.05$).

*Table 4.11 - Community Conservation Index scores for individual seasons and combined seasons (total) of pond sites within meadow, agricultural, forest and urban landscapes (0-5 low conservation value; >5-10 moderate conservation value; >10-15 fairly high conservation value; >15-20 high conservation value and >20 very high conservation value). Very high CCI scores are presented in bold italics and high CCI scores are presented in bold. * = pond dry in that season.*

	Spring	Summer	Autumn	Total
	Meadow			
M1	4.5	7.4	8.0	8.5
M2	13.4	9.0	9.4	14.4
M3	1.0	**19.6**	*	14.9
M4	3.5	7.0	10.4	10.6
M5	5.6	7.7	*	9.3
M6	9.5	7.1	8.3	8.7
M7	4.8	8.1	12.1	13.3
M8	14.3	8.6	12.5	13.8
M9	1.1	***25.8***	*	***21.9***
M10	***28.2***	14.8	12.3	***23.8***
M11	12.7	3.6	7.0	11.7
M12	8.5	9.3	9.1	10.1
M13	10.0	5.0	10.0	9.6
M14	14.0	11.5	15.0	**15.2**
M15	**18.0**	4.2	14.6	***23.4***
M16	14.4	8.8	**15.0**	**15.5**
M17	***20.6***	8.5	14.6	***24.3***
M18	12.1	10.9	14.4	**15.4**
M19	4.0	4.5	8.5	8.9
M20	**18.9**	6.7	9.1	**15.0**
M21	14.8	6.9	8.5	12.4
M22	13.4	12.9	8.2	13.2
M23	14.0	12.2	8.6	13.3
M24	12.8	7.8	**15.7**	**15.8**
M25	14.9	7.1	11.6	***24.5***
M26	*	14.0	*	14.0
M27	*	4.0	*	4.0
M28	*	8.3	13.6	12.9
M29	*	8.6	**17.5**	**16.2**
M30	8.18	3.4	6.3	6.9
M31	4.29	1.1	2.4	3.8
M32	*	8.9	*	8.9
M33	*	8.9	*	8.3
M34	*	3.7	*	3.7
M35	**15.7**	12.0	8.5	13.9
Mean	11.3	8.8	10.8	13.1
	Agricultural			
AP1	4.1	8.6	4.4	8.1
AP2	1.2	1.0	10.9	10.7
AP3	1.2	4.0	7.8	7.8
AP4	**17.9**	11.4	6.1	14.8
AP5	1.1	3.6	6.9	6.8
AP6	1.0	1.0	1.0	1.0
AP7	***22.0***	14.0	14.7	***23.2***
AP8	*	*	1.0	1.0
AP9	*	4.3	*	4.0
AP10	4.7	1.1	7.9	8.2
AP11	4.4	12.3	**14.0**	13.8
AP12	5.0	3.8	12.1	12.1
Mean	6.3	5.9	7.9	9.3

	Spring	Summer	Autumn	Total
	Forest			
FP1	4.5	4.0	7.4	8.2
FP2	4.0	1.0	1.1	3.8
FP3	10.9	3.5	1.0	8.8
FP4	13.4	6.5	1.0	11.1
FP5	9.6	10.4	8.2	8.9
FP6	4.3	1.0	4.1	4.1
FP7	*	1.0	*	1.0
Mean	7.8	3.9	3.8	6.5
	Urban			
UP1	6.7	1.1	4.2	7.7
UP2	1.2	1.0	1.0	1.1
UP3	1.00	1.0	1.0	1.0
UP4	1.00	1.0	*	1.0
UP5	10.3	8.3	9.2	9.4
UP6	11.0	3.8	**15.4**	13.0
UP7	4.5	1.1	*	4.5
UP8	10.4	7.4	6.7	11.9
UP9	4.0	11.1	*	10.7
UP10	1.1	1.0	7.0	6.3
UP11	8.6	8.6	8.1	8.3
UP12	1.0	*	*	1.0
UP13	7.6	6.7	4.8	7.6
UP14	14.4	8.6	3.9	13.3
UP15	9.0	9.0	9.3	10.5
UP16	3.7	3.8	4.0	4.4
UP17	12.2	8.0	12.6	13.1
UP18	8.9	3.5	6.6	8.6
UP19	**18.1**	3.9	10.	14.7
UP20	1.0	1.0	1.0	1.0
UP21	8.9	7.9	8.5	8.0
UP22	1.1	1.11	1.1	1.1
UP23	1.0	1.0	4.0	3.8
UP24	8.8	9.0	8.6	8.3
UP25	1.0	1.0	1.0	1.0
UP26	8.0	4.5	1.0	7.9
UP27	1.0	1.0	1.0	1.0
UP28	9.6	13.0	8.5	10.0
UP29	1.2	1.0	1.1	1.1
UP30	9.4	1.0	9.0	9.6
UP31	4.7	4.3	3.9	4.4
UP32	1.0	1.0	1.0	1.0
UP33	1.0	1.3	1.0	1.2
UP34	1.0	1.0	1.0	1.0
UP35	1.0	1.0	1.0	1.0
UP36	3.9	8.2	1.0	7.7
UP37	1.0	1.0	1.0	1.0
UP38	5.0	4.8	9.7	12.3
UP39	10.0	8.9	**16.5**	14.8
UP40	1.2	5.6	8.0	8.0
UP41	*	1.0	*	1.0
Mean	5.38	4.21	5.4	6.2

* = Pond dry in that season

4.3 Discussion

4.3.1 Aquatic macroinvertebrate biodiversity

A significant proportion of the national macroinvertebrate species pool was represented within the 95 ponds studied in Leicestershire (228 taxa) but at an individual (alpha) scale, taxon richness across the region was highly variable (2-73 taxa). Even in highly disturbed urban landscapes, total macroinvertebrate diversity (170) was similar to semi-natural meadow ponds (175) demonstrating the importance of urban pond biodiversity to regional and landscape biodiversity. Although there has been no other research which has examined the regional macroinvertebrate diversity between ponds in different land cover types typical of lowland regions, there have been a number of studies which have highlighted the contribution of pond habitats at a regional/landscape scale (Williams *et al.,* 2003; Davies *et al.,* 2008b; Fuentes-Rodríguez *et al.,* 2013). Similarly, Hassall *et al.* (2011) recorded high regional macroinvertebrate diversity (277 taxa) from 425 ponds across Cheshire, UK. Ponds have been identified to support a greater number of macroinvertebrate taxa than rivers and streams at a landscape-scale, although at an individual scale invertebrate richness was highly variable (Williams *et al.,* 2003). In Williams et al. (2003) study, the richest pond sites were comparable to river samples but the poorest pond sites were amongst the most ecologically deprived freshwater habitats, corresponding to the large regional diversity and highly variable alpha diversity among ponds in this study (Williams *et al.,* 2003; Biggs *et al.,* 2005; Davies *et al.,* 2008b).

The results from this chapter indicate semi-natural meadow ponds support the greatest macroinvertebrate diversity (total: 175 mean: 39) and provides evidence to partially accept the first hypothesis;

> *H_1: Aquatic macroinvertebrate diversity will be greatest in meadow ponds and lowest in urban ponds.*

The lowest macroinvertebrate diversity was recorded from forest ponds (total: 62 mean: 18) and not urban ponds (total: 170 mean: 21). However, most of the forest ponds were ephemeral, displaying a terrestrial and aquatic phase during the sampling period, which has been demonstrated to reduce the number of taxa within these ponds (Collinson *et al.,* 1995; Nicolet, 2001; Della Bella *et al.,* 2005). The taxon richness recorded within forest ponds in this study was significantly lower than the diversity recorded from 12 forest ponds in Dorset, UK (total: 174 mean: 30.8) and 42 forest ponds in Scotland (total: 160 mean: 23±11) (Jeffries, 1991; Armitage *et al.,* 2012). The forest ponds in this study were located in heavily shaded, closed canopy woodlands. Elsewhere, shading of pond habitat has been associated with reduced macroinvertebrate richness (Lundkivst *et al.,* 2002; Williams *et al.,* 2008; Sayer *et al.,* 2012) and forest cover may act as a physical barrier for colonization and dispersal. Similar to the findings in this research, high abundances of Culicidae (mosquito larvae) were recorded in forest ponds in Canberra, Australia, which were also heavily shaded (Mokany *et al.,* 2008). However, ponds shaded by trees may still support uncommon and rare taxa (Biggs *et al.,* 1994).

High alpha and gamma faunal diversity was demonstrated within agricultural ponds in this study (total: 126 mean: 34) which has been demonstrated in previous research (Ruggiero *et al.,* 2008; Gioria *et al.,* 2010; Hassall *et al.,* 2011). In many agricultural landscapes, ponds are not managed (Boothby *et al.,* 1995a) allowing pond succession and the development of a surrounding shrub layer and tree canopy (Sayer *et al.,* 2012). In addition, sedimentation (as a result of succession), can lead to the pond becoming terrestrialized (Sayer *et al.,* 2012). Through active management (re-establishing aquatic macrophyte beds, removal of sediment and tree cover), a range of pond successional stages can be maintained and faunal biodiversity within agricultural ponds can be greatly enhanced even within intensely farmed landscapes (Sayer *et al.,* 2012). The high regional macroinvertebrate diversity recorded in urban ponds demonstrates their value as a biodiversity resource (Goertzen and Suhling, 2013; Hassall, 2014) and potential to reduce biodiversity loss in heavily modified anthropogenic landscapes. See Chapter 5 for more detailed analysis and discussion of the biodiversity and conservation value of urban ponds.

Macroinvertebrate diversity was typically higher during the autumn season compared to the spring and summer seasons in all four pond types and represented 76% of the total invertebrate biodiversity recorded from these three seasons. Similarly, faunal richness was highest during the autumn months in 12 ephemeral forest ponds in Dorset, UK (Armitage *et al.,* 2012). Many pond surveys are restricted to single season surveys (commonly summer) (Armitage *et al.,* 2012), which may under represent total biodiversity and conservation value given the high taxon turnover in some ponds in this study (namely meadow and agricultural ponds). If invertebrate surveys can only be undertaken in one season, based on the results from this study, autumn (Sept-Oct) sampling would provide the best representation of total biodiversity. However, whilst the autumn survey provided a good representation of richness for most invertebrate groups (e.g., Odonata, Coleoptera and Hemiptera), this study demonstrated that trichopteran richness and abundance was lowest during the autumn sample period and could be under-represented in the final species list if a macroinvertebrate survey was undertaken only in autumn.

Emergent and submerged macrophytes have been well documented to support substantially higher macroinvertebrate diversity than other mesohabitats in ponds (Wilkinson, 1995; Water and San Giovanni, 2002; Gledhill *et al.,* 2008; Bazzanti *et al.,* 2010; Fuentes-Rodríguez *et al.,* 2013; Goertzen and Suhling, 2013) which supports the findings in this study and provides further evidence to accept the second hypothesis;

> *$H_{2:}$ Macroinvertebrate diversity will be highest in emergent and submerged macrophyte mesohabitats and lowest in open water mesohabitats.*

Aquatic macrophytes can provide many benefits to pond communities, such as a source of food, refuge from predation, diversification of habitats and oxygenation of the water (Biggs *et al.,* 1994a; Bazzanti *et al.,* 2010). Some aquatic macroinvertebrate taxa often show distinct preferences for particular aquatic macrophyte types including Odonata, Coleoptera (Bazzanti *et al.,* 2010), Zygoptera and Baetidae (Van de Meutter *et al.,* 2008) which have displayed preferences for submerged macrophytes whilst Chironomidae and Notonectidae have been identified to prefer emergent macrophytes (Bazzanti *et al.,* 2010) within pond environments. Similarly, in this study, Zygoptera were primarily associated with submerged macrophytes although, in contrast to Bazzanti et al. (2010) Chironomidae were also associated with submerged macrophytes. In addition, the high macroinvertebrate diversity recorded among submerged and emergent macrophytes was driven by high Gastropoda diversities recorded within both emergent and submerged macropyhtes; high Dytiscidae richness commonly recorded within submerged macrophytes and also Limnephilidae taxa which were commonly recorded in emergent macrophyte mesohabitats. Allowing a wide diversity of emergent and submerged macrophytes (and managing ponds to maintain structurally complex macrophyte mosaics (Biggs *et al.,* 1994)) to colonise ponds should ensure a wide range of macroinvertebrate habitat preferences are met and may greatly increase pond biodiversity at an alpha and gamma scale. Although, it should be noted that Corixidae were most commonly found in open water and submerged macrophyte mesohabitats indicating that some open water habitat should be maintained to ensure there is suitable habitat for open water macroinvertebrate taxa.

4.3.2 Community heterogeneity

Considerable heterogeneity in aquatic macroinvertebrate assemblages was identified between the ponds in this study. These results provide evidence to accept the third hypothesis;

> *H_3: There will be significant community heterogeneity between pond types.*

The marked macroinvertebrate dissimilarity between pond types can be attributed to the wide range of physicochemical conditions recorded among the ponds in this study. A wide variability of pond physicochemical conditions was also recorded by Angélibert *et al.* (2004), Søndergaard, (2005) and Oertli *et al.* (2008). The small catchment areas of ponds can result in highly distinct physicochemical conditions, even if ponds are in close proximity to each another. This can result in a wide range of habitats/conditions for macroinvertebrate taxa to exploit (Williams *et al.,* 2003; Davies *et al.,* 2008b). In addition, high macroinvertebrate community heterogeneity can also be attributed to stochastic events (related to dispersal limitation or priority effects), which can have a large influence on small water bodies (Scheffer *et al.*, 2006). The heterogeneous macroinvertebrate community assemblages recorded between meadow and urban ponds is likely to reflect meadow pond location in the natural landscape (nature reserves), their management practices (designed to benefit biodiversity), and the minimal anthropogenic disturbance. In addition, agricultural pond invertebrate communities were identified to be significantly different to urban pond communities which may reflect the lack of pond management of agricultural ponds and relatively open agricultural landscapes which may increase pond connectivity. Whilst the structurally complex and fragmented urban landscape can impair connectivity, the high levels of anthropogenic disturbance (e.g., urban runoff/pollution) and the management practices (often not for the benefit of biodiversity) that urban ponds are subject to can result in very different macroinvertebrate communities to meadow and agricultural ponds.

However, macroinvertebrate assemblages were identified to be highly heterogeneous among urban ponds which is likely to reflect the wide range of management practices undertaken and successional stages represented in the urban ponds studied. Similarly, Briers (2014) recorded significant dissimilarity in invertebrate assemblages spatially and temporally between urban drainage ponds in Dunfermline, Scotland. The temporal variation in invertebrate composition was attributed to the wide variation in physicochemical conditions and pollutant loads over the 5 year study period (Briers, 2014). The overlap in macroinvertebrate assemblages among forest ponds and agricultural ponds in this study most likely reflects the late successional stage of many of the agricultural ponds examined. Allowing the succession of all ponds in the landscape may reduce beta and gamma diversity as taxa typical of late succession ponds (that are often not present in early-mid succession ponds) will become ubiquitous at the expense of other taxa (particularly those associated with early - mid successional stages). Therefore if high regional diversity is a management goal for ponds, a range of pond successional stages (providing high environmental heterogeneity) should be maintained across the pondscape (Hassall *et al.,* 2012; Sayer *et al.,* 2012).

Seasonal differences in meadow and agricultural pond macroinvertebrate communities were recorded within this study. The rural location and relatively low anthropogenic influence on meadow and agricultural ponds may have enabled macroinvertebrate taxa to disperse and colonize other ponds and the expected natural seasonal turnover to occur. By contrast, in urban and forest ponds, there was little distinction between seasonal communities. This almost certainly reflects the structural complexity of both landscapes, impairing connectivity. In urban ponds, the high level of fragmentation and management can limit dispersal (active and passive) success to other pond habitats (Fahrig, 2003) and slow the turnover of invertebrate taxa. Over longer timescales (~10 years) macroinvertebrate communities have been shown to be heterogeneous and have significant turnover of macroinvertebrate taxa (Jeffries, 2011; Hassall *et al.,* 2012). The temporal heterogeneity displayed by ponds has been suggested to be the result of their biological history (contemporary pond communities partially reflect the communities that preceded them), previous management practices and key events (e.g., drought) (Jeffries, 2011).

4.3.3 Conservation value

Although research into ponds still lags someway behind lotic systems (Oertli *et al.,* 2009), the value of pond habitats to biodiversity conservation is beginning to be acknowledged (Nicolet *et al.,* 2007). At a policy level this has been demonstrated by the inclusion of ponds into the UK Biodiversity Action Plan (BRIG, 2008) in 2007, which has been replaced by the UK Post-2010 Biodiversity Framework (JNCC and DEFRA, 2012; Natural England, 2014b). Often, management strategies and legislation assess and develop the ecological status of freshwater habitats using diversity and conservation metrics (Gamito*,* 2010; Armitage *et al.,* 2012). There is a wide range of conservation metrics available (Rosset *et al.,* 2013) but for the purposes of this research the Community Conservation Index (CCI) was applied, which incorporates both species richness and rarity and places the sites in a national context (Armitage *et al.,* 2012). It was hypothesised that;

> *H_4: Meadow, agricultural and forest ponds will have a higher conservation value than urban ponds.*

The results from this study provided evidence to partially accept this hypothesis. A total of 31% of meadow ponds recorded high or very high CCI values but only one agricultural pond and no forest or urban ponds were of a high or very high CCI value. The relatively high conservation value of floodplain meadow ponds highlights the importance of this habitat for macroinvertebrate taxa. The low CCI value recorded for forest ponds in this study is in marked contrast to the study of Armitage *et al.* (2012) which indicated 5 of the 8 forest pond sites had high or very high CCI scores. This difference can be attributed to the location of forest ponds in the Armitage *et al.* (2012) study in open pathways within the woodland which reduced the shading of these ponds and provided colonization pathways, whilst the forest ponds in this study were located in dense, closed canopy woodlands, which greatly increased shading and can act as a physical barrier to colonization. In addition, the median CCI score for urban ponds in this study (7.6) was lower than that recorded for urban ponds in Halton, north-west England (Gledhill and James, 2012). However, it should be noted that the Gledhill and

James (2012) study did not include garden ponds which, in this research, recorded a significantly lower faunal richness than other urban ponds (see Chapter 5).

At a regional scale, ponds in this study supported significant macroinvertebrate richness including 13 species of conservation interest (12 were recorded from rural areas and 5 from urban areas). Similar findings were recorded from 20 rural ponds near Coleshill, UK, which recorded 14 nationally scarce invertebrate taxa (Williams *et al.,* 2003). At a landscape-scale, previous research recorded a significantly greater conservation value and number of nationally scarce invertebrate taxa ponds compared to river, stream and lake environments in the UK and Europe (Williams *et al.,* 2003; Biggs *et al.,* 2005; Davies *et al.,* 2008b). A total of 17% of ponds in this study potentially qualified as Pond Priority habitats (PPH) (11 meadow (12%), 2 agricultural (2%) and 3 urban (3%)), which is comparable to Williams *et al.,* (2010) suggestion that 20% of all UK lowland ponds could meet one of the PPH criteria. Despite supporting few macroinvertebrate taxa of conservation interest, 3 urban ponds qualified as PPH sites based on their high macroinvertebrate richness (>50 taxa), demonstrating the importance that ponds may have in preserving and enhancing aquatic biodiversity within anthropogenically disturbed landscapes.

Pond environments clearly support significant macroinvertebrate biodiversity (Williams *et al.,* 2003; Nicolet *et al.,* 2004; Céréghino *et al.,* 2008a; Gioria *et al.,* 2010). At an alpha scale, a large number of semi-natural meadow ponds, located in areas designated for nature conservation (all meadow ponds were located in nature reserves/SSSI sites) can support rare taxa and substantial invertebrate richness. Floodplain meadows in nature reserves inadvertently support the conservation of ponds and provide protection from anthropogenic disturbance, promoting the development of rich and diverse invertebrate communities (the biodiversity and conservation value of semi-natural floodplain meadow ponds will be explored more fully in Chapter 6). However, in anthropogenically disturbed landscapes (e.g., urban and agricultural ponds) their ecological value is much more variable. A large number of ponds with a low conservation value exist in close proximity to ponds of high conservation value. Nature and biodiversity conservation cannot depend solely on protected areas (Chester and Robson 2013), and conservation should be opportunistically increased wherever possible. In particular, biodiversity conservation needs to be further integrated into urban landscapes to protect freshwater of considerable conservation value from further anthropogenic disturbance and provide opportunities for the improvement of biodiversity within degraded urban ponds (see Chapter 5).

Although research into semi-natural pond landscapes where anthropogenic disturbance is low (such as the meadow ponds in this study) is limited to-date, results from the present study suggest that such work is essential and can provide information to the natural distribution of aquatic biota and the environmental processes that influence invertebrate distribution (Williams *et al.,* 2003). Semi-natural and natural ponds can provide reference/baseline conditions for the development of conservation and management strategies for ponds in anthropogenically disturbed landscapes. In order to increase the richness of ecologically poor ponds in disturbed landscapes to desired levels, a significant management effort is often required (e.g., increase aquatic macrophyte cover and tree (de-shading) and sediment removal (Sayer *et al.,* 2012). Although, even ponds currently of low biological quality can still provide an opportunity to allow the general public to engage with freshwater biodiversity issues and raise awareness of the considerable biological importance of ponds (Hassall, 2014).

4.4 Summary

This chapter has provided a comprehensive analysis of aquatic macroinvertebrate taxa in various landscapes typical of a European lowland landscape. At a regional scale, ponds are rich and valuable sites for aquatic macroinvertebrate taxa often exceeding diversity in lakes and rivers. Semi-natural meadow ponds supported the greatest biodiversity whilst forest and urban ponds supported the lowest diversity. High macroinvertebrate community dissimilarity was displayed between pond types which was attributed to the heterogeneity in physicochemical conditions and the variability in pond management practices and structural complexity between rural and urban areas. Across the region, 17% of ponds potentially qualified as a Priority Pond Habitat. However, semi-natural floodplain meadow ponds, located in areas protected for conservation, had considerably greater conservation value than ponds situated in anthropogenically disturbed landscapes (e.g., urban and agricultural) where taxon richness and conservation value was highly variable. Ponds must be seen as part of an integrated conservation package in lowland areas alongside lakes, rivers, streams and wetlands (Sayer, 2014). If the goal of conservation is to increase regional biodiversity, large-scale pond studies are critical to help develop an understanding of the regional distribution of freshwater biota and direct conservation and management strategies to where there is the greatest need. In addition, large-scale regional pond research should ensure that the funds for ecological conservation is targeted to where it is most urgently required and guarantee the long term protection of pond habitats and their biota.

Chapter 5. The macroinvertebrate biodiversity and conservation value of different types of urban pond

5.1 Introduction

Global urban landscape covers approximately 3% of the earth surface (Grimm *et al*., 2008) but is predicted to increase by up to 185% by 2030 (Seto *et al*., 2012). In addition global urban population is predicted to increase by up to 66% by 2050 (United Nations, 2014). Despite the relatively small area that cities and towns cover overall, urbanisation provides a significant threat to local and global biodiversity (Grimm *et al*., 2008; Hamer and McDonell, 2008; Shochat *et al*., 2010). Urbanisation is a primary driver of large-scale ecosystem change, resulting in the fragmentation of the natural environment (Goddard *et al*., 2010), an increase in biotic homogenization and a rise in the successful establishment of non-native taxa at the expense (local extinction) of native taxa (McKinney, 2006). In many instances this significantly reduces the biodiversity within the urban and proximal landscape (McKinney, 2002). Disturbances such as pollution and habitat modification generated by the expansion of urban landscapes have placed freshwater ecosystems under substantial pressure (Dudgeon *et al*., 2006; Gopal, 2013).

Alongside the growth in urban land cover, the density of buildings within urban spaces has increased significantly. Compact, high density commercial and residential spaces are being built as urban population growth continues to increase; however this urban 'densification' is at the expense of much of the urban green space that remains in towns and cities (Dallimer *et al*., 2011). Traditionally, ecological conservation has relied heavily on the designation of areas protected from development or modification by legislation and policy (Mcdonald *et al*., 2008). However, biodiversity conservation should not rely solely on the designation of protected areas as they are under threat from urban growth (Guneralp and Seto, 2013) and policy makers/environmental regulators may have to develop new strategies that are compatible with pervasive urban population growth (Mcdonald *et al*., 2008).

Within the wider rural landscape, ponds have been shown to support greater macroinvertebrate diversity (and numbers of rare/uncommon invertebrate species) at a regional scale than other freshwater bodies (Williams *et al*., 2003; Davies *et al*., 2008b). Their physicochemical heterogeneity provides a wide range of habitat niches for aquatic macroinvertebrate taxa (Williams *et al*., 2003) which in turn increases the variability (beta-diversity) of macroinvertebrate communities supported by ponds.

Ponds are abundant in the urban landscape (Goertzen and Suhling, 2013) often created as part of urban flood reduction strategies (Williams *et al*., 2013), to improve water quality (such as sustainable urban drainage systems (Heal *et al*., 2006; Briers, 2014)), for aesthetic and ornamental purposes (Hassall, 2014) and were historically built for industrial purposes (e.g., mill ponds); although most are no longer used for their original purpose but persist in the landscape (Wood *et al*., 2001). Their high physicochemical variability and abundance may make these small lentic waterbodies important sites for aquatic macroinvertebrates and augment aquatic biodiversity within urban landscapes.

5.1.1 Research/knowledge gaps

Historically, research into urban biodiversity has focused on birds (Blair, 1996; Chace and Walsh, 2006; Santoul *et al*., 2009; Ferenc *et al*., 2014), mammals (Baker and Harris, 2007; Parker *et al*., 2008)) and lotic ecosystems (Paul and Mayer 2001; Walsh *et al*., 2005; Price *et al*., 2011; Francis, 2014; García-Armisen *et al.,* 2014). Despite the threats to biodiversity from increasing urban land cover and density, there has been very limited research to date addressing aquatic biodiversity within urban ponds, but see; Le Viol *et al*. (2009) and Hassall and Anderson, (2015) for macroinvertebrate biodiversity within stormwater retention ponds; Vermonden *et al*. (2009) and Briers, (2014) for invertebrate biodiversity within sustainable urban drainage systems; Willigalla and Fartmann, (2012) and Goertzen and Suhling, (2013) for Odonata diversity within urban pond habitats and Gledhill *et al*. (2008) for invertebrate diversity within old and new urban developments. In particular, there has been a paucity of research into garden pond biodiversity (Monkay and Shine, 2003, Gaston *et al*., 2005a) and the potential of urban ponds to serve as refugia (Chester and Robson, 2013).

5.1.2 Chapter aims and hypotheses

In light of this research gap highlighted above this chapter aims to examine the biodiversity and conservation value of aquatic macroinvertebrate taxa within a range of urban pond types (see Chapter 1.4: Objective 3) by testing the following hypotheses:

H_1: Aquatic macroinvertebrate biodiversity and conservation value will be greatest in large park ponds and lowest in small garden ponds;

H_2: Macroinvertebrate biodiversity will vary significantly among urban ponds (β diversity) reflecting the highly variable environmental conditions in ponds.

Macroinvertebrate sampling, laboratory techniques and statistical analysis undertaken in this chapter are described in detail in Chapter 3.

5.2 Results

A comprehensive examination of 41 urban ponds in the town of Loughborough (Leicestershire, UK) and the surrounding anthropogenic environment was undertaken. The ponds were categorised into three urban pond types: i) 13 garden ponds - small water bodies located within a private or rented residential plot of land; ii) 16 'other' urban ponds - varying in size, anthropogenic purpose and located in high density, compact developments often on private land with controlled access (these comprised 9 urban drainage ponds - 5 of which were ephemeral in nature and dried at least once during the survey period, 4 located within school grounds and used as wildlife/education tools and 3 ponds surrounded by high density commercial developments) and; iii) 12 park ponds - situated within urban green spaces (e.g., parks), with variable water surface areas, heavily managed, primarily utilised for their amenity value and public access is actively encouraged (Hassall, 2014). Across all three types, urban ponds frequently have an anthropogenic base (concrete, synthetic lining), steep bank sides and may have an ephemeral or perennial hydrology depending on whether the pond is still actively managed.

5.2.1 Alpha and gamma diversity

A total of 170 macroinvertebrate taxa were identified within 18 orders and 60 families from the 41 urban ponds. Garden ponds supported a total of 44 taxa (range: 2-24), 'other' urban ponds recorded 91 taxa (range: 3-42) and park ponds supported 149 taxa (range: 4-61). A total of 77077 individuals were recorded from three sampling occasions corresponding to spring, summer and autumn 2012 from garden ponds (total: 11218, range: 45-2379), 'other' urban ponds (total: 32209, range: 39-6766) and park ponds (total: 33650, range: 303-6628). The number of macroinvertebrate families and taxa recorded within urban ponds is summarized in Table 5.1. The taxa most widely distributed within ponds across the urban landscape were Chironomidae (40 ponds), Oligochaeta (40 ponds), *Asellus aquaticus* (27 ponds), *Cloeon dipterum* (24 ponds) and Tipulidae (23 ponds). The greatest numbers of taxa were recorded from the orders; Coleoptera (43 taxa), Trichoptera (29 taxa), Hemiptera (28 taxa), Gastropoda (19 taxa) and Odonata (14 taxa). Urban ponds supported 127 macroinvertebrate taxa in spring 2012; 108 taxa in summer 2012 and; 116 taxa in autumn 2012. Two non-native macroinvertebrate species were recorded from the urban ponds; *Potamopyrgus antipodarum* (Hydrobiidae: Mollusca) was recorded from 4 'other' urban ponds and 5 park ponds; and *Crangonyx pseudogracilis* (Amphipoda: Crustacea) was identified from 5 garden ponds, 9 'other' urban ponds and 11 park ponds. Both species are widespread and common within freshwater systems in the United Kingdom (Macan, 1977 and Gledhill *et al*., 1993).

Table 5.1 - Total number of families and species of macroinvertebrate taxa recorded within urban ponds

Invertebrate Group	Families	Species
Turbellaria		
Tricladida*	1	1
Mollusca		
Gastropoda	9	19
Bivalvia*	1	1
Annelida		
Oligochaeta*	1	1
Hirudinea	3	7
Crustacea		
Amphipoda	2	2
Isopoda	1	2
Maxillopoda		
Argulidae*	1	1
Arachnida		
Hydrachnidiae**	1	1
Entognatha		
Collembola**	1	1
Insecta		
Ephemeroptera	2	5
Megaloptera	1	1
Lepidoptera	1	1
Odonata	4	14
Trichoptera	7	29
Hemiptera	6	28
Coleoptera	7	43
Diptera*	13	13
Total	62	170

*Taxa identified to family level only
**Taxa identified to order level only

Preliminary analysis indicated that faunal community abundance did not have a normal distribution and was therefore log_{10} transformed prior to statistical analysis. The taxon richness (ANOVA $F_{2, 40}$=28.053; p<0.001) and log_{10} community abundance (ANOVA $F_{2, 40}$=3.482; p<0.041) differed significantly between the three urban pond types (Figure 5.1). *Post hoc* analysis (Tukey test) indicated that park ponds (mean: 41) supported a significantly greater number of taxa than 'other' urban ponds (mean: 17) and garden ponds (mean: 9) (Figure 5.1). High variability in taxon richness was revealed within urban ponds. The greatest taxon richness recorded within a park pond was 61 whilst a garden pond had the most impoverished invertebrate community, supporting only 2 taxa. Mean taxon richness across the urban region within the ponds studied was 22. Nine park ponds supported macroinvertebrate assemblages with >40 taxa whilst only one 'other' urban pond and no garden ponds supported assemblages with >40 taxa. Six 'other' urban ponds contained macroinvertebrate communities with >20 species whilst, only one garden pond supported >20 taxa. Highly impoverished invertebrate communities were recorded within all three pond types; 1 park pond, 4 'other' urban ponds and 8 garden ponds had macroinvertebrate assemblages with <10 taxa. The *post hoc* Tukey test indicated that invertebrate community abundance was significantly higher in park ponds than garden ponds although, across all three urban pond types considerable variability was recorded (Figure 5.1; Appendix 5).

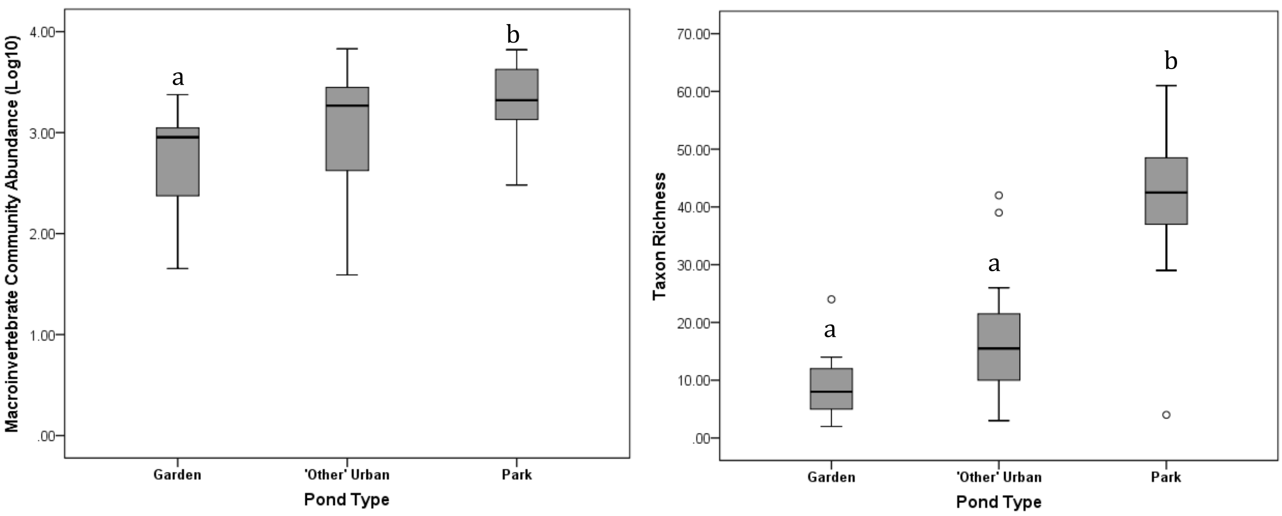

Figure 5.1 - Taxon richness and log_{10} community abundance within ponds in an urban landscape: garden, 'other' urban and park ponds. Central black bar = median, box = interquartile range, whiskers = total maximum and minimum range. Open circle = outlier defined on the basis of being >1.5 times the interquartile range from the rest of the values. Pond types/groups that are significantly different in post hoc pairwise Tukey test are indicated with different letters (a or b).

One-way Analysis of Variance (ANOVA) identified significant differences among garden, 'other' urban and park ponds for alpha diversity indices; Shannon Wiener diversity index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index, Fisher's alpha and Berger Parker Dominance index (Table 5.2).

Table 5.2 - One-way Analysis of Variance between alpha diversity indices and urban pond type. Significant values (p≤0.05) are presented in bold.

Alpha Diversity Indices	F. Ratio	P. Value
Shannon Wiener diversity index	11.944	**0.000**
Simpson diversity index	10.163	**0.000**
Margalef diversity index	25.994	**0.000**
McIntosh diversity index	10.289	**0.000**
Fisher's alpha	25.810	**0.000**
Berger Parker Dominance index	9.380	**0.000**

The *post hoc* Tukey test indicated that Fisher's alpha and Margalef diversity scores were significantly greater in park ponds than 'other' urban and garden ponds (ANOVA $p<0.05$). Although, *post hoc* analysis also indicated that Shannon Wiener, Simpsons and McIntosh diversity indices scores were significantly greater in 'other' urban and park ponds than garden ponds but that there was no difference in the alpha diversity scores between park ponds and 'other' urban ponds (ANOVA $p<0.05$). The Berger Parker Dominance index scores were significantly greater for garden ponds than park or 'other' urban ponds, indicating that garden pond macroinvertebrate communities were dominated by a small number of taxa.

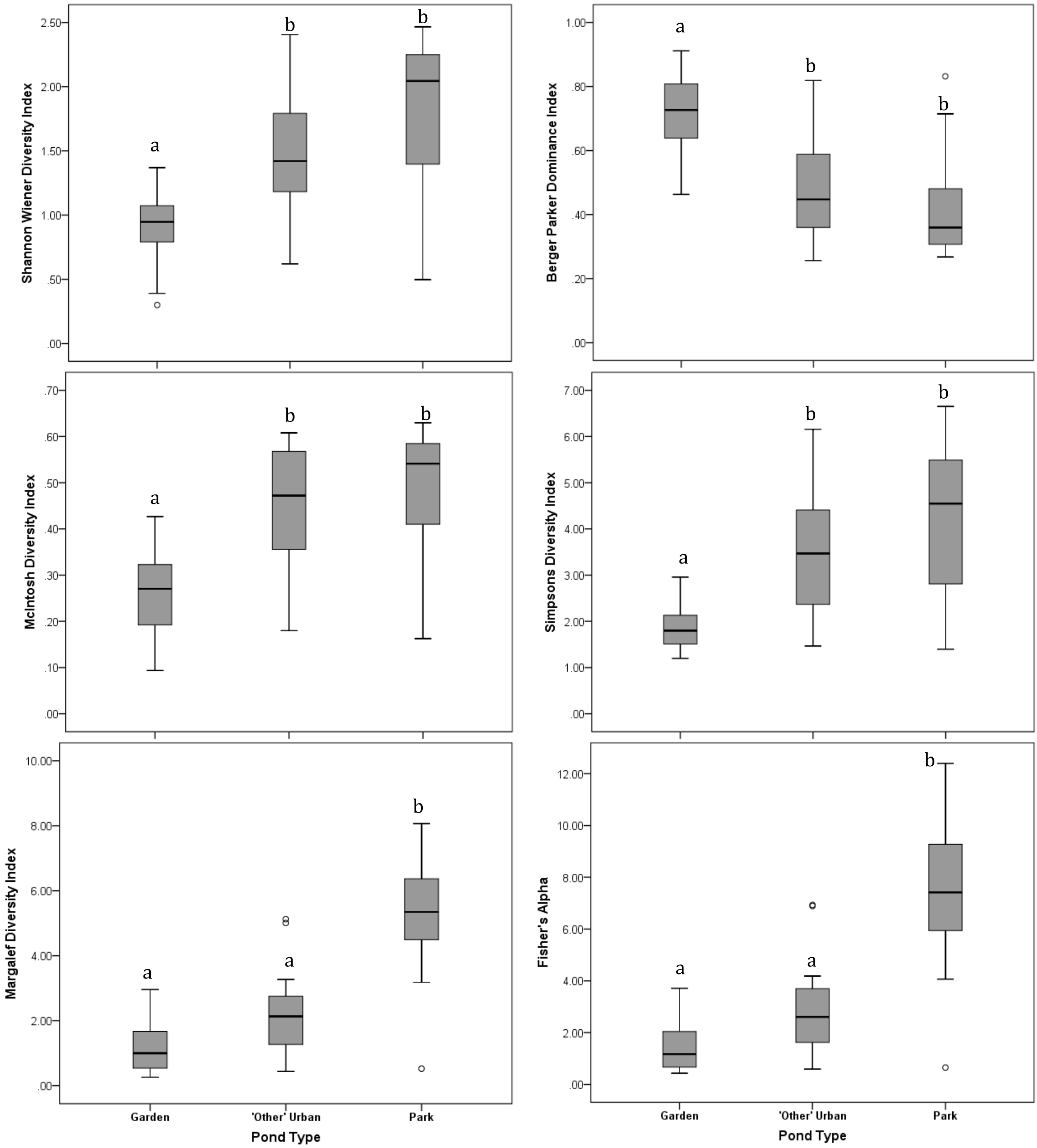

Figure 5.2 - Alpha diversity indices; Shannon Wiener diversity index, Simpson diversity index, McIntosh diversity index, Berger Parker Dominance index, Margalef diversity index and Fisher's alpha within garden, 'other' urban and park ponds. Central black bar = median, box = interquartile range, whiskers = total maximum and minimum range, open circle = outlier defined on the basis of being >1.5 times the interquartile range from the rest of the scores. Pond types/groups that are significantly different in post hoc pairwise Tukey test are indicated with different letters (a or b).

5.2.2 Mesohabitat macroinvertebrate diversity

A wide range of mesohabitats were present within urban ponds, for the purposes of this chapter they were placed into 4 categories; open water (OW), emergent macrophytes (EM), submerged macrophytes (SM) and floating macrophytes (FM). Open water was the most extensive and frequently occurring mesohabitat, occurring 77 times across all three sampling seasons. Emergent macrophytes were recorded 49 times, submerged macrophytes were present 37 times and floating macrophytes were recorded on 24 occasions. Emergent, submerged and floating macrophytes were common across all three urban pond types however, 50% of the floating macrophyte mesohabitats were recorded from garden ponds.

Nested ANOVA identified a significant difference in community abundance and taxon richness among the mesohabitats (Table 5.3). *Post hoc* analysis (Sidak test) indicated that $\log_{10}$ community abundance was significantly greater in submerged macrophytes than open water mesohabitats ($p<0.05$) (Figure 5.3). Taxon richness and Margalef diversity index was recorded to be significantly higher in emergent and submerged macrophytes than open water ($p<0.05$) (Figure 5.3). Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity index, McIntosh Diversity index and Fisher's alpha did not differ significantly between open water, emergent macrophyte, submerged macrophyte and floating macrophyte mesohabitats in urban ponds (Table 5.3).

Table 5.3 - Nested ANOVA between log_{10} community abundance, taxon richness and alpha diversity indices and mesohabitat nested within pond type. Significant values (p≤0.05) are presented in bold.

		Pond Type (Mesohabitat)
Log_{10} community abundance	*F.*	2.770
	P.	**0.005**
Taxon richness	*F.*	3.184
	P.	**0.001**
Shannon Wiener diversity index	*F.*	1.009
	P.	0.435
Berger Parker Dominance index	*F.*	1.270
	P.	0.256
Simpsons diversity index	*F.*	0.584
	P.	0.809
Margalef diversity index	*F.*	1.926
	P.	0.051
McIntosh diversity index	*F.*	0.944
	P.	0.489
Fisher's alpha	*F.*	1.467
	P.	0.164

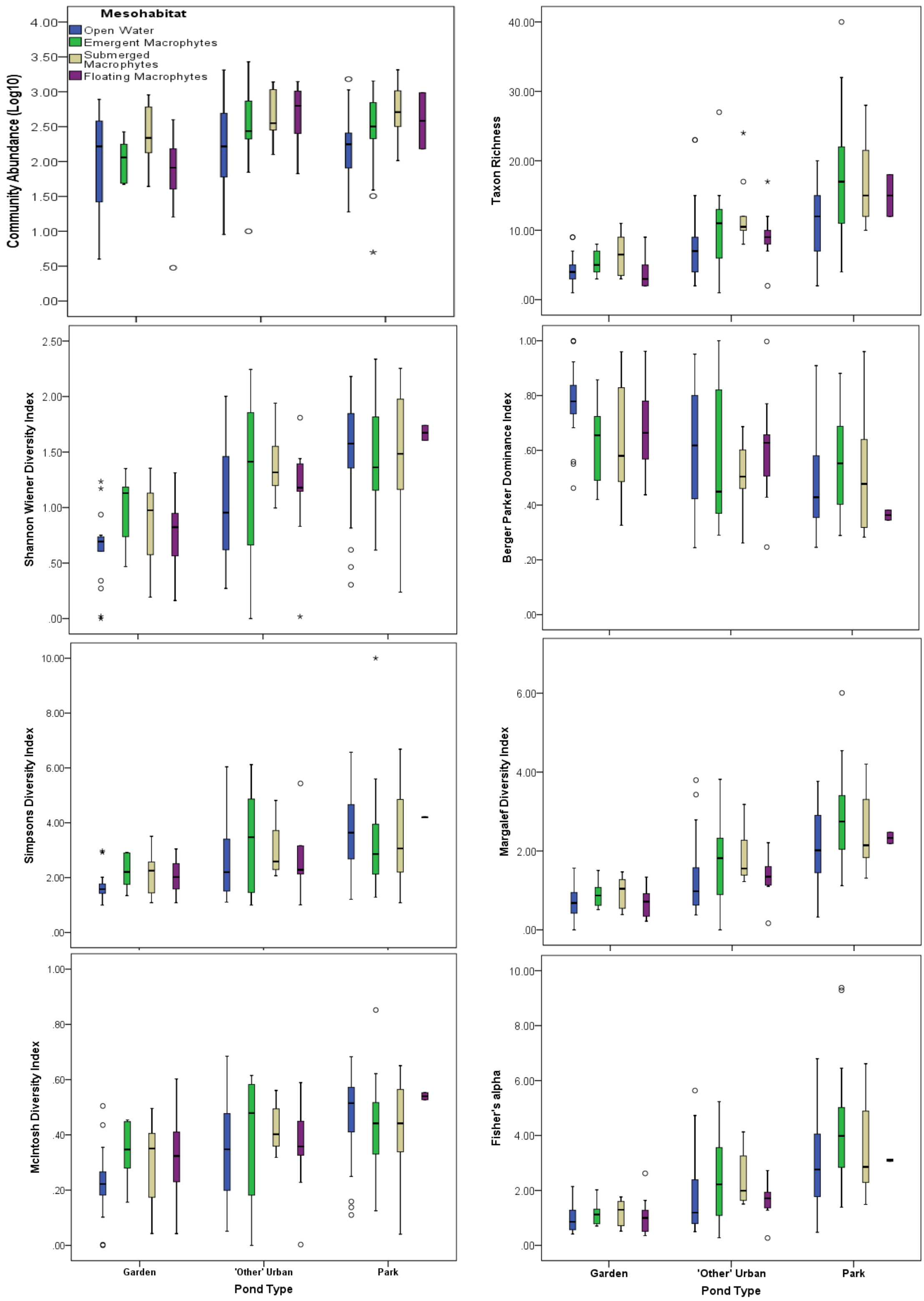

*Figure 5.3 - Comparisons of the $\log_{10}$ community abundance, taxon richness, Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha within the different mesohabitats: open water, emergent macrophytes, submerged macrophytes and floating macrophytes from the three urban pond types: garden, 'other' urban and park. Central black bar = median, box = interquartile range, whiskers = total maximum and minimum range. Open circle = outlier defined on the basis of being >1.5 times the interquartile range from the rest of the scores. * = outlier defined on the basis of being >3 times the interquartile range from the rest of the scores.*

5.2.3 Pond physicochemistry

Physicochemical variables were examined for a normal distribution and pond surface area, depth, pond water shaded, pond margin shaded, emergent macrophytes, submerged macrophytes and floating macrophytes were all $\log_{10}$ transformed. The *post hoc* Tukey test indicated park ponds to have a significantly greater mean surface area and depth (ANOVA $p<0.01$) than 'other' urban ponds and garden ponds when all sampling seasons were considered (Table 5.4). 'Other' urban ponds also had a greater mean surface area than garden ponds (ANOVA $p<0.01$). Garden ponds had a significantly higher proportion of their surface area covered by floating macrophytes than the other pond types (ANOVA $p<0.05$). Conductivity, dissolved oxygen, pH, water surface area/pond margin shaded, submerged macrophytes and emergent macrophytes were not significantly different between garden, 'other' urban and park pond types (all ANOVA $p>0.05$). Physicochemical conditions varied widely among the urban ponds (Table 5.4).

Fish communities were recorded from 19 ponds (8 garden, 9 park and 2 'other' urban ponds). No significant difference in macroinvertebrate biodiversity (community abundance, taxon richness and alpha diversity indices) was recorded for ponds with or without fish (ANOVA $p>0.05$). However, examination of the relationship between community indices and physicochemical vectors indicated that water surface area recorded the most significant correlations (ANOVA $p<0.01$) with community abundance, taxon richness, Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha (Table 5.5 and Figure 5.4). Taxon richness ($r=0.822$), Margalef diversity index ($r=0.822$), Fisher's alpha ($r=0.816$) and the Shannon Wiener diversity index ($r=0.704$) had a strong positive correlation with water surface area whilst McIntosh diversity index ($r=0.61$) and community abundance ($r=0.43$) had a moderate positive correlation. Berger Parker Dominance index ($r=-0.599$) had a moderate negative correlation with water surface area (Figure 5.4).

Table 5.4 - Summary table (mean and range) of measured environmental variables for urban pond types: garden, 'other' urban and park ponds. SWS: pond surface water shaded, PMS: pond margin shaded, EM: emergent macrophytes, SM: submerged macrophytes, FM: floating macrophytes, COND: conductivity, DO: dissolved oxygen.

	Garden			**'Other' Urban**			**Park**		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Area (m^2)	10.8	1	86.5	149.8	3	1407	2454.7	154.1	9309
Depth (cm)	38.5	14.5	70.4	33	4	82.7	144.8	36.7	200
SWS (%)	20.9	0	100	24	0	93.3	5.2	0	20
PMS (%)	20.5	0	100	26.3	0	98.3	41.6	0	99
EM (%)	10.7	0	15	39.9	0	100	13.9	0	43.3
SM (%)	17.9	0	31.7	25.8	0	90	18.5	0	58.3
FM (%)	32.3	6.7	96.7	12.8	0	96.7	2	0	15
pH	7	7.2	8.3	7.6	6.3	8.4	7.8	6.8	8.5
COND	420	355.7	784	535.5	89.7	132	543.9	63.7	55.9
DO (%)	69	13.1	118	64.6	17.4	105.2	82.5	1024	107.5

Table 5.5 - Summary of Pearson's Correlation Coefficients between environmental variables (SWS: surface water shaded, PMS: pond margin shaded, EM: emergent macrophytes, SM: submerged macrophytes, FM: floating macrophytes, COND: conductivity and DO: dissolved oxygen) and ecological indices

	Taxon richness	Shannon Wiener diversity index	Berger Parker Dominance index	Log_{10} Community abundance	Simpson diversity index	Margalef diversity index	McIntosh diversity index	Fisher's alpha
Log_{10} Area	0.822**	0.704**	-0.600**	0.432**	0.680**	0.822**	0.610**	0.816**
Log_{10} Depth	0.601**	0.313*	-0.121	0.445**	0.243	0.573**	0.130	0.564**
Log_{10} % SWS	0.000	0.106	-0.224	0.359*	0.090	-0.030	0.176	-0.048
Log_{10} PMS	0.297	0.348*	-0.387**	0.399**	0.345*	0.281	0.361*	0.281
Log_{10} EM	0.178	0.284	-0.292	0.015	0.238	0.195	0.317*	0.180
Log_{10} SM	0.304	0.198	-0.069	0.359*	0.092	0.283	0.093	0.256
Log_{10} FM	-0.347*	-0.318*	0.291	0.126	-0.348*	-0.377*	-0.307	-0.394*
Log_{10} COND	-0.006	0.156	-0.245	-0.095	0.217	0.040	0.236	0.066
Log_{10} DO	0.346*	0.267	-0.175	0.160	0.203	0.370*	0.183	0.359*
pH	0.006	0.015	0.072	-0.208	0.045	0.051	-0.059	0.073

*p<0.05
**p<0.01

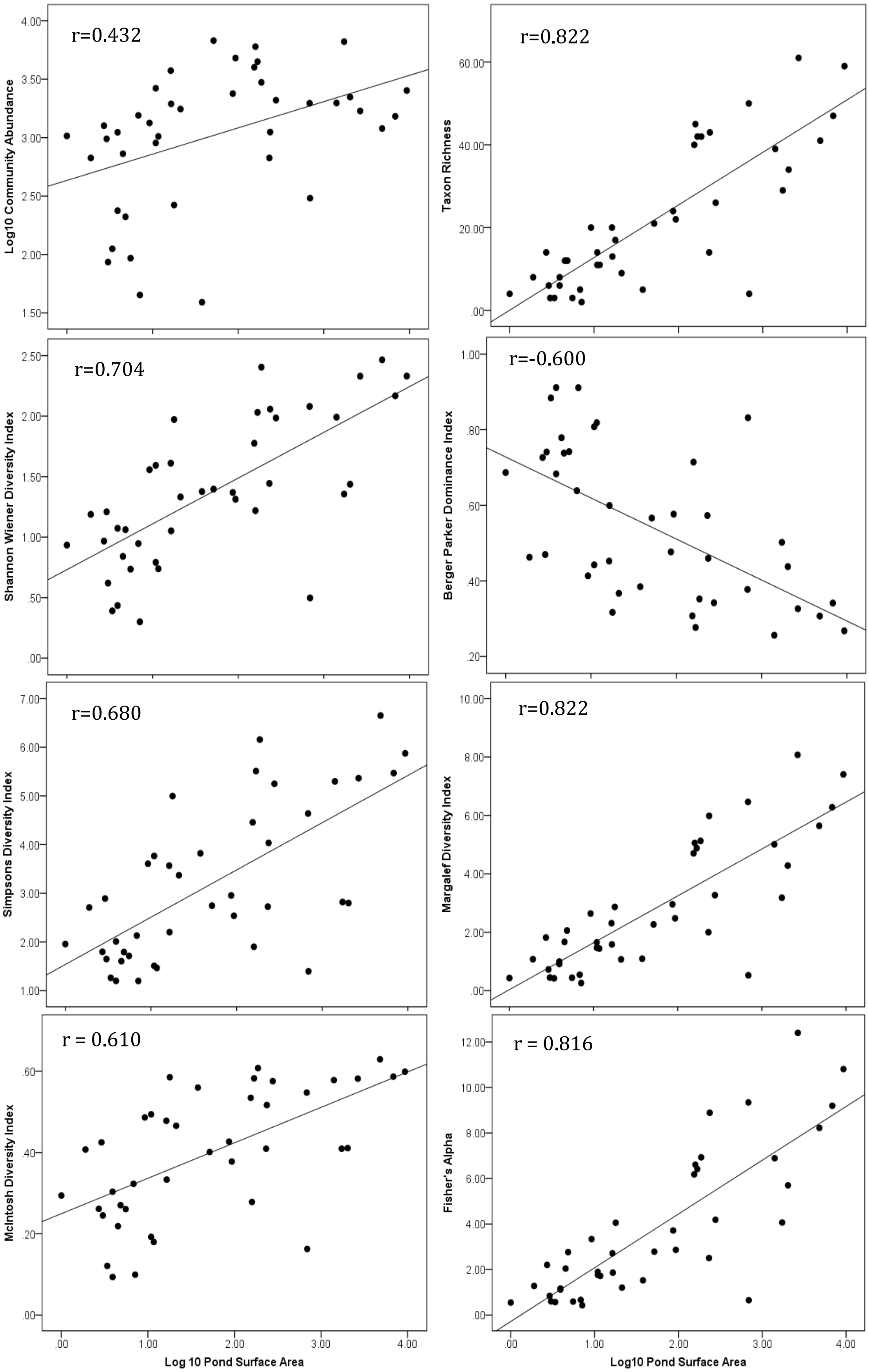

Figure 5.4 - Scatter plot of correlation between log_{10} pond surface area and ecological indices: log_{10} community abundance, taxon richness, Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha

5.2.4 Community heterogeneity

A significant difference in Jaccard's Coefficient of Similarity (ANOVA $F_{2, 263}$=10.897; p<0.001) and Sørensen Similarity index (ANOVA $F_{2, 263}$ =10.826; p<0.001) was recorded between the three urban pond types (Table 5.6). The *post hoc* Tukey test identified Jaccard's Coefficient of Similarity and the Sørensen Similarity index to be significantly lower in 'other' urban ponds than garden and park ponds which suggests that substantial heterogeneity (fewer species in common) was displayed by assemblages within 'other' urban ponds. However, there was a greater overlap and uniformity of aquatic invertebrate communities within garden and park ponds (Table 5.6). Both Jaccard's Coefficient of Similarity and Sørensen Similarity index indicated that across the urban region individual ponds had a wide variability (high beta-diversity) in their macroinvertebrate community composition. The top four macroinvertebrate taxa identified as contributing most to the dissimilarity (as a percentage) between urban pond types is presented in Table 5.7.

Table 5.6 - Mean Jaccard's Coefficient of Similarity and Sørensen Similarity index within the three urban pond types and across the urban landscape

	Garden Ponds	'Other' Urban Ponds	Park Ponds	Urban Landscape (all ponds)
Mean Jaccard's Coefficient of Similarity	0.27	0.19	0.24	0.18
Mean Sørensen Similarity index	0.41	0.32	0.38	0.30

Table 5.7 – Summary table of top 4 aquatic macroinvertebrates identified by SIMPER as most strongly influencing between pond type dissimilarity. Number in parenthesis indicates the percentage contribution to pond dissimilarity. n = number of pond sites and j = total number of taxa. x/x represents the total number of taxa common between the pond types.

	Garden Ponds	'Other' Urban Ponds	Park Ponds
Garden Ponds	*n = 13* *j = 44*	*OUP/GP = 25*	*PP/GP = 38*
'Other' Urban Ponds	*Asellus aquaticus* (7.3) *Crangonyx pseudogracilis* (7) Oligochaeta (5.8) Chironomidae (5.4)	*n = 16* *j = 91*	*PP/OUP = 77*
Park Ponds	*Crangonyx pseudogracilis* (5) *Cloeon dipterum* (4.3) *Asellus aquaticus* (4.2) Oligochaeta (2.6)	*Cloeon dipterum* (4) *Crangonyx pseudogracilis* (4) *Asellus aquaticus* (3.9) *Lymnaea peregra* (2.7)	n = 12 j = 149

An accurate representation of the dissimilarity between the urban ponds is presented in the NMDS biplot as a two dimensional stress level of ≤ 0.2 was calculated. The species abundance data was log (X+1) transformed prior to analysis. There were significant differences in macroinvertebrate community assemblages among the three pond types (ANOSIM $p<0.001$). A clear distinction between park ponds and garden ponds is demonstrated in the NMDS biplot (Figure 5.5) suggesting that the two pond types supported dissimilar invertebrate communities. The majority of park ponds were located towards the left of the first axis whilst most of the garden ponds were placed towards the right of axis one. This was corroborated by ANOSIM pairwise tests which indicated that garden ponds supported significantly different macroinvertebrate community compositions to park ponds ($p<0.001$) and 'other' urban ponds ($p<0.05$). 'Other' urban ponds were widely dispersed within the NMDS ordination space indicating that within this pond type there was substantial heterogeneity in macroinvertebrate community composition (Figure 5.5). This was reinforced by Jaccard's Coefficient and Sørensen Similarity index, which also identified a significant heterogeneity in macroinvertebrate assemblages within 'other' urban ponds (Table 5.5).

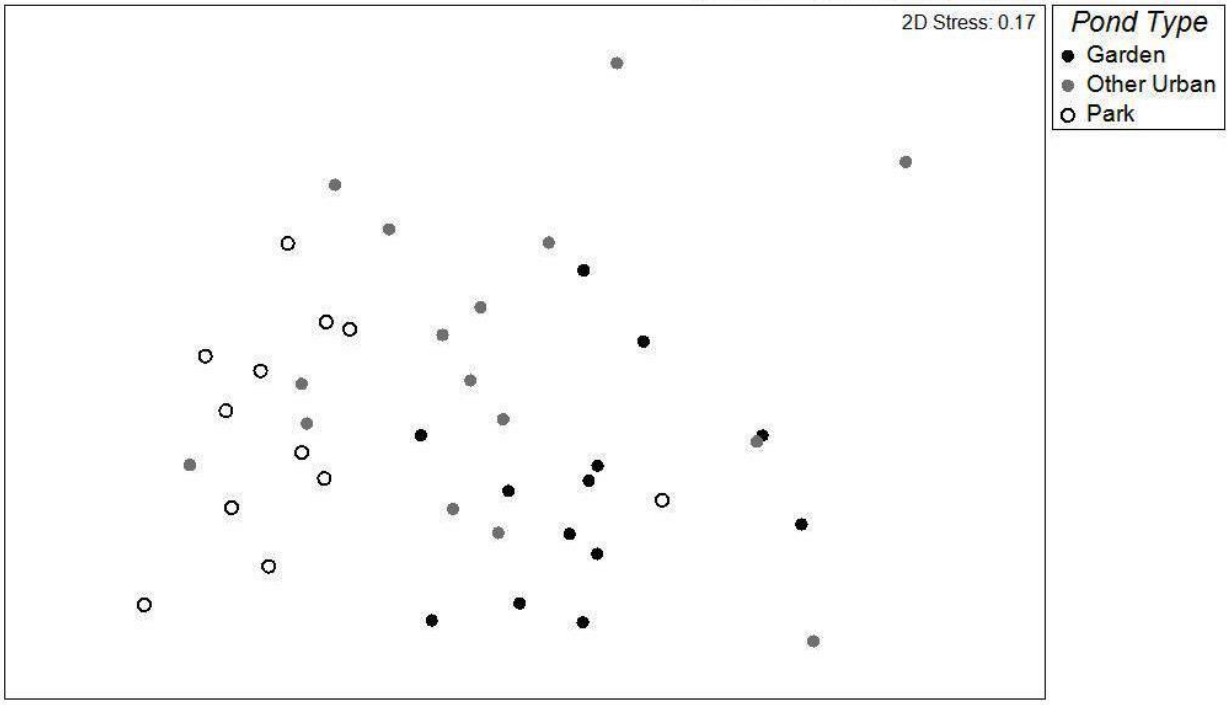

Figure 5.5 - Two dimensional NMDS biplot of dissimilarity (Bray-Curtis) of macroinvertebrate communities within urban pond sites (two-dimensional stress: 0.17)

Figure 5.6 presents the NMDS biplots (three separate NMDS analyses were undertaken) for the spring, summer and autumn season macroinvertebrate communities from the three urban pond types. No significant distinction between the seasonal communities in garden, 'other' urban and park ponds was recorded (ANOSIM $p>0.05$). The spring, summer and autumn macroinvertebrate communities from garden, 'other' urban and park ponds overlapped considerably in their respective NMDS biplots (Figure 5.6). This indicates that the seasonal macroinvertebrate communities were homogenous and there was little turnover of macroinvertebrate taxa throughout the three sampling periods.

5.2.5 Macroinvertebrate dispersal

The dispersal mechanism assigned to each macroinvertebrate taxa within this research was based on the designations given in Tachet *et al*. (2003) and Van de Meutter *et al*. (2006). Across all three urban pond types there was a greater proportion of actively dispersing macroinvertebrate taxa (taxa with flying adults) to passively dispersing taxa within macroinvertebrate communities (Figure 5.7). Actively dispersing taxa (including species of Coleoptera, Odonata and Hemiptera) dominated park pond communities, encompassing on average 63% of the species richness within invertebrate communities.

Whilst, on average 58% and 54% of the community were actively dispersing taxa within 'other' urban and garden ponds respectively. However, the numbers of actively and passively dispersing taxa between the three urban pond types were not recorded to be significantly different (Kruskal-Wallis $p>0.05$).

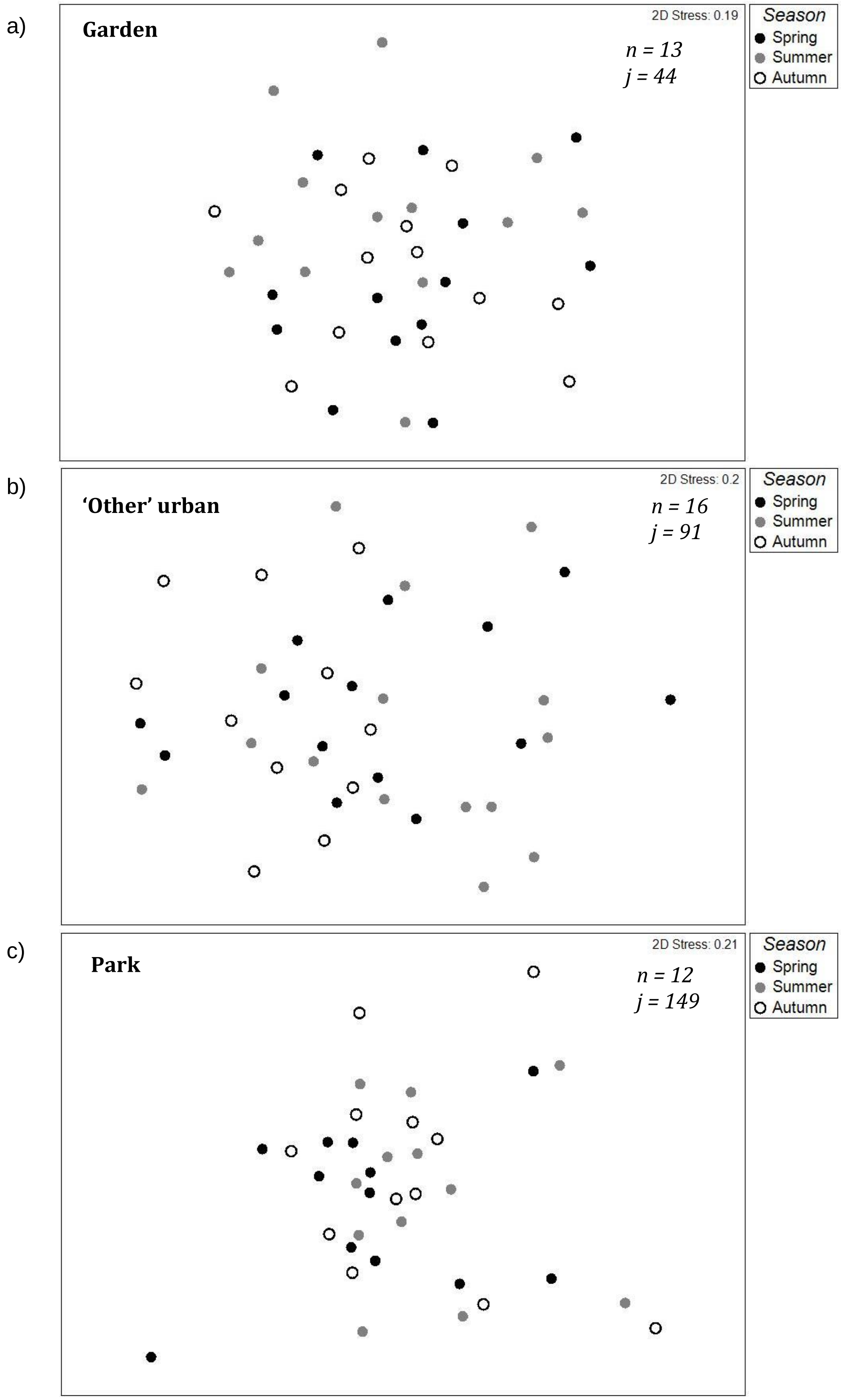

Figure 5.6 - Two dimensional NMDS plot of dissimilarity (Bray-Curtis) of seasonal (spring, summer and autumn) invertebrate communities within the three urban pond types: (a) garden (b) 'other' urban and (c) park. n = number of pond sites and j = total number of taxa.

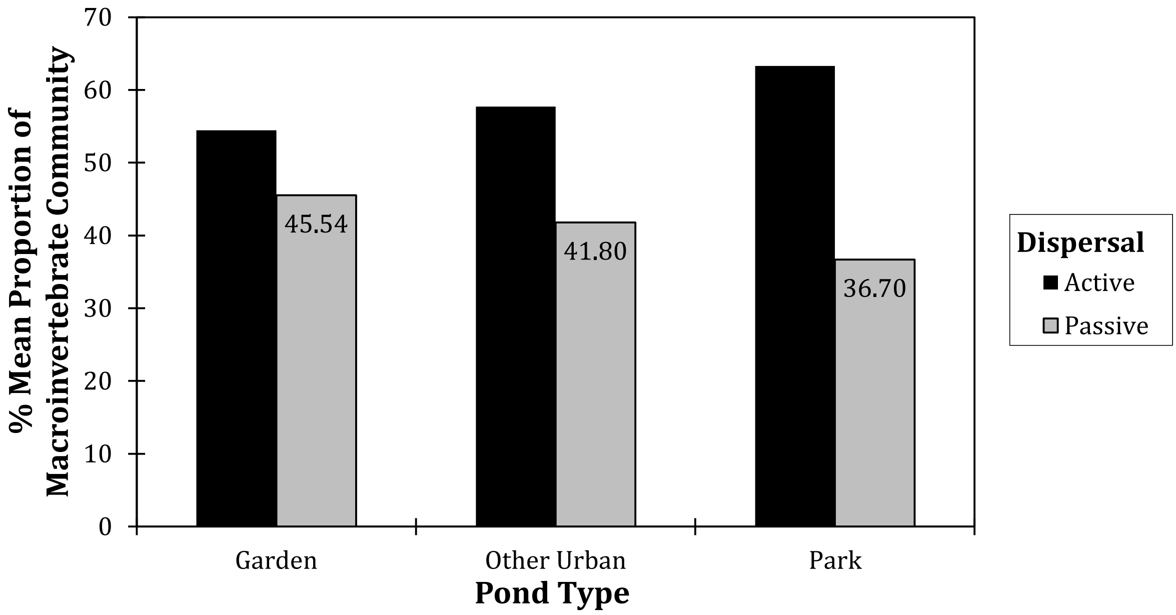

Figure 5.7 - Proportion (mean %) of actively and passively dispersing macroinvertebrate taxa within garden, 'other' urban and park ponds

5.2.6 Conservation Value

5.2.6.1 UK Post-2010 Biodiversity Framework (England) Pond Priority Habitat (PPH)

A total of 4 nationally scarce and nationally notable Coleoptera species were recorded from the urban ponds; *Helophorus strigifrons* (Hydrophilidae: *Helophorus*), *Helochares punctatus* (Hydrophilidae: *Helochares*), *Agabus uliginosus* (Dytiscidae: *Agabus*), *Gyrinus distinctus* (Gyrinidae: *Gyrinus*) and a single Zygoptera *Coenagrion pulchellum* (Coenagrionidae: *Coenagrion*) (Table 5.8). The UK Post-2010 Biodiversity Framework for England (previously the Biodiversity Action Plan (Natural England, 2014a)), which includes ponds as a priority habitat, is the key procedure through which ponds can receive detailed conservation/management plans and some statutory conservation protection. Using the Priority Pond Habitat (PPH) criteria (BRIG, 2008), three ponds met the requirements as they supported invertebrate communities with >50 taxa, qualifying as PPH's and should receive consideration from policy makers. A complete assessment of PPH criteria was not possible as the Predictive System for Multimetrics (PSYM) score could not be calculated.

Table 5.8 - Aquatic macroinvertebrate species of conservation interest with their designations and locale

Family	Species	Conservation Designation	Sample Location/s
Coenagrionidae	*Coenagrion pulchellum*	IUCN Lower Risk - Near Threatened	1 Park Pond
Gyrinidae	*Gyrinus distinctus*	Nationally Scarce	1 Park Pond
Dytiscidae	*Agabus uliginosus*	IUCN Lower Risk - Near Threatened Nationally Notable	1 Park Pond
Hydrophilidae	*Helochares punctatus*	Nationally Scarce	1 Park Pond
Hydrophilidae	*Helophorus strigifrons*	Nationally Scarce Nationally Notable	1 Park Pond 1 'Other' Urban Pond

5.2.6.2 Community Conservation Index (CCI)

The Community Conservation Index (CCI) incorporates both the rarity of individual macroinvertebrate taxa (based on legislative conservation designations and information from authoritative sources) and the overall community assemblage (Chad and Extence (2004); see Appendix 4). The rarity score given to each macroinvertebrate taxa within this study was based on the rarity scores assigned to macroinvertebrate taxa by Chad and Extence (2004). When analysing the total species data (three seasons combined) CCI scores were significantly greater in park ponds than garden or 'other' urban ponds (ANOVA $F_{2, 40}$=8.781; p<0.001). Fairly high conservation value was recorded for 9 urban pond communities (7 park ponds and 2 'other' urban ponds) (Table 5.9). Only moderate conservation values (4 ponds) and low conservation values (9 ponds) were calculated for garden pond communities. 'Other' urban ponds were also dominated by low (8 ponds) and moderate conservation values (6 ponds) whereas, only 1 park pond was of a low conservation value and 3 had a moderate conservation value (Table 5.9).

The CCI for urban ponds within each season (spring, summer and autumn) was calculated in order to be comparable to the large number of pond surveys which are limited to a single season (Armitage *et al.,* 2012). Throughout each season there were a minimum of two ponds that had macroinvertebrate communities with at least a fairly high conservation value (Table 5.9). CCI was highest in the autumn season where 2 ponds had a high conservation value (two park ponds) however; there was no statistically significant difference (p>0.05) in the CCI between the spring, summer and autumn seasons.

Table 5.9 - Community Conservation Index (CCI) for individual seasons and the combined seasons (total) from the 41 urban pond sites. GP = garden pond; OU = 'other' urban ponds; PP = park ponds, (0-5 low conservation value: >5-10 moderate conservation value: >10-15 fairly high conservation value: >15-20 high conservation value and >20 very high conservation value). Fairly high conservation scores are presented in bold and high conservation value scores are presented in bold italic.

	Spring	Summer	Autumn	Total
Garden ponds				
GP1	1.0	1.0	1.0	1.0
GP2	8.0	4.5	1.0	7.9
GP3	1.0	1.0	1.0	1.0
GP4	9.5	**13.0**	8.5	10.0
GP5	1.2	1.0	1.1	1.1
GP6	9.4	1.0	9.0	9.6
GP7	4.7	4.3	3.9	4.4
GP8	1.0	1.0	1.0	1.0
GP9	1.0	1.3	1.0	1.2
GP10	1.0	1.0	1.0	1.0
GP11	1.0	1.0	1.0	1.0
GP12	3.9	8.2	1.0	7.7
GP13	1.0	1.0	1.0	1.0
Mean	3.4	3	2.4	3.7
Other Urban Ponds				
OUP1	6.7	1.1	4.2	7.7
OUP2	1.2	1.0	1.0	1.1
OUP3	1.0	1.0	1.0	1.0
OUP4	10.3	8.3	9.2	9.4
OUP5	1.1	1.0	7.0	6.3
OUP6	8.6	8.6	8.06	8.3
OUP7	1.0	1.0	*	1.0
OUP8	4.5	1.1	*	4.5
OUP9	10.3	7.4	6.7	**11.8**
OUP10	4.0	**11.1**	*	**10.7**
OUP11	1.0	*	*	1.0
OUP12	*	1.0	*	1.0
OUP13	8.9	7.9	8.5	8.0
OUP14	1.1	1.1	1.1	1.1
OUP15	1.0	1.0	4.0	3.8
OUP16	8.8	9.0	8.6	8.3
Mean	4.6	4.1	5.4	5.3
Park Ponds				
PP1	1.0	1.0	1.0	1.0
PP2	9.0	9.0	9.3	**10.5**
PP3	14.4	8.6	3.9	**13.3**
PP4	***18.1***	3.9	10.0	**14.7**
PP5	3.7	3.8	4.0	4.4
PP6	12.2	8.0	**12.6**	**13.1**
PP7	8.9	3.5	6.6	8.6
PP8	7.6	6.7	4.8	7.6
PP9	5.0	4.8	9.7	**12.3**
PP10	10.0	8.9	**16.5**	**14.8**
PP11	1.2	5.6	8.0	8.0
PP12	**11.0**	3.8	**15.4**	**13.0**
Mean	8.5	5.6	8.5	10.1

*Pond dry in that season

5.3 Discussion

5.3.1 Macroinvertebrate diversity

We found strong evidence to accept our first hypothesis:

> *H_1: Aquatic macroinvertebrate biodiversity and conservation value will be greatest in large park ponds and lowest in small garden ponds.*

Garden ponds supported the lowest invertebrate diversity among the three urban pond types and were frequently dominated by Diptera larvae. However, it is important to acknowledge that Diptera were only identified to family level in this study and it is likely that garden ponds may support high dipteran species diversity, which has not been quantified in this study. Garden ponds in Sheffield, UK, were also dominated by Diptera larvae and supported a limited number of invertebrate taxa (Gaston *et al*., 2005a). Park ponds supported high macroinvertebrate diversity in this study (149) and was greater than that recorded from urban ponds in Halton (Lancashire): total = 119 taxa, and urban drainage ponds in the UK: Dunfermline (Fife) total = 66 taxa (Briers, 2014; Gledhill *et al*., 2008). Faunal richness was revealed to be highest in emergent and submerged macrophyte mesohabitats and lowest in open water mesohabitats. Similarly, Odonata diversity was associated most with aquatic macrophytes (Goertzen and Suhling, 2013) and Gledhill *et al*. (2008) identified a strong correlation between macroinvertebrate richness and macrophyte richness in urban ponds in north-west England. Aquatic macrophytes are not only a source of food for invertebrates but provide areas for egg-laying, materials for case building for Trichoptera and refuge/protection from predation by other macroinvertebrate and vertebrate (fish and amphibians) taxa (Biggs *et al*., 1994a).

A significant proportion of the regional macroinvertebrate species pool was represented within the urban ponds in this study (170 taxa). The total biodiversity recorded within urban ponds was comparable to ponds in the wider landscape around the town of Loughborough (semi-natural meadow ponds = 175 taxa; agricultural ponds = 127 taxa). High regional invertebrate diversity has also been recorded within aquatic urban systems in the Netherlands (Vermonden *et al*., 2009) and for other organisms such as waterbirds (Santoul *et al*., 2009) and amphibians (Brand and Snodgrass, 2009).

However, at an alpha (individual) scale macroinvertebrate diversity within urban ponds in this study was variable (ranging from 2 to 61 taxa), and the average number of taxa (22) was markedly lower than that recorded in the in the wider landscape (meadow ponds = 36; agricultural ponds = 34, see Chapter 4). This almost certainly reflects both the physical and chemical heterogeneity of the ponds, but also their location within structurally complex and highly fragmented anthropogenic settings. Many of the most taxon rich park ponds were located in 'green spaces' which may have acted as a buffer zone protecting aquatic taxa from runoff from anthropogenic surfaces and disturbances. The importance of buffer zones in the conservation of amphibian populations has been highlighted (Semlitsch and Bodie, 2003; Rubbo and Kiesecker, 2005), although there has been limited research assessing their effectiveness in relation to macroinvertebrate biodiversity within ponds (Langley *et al*., 1995; Gledhill *et al*., 2008).

A number of taxa in garden ponds in this study (Trichoptera larvae: *Hydropsyche angustipennis, Limnephilus lunatus, Limnephilus rhombicus, Beraea pullata* and *Mystacides longicornis*) are more typically associated with lotic environments (Edington and Hildrew, 1995; Wallace *et al*., 2003). Many of the garden ponds contained artificial flowing water features (fountains or re-circulating water) that were designed to be aesthetically pleasing, facilitate oxygenation of the water and/or to prevent algae/floating vegetation from covering the pond surface. These artificial water features, powered by electrical pumps, created a lotic environment in inflowing areas, which provided habitat for lotic trichopteran and dipteran taxa.

Urbanization is often closely associated with an increase in non-native invasive species and biotic homogenization (Holway and Suarez, 2006; McKinney, 2006). However, only two non-native macroinvertebrate taxa were recorded from urban ponds in this study; *C. pseudogracilis* and *P. antipodarum*, both of which have not been recorded to significantly impact native macroinvertebrate taxa and are widespread and common across the United Kingdom (Macan, 1977; Gledhill *et al.,* 1993). The discrete, patchy nature of urban ponds (not hydrologically connected to other waterbodies) may reflect the reduced numbers of non-native/invasive taxa recorded as there are few dispersal pathways available to the invasive species.

A positive association was observed between macroinvertebrate diversity and pond surface area in this study and is a pattern that has been documented in some (e.g., Nilsson and Svensson, 1995; Biggs *et al*., 2005; Ruggiero *et al*., 2008) but not all pond biodiversity studies (Scheffer *et al*., 2006; Nakanishi *et al*., 2014). Oertli *et al*. (2002) demonstrated that the influence of pond size can vary depending on the macroinvertebrate group; Odonata had a relatively strong correlation with pond size, whilst Coleoptera, Sphaeriidae and overall faunal richness displayed a weak association with pond size. The small size of garden ponds (typically <10 m^2), their management practices (e.g., maintenance of open water, reduced macrophyte cover, actively managed to prevent succession) and their high turn-over, due to changes in house ownership and garden management fashions, may significantly limit the ability of garden ponds to replicate the habitat diversity of ponds within the wider urban and rural landscape (Gaston *et al*., 2005b). Garden ponds are often surrounded by walls, fences or buildings (barriers), typical of urban landscapes. These physical barriers may significantly reduce pond connectivity and the ability of invertebrate taxa to disperse or colonize new habitats, even if they are in close geographical proximity. However, despite these limitations, they may contribute to the regional species pool (Gaston *et al*., 2005a; Gledhill *et al*., 2008). Given the high abundances of garden ponds, estimated to be between 2.5-3.5 million in the UK (Davies *et al*., 2009b), future research is required to examine their potential to serve as refugium for macroinvertebrate communities. Greater public awareness and guidance regarding the best management practices may also enhance the biodiversity value of garden ponds in the future.

Urban ponds are often built to support ornamental fish populations, especially garden and park ponds (Hassall, 2014). Previous studies have indicated that ponds with fish typically support lower invertebrate diversity than fishless ponds (Wood *et al*., 2001; Abjörnsson *et al*., 2002). However, no significant effects of the presence of fish on macroinvertebrate diversity or community composition were recorded among the urban ponds in this study. This may reflect the low to moderate fish stocking densities and also the protection provided by emergent and submerged macrophyte beds from predation (Diehl, 1992; Biggs *et al*., 1994; Stansfield *et al*., 1997).

5.3.2 Macroinvertebrate community heterogeneity

Substantial macroinvertebrate community heterogeneity was observed within and between urban pond types and provides evidence to support our second hypothesis:

H_2: Macroinvertebrate biodiversity will vary significantly among urban ponds (β diversity) reflecting the highly variable environmental conditions in ponds.

The high community dissimilarity recorded demonstrates that urban ponds provide a range of habitats/niches for invertebrate taxa to utilise. 'Other' urban ponds in this study were shown to have a high dissimilarity in community composition. This reflects the varying pond successional stages, the diverse physicochemical characteristics and variable hydrological regimes observed among the urban ponds (Biggs *et al*., 1994; Williams *et al*., 2003; Nicolet *et al*., 2004; Biggs *et al*., 2005; Ruhi *et al*., 2013). This inter-pond, spatial dissimilarity also reflects the spectrum of management levels that urban ponds are subject to; ranging from regular active management through to an absence of intervention. However there was no significant seasonal dissimilarity/turnover of macroinvertebrate communities from garden, 'other' urban and park ponds. This most likely reflects the reduced connectivity of urban waterbodies and the consequent reduction in dispersal and colonization potential for many macroinvertebrate taxa, especially those that disperse passively. Over a longer time scale (5 years) Briers, (2014) recorded macroinvertebrate community composition from urban drainage ponds to become increasingly dissimilar. This was identified to be the result of the large temporal variation in physicochemical characteristics, especially of nutrient loads (Briers, 2014). Macroinvertebrate communities from ponds in the wider landscape have also been shown to display significant temporal heterogeneity and turnover of species, which can result in temporal variation in the conservation value of pond habitats (Jeffries, 2005, Jeffries, 2011; Hassall *et al*., 2012). Future research is required to examine the nature of temporal heterogeneity of urban pond communities and the implications for urban biodiversity conservation.

5.3.3 Conservation value

The growing need for the protection and conservation of freshwater biodiversity has been raised on the international political agenda in recent years. The United Nations launched and supported an international decade for action on 'water for life' 2005-2015 with a special emphasis on highly modified and fragmented landscapes (Dudgeon *et al*., 2006). Despite their largely anthropogenic origin and the presence of several non-native taxa (*C. pseudogracilis* and *P. antipodarum*), a number of ponds were of significant conservation value supporting a total of 4 nationally rare species (4 Coleoptera) and 3 urban ponds supported invertebrate assemblages with ≥50 invertebrate taxa. Urban ponds potentially have a vital role to play in reducing aquatic habitat fragmentation and serving as stepping stones in anthropogenically disturbed landscapes (Chester and Robson, 2013). Urban ponds not only aid ongoing conservation efforts but may actively enhance freshwater biodiversity in the wider region (Le Viol *et al*., 2009; Vermonden, *et al*., 2009; Briers, 2014). The majority of taxa supported within urban ponds were generalist taxa. However, urban ponds may be particularly important habitats for motile taxa such as Coleoptera and Odonata which can opportunistically colonize available habitat aerially (Scher and Thiery, 2005; Goertzen and Suhling, 2013). A number of these active colonizers with an aerial adult life-stage were well represented and among the most species rich groups recorded (Coleoptera, Trichoptera and Hemiptera) in the urban ponds studied. A key determinant of Odonata biodiversity within individual ponds is vegetation diversity with the surrounding landscape being less critical to this group due to high vagility (Goertzen and Suhling, 2013). *Ischnura elegans* was the most abundant damselfly within urban ponds in this study. *I. elegans* was also widely distributed and abundant in urban park ponds in Dortmund, Germany and appeared to thrive in locations that were frequently managed/disturbed (Goertzen and Suhling, 2013). It has also been shown to be tolerant to a wide range of water quality conditions typical of garden ponds (Solimini *et al*., 1997).

The results clearly demonstrate that many urban ponds can support species rich invertebrate communities of conservation value. The Community Conservation Index indicated that nine of the urban ponds were of 'fairly high' conservation value. However, this study, and others (Noble and Hassall, 2014) have also demonstrated that a large number of urban ponds are species poor and of a low conservation value. Poor quality urban ponds are often not reported as they are considered uninteresting (Hassall, 2014). It has been identified that approximately 80% of ponds in England and Wales are of a poor or very poor quality (Williams *et al*., 2010). Pond warden schemes enlist volunteers to ensure the conservation and maintenance of ponds (Boothby, 1995; DCPWA, 2014; Footprint Trust, 2014). Pond warden schemes allow a larger number of urban ponds to be monitored and managed in a more strategic manor and could greatly improve the ecological quality of degraded urban ponds at a national scale.

It is also important to recognise that ponds located in urban spaces (e.g., school, or public park) provide an opportunity for the general public to interact with freshwater ecosystems and even if individual sites have 'low' conservation value they may help to engage the non-scientific community in biological conservation and raise awareness of the importance and management needs of small freshwater habitats (Hassall, 2014). Recreational activities including boating, fishing and general exercise are provided by urban ponds which can connect the urban community to the natural environment (Lundy and Wade, 2011). Urban waterbodies also provide an environment for more passive activities, drawing on their aesthetic value, providing a habitat for tranquillity and reflection which may improve well-being of the general public (Lundy and Wade, 2011).

5.4 Summary

Urban ponds can support rich and diverse macroinvertebrate communities. When the three different types of urban pond (garden, 'other' urban and park) were considered, park ponds had the highest conservation value and greatest macroinvertebrate diversity whilst garden ponds were the most taxa poor and had lower conservation value. At a regional scale urban pond biodiversity was comparable to biodiversity in the wider rural landscape. Pond size was found to be strongly associated with macroinvertebrate diversity and the high beta-diversity recorded demonstrates that individual ponds may support different communities and that they make an important contribution to regional diversity. Irrespective of their biodiversity and conservation value, it is important to recognise that urban ponds serve a number of societal functions and provide an opportunity for public engagement with freshwater habitats in addition to supporting biodiversity. Recognition of the significant contribution that ponds make to urban freshwater biodiversity is therefore important for the future conservation and management of urban ponds and other artificial waterbodies. This is vital for the ongoing protection of sites and biota from further habitat fragmentation in urban landscapes.

Chapter 6. Macroinvertebrate biodiversity and conservation value of ephemeral ponds in two floodplain meadow landscapes

6.1 Introduction

Ephemeral ponds can be defined as small lentic water bodies that experience a recurrent dry/desiccation phase (Williams *et al.,* 2001). The duration of the wet phase can be highly variable and be either predictable or unpredictable (Williams, 1997). The physicochemical conditions of ephemeral ponds are demanding and often become extreme as the pond dries (Williams, 1996; Bagella *et al.,* 2010). Ephemeral ponds are commonly associated with semi-arid climates, but they are common and abundant landscape features globally and in Britain occur in a wide range of habitats including intensively farmed agricultural areas, floodplain meadows, semi-natural forests and urban landscapes (Collinson *et al.,* 1995). A total of 25% of all UK ponds (119,500) may be semi-permanent (drying in years with below average precipitation) and at least 5% (23,900) are likely to be ephemeral (drying every year) (Williams *et al.,* 2010).

Wider recognition and awareness of the contribution that ephemeral ponds make to aquatic biodiversity and conservation has significantly increased in recent years (Nicolet *et al.,* 2004; Armitage *et al.,* 2012) although, research into ephemeral pond biodiversity still lags behind that of perennial ponds and other fresh waterbodies (Williams *et al.,* 2001). Despite the demanding and harsh physicochemical environment (as a result of periodic drying) ephemeral ponds have been demonstrated to be important habitats for freshwater fauna with a range of macroinvertebrate taxa adapted to and able to exploit ephemeral pond habitats (Bazzanti *et al.,* 2010). Ephemeral ponds can support a high taxon richness of rare and endemic species (Boix *et al.,* 2001; Nicolet *et al.,* 2004; Bilton *et al.,* 2009; Díaz-Paniagua *et al.,* 2010; Armitage *et al.,* 2012) and in some cases support a greater number of rare taxa than perennial ponds (Collinson *et al.,* 1995; Nicolet, 2001). However, ephemeral ponds often support a lower total macroinvertebrate richness and abundance than perennial ponds (Nicolet, 2001). Two of the UK's rarest macroinvertebrate species; the fairy shrimp (*Chirocephalus diaphanus*) and tadpole shrimp (*Triops cancriformis*) are reliant on ephemeral pond habitats

(Williams, 1997). Vertebrate predators are typically absent from ephemeral ponds as they cannot survive the dry phase, this can greatly reduce the predation pressure and increase the abundance/richness of open water macroinvertebrate taxa and taxa that are often out competed in perennial ponds (Brönmark and Hansson, 2005; De Meester *et al.,* 2005). Although, predatory macroinvertebrate taxa have been demonstrated to significantly influence prey populations and community assemblage in ephemeral ponds with longer hydroperiods (Bilton *et al.,* 2001; Williams, 2006).

Floodplain landscapes are often sites of exceptionally high aquatic, terrestrial and semi-aquatic biodiversity (Ward *et al.,* 1999; Helfield *et al.,* 2012) driven by lateral connectivity to the river (inundation of river floodwater) providing water, nutrients and resources to the floodplain (Junk, 1989). Ponds located on floodplain meadows provide important habitat for a wide range of flora and fauna (Gergel, 2002). Natural flooding of riverine landscapes creates and maintains a gradient in hydroperiod and results in a network of hydrologically connected perennial and ephemeral waterbodies at a range of successional stages which can provide a wide diversity of aquatic habitats to support floral and faunal floodplain communities and may represent locations of high alpha, beta and gamma diversity (Gergel, 2002; Paillex *et al.,* 2013). However, due to extensive anthropogenic activities such as river regulation, channelization and the building of embankments to reduce flood risk and to protect anthropogenic infrastructure and agricultural activities on the floodplain, many rivers are hydrologically disconnected from the floodplain (Nilsson *et al.,* 2005; Paillex *et al.,* 2013). This has resulted in a long term trend of terrestrialization of floodplain habitats and the reduction in freshwater biodiversity (Tockner and Stanford, 2002; Reckendorfer *et al.,* 2006). There has been a recent drive to reconnect rivers with their floodplains to rehabilitate and restore aquatic habitats (wetlands and ponds) on the floodplain and support faunal and floral biodiversity (Reckendorfer *et al.,* 2006; Paillex *et al.,* 2013). However, most natural river-floodplain ecosystems remain highly fragmented and endangered in European lowland landscapes (Ward *et al.,* 1999; Schindler *et al.,* 2013).

6.1.1 Research/knowledge gaps

Ephemeral pond ecology from Mediterranean (semi-arid) regions has received substantial research interest in recent years (e.g., Beja and Alcazar, 2003; Florencio *et al.,* 2013, 2014; Ruhi *et al.,* 2014) and Mediterranean temporary ponds have been given statutory protection as a Priority Habitat under the Habitats Directive (EC, 1992). However ephemeral pond invertebrate communities within European lowland landscapes have received markedly less research attention and there remain major gaps in our understanding of the ecology of these ephemeral waterbodies (Nicolet *et al.,* 2004). In northern Europe ephemeral ponds receive no statutory protection but may be specifically covered as pond Priority Habitats in the UK under the UK Post-2010 Biodiversity Framework (Bilton *et al.,* 2009).

There has been little research attention focused on the ecology of ephemeral or perennial ponds in the East Midlands, UK. Ephemeral pond research in the UK has typically focussed on the Lizard Peninsula (Cornwall) and the New Forest (Hampshire) (Nicolet*,* 2001; Bilton *et al.,* 2009; McAbendroth *et al.,* 2005; Gutierrez-Estrada and Bilton, 2010), and northern England (Davy-Bowker, 2002; Jeffries, 2011). However, a few studies have been UK wide (e.g., Nicolet *et al.,* 2004). Ephemeral ponds located on unregulated flood plain meadows in temperate lowland regions have been largely neglected in the published literature and there has been limited published research which has specifically characterized the difference between perennial and ephemeral pond invertebrate communities on unregulated floodplain meadows.

6.1.2 Chapter aims and hypotheses

This chapter aims to address the identified knowledge gaps by quantifying the macroinvertebrate biodiversity and conservation value of ephemeral and perennial ponds located on two large unregulated flood plain meadows that are traditionally managed by Leicestershire and Rutland Wildlife Trust (see Chapter 1.4: Objective 4). This chapter will also examine the community heterogeneity within ephemeral and perennial ponds. The following hypotheses will be tested;

H_1: Macroinvertebrate biodiversity will be higher in perennial floodplain meadow ponds than ephemeral floodplain meadow ponds;

H_2: Ephemeral ponds will support significantly different macroinvertebrate communities compared to perennial ponds;

H_3: Actively dispersing and non-predatory taxa will constitute a greater proportion of the invertebrate communities within ephemeral floodplain meadow ponds than in perennial ponds;

H_4: The conservation value of both perennial and ephemeral floodplain meadow ponds will be high.

The fieldwork, laboratory and statistical methods utilised in this chapter are outlined in Chapter 3.

6.2 Results

A comprehensive examination of 34 ponds was undertaken in two unregulated floodplain meadows adjacent to the River Soar, Leicestershire (Cossington Meadow-CM and Loughborough Big Meadow-LBM).

Both meadows lie on the River Soar floodplain, CM is often flooded by the River Soar during winter, whilst LBM is less regularly flooded. Fluvial gravel and sand were historically quarried from Cossington Meadow but since 2004 has been a nature reserve supporting a variety of floodplain meadow, woodland and freshwater habitats (perennial and ephemeral ponds, lakes and ditches) all in close proximity to the River Soar (LRWT, 2014a). The majority of the larger ponds and lakes in CM are of anthropogenic origin (relicts of quarrying) but since their creation all have been subject to limited direct management and are minimally affected by agriculture (low density grazing) activities associated with traditional meadow systems. Many of the ponds sampled were >10 years old however, some ponds were <2 years old, dug adjacent to the River Soar to develop a floodplain wetland. LBM is part of a Site of Special Scientific interest (SSSI) and is one of the few remaining traditional Lammas Meadow sites in the UK (LRWT, 2014b). LBM is dominated by naturally formed ponds with an ephemeral hydrology and has historically been managed as a flood meadow (LRWT, 2014b). The meadow ponds studied were comprised of 2 groups: i) 20 perennial meadow ponds - water bodies which contained water all year round and; ii) 14 ephemeral meadow ponds - ponds which became dry at least once during the study period. Floodwater recharge from the River Soar was the primary driver of the hydroperiodicity for the ephemeral ponds studied. The ephemeral ponds were additionally separated into CM or LBM ephemeral ponds and their macroinvertebrate diversity examined.

6.2.1 Alpha and gamma diversity

A total of 173 taxa were identified within 16 orders and 56 families from the ponds in the two meadow sites when all sampling dates were considered (corresponding to the spring, summer and autumn 2012 seasons). Perennial ponds contained a total 164 taxa and 93 taxa were recorded from ephemeral ponds. Similar numbers of taxa were recorded from ephemeral ponds in CM (66) and LBM (67). A total of 72483 macroinvertebrate individuals were recorded from the two meadow pond landscapes when all sampling dates were considered. Perennial ponds supported a total of 63093 individuals and ephemeral ponds contained 9390 individuals. The greatest numbers of taxa were recorded from the orders; Coleoptera (54), Hemiptera (28), Trichoptera (22) and Gastropoda (21). The taxa most widely distributed across the meadow pond sites were Chironomidae (32 ponds) Oligochaeta (30 ponds), *Crangonyx pseudogracilis* (28 ponds) and Dytiscidae larvae (26 ponds) (Figure 6.1). Oligochaeta and Chironomidae were the most widely distributed taxa from both ephemeral and perennial ponds, although *Lymnaea peregra* was identified from all perennial ponds but was only recorded within 4 ephemeral ponds.

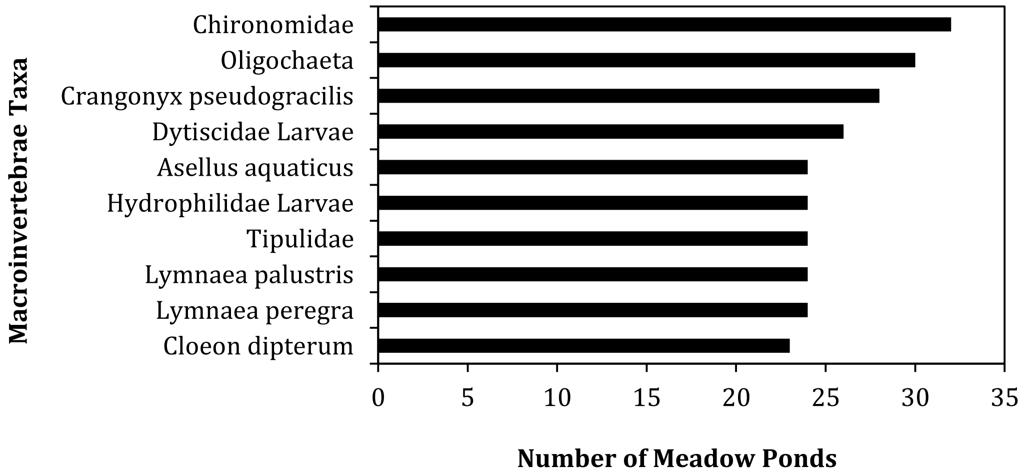

Figure 6.1 - Macroinvertebrate taxa most widely distributed throughout the study region

Two non-native macroinvertebrate species were recorded from the ephemeral and perennial meadow ponds. *Potamopyrgus antipodarum* (Hydrobiidae: Mollusca) was recorded from 5 perennial meadow ponds and 1 ephemeral meadow pond. *P. antipodarum* was highly abundant within the perennial ponds it inhabited accounting for up to 18% of the community abundance. *Crangonyx pseudogracilis* (Amphipoda: Crustacea) was identified from all perennial ponds, and 8 ephemeral ponds. The amphipod was abundant in many of the perennial meadow sites where it occurred, accounting for up to 44% of the community abundance. Within freshwater systems both species are abundant and widespread throughout the United Kingdom (Macan, 1977 and Gledhill *et al.,* 1993).

A total of 9 macroinvertebrate taxa were unique to ephemeral ponds (Gastropoda: *Lymnaea truncaulata,* Odonata: *Libellula quadrimaculata,* Trichoptera: *Limnephilus aricula, Limnephilus centralis, Limnephilus griseus,* Hemiptera: *Gerris gibbifer,* Coleoptera: Elminthidae larvae, *Helophorus dorsalis and Paracymus scutellaris*). CM and LBM ephemeral ponds both supported >20 taxa that were unique to that meadow (Table 6.1). There were twice the numbers of unique taxa which disperse passively recorded from ephemeral ponds in LBM compared to CM ephemeral ponds. Faunal dispersal mechanisms will be examined in greater detail in section 6.7.

Table 6.1 - The number of taxa recorded from each macroinvertebrate order that were unique to ephemeral ponds in CM or LBM

	Ephemeral Ponds	
	CM	**LBM**
Gastropoda	3	4
Bivalvia	0	1
Hirudinea	1	3
Ephemeroptera	2	0
Odonata	2	2
Trichoptera	4	0
Hemiptera	5	2
Coleoptera	7	9
Diptera	1	2

Preliminary analysis identified that macroinvertebrate community abundance did not have a normal distribution and was transformed (log_{10}) prior to statistical analysis. Across the study region mean taxon richness within meadow ponds was 39 taxa. Macroinvertebrate taxon richness varied widely among meadow pond sites ranging from 5 taxa (ephemeral pond) to 73 taxa (perennial pond). One-way Analysis of Variance (ANOVA) indicated that there was a significant difference in community abundance, taxon number, Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity, McIntosh diversity and Fisher's alpha between perennial and ephemeral ponds (Table 6.2).

Table 6.2 - One-way Analysis of Variance (ANOVA) between log_{10} community abundance, taxon richness and alpha diversity indices and perennial and ephemeral meadow ponds. Significant values ($p \leq 0.05$) are presented in bold.

	Df	F. Ratio	P. Value
Taxon richness	1, 33	67.734	**0.000**
Shannon Wiener diversity index	1, 33	24.769	**0.000**
Berger Parker Dominance index	1, 33	14.553	**0.001**
Simpsons diversity index	1, 33	10.608	**0.003**
Margalef diversity index	1, 33	52.357	**0.000**
McIntosh diversity index	1, 33	15.596	**0.000**
Fisher's alpha	1, 33	43.102	**0.000**
Log_{10} community abundance	1, 33	59.279	**0.000**

Perennial ponds supported substantially higher taxon richness (mean: 53 range: 20-73) compared to ephemeral ponds (mean: 19 range: 5-40) (Figure 6.2). A total of 19 out of the 20 perennial ponds supported macroinvertebrate assemblages with >40 taxa whilst 11 supported communities with >50 taxa when all sampling dates were considered. In contrast only 2 of the 14 ephemeral ponds had communities with >30 taxa and 6 ponds supported <10 taxa when all sampling dates were considered. Macroinvertebrate community abundance was identified to be significantly lower in ephemeral ponds (mean: 671 range: 85-2296) than perennial ponds (mean: 3155 range: 891-5661) (Figure 6.2). The macroinvertebrate assemblages within ephemeral and perennial ponds were generally dominated by coleopteran taxa (Figure 6.3). Greater than 20% of the mean number of taxa in perennial ponds were Hemiptera, whereas among ephemeral ponds Hemiptera taxa constituted <10% of the invertebrate community. On average, 15% of macroinvertebrate taxa supported within ephemeral ponds were dipteran larvae whilst in perennial ponds <10% on average were dipteran larvae (Figure 6.3).

In ephemeral ponds from both CM and LBM coleopteran (CM: 30% LBM: 27%) and dipteran (CM: 16% LBM: 16%) taxa dominated the macroinvertebrate communities. However, on average, Gastropoda (CM: 12% LBM: 17%) taxa constituted a greater proportion of LBM than CM ephemeral pond taxon richness whilst the opposite pattern was recorded for Hemiptera taxa (CM: 12% LBM: 7%).

a)

b)

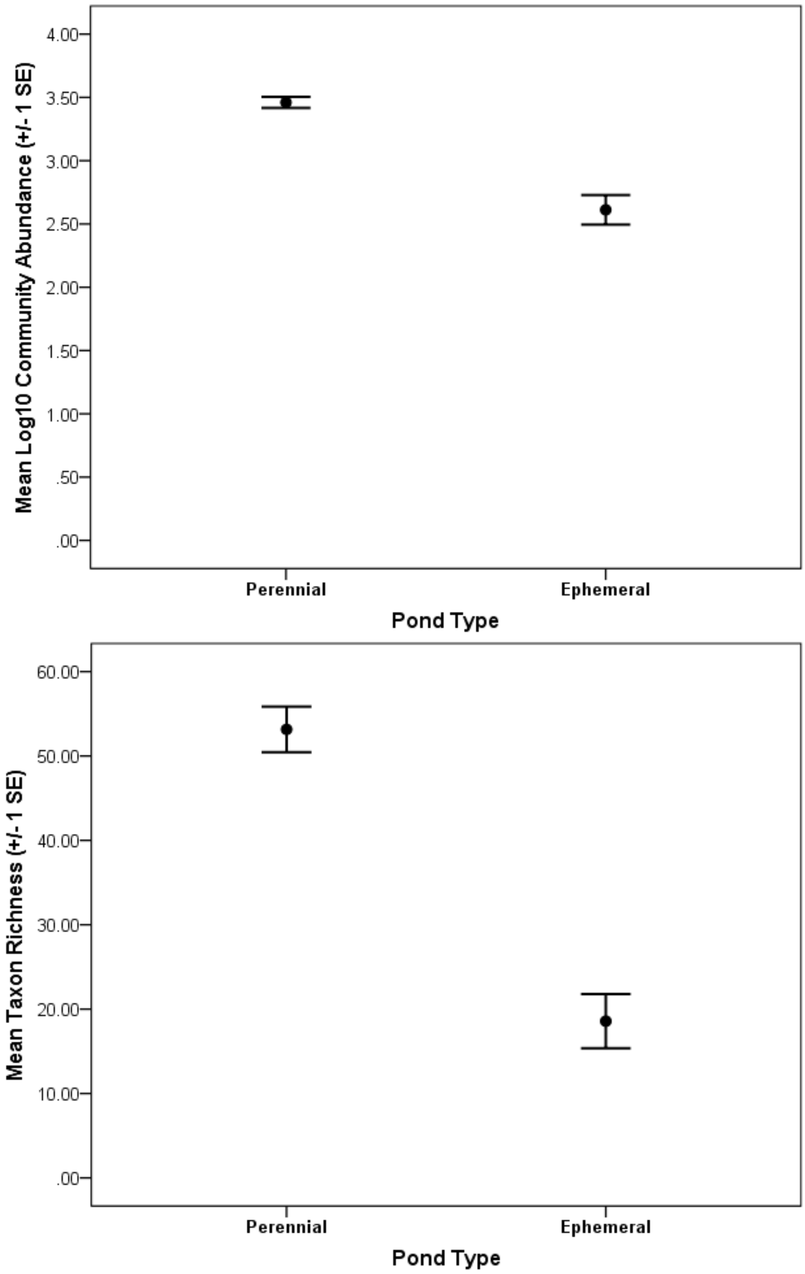

Figure 6.2 - Log_{10} community abundance (a) and taxon richness (b) within ephemeral and perennial meadow ponds

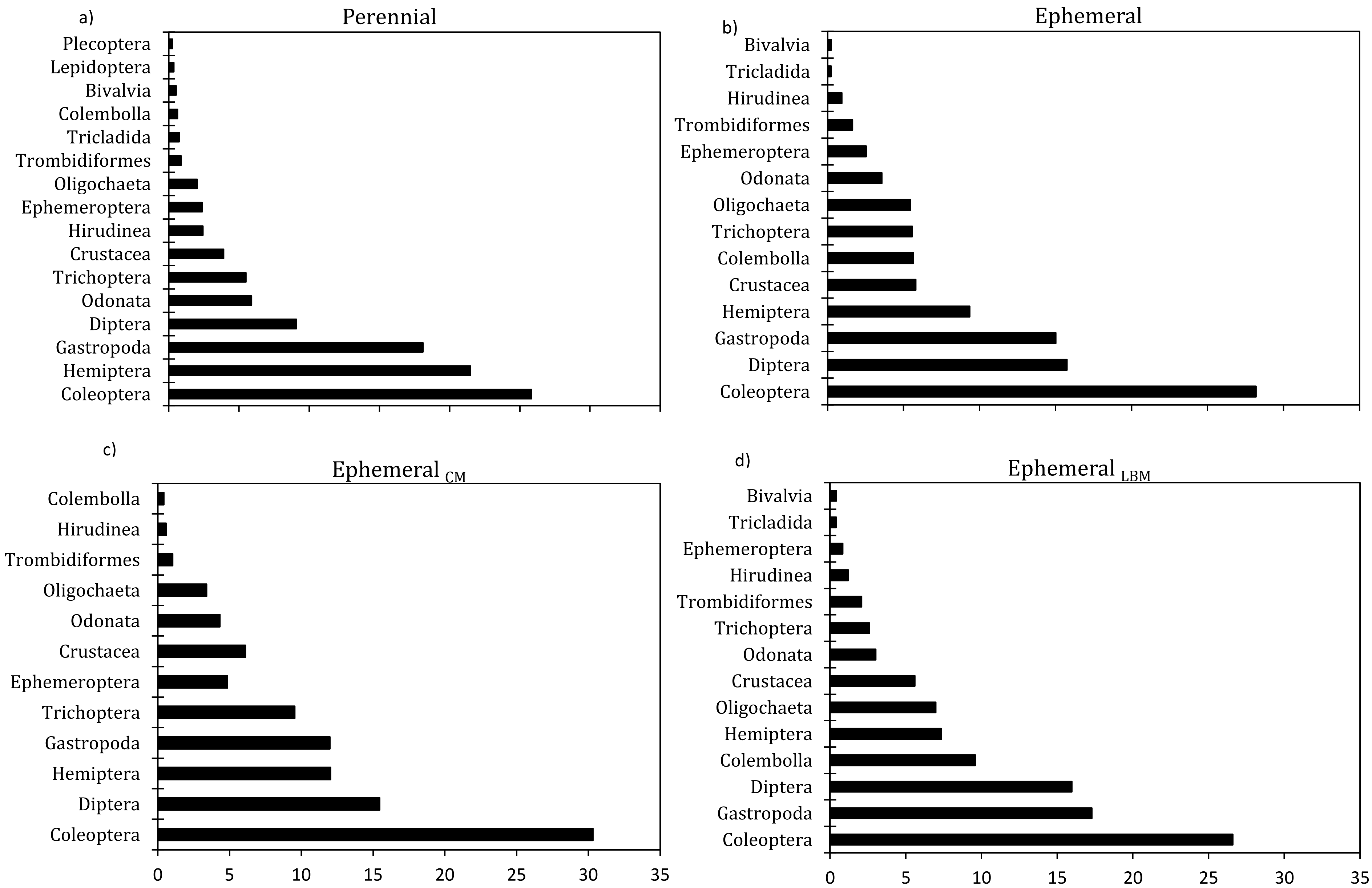

Figure 6.3 - Mean percentage of taxa per pond from the main macroinvertebrate orders: a) perennial meadow ponds, b) ephemeral meadow ponds, c) CM ephemeral ponds and d) LBM ephemeral ponds

Perennial ponds had a significantly higher Shannon Wiener diversity index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha than ephemeral ponds from the two meadow landscapes (Figure 6.4). The Berger Parker Dominance index was significantly higher in ephemeral meadow ponds than perennial meadow ponds demonstrating that the macroinvertebrate communities within ephemeral ponds were dominated by a few taxa (notably Chironomidae) (Figure 6.4). Mean taxon richness was higher in CM ephemeral ponds (22) than LBM ephemeral ponds (16) although it was not statistically significant ($p>0.05$). No significant difference in community abundance ($\log_{10}$), Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha was recorded between ephemeral ponds in the CM and LBM study sites.

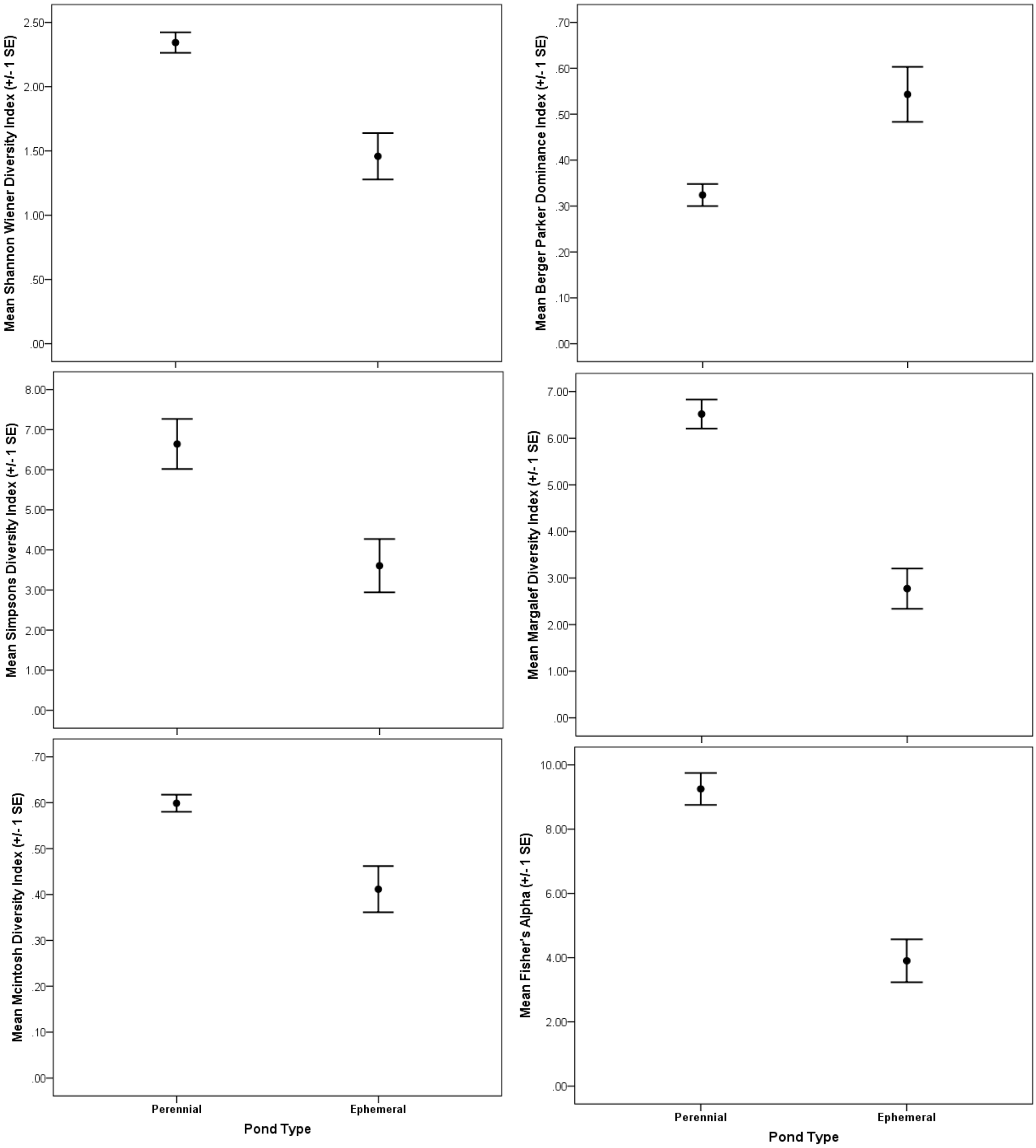

Figure 6.4 - Alpha diversity indices: Shannon Wiener diversity index, Berger Parker Dominance index, Simpson diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha within ephemeral and perennial meadow ponds

6.2.2 Meadow pond mesohabitat macroinvertebrate diversity

A wide range of mesohabitats were present within perennial and ephemeral meadow ponds, but for the purposes of this chapter they were placed into 3 categories; open water (OW), emergent macrophytes (EM) and submerged macrophytes (SM). The most frequently occurring mesohabitat was open water, occurring 63 times across all three sampling seasons. Submerged macrophyte habitats occurred 54 times and emergent macrophyte habitats were present 29 times across all three sampling seasons.

Nested ANOVA identified a significant difference in community abundance, taxon richness, Shannon Wiener diversity index, Margalef diversity and Fisher's alpha among ephemeral and perennial meadow pond mesohabitats (Table 6.3). However, there was no significant difference in Berger Parker Dominance index, Simpsons diversity index and McIntosh diversity index among the mesohabitats in the meadow ponds (Table 6.3). The *post hoc* Sidak test indicated emergent macrophyte and submerged macrophyte mesohabitats supported significantly higher taxon richness, Margalef diversity and Fisher's alpha values than open water in the meadow ponds (Figure 6.5). Only emergent macrophyte mesohabitats recorded significantly higher community abundance and Shannon Wiener diversity values than open water habitats from the meadow ponds (Figure 6.5).

Community abundance, taxon richness, Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index, and Fisher's alpha values were not recorded to be significantly different among the mesohabitats in ephemeral ponds from LBM and CM (Nested ANOVA $p>0.05$).

Table 6.3 - Nested ANOVA between log_{10} community abundance, taxon richness and alpha diversity indices and mesohabitat nested within pond type. Significant values (p≤0.05) are presented in bold.

		Pond Type (Mesohabitat)
Log_{10} community abundance	*F.*	3.564
	P.	**0.008**
Taxon richness	*F.*	10.220
	P.	**0.000**
Shannon Wiener diversity index	*F.*	2.873
	P.	**0.025**
Berger Parker Dominance index	*F.*	1.309
	P.	0.270
Simpsons diversity index	*F.*	1.354
	P.	0.253
Margalef diversity index	*F.*	11.186
	P.	**0.000**
McIntosh diversity index	*F.*	1.374
	P.	0.246
Fisher's alpha	*F.*	10.557
	P.	**0.000**

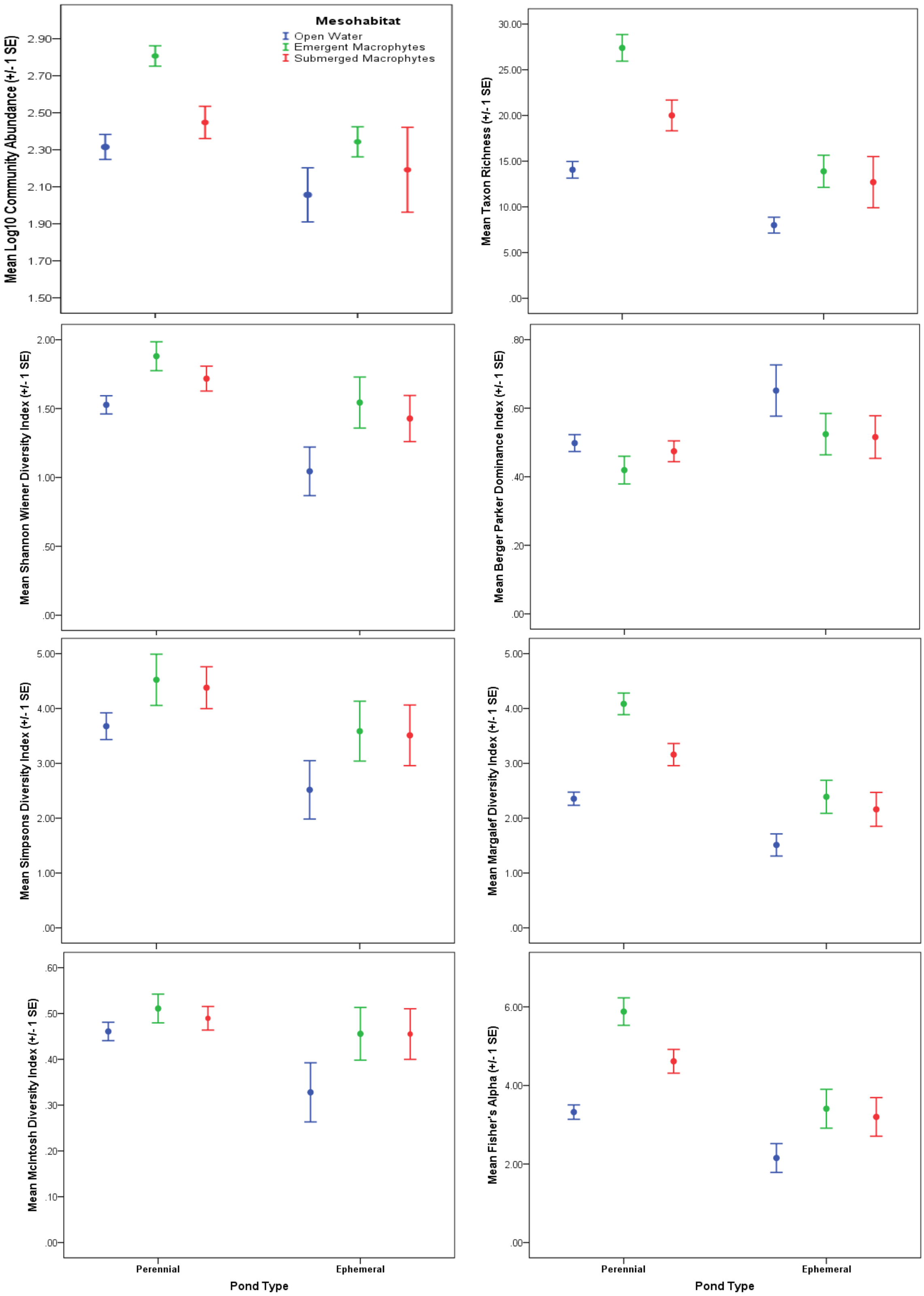

Figure 6.5 - Comparisons of the $\log_{10}$ community abundance, taxon richness, Shannon Wiener diversity index, Berger Parker Dominance index, Simpsons diversity index, Margalef diversity index, McIntosh diversity index and Fisher's alpha within the different mesohabitats: open water, emergent macrophytes and submerged macrophytes from the perennial and ephemeral meadow ponds

6.2.3 Pond physicochemistry

Pond physicochemical parameters were tested for a normal distribution; area, depth, pond margin shaded, surface water shaded, submerged, emergent, and floating macrophytes were log_{10} transformed following inspection of the frequency distribution plots. Considerable heterogeneity of the physicochemical conditions was recorded among ephemeral and perennial ponds from the two meadow sites (Table 6.4). Perennial ponds had significantly deeper pond basins than ephemeral ponds (ANOVA $F_{1, 33}$=37.652; p<0.001). Perennial ponds were slightly alkaline and pH was significantly higher than that of ephemeral ponds (ANOVA $F_{1, 33}$=11.122; p<0.002). Conductivity was also significantly higher in perennial than ephemeral ponds (ANOVA $F_{1, 33}$=18.284; p<0.001). The proportion (%) of the pond covered by emergent macrophytes was significantly higher in ephemeral ponds compared to perennial ponds (ANOVA $F_{1, 33}$=5.523; p<0.025) (Table 6.4). Surface area, surface water shaded, pond margin shaded, submerged macrophytes and dissolved oxygen did not differ significantly between ephemeral and perennial ponds (p>0.005). Fish were present in 19 of the 20 perennial ponds, but were absent from all ephemeral ponds. This is almost certainly because the seasonal drying of the basin prevented fish populations from becoming established.

Ephemeral ponds from CM had slightly alkaline pH values which were found to be significantly higher than that of LBM ephemeral ponds (ANOVA $F_{1, 13}$=85.638; p<0.001) (Table 6.4). Mean dissolved oxygen was significantly higher in CM ephemeral ponds than LBM ephemeral ponds (ANOVA $F_{1, 13}$=31.857; p<0.001) (Table 6.4). The other physicochemical parameters were not significantly different between ephemeral ponds from CM and LBM.

Table 6.4 - Summary table (mean and range) of measured environmental variables for ephemeral and perennial ponds across the two meadow sites and only the ephemeral ponds from CM and LBM; SWS: pond surface water shaded, PMS: pond margin shaded, EM: emergent macrophytes, SM: submerged macrophytes, FM: floating macrophytes, COND: conductivity, DO: dissolved oxygen

	Perennial			**Ephemeral**			**Ephemeral $_{CM}$**			**Ephemeral $_{LBM}$**		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Area (m^2)	828.2	12.5	11922.7	229.6	10	1258	91.5	11.9	315	333.2	10.3	1258
Depth (cm)	64.8	26.5	200	25.5	8	100	11.9	8	22	35.7	15	100
SWS (%)	8.7	0	93.3	2.9	0	30	1.7	0	10	3.8	0	30
PMS (%)	9.7	0	96.7	7.3	0	85	2.8	0	16.7	10.6	0	85
EM (%)	11	1	45	37.1	0	86.7	28.7	0	66.7	43.3	0	86.7
SM (%)	24.5	3.7	73	35.7	0	100	29.8	0	72.5	40.2	5	100
pH	8.3	7.2	9.1	7.5	6.4	8.7	8.4	7.8	8.7	6.9	6.4	7.2
COND	772.9	422.3	1494	418.2	80	987	441.5	353.5	521	400.7	80.0	987.0
DO (%)	87.9	28.3	111.9	77.9	55	120	97.5	78.5	120	63.3	55.5	71.5

6.2.4 Community heterogeneity

A significant difference in the macroinvertebrate community composition within ephemeral and perennial ponds from the floodplain meadows was identified (ANOSIM $p<0.005$). The NMDS biplot (2D stress: 0.14) demonstrates a clear distinction between ephemeral and perennial ponds (Figure 6.6). The perennial ponds were tightly clustered towards the left of the NMDS ordination plot indicating that there was considerable overlap (similarity) in macroinvertebrate taxa among perennial ponds. In contrast, ephemeral ponds were widely dispersed throughout the NMDS biplot indicating that there was significant community heterogeneity among ephemeral pond invertebrate assemblages (Figure 6.6). The perennial ponds most tightly clustered in the NMDS ordination plot were located on Cossington Meadow in close proximity to each other and were directly adjacent to the River Soar (Figure 6.6).

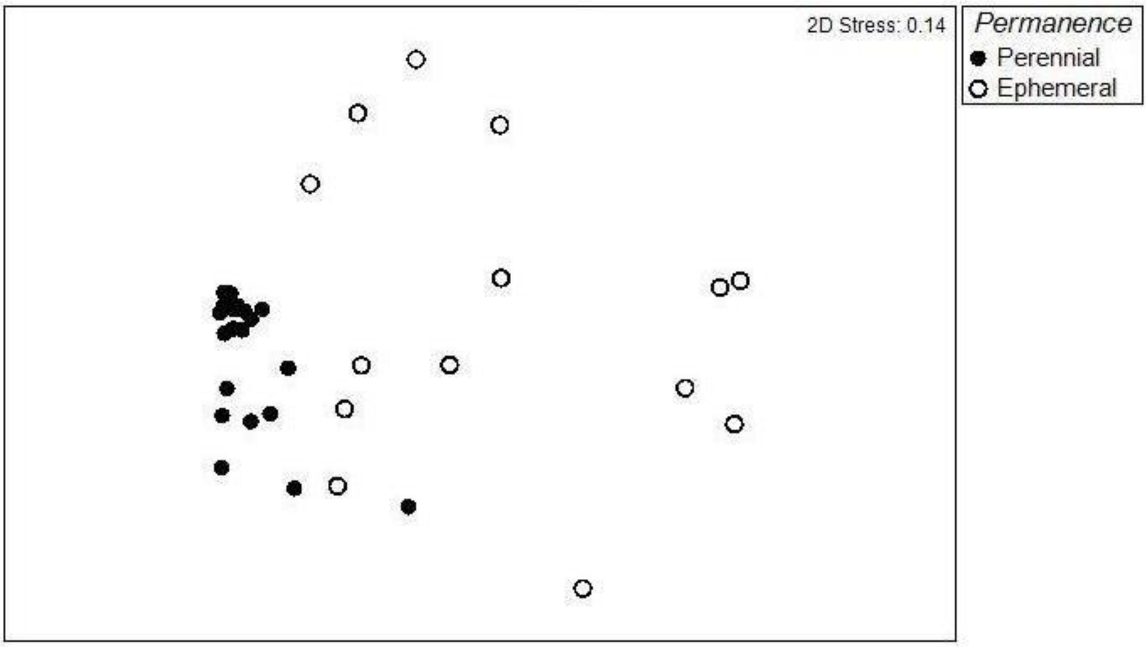

Figure 6.6 - NMDS ordination biplot of macroinvertebrate composition of the ephemeral and perennial floodplain meadow ponds

Macroinvertebrate communities were identified to be significantly different between ephemeral ponds in both CM and LBM (ANOSIM $p<0.01$). A clear distinction between the ephemeral ponds from LBM and CM is demonstrated within the NMDS ordination (2D stress: 0.15) (Figure 6.7). Ephemeral ponds from CM were located towards the right of the ordination space whilst LBM ephemeral ponds were situated towards the left of the ordination plot (Figure 6.7). Individual ephemeral ponds from LBM and CM were widely dispersed in the ordination space indicating that there was substantial dissimilarity among the communities within ephemeral ponds (Figure 6.7).

b)

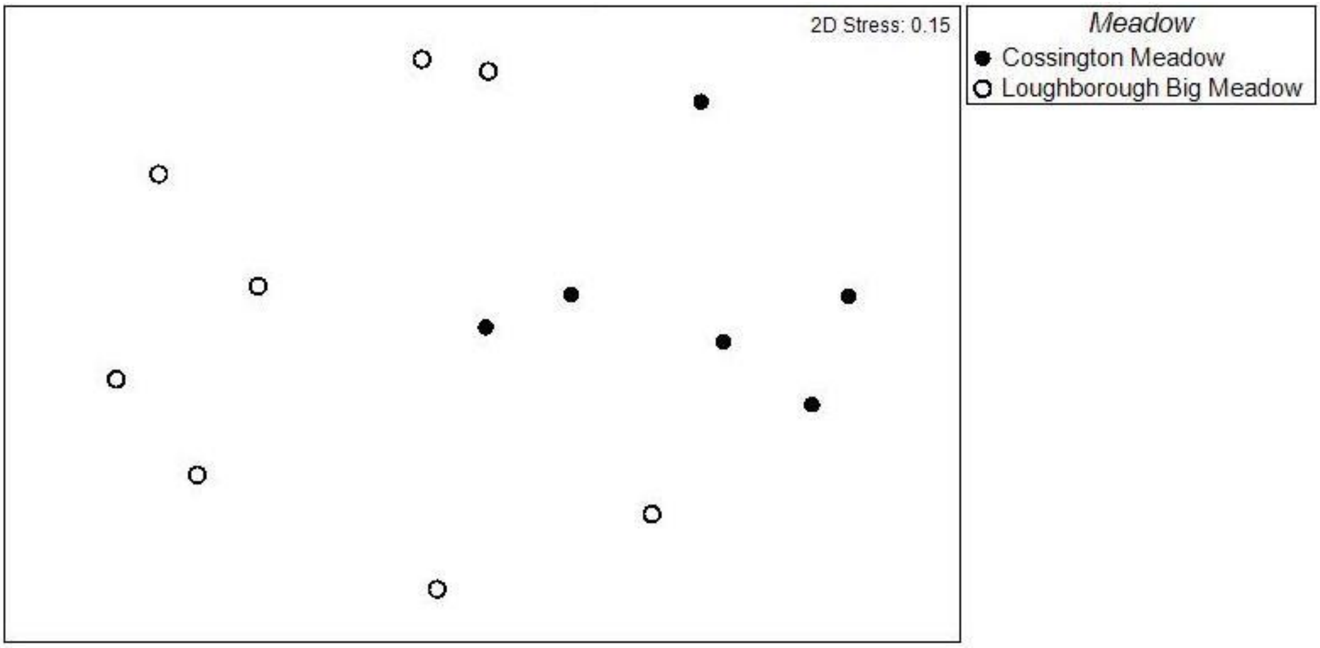

Figure 6.7 - NMDS ordination biplot of macroinvertebrate composition of the ephemeral ponds within Cossington Meadow and Loughborough Big Meadow

Ephemeral meadow ponds had a significantly lower Jaccard's Coefficient of Similarity (C_j) (ANOVA $F_{1,\ 280}$=219.623; $p<0.001$) and Sørensen Similarity (*QS*) (ANOVA $F_{1,\ 280}$=253.282; $p<0.001$) values compared to perennial meadow ponds (Table 6.5). This suggests that macroinvertebrate communities within ephemeral ponds were heterogeneous whilst perennial ponds supported more similar invertebrate assemblages (correlating with the NMDS analysis). Similar C_j and *QS* scores were recorded between ephemeral ponds from CM or LBM meadows (Table 6.5). Ephemeral ponds from CM and LBM both had low mean C_j and *QS* values indicating greater community dissimilarity within the ephemeral ponds (Table 6.5).

Table 6.5 - Mean Jaccard's Coefficient (C_j) of Similarity and Sørensen Similarity (QS) index for; perennial and ephemeral meadow ponds, ephemeral ponds in CM and LBM and all sample sites combined (region)

	Perennial	**Ephemeral**	**Ephemeral $_{CM}$**	**Ephemeral $_{LBM}$**	**Region**
Mean Jaccard's Coefficient of Similarity	0.39	0.17	0.23	0.2	0.25
Mean Sørensen Similarity index	0.55	0.28	0.37	0.32	0.37

SIMPER analysis indicated that two gastropods (Physidae and *Lymnaea peregra*), and two Corixidae (*Sigara dorsalis* and Corixidae nymph) contributed most to the community dissimilarity between ephemeral and perennial ponds (Table 6.6). All four taxa were abundant in the majority of perennial ponds but were absent from most ephemeral ponds. The non-biting midge (Chironomidae), two Coleoptera larvae (Dytiscidae and Hydrophilidae) and a gastropod (*Anisus leucostoma*) contributed most to the heterogeneity between ephemeral pond macroinvertebrate assemblages in CM and LBM (Table 6.6).

Table 6.6 - Summary of top 4 aquatic macroinvertebrate taxa identified by SIMPER as contributing most to community dissimilarity between: a) perennial and ephemeral ponds and; b) ephemeral ponds in CM and LBM. Note - number in parenthesis indicates the percentage contribution to pond dissimilarity. n = number of pond sites and j = total number of taxa. x/x represents the total number of taxa common between the pond types.

a)	**Meadow Perennial**	**Meadow Ephemeral**
Meadow Perennial	*n = 20* *j = 164*	*P/E = 84*
Meadow Ephemeral	Physidae (3.7) *Lymnaea peregra* (3.5) *Sigara dorsalis* (3.2) Corixidae nymph (2.9)	*n = 14* *j = 93*

b)	**b) CM Ephemeral ponds**	**LBM Ephemeral ponds**
CM Ephemeral ponds	*n = 6* *j = 66*	*CM/LBM = 40*
LBM Ephemeral ponds	Chironomidae (6.6) Dytiscidae larvae (5.5) *Anisus leucostoma (5.3)* Hydrophilidae larvae (4.3)	*n = 8* *j =67*

6.2.5 Macroinvertebrate predation/dispersal

Statistical analysis was undertaken to examine the difference in the proportion of predators/non-predators and actively/passively dispersing macroinvertebrate taxa between perennial and ephemeral pond communities. The dispersal and feeding type attributed to individual macroinvertebrate taxa in this analysis was based on the classification of macroinvertebrate biological traits presented by Tachet *et al.* (2003) and Merritt and Cummins (1996). Within ephemeral and perennial ponds non-predatory taxa (including; Gastropoda, Ephemeroptera, and Hydrophilidae taxa) comprised a greater mean proportion of the macroinvertebrate community than predatory macroinvertebrate taxa (Figure 6.8). Macroinvertebrate communities within ephemeral meadow ponds had a significantly higher mean proportion of non-predatory taxa compared to perennial meadow ponds (perennial pond: 58% ephemeral pond: 77% (Kruskal-Wallis Test $p<0.005$)) (Figure 6.8). Consequently, perennial pond communities contained a greater mean proportion of predatory taxa than ephemeral ponds (perennial pond: 42% ephemeral pond: 23%). The average proportion of taxa that were non-predatory was higher among ephemeral ponds in LBM than CM although this was not statistically significant (Figure 6.8).

Actively dispersing invertebrates (taxa with the ability of flight) comprised a greater proportion the invertebrate community within ephemeral and perennial ponds than passively dispersing taxa. There was a greater proportion of actively dispersing taxa in perennial ponds than ephemeral pond communities (Figure 6.9), although the proportion of actively and passively dispersing taxa was not statistically different between ephemeral and perennial ponds (Kruskal-Wallis Test $p>0.05$). Macroinvertebrate communities within ephemeral ponds in CM contained a higher proportion of actively dispersing taxa than ephemeral ponds in LBM (CM: 65.3% LBM: 44.7% (Figure 6.9); although this was not statistically significant.

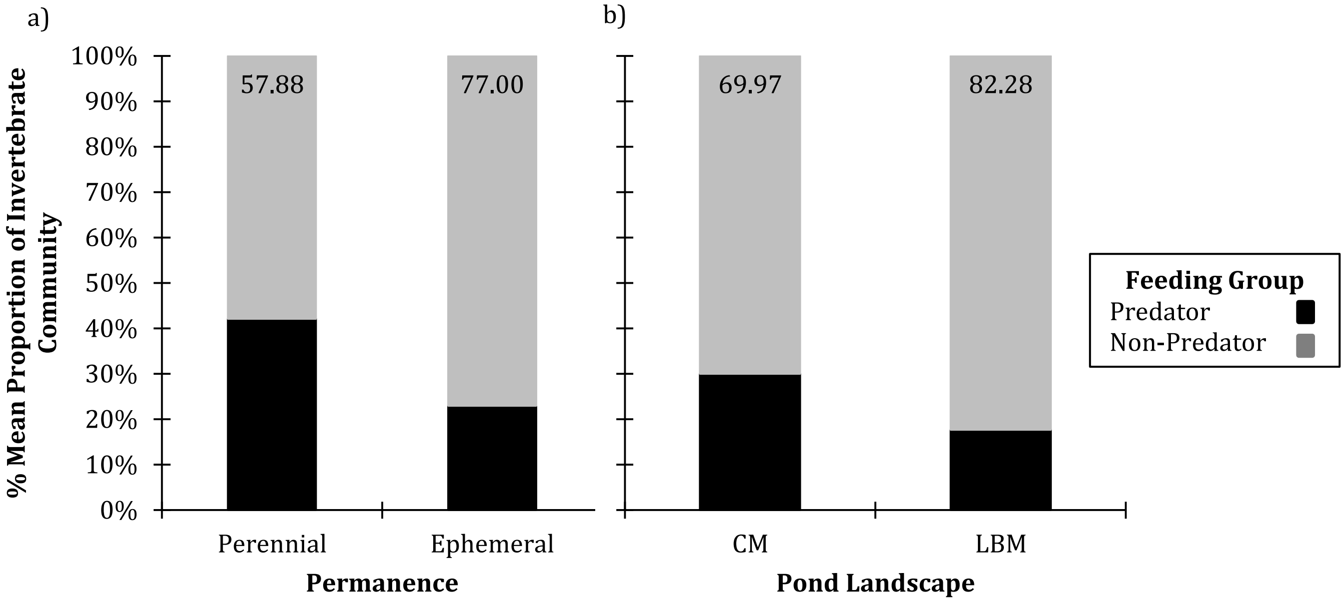

Figure 6.8 - Proportion (mean %) of predator and non-predator invertebrate taxa per pond in: a) ephemeral and perennial ponds and b) ephemeral ponds in Cossington Meadow (CM) and Loughborough Big Meadow (LBM)

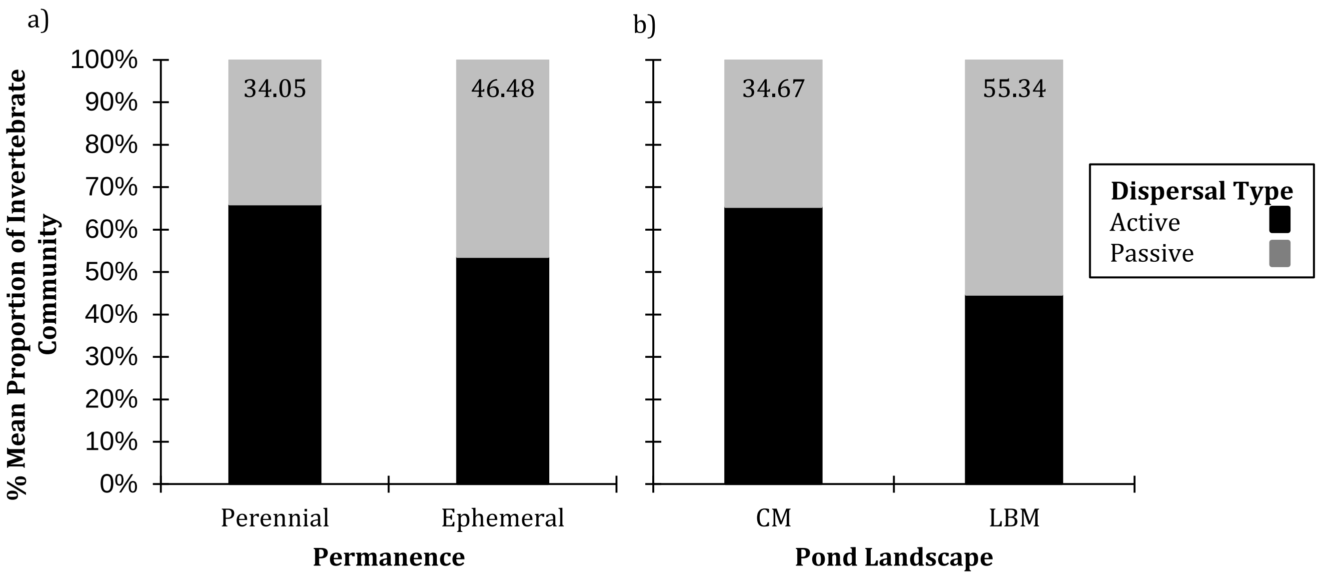

Figure 6.9 - Proportion (mean %) of actively and passively dispersing invertebrate taxa per pond in: a) ephemeral and perennial ponds and b) ephemeral ponds in Cossington Meadow (CM) and Loughborough Big Meadow (LBM).

6.2.6 Conservation value

A total of 7 taxa (all Coleoptera) with UK conservation designations were recorded from the meadow ponds within 8 perennial ponds and 5 ephemeral ponds. *Helophorus dorsalis* (Hydrophilidae: *Helophorus*) and *Paracymus scutellaris* (Hydrophilidae: *Paracymus*) were only recorded from ephemeral ponds whilst *Berosus luridus* (Hydrophilidae: *Berosus*), *Ilybius subaeneus* (Dytiscidae: *Ilybius*) and *Agabus conspersus* (Dytiscidae: *Agabus*) were recorded only from perennial ponds (Table 6.7). *Hygrotus nigrolineatus* (Dytiscidae: *Hygrotus*) and *Rhantus frontalis* (Dytiscidae: *Rhantus*) were recorded within both ephemeral and perennial ponds (Table 6.7). All 7 taxa with conservation designations were recorded from CM whereas only *Rhantus frontalis* was recorded from LBM.

Table 6.7 - Macroinvertebrate taxa of conservation interest with their designations and location/s

Family	Species	Conservation Designation	Sample Location/s
Dytiscidae	*Agabus conspersus*	Nationally Scarce Nationally Notable	1 Perennial Pond
Dytiscidae	*Hygrotus nigrolineatus*	Nationally Scarce Nationally Notable	3 Perennial Ponds 1 Ephemeral Pond
Dytiscidae	*Ilybius subaeneus*	Nationally Scarce	1 Perennial Pond
Dytiscidae	*Rhantus frontalis*	Nationally Scarce Nationally Notable	4 Perennial Ponds 2 Ephemeral Ponds
Hydrophilidae	*Berosus luridus*	IUCN Lower Risk - Near Threatened Nationally Notable	1 Perennial Pond
Hydrophilidae	*Helophorus dorsalis*	Nationally Scarce Nationally Notable	1 Ephemeral Pond
Hydrophilidae	*Paracymus scutellaris*	Nationally Scarce	1 Ephemeral Pond

6.2.6.1 UK Post-2010 Biodiversity Framework (England) Pond Priority Habitat (PPH)

Becoming a Pond Priority Habitat in England under the UK Post-2010 Biodiversity Framework (previously the Biodiversity Action Plan (Natural England, 2014b)), is the main process through which ponds can receive some statutory protection, detailed conservation/management plans and consideration from policy makers (Williams *et al.,* 2010). Using the PPH pond assessment criteria (BRIG, 2008) a total of 11 perennial meadow ponds (31% of all meadow ponds sampled) would qualify as a PPH but no ephemeral ponds met these requirements. All 11 perennial ponds supported macroinvertebrate communities with >50 taxa when all sampling dates were considered.

6.2.6.2 Community Conservation Index (CCI)

Macroinvertebrate communities within 11 meadow ponds were of high (6 ponds) or very high (5 ponds) conservation value (Table 6.8). No significant difference in Community Conservation Index scores were recorded between perennial or ephemeral meadow ponds ($p>0.05$) when faunal data from all three sampling dates was combined. This suggests that although ephemeral ponds support a lower diversity of taxa compared to perennial ponds they supported similar numbers of rare and less commonly occurring taxa. A total of 3 perennial ponds had a very high conservation value and 5 had a high conservation value whilst 2 ephemeral meadow ponds demonstrated a very high conservation value and 1 recorded a high conservation value (Table 6.8). The majority of ephemeral ponds were of a moderate (5 ponds) or fairly high (4 ponds) conservation value whereas perennial meadow ponds were dominated by ponds with a fairly high (7 ponds) or high (5 ponds) conservation value (Table 6.16). The CCI scores did not differ significantly ($p>0.05$) between ephemeral ponds in LBM and CM. However, there were 2 ephemeral ponds with a very high conservation value from CM whereas only one ephemeral pond from LBM demonstrated a high conservation value and was dominated by ephemeral ponds with a low conservation value (Table 6.8).

To enable a comparison with other pond biodiversity research/literature that are restricted to a single season macroinvertebrate survey the Community Conservation Index was assessed for each sampling season (Armitage *et al.,* 2012). Throughout each season there were at least 2 ephemeral or perennial ponds that were of a high or very conservation value (Table 6.8). The spring season had the greatest number of ponds with high/very high conservation value (spring: 5 ponds, autumn: 3 ponds, and summer: 2 ponds) although, there was no overall significant difference in CCI scores between the spring, summer and autumn seasons ($P >0.05$).

Table 6.8 - Individual seasons and total (combined season) Community Conservation Index (CCI) scores from the 25 meadow pond sites. CMP - Cossington Meadow perennial; CME - Cossington Meadow ephemeral; LMP - Loughborough Big Meadow perennial; LME - Loughborough Big Meadow ephemeral (0-5 low conservation value; >5-10 moderate conservation value; >10-15 fairly high conservation value; >15-20 high conservation value and >20 very high conservation value). Very high CCI scores are presented in bold italics and high CCI scores and presented in bold.

	Spring	Summer	Autumn	Total
	Perennial			
CMP1	4.5	7.4	8	8.5
CMP2	3.5	7	10.4	10.6
CMP3	13.4	9	9.4	14.4
CMP4	9.5	7.1	8.3	8.7
CMP5	4.8	8.1	12.1	13.3
CMP6	14.3	8.6	12.5	13.8
CMP7	8.5	9.3	9.1	9.9
CMP8	14	11.5	15	**15.2**
CMP9	**18**	4.2	14.6	***23.4***
CMP10	14.4	8.8	**15**	**15.5**
CMP11	***20.6***	8.5	14.6	***24.3***
CMP12	12.1	10.9	14.4	**15.4**
CMP13	4	4.5	8.5	8.9
CMP14	**18.9**	6.7	9.1	**15**
CMP15	14.8	6.9	8.5	12.4
CMP16	13.4	12.9	8.2	13.2
CMP17	14	12.2	8.6	13.3
CMP18	12.8	7.8	**15.7**	**15.8**
CMP19	14.9	7	11.6	***24.5***
LMP1	4.3	1.1	2.4	3.8
Mean	11.7	8	10.8	14
	Ephemeral			
CME1	1	**19.6**	*	14.9
CME2	5.6	7.7	*	9.3
CME3	1.1	***25.8***	*	***21.9***
CME4	***28.2***	14.8	12.3	***23.8***
CME5	12.7	3.6	7	11.7
CME6	10	5	10	9.6
LME1	*	14	*	14
LME2	*	4	*	4
LME3	*	8.3	13.6	12.9
LME4	*	8.6	**17.5**	**16.2**
LME5	8.2	3.4	6.3	6.9
LME6	*	8.9	*	8.9
LME7	*	8.9	*	8.3
LME8	*	3.7	*	3.7
Mean	9.5	9.7	11.1	11.9

*Pond dry in that season

6.3 Discussion

6.3.1 Macroinvertebrate diversity

The results from this chapter indicate that the ephemeral meadow pond habitats examined supported significantly lower aquatic macroinvertebrate taxon richness than perennial meadow pond sites and provides evidence to accept the first hypothesis;

> *H_1: Macroinvertebrate diversity will be higher in perennial floodplain meadow ponds than ephemeral floodplain meadow ponds.*

Perennial ponds supported a mean taxon richness of 53 whilst ephemeral ponds recorded a mean richness of 19 taxa in this study. A study of 10 ephemeral ponds in Oxfordshire, UK, reported an average of 17 taxa per pond whilst 29 perennial ponds in the same study supported an average of 35 aquatic macroinvertebrate taxa (Collinson *et al.,* 1995). Near Rome, Italy, 8 perennial ponds supported significantly greater macroinvertebrate richness than 13 ephemeral ponds (Della Bella *et al.,* 2005). However, Bazzanti *et al.* (2003) did not record any significant difference in macroinvertebrate richness between ephemeral and perennial ponds. This study and others (Collinson *et al.,* 1995; Nicolet*,* 2001; Della Bella *et al.,* 2005) does not demonstrate that ephemeral ponds are ecologically impoverished/unimportant, only that they support fewer aquatic invertebrates compared with perennial ponds (Collinson *et al.,* 1995). It is important to acknowledge that riparian fauna is often not included in ephemeral pond biodiversity research (Della Bella *et al.,* 2005). Only examining the aquatic invertebrate communities in ephemeral ponds could lead to an underestimation of their overall contribution to biodiversity (Collinson *et al.,* 1995; Drake, 2001). A large number of terrestrial or semi-aquatic macroinvertebrates such as ground beetles (Coleoptera: Carabidae) or rove beetles (Coleoptera: Staphylinidae) and spring tails (Insecta: Collembola) utilise ponds and could contribute a significant proportion of the diversity of ephemeral ponds. A rich diversity of ground and rove beetles, (including a large number of beetles with a conservation designation), were recorded from lowland ephemeral ponds across the UK and had an equivalent diversity to that of the aquatic beetles recorded (Lott, 2001).

In this study, vegetated zones within and at the margins of ephemeral and perennial meadow ponds supported higher invertebrate diversity than unvegetated zones. Similar findings were reported by Bazzanti *et al.* (2010) and indicated that unvegetated zones were significantly species poorer than vegetated zones in ephemeral ponds. The benefits and influence of aquatic macrophyte habitats for macroinvertebrates have been well documented (Biggs, 1994a; Williams *et al.,* 1999; Della Bella *et al.,* 2005).

A significant proportion of the regional aquatic macroinvertebrate taxa were represented among ephemeral and perennial floodplain meadow ponds (173 taxa). The total ephemeral pond biodiversity (93 taxa) was markedly lower than that recorded in forested ephemeral ponds in Southern England (174 taxa), ephemeral ponds in the New Forest (Hampshire) and Lizard Peninsula (Cornwall) (165 taxa) and lowland ephemeral ponds across the UK (242 taxa) (Nicolet *et al.,* 2004; Bilton *et al.,* 2009; Armitage *et al.,* 2012). However, direct comparison of biodiversity between studies is not straightforward since the taxonomic resolution varies between studies. Diptera were only identified to family level in this study, whilst Armitage et al. (2012) and Bilton et al. (2009) resolved Diptera to genus or species level. As a result, the true macroinvertebrate biodiversity of the floodplain ponds examined in the current investigation is almost certainly significantly higher than that reported. Most of the macroinvertebrate groups were represented in ephemeral ponds in this study, especially Coleoptera, mirroring to the findings of Nicolet *et al.* (2004). At an individual scale aquatic macroinvertebrate diversity was highly variable ranging from 5 to 40 taxa in ephemeral ponds. This almost certainly reflects the wide variability in hydroperiod length and physicochemical conditions recorded within ephemeral ponds. Previous research has demonstrated that aquatic invertebrate richness increases as the length of the wet phase increases (Spencer *et al.,* 1999; Brooks, 2000; Boix *et al.,* 2001; Eitam *et al.,* 2004; Tarr *et al.,* 2005). Two non-native taxa were recorded within the floodplain meadow ponds; *C. pseudogracilis* and *P. antipodarum*. Both species are widespread and common throughout the UK (Macan, 1977; Gledhill *et al.,* 1993) but both had a much greater incidence and abundance in perennial ponds than ephemeral ponds. The periodic desiccation of ephemeral ponds is most likely to have prevented the establishment of large populations of these two invasive species.

The results from this chapter illustrate that a similar proportion of actively and passively dispersing macroinvertebrate taxa were recorded between the ephemeral and perennial ponds which provides evidence to partially reject the third hypothesis;

H_3: Actively dispersing and non-predatory taxa will constitute a greater proportion of the invertebrate communities within ephemeral floodplain meadow ponds than in perennial ponds.

These findings appear to contradict with the findings of a number of other ephemeral pond studies which recorded a greater incidence of highly mobile taxa (actively dispersing) in ephemeral ponds compared to perennial ponds (Nicolet, 2001). The greater proportion of non-mobile taxa in the ephemeral floodplain meadow ponds studied may be the result of regular inundation of flood water and the consequent mixing of water over the floodplain which facilitates the migration of passively dispersing taxa from perennial habitats to ephemeral pond habitats (Williams *et al.,* 2003). The hydrological connectivity of ephemeral ponds to perennial ponds has been suggested to promote the colonization of a number of perennial macroinvertebrate taxa in ephemeral ponds of floodplains in the UK (Nicolet *et al.,* 2004). Rundle *et al*. (2002) suggested that there was a non-random distribution of actively dispersing invertebrates which pursue more stable perennial water bodies whilst the distribution of passively dispersing microcrustacea were influenced more by their adaptations to the ephemeral habitat.

A significantly greater proportion of the macroinvertebrate community in ephemeral ponds were non-predatory taxa compared to perennial pond communities. Habitat duration (length of wet phase) has been demonstrated to be an important regulator of predatory taxa in ephemeral ponds (Bilton *et al.,* 2001; Schneider, 1999). Ephemeral ponds with shorter hydroperiods (many of the ponds in this study had hydroperiods of <4months) do not often support vertebrate predators (e.g., fish) and reduces the occurrence of large invertebrate predators (e.g., Coleoptera/Odonata) as predaceous taxa often have generation times that are too long to be completed in short hydroperiod ponds (Bilton *et al.,* 2001; De Meester *et al.,* 2005; Williams, 2006). This can significantly reduce the predation pressure in ephemeral ponds and enable a greater diversity of non-predatory macroinvertebrates to colonize including species of Gastropoda, Crustacea, Ephemeroptera and Diptera which often demonstrate rapid growth/desiccation resistant eggs and other adaptations to survive in ephemeral ponds (see Chapter 2.2.5) (Wiggins, 1980; Williams, 1985; Bratton and Fryer, 1990; Welborn, 1996; Drake, 2001; Brendonck *et al.,* 2002; Nicolet *et al.,* 2004; Williams, 2006).

6.3.2 Community heterogeneity

Despite the close proximity of ephemeral and perennial meadow ponds and the inundation of the ponds by River Soar flood water, they demonstrated substantial community heterogeneity providing evidence to support the second hypothesis;

> *H_2: Ephemeral ponds will support significantly different macroinvertebrate communities compared to perennial ponds*.

It has been widely documented that ephemeral ponds frequently support distinct communities compared to perennial waterbodies (Collinson *et al.,* 1995; Nicolet, 2001; Della Bella *et al.,* 2005). Despite regular inundation from flood water a number of taxa were only recorded from ephemeral ponds. *A. Leucostoma* (Gastropoda: Planorbidae) *L. trunculata* (Gastropoda: Lymnaeidae), *L. aricula, L. griseus* and *L. centralis* (Trichoptera: Limnephilidae) are all ephemeral pond specialists and not often recorded in permanent waterbodies (Macan, 1977; Edington and Hildrew, 1995). Most trichopteran taxa recorded in ephemeral ponds were from the family Limnephilidae which typically emerge as adults before the pond basin dries and wait for the pond to refill during the autumn before laying their eggs (Bratton, 1990). *Libelulla quadrimaculata* (Odonata: Libellulidae) which have a longer larval phase were also recorded in the ephemeral meadow ponds. This and other Odonata species have been reported to enter a state of diapause in the pond sediment (Corbet, 1999). Perennial ponds had relatively similar community assemblages whilst ephemeral ponds displayed a large dissimilarity in community compositions. The invertebrate community dissimilarity displayed by ephemeral ponds is almost certainly a reflection of the wide variability in hydroperiod length and physicochemical conditions recorded within the ephemeral floodplain meadow ponds. The results of this study also indicate that many taxa recorded from ephemeral ponds are also supported in perennial pond habitats. Such findings were also reported for other ephemeral pond studies (Collinson *et al.,* 1995; Bazzanti *et al.,* 2003; Nicolet *et al.,* 2004; Bilton *et al.,* 2009). The high density of ephemeral and perennial ponds and regular flooding by the River Soar may have increased the frequency of stochastic dispersal events (Nicolet *et al.,* 2004). Dipteran taxa were common and abundant in ephemeral ponds which is consistent with other ephemeral pond research (Boix *et al.,* 2001). Even though few adaptive strategies (to manage the periodic drying) have been noted for Diptera in UK ephemeral ponds they have all the prerequisites required for surviving in ephemeral pond habitats; reaching maturity before the system dries, ability to rapidly recolonize via aerial dispersal and mechanisms to survive dry period (Drake, 2001).

6.3.3 Conservation value

The importance of pond habitats for aquatic biodiversity has been acknowledged in the academic literature (Oertli *et al.,* 2009; Williams *et al.,* 2003) and is reflected in the consideration of perennial ponds in policy decisions (BRIG, 2008). Whilst ephemeral ponds in Mediterranean regions have received some legislative protection (BRIG, 2008; Oertli *et al.,* 2009), the acknowledgement of ephemeral ponds to ecological conservation in European lowlands, such as the UK, lags some way behind its perennial counterpart (Williams *et al.,* 2001). The results of this study indicate that floodplain meadow ponds provide a valuable and important habitat for aquatic macroinvertebrate taxa (11 ponds were of a high or very high conservation value), supporting a wide diversity of taxa and a number of taxa of conservation interest at an alpha and gamma scale. These results provide evidence to accept the fourth hypothesis;

> *H_4: The conservation value of both perennial and ephemeral floodplain meadow ponds will be high.*

A total of 31% of floodplain meadow ponds (all perennial) studied in this chapter potentially qualify as a Priority Pond Habitat (PPH) which was greater than that predicted for all UK ponds (suggested that 20% of UK ponds could meet one of the PPH criteria) (Williams *et al.,* 2010). Although greater macroinvertebrate richness was recorded within perennial ponds, similar numbers of aquatic macroinvertebrate taxa with a conservation designation and less commonly occurring taxa were recorded between ephemeral and perennial meadow ponds. Previous research has demonstrated that ephemeral ponds support a comparable and often higher number of rare and endemic taxa than perennial ponds despite typically supporting lower taxon abundance and richness (Collinson *et al.,* 1995; Nicolet, 2001; Díaz-Paniagua *et al.,* 2010; Armitage *et al.,* 2012). Ephemeral ponds in this study also supported a number of macroinvertebrate taxa, particularly ephemeral pond specialists, not recorded in the perennial floodplain meadow ponds. These results support the findings of other studies which report that ephemeral ponds can provide suitable habitat for macroinvertebrate taxa that are often out competed or cannot survive in perennial ponds (Collinson *et al.,* 1995; Grillas *et al.,* 2004; Nicolet *et al.,* 2004; Díaz-Paniagua *et al.,* 2010).

The meadow ponds in this chapter were protected and located in nature conservation areas. The protection offered by the nature reserve status has enabled a high density of ephemeral and perennial ponds to be maintained. The substantial regional biodiversity of floodplain meadow ponds and the large community heterogeneity displayed between ephemeral and perennial meadow ponds highlights the importance of this habitat for the wider protection and enhancement of macroinvertebrate biodiversity. Ephemeral and perennial ponds provide different ecological niches for invertebrate taxa to utilise and in order to maximise biodiversity on floodplain meadows, landscape management practices should aim to maintain a wide variety of ponds with a range of hydroperiod lengths and physicochemical conditions (Biggs *et al.,* 1994a; Williams *et al.,* 2003; Bilton *et al.,* 2008).

The natural inundation of the floodplain meadows by the River Soar observed at Cossington Meadow and Loughborough Big Meadow is characteristic, prior to any river regulation, of the dynamic relationship between river and floodplain in lowland riverine landscapes across the temperate lowland landscape. Research into unregulated (semi)natural floodplain meadows is essential and can provide information regarding the natural distribution of aquatic biota and the environmental processes that influence invertebrate distribution in these dynamic landscapes (Williams *et al.,* 2003). Quantifying the aquatic invertebrate diversity of semi-natural floodplain meadow ponds will provide reference conditions for the development of conservation and restoration (reconnection) strategies for aquatic habitats in regulated floodplain landscapes.

6.4 Summary

This chapter, consistent with limited other research (Collinson *et al.,* 1995; Nicolet, 2001; Della Bella *et al.,* 2005), identified perennial floodplain meadow ponds to support greater aquatic macroinvertebrate diversity than their ephemeral counterparts. Notwithstanding, ephemeral meadow ponds supported a similar number of invertebrate taxa of conservation interest and demonstrated a distinctive community assemblage to perennial meadow ponds despite regular mixing of perennial and ephemeral waterbodies. This suggests that at a regional scale, ephemeral ponds provide a valuable biodiversity resource in European lowland landscapes. Landscape management and floodplain restoration practices should maintain a mosaic and wide variety of freshwater habitats to maximise the biodiversity and conservation value of meadow landscapes as both common and rare taxa rely on a variety of pond types. In particular, a wide range of hydroperiod lengths should be maintained for those macroinvertebrate species that rely on the periodic drying. The distinctive contribution of ephemeral floodplain meadow ponds to macroinvertebrate biodiversity needs to be acknowledged by both freshwater scientists and conservation managers.

Chapter 7. Local (physicochemical & biological) and spatial (connectivity) determinants of pond macroinvertebrate community composition

7.1 Introduction

Macroinvertebrate communities within ponds are influenced by an interplay of physicochemical, biological and spatial factors including; pond connectivity to other aquatic habitats, altitude, surface area, depth, pH, conductivity, temperature, macrophyte coverage, shading, hydroperiodicity (pond drying) and fish predation (Williams, 1996; Oertli *et al.,* 2002; Cottenie *et al.,* 2003; Biggs *et al.,* 2005; Hinden *et al.,* 2005; Chaichana *et al.,* 2011; Hassall *et al.,* 2011). There has been debate in the academic literature surrounding the influence of pond size on macroinvertebrate communities, with some research identifying a strong influence (Biggs *et al.,* 2005; Shieh and Chi, 2010) whilst other studies have suggested pond size exerts a weak influence (Oertli *et al.,* 2002). Previous research has demonstrated that cyclical pond drying and desiccation is a key determinant of macroinvertebrate community assemblage within ephemeral ponds (Bilton *et al.,* 2001; Brönmark and Hansson, 2005; Williams, 2006).

A considerable volume of research examining the environmental factors influencing macroinvertebrate community composition has focussed exclusively on local variables (physicochemical and biological) and many have failed to examine potential spatial/regional determinants on community composition such as connectivity. Landscape connectivity can be defined as "the degree to which the landscape impedes or facilitates movement along resource patches" (Taylor *et al.,* 1993: 571). Connectivity can be categorised into two types: structural - centred on the physical arrangement of the landscape; and functional - the actual movement of taxa through the landscape (behavioural response of taxa to the structure of the landscape) (Crooks and Sanjayan, 2006; Ribeiro *et al.,* 2011). For the purposes of this research structural connectivity (pond proximity and connectivity: see Chapter 3.3.1) was measured, as it is most commonly used in biodiversity and conservation research. In addition, it is relatively easy to measure using GIS software tools (Taylor *et al.,* 2006), although, it has been criticised for generalising the response of taxa to landscape structure (Ribeiro *et al.,* 2011). Functional connectivity can provide a detailed assessment of the response of taxa to the landscape, although this requires substantial research time (a number of years to determine baseline characteristics) and was beyond the scope of this research project.

The importance of spatial factors (connectivity/pond proximity) has increasingly been acknowledged in community ecology (Vanschoenwinkel *et al.,* 2007). The metacommunity theory provides four theoretical paradigms (see Chapter 2.5.1), to explain the variation and distribution of macroinvertebrate taxa among sites in a metacommunity based on the differing influence of local (physicochemical/biological) and spatial (dispersal) factors (see Chapter 2.5.1) (Leibold *et al.,* 2004; Ng *et al.,* 2009). Pond connectivity has been shown to be an important influence on invertebrate structure and a control on the biodiversity of pond habitats (Cottenie *et al.,* 2003; Cottenie and De Meester, 2004; Briers and Biggs, 2005; Werner *et al.,* 2007; Gledhill *et al.,* 2008). Ponds with a greater proximity to other water bodies often support greater macroinvertebrate species richness compared to those with reduced proximity (Williams *et al.,* 2008) as there is greater potential for the dispersal and colonization of macroinvertebrate taxa and recolonization after extinction events. A limited number of studies have examined the importance of local and spatial factors on aquatic invertebrate communities at small spatial scales; the majority of these identified local variables to be dominant over spatial parameters (*zooplankton* - Pinel-Alloul *et al.,* 1995; Cottenie *et al.,* 2003; Cottenie and De Meester, 2003; Cottenie and De Meester, 2004; *macroinvertebrates* - Vanschoenwinkel *et al.,* 2007; Florencio *et al.,* 2014). For example, using variance partitioning, local and spatial correlates were found to be an important influence on the distribution of passively dispersing macroinvertebrate taxa but only local parameters appeared to influence actively dispersing taxa within 36 temporary rock pools in South Africa (Vanschoenwinkel *et al.,* 2007).

7.1.1 Research/knowledge gaps

Research addressing connectivity has typically focussed on terrestrial landscapes (Tischendorf and Fahrig, 2000; Frey-Ehrenbold *et al.,* 2013; Gil-Tena *et al.,* 2013; Braaker *et al.,* 2014). In aquatic systems, the importance of pond connectivity for amphibian diversity has been well defined (Werner *et al.,* 2007; Ribeiro *et al.,* 2011). In comparison, there is a paucity of research which has examined the individual and combined importance of local and spatial variables on pond macroinvertebrate communities (limited research has been undertaken on zooplankton - Cottenie *et al.,* 2003; Cottenie and De Meester, 2004) especially at the regional scale and over a range of landscape types (see Vanschoenwinkel *et al.* (2007) for a smaller-scale, temporary pond connectivity study). In particular, research addressing the local and spatial controls of macroinvertebrate community composition at larger scales and within urban and ephemeral water bodies has been poorly studied to date (Noble and Hassall, 2014).

7.1.2 Chapter aims and hypotheses

In light of the above knowledge gaps, and developing on from previous chapters, the overall aim of this chapter is to quantify the unique and combined contribution of local (physicochemical and biological) and spatial factors influencing macroinvertebrate assemblages from ponds across the entire study region, within meadow and urban landscapes and among ephemeral ponds (see Chapter 1.4: Objective 5). The following hypotheses will be tested;

H_1: A combination of physicochemical, biological and spatial factors will influence communities at a regional scale;

H_2: Spatial factors will exert a greater influence on meadow pond communities than urban or ephemeral pond communities;

H_3: Physicochemical parameters will be the dominant influence on macroinvertebrate assemblage at a regional and landscape (ephemeral, meadow and urban) scale;

H_{4a}: Dissimilarity in community composition between pond sites will increase with geographic distance at a regional scale and among meadow and ephemeral ponds;

H_{4b}: There will be no difference in community dissimilarity with geographic distance among urban ponds.

The methodological processes (fieldwork and statistical) undertaken in this chapter are described in detail in Chapter 3.

7.2 Results

Thirteen *physicochemical* (area, depth, pH, conductivity, dissolved oxygen, dry phase length (number of months pond basin was dry), percentage of pond margin shaded); *biological* (fish presence, percentage coverage of emergent, submerged and floating macrophytes); and *spatial* (pond connectivity and pond proximity; see Chapter 3.3.1) variables were included in a Canonical Correspondence Analyses (CCA) of the regional, urban, meadow and ephemeral ponds. Due to natural seasonal variability in community composition, seasonal data from individual pond sites were combined and mean values of environmental parameters derived. Environmental variables were $\log_{10}$ transformed prior to analysis to reduce skewness and create a uniform scale (Legendre and Birks, 2012). Species-abundance (count) data was log transformed in CANOCO to reduce the influence of commonly occurring and abundant species. Species data was additionally downweighted to reduce the influence of rare and less commonly occurring taxa. Detrended Correspondence Analysis (DCA) indicated that gradient lengths were large enough (>3) for regional, urban, meadow and ephemeral ponds and that the unimodal CCA method was the most appropriate to examine the influence of local and spatial variables on the macroinvertebrate communities at a regional scale and among urban, meadow and ephemeral ponds (Lepš and Šmilauer, 2003). PCA analysis indicated there was little multicollinearity among the physicochemical variables. In addition, the variance inflation factors of all significant environmental parameters was below 5 for regional, urban, meadow and ephemeral pond CCA suggesting there was little co-linearity between parameters (Martel *et al.,* 2007). Using CANOCO 4.5, a forward selection procedure using 999 Monte Carlo random permutation tests and Bonferroni correction (1st variable: p=0.05) was applied to the CCA to identify those variables that contributed most to the variability in macroinvertebrate assemblages and should be retained in the final CCA models.

7.2.1 Influence of environmental variables on pond macroinvertebrate assemblages at a regional scale

A total of 95 ponds across the region were used in the regional analysis. Nine physicochemical variables (*physicochemical*: pond surface area, the dry phase, pH and dissolved oxygen, *biological*: emergent macrophytes, submerged macrophytes and fish presence, *spatial:* pond proximity and connectivity) were identified as significantly influencing the variation in macroinvertebrate community data at a regional scale and were included in the final CCA model (Table 7.1; Figure 7.1).

Table 7.1 - Significance of environmental parameters in explaining the variation in macroinvertebrate community composition using forward selection Monte Carlo permutation tests (999) and Bonferroni correction

Environmental Characteristic	Environmental Group	Code in Figures 7.1 and 7.2	F. Ratio	P. Value
pH	Physicochemical	pH	2.84	0.001
Dissolved oxygen	Physicochemical	DO	1.89	0.03
Dry phase	Physicochemical	Dry phase	4.98	0.001
Pond surface area	Physicochemical	Surface Area	2.43	0.001
Fish presence	Biological	Fish	2.96	0.001
Submerged macrophytes	Biological	SM	2.30	0.001
Emergent macrophytes	Biological	EM	1.95	0.001
Pond proximity	Spatial	Prox	5.81	0.001
Connectivity	Spatial	Connect	4.40	0.001

The canonical axes of the total model were highly significant (Monte Carlo significance test: $F=2.986$; $p<0.002$) and the first four axes explained 20.9% of the variation in species data and 75.8% of the species-environment relationship; axis 1 explained 9.4% of the species data and 34% of the species-environmental relationship; the second canonical axis accounted for 5.1% of the species data and 18.5% of the species-environment relationship. A relatively clear distinction between meadow and urban pond community assemblage was demonstrated by the CCA (Figure 7.1a); macroinvertebrate assemblages within urban ponds were located towards the positive end of axis one, whereas meadow ponds were ordinated towards the negative end of axis one. However, there was some overlap among urban and meadow ponds indicating there were some similarities in macroinvertebrate community composition. Axis two largely separated pond sites along an ephemerality (dry phase) gradient. Perennial ponds were located towards the negative end of axis two whilst ponds with an ephemeral regime were located towards the positive end of axis two. Urban ponds were associated with a greater occurrence of fish, reduced surface area and emergent macrophytes and reduced pond connectivity and pond proximity. Greater connectivity and pond proximity separated meadow ponds from the other pond habitats, although meadow ponds were also associated with a greater surface area, dissolved oxygen and higher pH levels (Figure 7.1a). Forest and agricultural ponds were associated with lower pH and dissolved oxygen levels and greater emergent macrophyte coverage.

Pond sites with greater macroinvertebrate community abundance, taxon number and the Shannon Wiener diversity index were associated with greater pond connectivity, proximity to other ponds and larger surface areas (Figure 7.1b, 7.1c, 7.1d). Less diverse pond sites were associated with an ephemeral hydrology, reduced pond connectedness, lower pH and dissolved oxygen levels (Figure 7.1b, 7.1c, 7.1d). Fish presence was also unexpectedly identified to be related to higher macroinvertebrate diversity, although the majority of pond sites demonstrated low fish densities thus were unlikely to have a large negative impact on community assemblage.

Several species of Hemiptera (e.g., *Sigara concinna,* (71) *Corixa panzeri,* (65) *Corixa praeusta*, (62), *Sigara lateralis* (75) and Corixidae nymph (67)) and Coleoptera (e.g., *Hygrotus* - 3 species (91, 93, 94), *Hydroporus* - 2 species (88, 89), *Colymbetes fuscus* (86) and *Hygrobia hermanni* (99)) were associated with ponds that had a high connectivity and proximity to other ponds (Figure 7.2). Taxa corresponding to the numbers displayed on the species CCA output are presented in Table 7.2. The majority of Odonata were clustered in the middle of the ordination indicating that they were recorded within a range of pond types and influenced by a wide range of environmental parameters (Figure 7.2). Gastropoda *Planorbis carinatus* (6) and *Planorbis corneus* (7) were closely associated with the proportion of pond covered by submerged macrophytes and *Gyraulus albus* (5), *Segmintina nitida* (13) and *Potamopygrus antipodarum* (15) were associated with larger pond surface areas. The separation between meadow and urban ponds was driven by high abundances of Coleoptera and Hemiptera in the meadow ponds and greater abundances of Diptera in urban ponds (Figure 7.2). Additionally, a number of Coleoptera species including *Helophorus minutus* (110)*, Anacaena globulus* (104) and Scritidae larvae (113)*;* the Trichoptera *Limnephilus binotatus* (50); the Entognatha Collembola (126) and the Gastropoda *Anisus leucostoma* (A temporary water specialist (10)) had a greater association with ephemeral pond habitats (Figure 7.2).

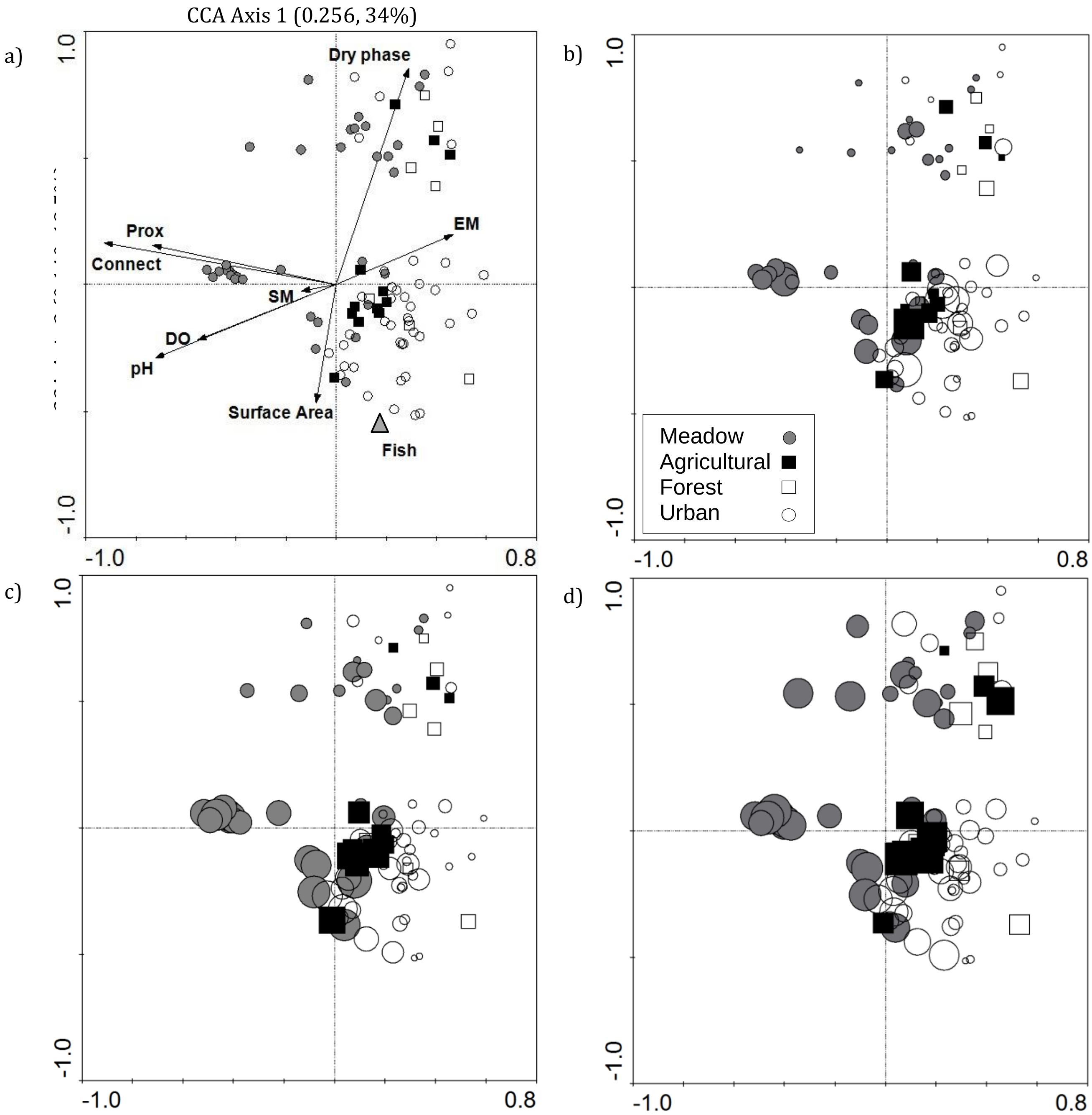

Figure 7.1 - Canonical Correspondence Analysis of meadow, agricultural, forest and urban pond macroinvertebrate communities and a) pond sites and significant environmental parameters (Connect – connectivity, Prox - pond proximity, DO - dissolved oxygen, EM - emergent macrophyte, SM - submerged macrophytes, Fish - Fish presence. Note - only significant environmental variables are presented); b) community abundance bubble plot; c) taxon richness bubble plot and; d) Shannon Wiener diversity index bubble plot. The size of each bubble (pond site) is proportional to: b) community abundance, c) taxon richness and d) Shannon Wiener diversity index.

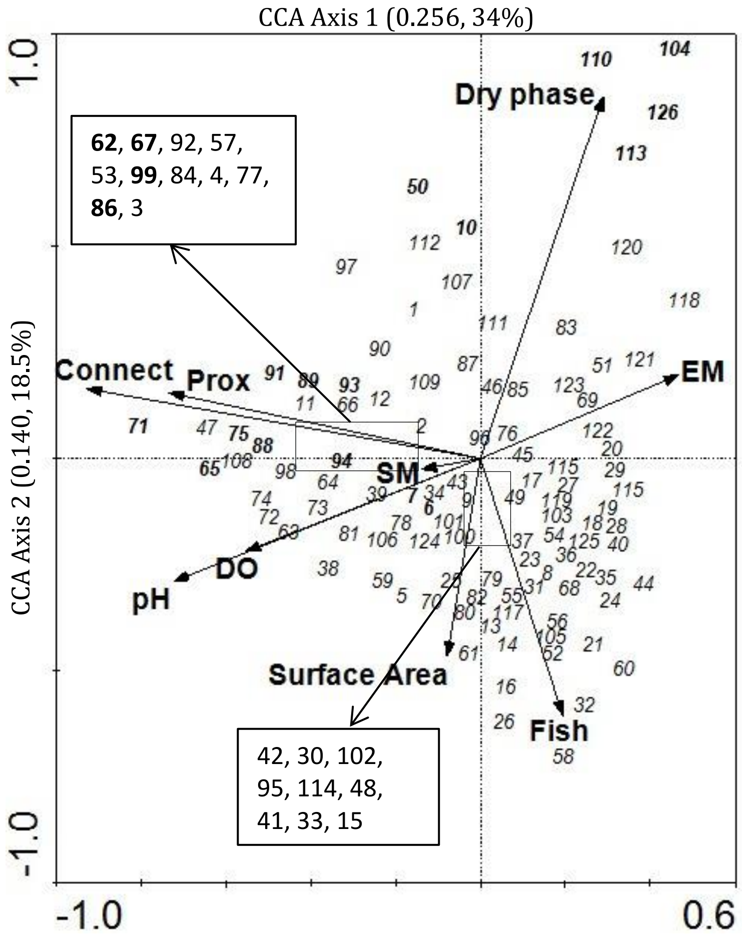

Figure 7.2 - CCA ordination of regional macroinvertebrate taxa in relation to physicochemical, biological and spatial environmental parameters (connect - connectivity, Prox - pond proximity, DO - dissolved oxygen, EM - emergent macrophyte, SM - submerged macrophyte, Fish - fish presence). Only taxa that were recorded from at least ≥6 pond sites were included in the final output. Note - only significant environmental variables are presented in the final output. Macroinvertebrate taxa which correspond to the number displayed in the CCA output are presented in Table 7.2.

Table 7.2 - Regional macroinvertebrate taxa and their representative number displayed in the CCA biplot. Note - only macroinvertebrate taxa recorded from ≥6 ponds were displayed in the final CCA output.

Taxa					
Lymnaea palustris	1	Aeshna Instar I+II	43	*Agabus sturmii*	85
Lymnaea peregra	2	*Aeshna mixta*	44	*Colymbetes fuscus*	86
Lymnaea stagnalis	3	*Anax imperator*	45	Dytiscidae larvae	87
Physidae	4	*Libellula depressa*	46	*Hydroporus angustatus*	88
Gyraulus albus	5	Trichoptera Pupae	47	*Hydroporus palustris*	89
Planorbis carinatus	6	*Phryganea bipunctata*	48	*Hydroporus pubescens*	90
Planorbarius corneus	7	*Glyphotaelius pellucidus*	49	*Hygrotus confluens*	91
Armiger crista	8	*Limnephilus binotatus*	50	*Hygrotus inaequalis*	92
Gyraulus laevis	9	*Limnephilus decipiens*	51	*Hygrotus impressopunctatus*	93
Anisus leucostoma	10	*Limnephilus flavicornis*	52	*Hygrotus versicolor*	94
Planorbis planorbis	11	*Limnephilus incisus/affinis*	53	*Hyphydrus ovatus*	95
Anisus vortex	12	*Limnephilus lunatus*	54	*Laccophilus minutus*	96
Segmentina nitida	13	Limnephilus instar I+II	55	*Rhantus frontalis*	97
Bythnia tentaculata	14	*Limnephilus marmoratus*	56	*Rhantus suturalis*	98
Potamopyrgus antipodarum	15	*Limnephilus vittatus*	57	*Hygrobia hermanni*	99
Acroloxus lacustris	16	*Mystacides longicornis*	58	*Haliplus confinis*	100
Valvata piscinalis	17	*Triaenodes bicolor*	59	Haliplus Ruficollis Group	101
Zonitidae	18	*Cyrnus trimaculatus*	60	Haliplus larvae	102
Pisidiidae	19	*Holocentropus dubius*	61	*Haliplus lineatocollis*	103
Oligochaeta	20	*Callicorixa praeusta*	62	*Anacaena globulus*	104
Erpobdella octoculata	21	*Callicorixa wollastoni*	63	*Enochrus testaceus*	105
Erpobdella testacea	22	*Corixa dentipes*	64	*Helochares lividus*	106
Glossiphonia complanata	23	*Corixa panzeri*	65	Helophorus terrestrial	107
Helobdella stagnalis	24	*Corixa punctata*	66	*Helophorus griseus*	108
Theromyzon tessulatum	25	Corixidae nymph	67	*Helophorus (cf.) longitarsis*	109
Piscicola geometra	26	*Hesperocorixa linnaei*	68	*Helophorus minutus*	110
Crangonyx pseudogracilis	27	*Hesperocorixa sahlbergi*	69	*Hydrobius fuscipes*	111
Asellus aquaticus	28	*Micronecta poweri*	70	Hydrophilidae larvae	112
Asellus meridianus	29	*Sigara concinnna*	71	Scirtidae larvae	113
Cloeon dipterum	30	*Sigara distincta*	72	Ceratopogonidae	114
Cloeon simile	31	*Sigara dorsalis*	73	Chaoboridae	115
Caenis horaria	32	*Sigara falleni*	74	Chironomidae	116
Caenis luctuosa	33	*Sigara lateralis*	75	Chrysomelidae	117
Caenis robusta	34	*Gerris lacustris*	76	Culicidae	118
Sialis lutaria	35	Gerridae nymph	77	Dixidae	119
Cataclysta lemnata	36	*Notonecta glauca*	78	Ephydridae	120
Coenagrion puella	37	*Notonecta maculata*	79	Psychodidae	121
Erythromma najas	38	Notonectidae nymph	80	Stratiomyidae	122
Ischnura elegans	39	*Ilyocoris cimicoides*	81	Tipulidae	123
Pyrrhosoma nymphula	40	*Noterus clavicornis*	82	Hydrachnidiae	124
Coenagrionidae instar I+II	41	*Agabus bipustulatus*	83	Planariidae	125
Aeshna cyanea	42	*Agabus nebulosus*	84	Collembola	126

Physicochemical parameters displayed a significant influence on macroinvertebrate community composition following variance partitioning analysis (Figure 7.3). A total of 27.5% of the variability in macroinvertebrate assemblages was explained by the set of physicochemical (surface area, dry phase, pH, dissolved oxygen), biological (emergent and submerged macrophytes, fish presence) and spatial (pond connectivity and pond proximity) parameters. Physicochemical characteristics (P|B+SP) uniquely explained 9.2% (although explained 33% of explainable variance), biological parameters (B|P+SP) explained 4.9% and spatial variables (SP|B+P) explained 3.2% of the total variance (Figure 7.3). A combination of physicochemical and spatial variables (P+SP|B) explained 4% of the total variation, higher than the unique explanation of spatial. The results demonstrate that physicochemical factors exerted the greatest influence on macroinvertebrate community composition and additionally highlight the importance of the interaction of physicochemical, biological and spatial parameters in structuring macroinvertebrate communities within pond habitats at a regional scale.

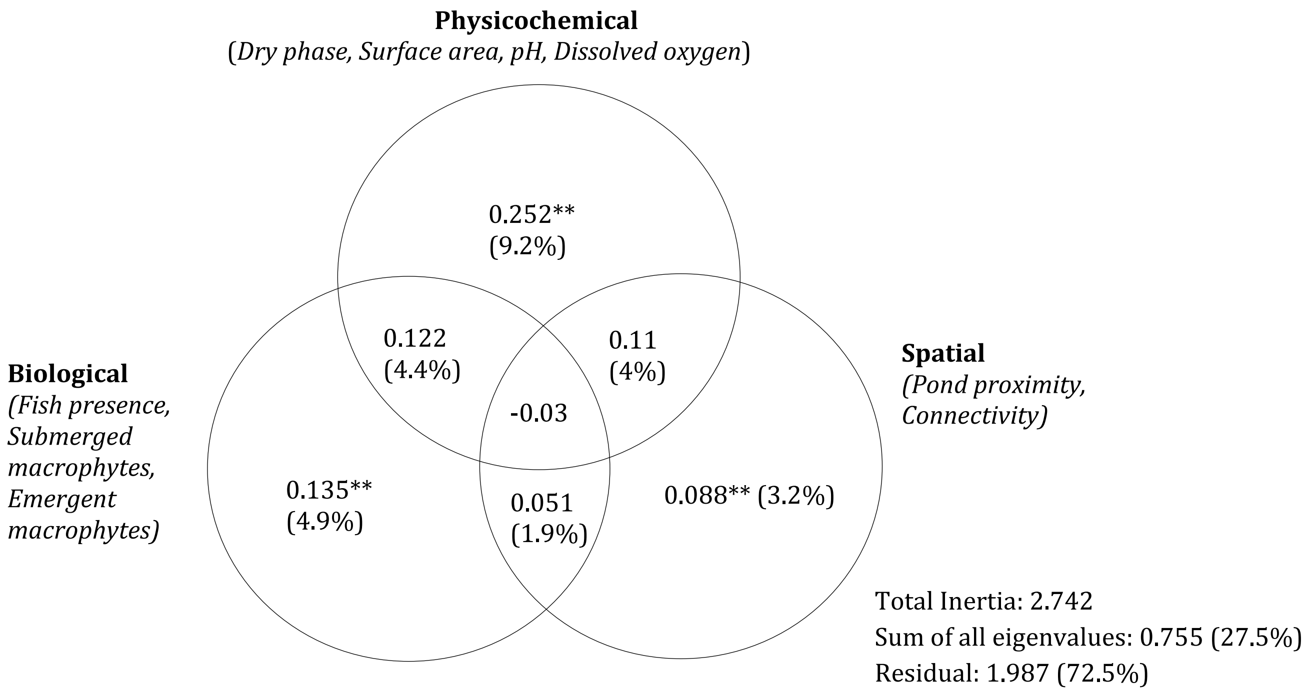

*Figure 7.3 - Variance partitioning of the relative influence of physicochemical, biological and spatial variables on macroinvertebrate composition at a regional scale. Values represent the proportion of the total variation (2.742). Percentage contribution of the total variance is presented in parenthesis. ** p<0.001.*

7.2.2 Influence of local and spatial parameters on macroinvertebrate assemblage among urban ponds

Canonical Correspondence Analysis of the urban pond (a total of 41 urban ponds were studied) macroinvertebrate community data and environmental parameters highlighted clear differences between the garden, 'other' urban and park pond types. The canonical axes were highly significant (Monte Carlo significance test: $F=1.617$; $p<0.001$) with the first four axes explaining 22% of the variation in species data (axis 1: 8.3%, axis 2: 6.3%, axis 3: 4.1% and axis 4: 3.3%) and 92.4% of the taxa-environment relationship (axis 1: 34.8%, axis 2: 26.5%, axis 3: 17.2% and axis 4: 13.9%) on the first four axes. Forward selection with Bonferroni correction identified 5 significant environmental parameters correlated with the first two canonical axes; water surface area, submerged macrophytes, emergent macrophytes (all $p<0.005$), the dry phase and pH ($p<0.05$) (Table 7.3; Figure 7.4).

Table 7.3 - Significance of environmental parameters in explaining the variation in macroinvertebrate community composition in urban ponds using Monte Carlo permutation tests (999) and Bonferroni correction

Environmental Characteristic	Environmental Group	Code in Figures 7.4 and 7.5	F. Ratio	P. Value
pH	Physicochemical	pH	1.76	0.003
Dry phase	Physicochemical	Dry phase	1.65	0.010
Pond surface area	Physicochemical	Surface Area	2.94	0.001
Emergent macrophytes	Biological	EM	2.09	0.001
Submerged macrophytes	Biological	SM	1.95	0.001

When the invertebrate assemblages of the three urban pond types were examined in relation to environmental variables, garden and park ponds were relatively distinct, but 'other' urban ponds were more widely dispersed in the biplot and overlapped both park and garden ponds (Figure 7.4a). Park and garden pond invertebrate communities were largely separated on the first canonical axis by a surface area gradient and on the second canonical axis by an emergent macrophytes (proportion of pond covered) gradient (Figure 7.4a). Park ponds were characterised by a greater water surface area, emergent and submerged macrophyte coverage, whilst garden ponds were characterised by smaller surface areas and a lower proportion of the pond covered by emergent and submerged macrophytes (Figure 7.4a). 'Other' urban ponds had highly variable environmental characteristics but were associated with greater proportions of emergent macrophyte cover and a small total surface area. Ephemeral pond (5 'other' urban ponds) communities were influenced largely by the periodic drying of the pond basin and plotted at the negative end of axis 2 (Figure 7.4a). Urban ponds with the greatest macroinvertebrate abundance, taxon richness and Shannon Wiener diversity index, were typically associated with greater water surface area, pH, submerged and emergent macrophytes (Figure 7.4b, Figure 7.4c and Figure 7.4d). Spatial variables (connectivity and pond proximity) were found to not have a significant influence on urban pond macroinvertebrate assemblage.

The CCA faunal plot indicated several species of Odonata (e.g., *Erythromma najas* (44)), Hemiptera (e.g., *Ilyocoris cimicoides* (109) and *Corixa panzeri* (87) and Notonectidae nymph (107)), Coleoptera (e.g., Gyrinidae - 3 species (112, 113, and 114) *Noterus clavicornis* (115) and *Hygrotus confluens* (127)) and Gastropoda (*Gyraulus albus* (5) *and Anisus vortex* (12)) were associated with ponds with larger surface areas (Figure 7.5). The taxa present in urban ponds and their corresponding number within the urban species CCA biplot is presented in Table 7.4. In addition, a number of Coleoptera taxa (e.g., *Agabus* - 2 species (116, 118); and *Hydroporus pubescens* (125)), were associated with emergent macrophytes. Ponds with a greater proportion of their area covered by submerged macrophytes were associated with several species Hemiptera (e.g., Corixidae - 4 species (95, 96, 97, 98) and Trichoptera (e.g., *Phryganea bipunctata* (55) and *Molanna angustata* (73)) (Figure 7.5). Several Hirudinea recorded within urban ponds were associated with higher pH levels. Although, Diptera (e.g., Chironomidae (157) and Culicidae (158)) were associated with ponds with a smaller surface area and less emergent and submerged macrophytes. Taxa commonly recorded from ponds with an ephemeral hydrology (Scritidae larvae (154), *Limnephilus binotatus* (61), *Limnephilus aricula* (60)) and a few taxa typically recorded from perennial waterbodies (Psychodidae (163) and Hydrophilidae larvae (151)) were associated with ephemeral ponds and plotted at the negative end of CCA - axis 2 (Figure 6). Relatively high abundances of Diptera larvae (Chironomidae (157), Culicidae (158), Ephydridae (161) and Empididae (162)) were typically recorded within garden ponds whilst park ponds recorded greater abundances of Hemiptera, Coleoptera and Odonata (Figure 7.5). *G. pulex* (30) was recorded only from one ephemeral urban pond, but this is almost certainly the result of colonization from overland flooding from a nearby urban stream.

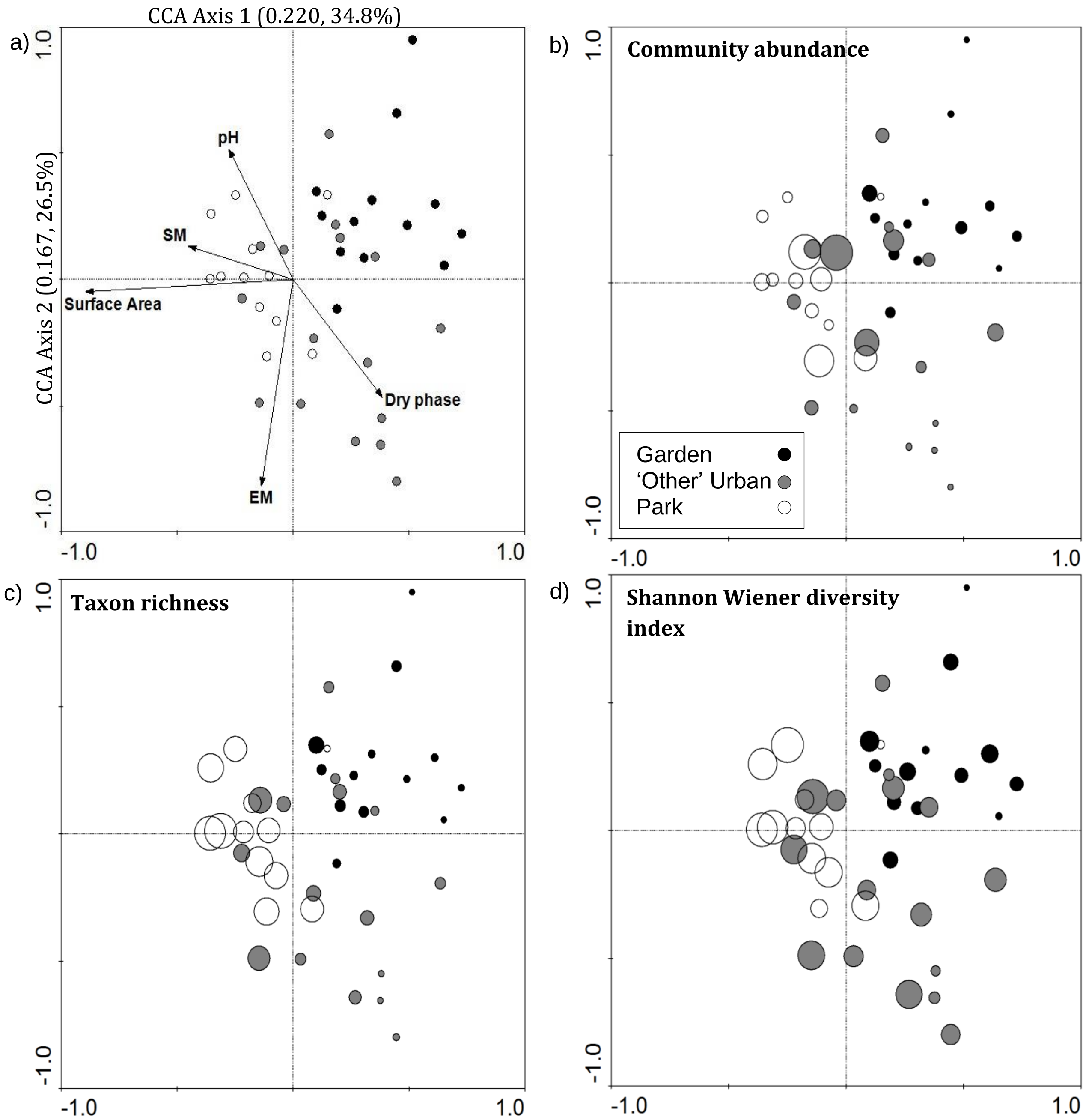

Figure 7.4 - Canonical Correspondence Analysis for garden, 'other' urban and park pond macroinvertebrate communities; a) pond sites and significant environmental parameters (EM - emergent macrophyte; SM - submerged macrophyte; DO - dissolved oxygen. Note - only significant environmental variables are presented); b) community abundance bubble plot; c) taxon number bubble plot and; d) Shannon Wiener diversity index bubble plot. The size of each bubble (pond site) is proportional to: b) community abundance, c) taxon richness and d) Shannon Wiener diversity index.

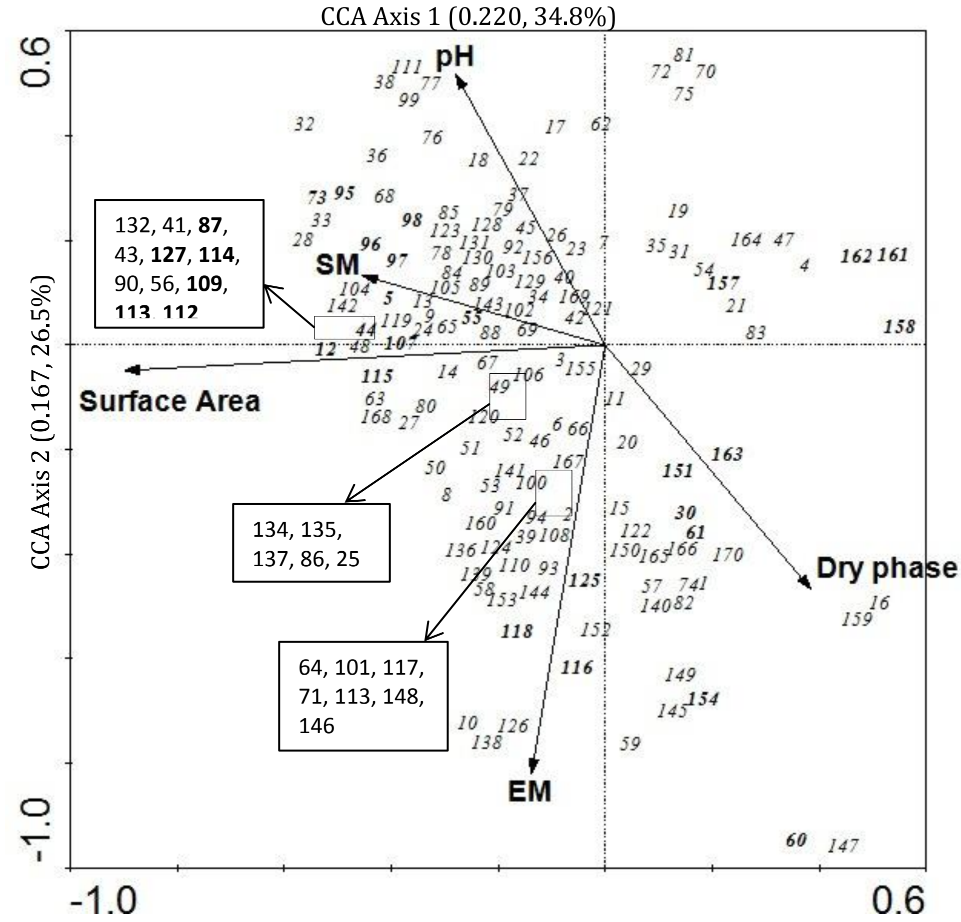

Figure 7.5 - CCA ordination of macroinvertebrate taxa in relation to physicochemical and biological environmental parameters from urban ponds (EM - emergent macrophytes, SM - submerged macrophytes). Note - only significant environmental variables are presented in the final output. Macroinvertebrate taxa which correspond to the number displayed in the CCA output are presented in Table 7.3.

Table 7.4 - Urban pond macroinvertebrate taxa and their representative number displayed in the CCA biplot.

Taxa							
Lymnaea palustris	1	*Erythromma najas*	44	*Corixa panzeri*	87	*Hyphydrus ovatus*	130
Lymnaea peregra	2	*Ischnura elegans*	45	*Corixa punctata*	88	*Laccophilus minutus*	131
Lymnaea stagnalis	3	*Pyrrhosoma nymphula*	46	Corixidae nymph	89	*Rhantus suturalis*	132
Physidae	4	*Lestes sponsa*	47	*Cymatia bonsdorffi*	90	*Hygrobia hermanni*	133
Gyraulus albus	5	Coenagrionidae instar I+II	48	*Hesperocoroxa castanea*	91	*Haliplus confinis*	134
Planorbis carinatus	6	*Aeshna cyanea*	49	*Hesperocorixa linnaei*	92	Haliplus Ruficollis Group	135
Planorbarius corneus	7	Aeshna instar I+II	50	*Hesperocorixa moesta*	93	*Haliplus laminatus*	136
Armiger crista	8	*Aeshna grandis*	51	*Hesperocorixa sahlbergi*	94	Haliplus larvae	137
Gyraulus laevis	9	*Aeshna mixta*	52	*Micronecta poweri*	95	*Haliplus lineatocollis*	138
Anisus leucostoma	10	*Anax imperator*	53	*Sigara distincta*	96	*Haliplus obliquus*	139
Planorbis planorbis	11	*Libellula depressa*	54	*Sigara dorsalis*	97	*Anacaena globulus*	140
Anisus vortex	12	*Phryganea bipunctata*	55	*Sigara falleni*	98	*Anacaena limbata*	141
Segmentina nitida	13	*Anabolia nervosa*	56	*Sigara fossarum*	99	*Enochrus testaceus*	142
Bythnia tentaculata	14	*Apatamia muliebris*	57	*Sigara lateralis*	100	*Helochares lividus*	143
Potamopyrgus antipodarum	15	*Glyphotaelius pellucidus*	58	*Gerris gibbifer*	101	*Helochares punctatus*	144
Succinea putris	16	*Grammotaulius nigropunctatus*	59	*Gerris lacustris*	102	Helophorus terrestrial	145
Acroloxus lacustris	17	*Limnephilus aricula*	60	Gerridae nymph	103	*Helophorus griseus*	146
Valvata piscinalis	18	*Limnephilus binotatus*	61	*Hydrometra stagnorum*	104	*Helophorus minutus*	147
Zonitidae	19	*Limnephilus decipiens*	62	*Notonecta glauca*	105	*Helophorus obscurus*	148
Pisidiidae	20	*Limnephilus flavicornis*	63	*Notonecta maculata*	106	*Helophorus strigifrons*	149
Oligochaeta	21	*Limnephilus griseus*	64	Notonectidae nymph	107	*Hydrobius fuscipes*	150
Erpobdella octoculata	22	*Limnephilus incisus/affinis*	65	*Notonecta obliqua*	108	Hydrophilidae larvae	151
Erpobdella testacea	23	*Limnephilus lunatus*	66	*Ilyocoris cimicoides*	109	*Laccobius bipunctatus*	152
Batracobdella paludosa	24	Limnephilus instar I+II	67	*Nepa cinerea*	110	*Sphaeridiinae*	153
Glossiphonia complanata	25	*Limnephilus marmoratus*	68	*Ranata linearis*	111	Scirtidae larvae	154
Helobdella stagnalis	26	*Limnephilus nigriceps*	69	*Gyrinus distinctus*	112	Ceratopogonidae	155
Theromyzon tessulatum	27	*Limnephilus rombicus*	70	*Gyrinus marinus*	113	Chaoboridae	156
Piscicola geometra	28	*Limnephilus vittatus*	71	*Gyrinus substriatus*	114	Chironomidae	157
Crangonyx pseudogracilis	29	*Beraea pullata*	72	*Noterus clavicornis*	115	Culicidae	158
Gammarus pulex	30	*Molanna angustata*	73	*Agabus bipustulatus*	116	Dicranota	159
Asellus aquaticus	31	*Athripsodes aterrimus*	74	*Agabus nebulosus*	117	Dixidae	160
Asellus meridianus	32	*Ceralea fulva*	75	*Agabus sturmii*	118	Ephydridae	161
Argulidae	33	*Mystacides longicornis*	76	*Agabus uliginosus*	119	Empididae	162
Cloeon dipterum	34	*Mystacides azurea*	77	*Colymbetes fuscus*	120	Psychodidae	163
Cloeon simile	35	*Triaenodes bicolor*	78	*Dytiscus marginalis*	121	Simuliidae	164
Caenis horaria	36	*Cyrnus trimaculatus*	79	Dytiscidae larvae	122	Stratiomyidae	165
Caenis luctuosa	37	*Holocentropus dubius*	80	*Hydroporus incognitus*	123	Syrphidae	166
Caenis robusta	38	*Holocentropus picicornis*	81	*Hydroporus palustris*	124	Tipulidae	167
Sialis lutaria	39	*Polycentropus flavomaculatus*	82	*Hydroporus pubescens*	125	Hydrachnidiae	168
Cataclysta lemnata	40	*Hydropsyche angustipennis*	83	*Hydroporus striola*	126	Planariidae	169
Coenagrion pulchellum	41	*Callicorixa praeusta*	84	*Hygrotus confluens*	127	Collembola	170
Coenagrion puella	42	*Callicorixa wollastoni*	85	*Hygrotus inaequalis*	128		
Enallagma cyathigerum	43	*Corixa dentipes*	86	*Hygrotus versicolor*	129		

Physicochemical parameters were identified to be the dominant influence on macroinvertebrate community composition among urban ponds (Figure 7.6). The total variability in macroinvertebrate community composition explained by physicochemical and biological variables was 23.8%. Spatial factors were determined to have no significant influence on urban pond macroinvertebrate community composition. Physicochemical factors alone (P|B) explained 9.4% (39% of explainable variance) and biological factors (B|P) uniquely explained 5.8% of the total variance within the data. A total of 8.7% of the total variation in macroinvertebrate assemblages could be explained by a combination of physicochemical and biological factors (P+B). The results highlight the importance of the physicochemical variables and the inter-relationship between physicochemical and biological factors in determining macroinvertebrate community composition.

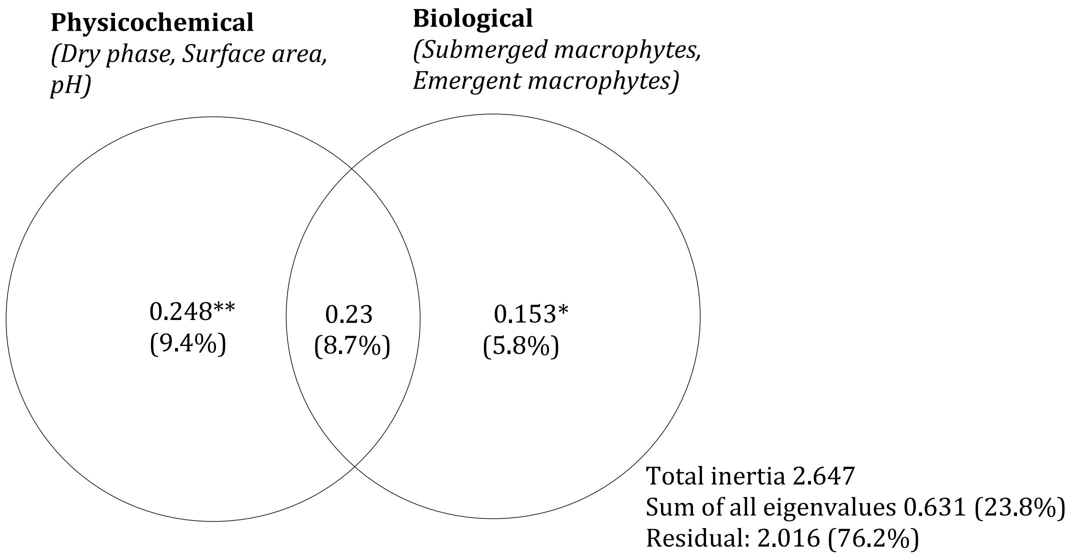

*Figure 7.6 - Variance partitioning of the relative influence of physicochemical and biological variables on macroinvertebrate composition from urban ponds. Values represent a proportion of the total variation (2.647). Percentage contributions of the total variance are presented in the parenthesis. * = p<0.05 ** = p<0.001.*

7.2.3 Influence of local and spatial parameters on macroinvertebrate assemblage among meadow ponds

A total of 20 perennial and 14 ephemeral meadow ponds from Cossington Meadow and Loughborough Big Meadow (see Chapter 3.2) were studied. Canonical Correspondence Analysis of the meadow pond macroinvertebrate community data and environmental parameters highlighted clear differences between the perennial and ephemeral meadow ponds. The canonical axes were highly significant (Monte Carlo significance tests $F=2.061$; $p<0.002$) with the first four axes explaining 30.1% of the variation in species data (axis 1: 12.8%, axis 2: 8.4%, axis 3: 4.8% and axis 4: 4.1%) and 89.5% of the taxa-environment relationship (axis 1: 38.2%, axis 2: 24.7%, axis 3: 14.3% and axis 4: 12.3%) on the first four axes. Five environmental variables (*spatial* - connectivity, pond proximity and *physicochemical* - pond surface area, the dry phase and conductivity) were identified to significantly influence the macroinvertebrate community assemblage within perennial and ephemeral meadow ponds (Table 7.5). No biological variables significantly influenced macroinvertebrate communities from meadow ponds.

Table 7.5 - Significance of environmental parameters in explaining the variation in macroinvertebrate community composition from meadow pond habitats using forward selection Monte Carlo permutation tests (999) and Bonferroni correction

Physicochemical Characteristic	Environmental Group	Code in Figures 7.7 and 7.8	F. Ratio	P. Value
Connectivity	Spatial	Connect	4.29	0.001
Pond proximity	Spatial	Pond Prox	2.27	0.001
Dry phase	Physicochemical	Dry phase	2.57	0.001
Pond surface area	Physicochemical	Surface Area	1.86	0.012
Conductivity	Physicochemical	Cond	2.01	0.001

The CCA demonstrates a clear distinction between perennial meadow ponds (located in the middle of the ordination and towards the negative end of axis two) and ephemeral meadow ponds (situated towards the positive end of axis two) macroinvertebrate communities (Figure 7.7). A tight clustering of 12 perennial ponds was closely associated with high pond connectivity (Figure 7.7). These ponds were located on the River Soar floodplain directly connected to each other and to the River Soar. They were inundated twice by flood water from the River Soar during the sampling period. The second clustering of perennial meadow ponds was associated with larger surface areas (Figure 7.7). The dry phase was identified to be the most important parameter influencing macroinvertebrate community assemblage among ephemeral meadow ponds (Figure 7.7). Reduced conductivity (<550) and greater pond isolation were also typically associated with ephemeral meadow ponds (Figure 7.7). High community abundance and taxon richness were associated with greater pond connectivity and surface areas whilst the seasonal drying of ephemeral ponds was associated with lower community abundance and taxon richness (Figure 7.7b, 7.7c). Most meadow ponds had a high Shannon Wiener diversity index, but the lowest Shannon Wiener diversity indices were associated with ephemeral ponds (Figure 7.7d).

A large number of actively dispersing macroinvertebrate taxa including; Coleoptera (e.g., Agabus - 2 species (110, 111), *Hydroporous* - 2 species (116, 118), *Hygrotus* - 4 species (121, 122, 123, 125)); Hemiptera (e.g., Corixidae - 5 species (81, 82, 88, 89, 91)) and Odonata (e.g., *Erythromma najas* (42), *Calopteryx virgo* (46), *Pyrrhosoma nymphula* (44)) were associated with highly connected ponds (Figure 7.8). Taxa corresponding to the numbers displayed on the species CCA output are presented in Table 7.6. Several species of Trichoptera (e.g., *Limnephilus lunatus* (68) *Limnephilus marmoratus* (70)) and passively dispersing macroinvertebrates such as Gastropoda (e.g., *Acroloxus lacustris* (18) and *Potamopyrgus antipodarum* (16)) and Hirudinea (e.g., *Erpobdella testacea* (25), *Glossiphonia complanata* (26) and *Helobdella stagnalis* (27)) were recorded in greater abundances in ponds with larger surface areas (Figure 7.8). However, the Gastropoda *Planorbarius corneus* (8)) was recorded in higher abundances in highly connected ponds. Several species of Diptera (e.g., Culicidae (163), Psychodidae (167)) supported greater abundances within ponds with a lower connectivity (Figure 7.8). Considerably greater numbers of taxa were associated with perennial ponds than ephemeral ponds however; several species of Trichoptera (e.g., *Limnephilus aricula* (60), *Limnephilus centralis* (62), *Limnephilus griseus* (66)), and Coleoptera (e.g., *Helophorus minutus* (151), *Acilus sulcatus* (107), Scritidae larvae (158), Elminthidae larvae (132)) and a single Gastropoda (*Anisus leucostoma* (11)) had a greater association with ephemeral pond habitats (Figure 7.8).

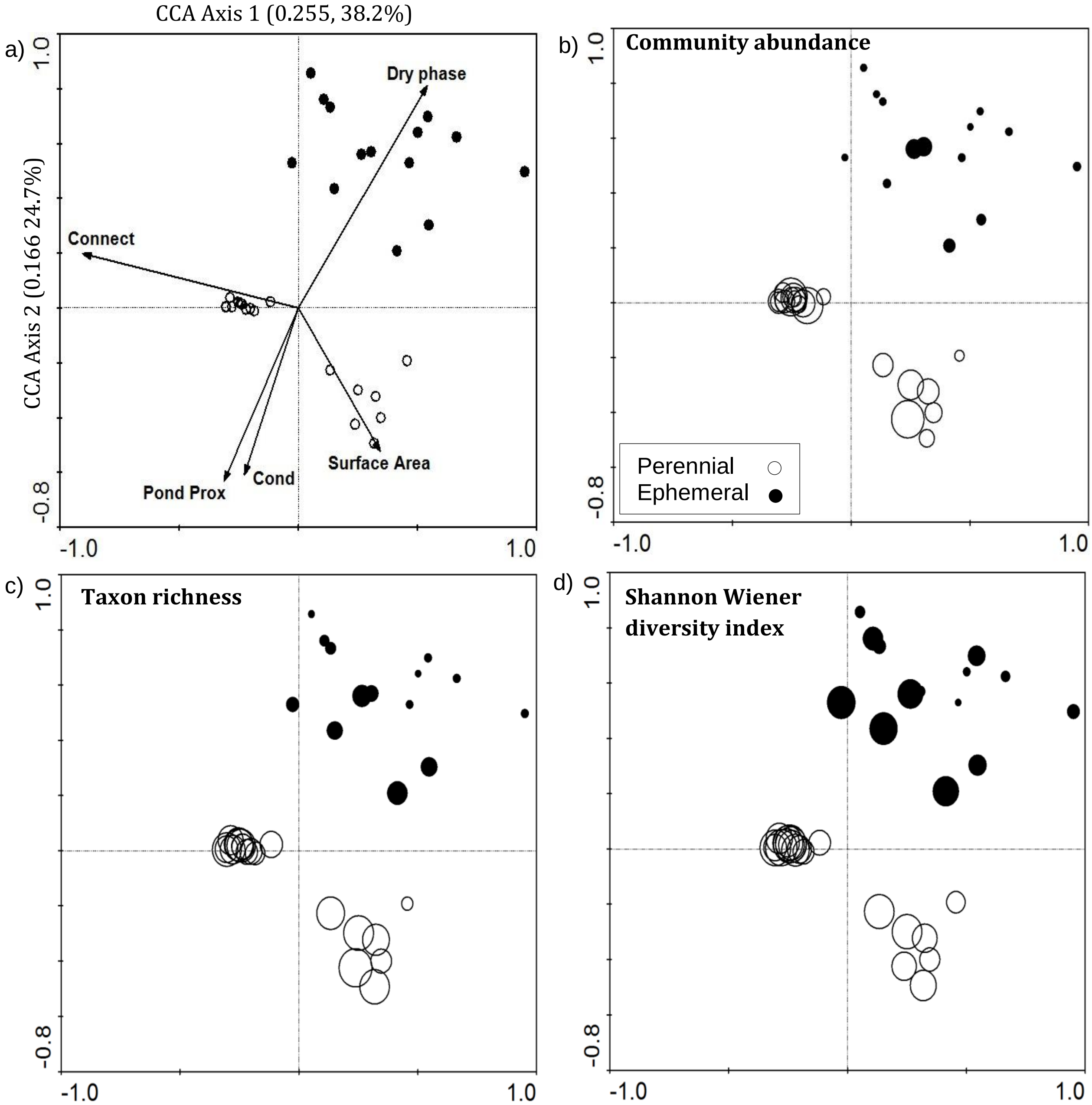

Figure 7.7 - Canonical Correspondence Analysis of perennial and ephemeral meadow pond macroinvertebrate communities and; a) pond sites and significant environmental parameters (Connect - connectivity, Pond Prox - pond proximity, Cond - conductivity). Note - only significant environmental variables are presented; b) community abundance bubble plot; c) taxon richness bubble plot and; d) Shannon Wiener diversity index bubble plot. The size of each bubble (pond site) is proportional to: b) community abundance, c) taxon richness and d) Shannon Wiener diversity index.

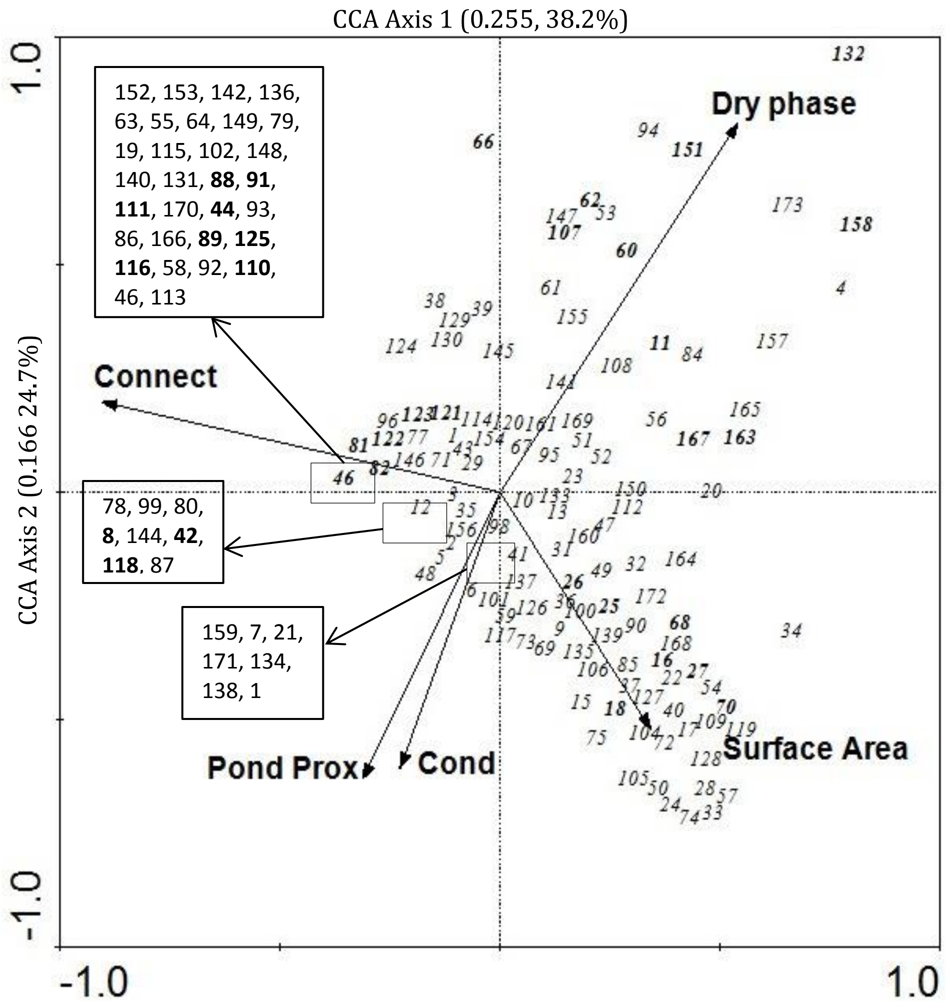

Figure 7.8 - CCA ordination of macroinvertebrate taxa in relation to physicochemical and spatial environmental parameters from meadow ponds (Connect - connectivity, Pond Prox - pond proximity, Cond - conductivity). Note - only significant environmental variables are presented in the final output. Macroinvertebrate taxa which correspond to the number displayed in the CCA output are presented in Table 7.6.

Table 7.6 - Meadow pond macroinvertebrate taxa and their representative number displayed in the CCA biplot.

Taxa							
Lymnaea palustris	*1*	*Lestes sponsa*	*45*	*Sigara falleni*	*89*	*Hygrobia hermanni*	*133*
Lymnaea peregra	*2*	*Calopteryx virgo*	*46*	*Sigara fossarum*	*90*	*Haliplus confinis*	*134*
Lymnaea stagnalis	*3*	Coenagrionidae instar I+II	*47*	*Sigara lateralis*	*91*	*Haliplus flavicolis*	*135*
Lymnaea truncatula	*4*	*Aeshna cyanea*	*48*	*Sigara limitata*	*92*	*Haliplus fluviatilis*	*136*
Physidae	5	Aeshna Instar I+II	*49*	*Sigara nigrolineata*	*93*	Haliplus Ruficollis Group	*137*
Gyraulus albus	*6*	*Aeshna mixta*	50	*Gerris gibbifer*	*94*	Haliplus larvae	*138*
Planorbis carinatus	*7*	*Anax imperator*	*51*	*Gerris lacustris*	95	*Haliplus lineatocollis*	*139*
Planorbarius corneus	*8*	*Libellula depressa*	*52*	Gerridae nymph	*96*	*Berosus luridus*	140
Armiger crista	*9*	*Libellula quadrimaculata*	*53*	*Hydrometra stagnorum*	*97*	Cercyon	*141*
Gyraulus laevis	*10*	*Sympetrum striolatum*	*54*	*Notonecta glauca*	*98*	*Cercyon marinus*	*142*
Anisus leucostoma	*11*	Trichoptera pupae	*55*	*Notonecta maculata*	*99*	*Enochrus testaceus*	*143*
Planorbis planorbis	*12*	*Phryganea bipunctata*	*56*	Notonectidae nymph	*100*	*Helochares lividus*	*144*
Anisus vortex	*13*	*Anabolia nervosa*	*57*	*Ilyocoris cimicoides*	*101*	Helophorus terrestrial	*145*
Segmentina nitida	14	*Chaetopteryx villosa*	*58*	Ilyocoris Cimicoides Nymph	*102*	*Helopohrus brevipalpis*	*146*
Bythnia tentaculata	*15*	*Glyphotaelius pellucidus*	59	*Nepa cinerea*	*103*	*Helophorus dorsalis*	*147*
Potamopyrgus antipodarum	*16*	*Limnephilus aricula*	*60*	*Ranata linearis*	104	*Helophorus griseus*	*148*
Succinea putris	*17*	*Limnephilus binotatus*	*61*	*Gyrinus substriatus*	*105*	*Helophorus (cf.) griseus*	149
Acroloxus lacustris	*18*	*Limnephilus centralis*	*62*	*Noterus clavicornis*	*106*	*Helophorus (cf.) longitarsis*	*150*
Valvata cristata	*19*	*Limnephilus decipiens*	*63*	*Acilius sulcatus*	*107*	*Helophorus minutus*	*151*
Valvata piscinalis	*20*	*Limnephilus extricatus*	*64*	*Agabus bipustulatus*	*108*	*Helophorus obscurus*	*152*
Zonitidae	*21*	*Limnephilus flavicornis*	*65*	*Agabus didymus*	*109*	Helophorus Other	*153*
Pisidiidae	*22*	*Limnephilus griseus*	*66*	*Agabus conspersus*	*110*	*Hydrobius fuscipes*	*154*
Oligochaeta	23	*Limnephilus incisus/affinis*	*67*	*Agabus nebulosus*	*111*	Hydrophilidae larvae	*155*
Erpobdella octoculata	*24*	*Limnephilus lunatus*	68	*Agabus sturmii*	*112*	*Laccobius biguttatus*	*156*
Erpobdella testacea	*25*	Limnephilus instar I+II	*69*	*Colymbetes fuscus*	113	*Paracymus scutellaris*	*157*
Glossiphonia complanata	*26*	*Limnephilus marmoratus*	*70*	Dytiscidae larvae	*114*	Scirtidae larvae	158
Helobdella stagnalis	*27*	*Limnephilus vittatus*	*71*	*Hydroglyphus geminus*	*115*	Ceratopogonidae	*159*
Hemiclepsis marginata	*28*	*Mystacides longicornis*	*72*	*Hydroporus angustatus*	*116*	Chaoboridae	*160*
Theromyzon tessulatum	*29*	*Triaenodes bicolor*	*73*	*Hydroporus incognitus*	*117*	Chironomidae	*161*
Piscicola geometra	*30*	*Cyrnus flavidus*	*74*	*Hydroporus palustris*	*118*	Chrysomelidae	*162*
Crangonyx pseudogracilis	*31*	*Holocentropus dubius*	*75*	*Hydroporus planus*	*119*	Culicidae	*163*
Asellus aquaticus	32	*Holocentropus picicornis*	*76*	*Hydroporus pubescens*	*120*	Dixidae	*164*
Asellus meridianus	*33*	*Callicorixa praeusta*	77	*Hygrotus confluens*	*121*	Ephydridae	*165*
Taeniopterygidae	*34*	*Callicorixa wollastoni*	*78*	*Hygrotus inaequalis*	122	Empididae	*166*
Cloeon dipterum	*35*	*Corixa dentipes*	*79*	*Hygrotus impressopunctatus*	*123*	Psychodidae	167
Cloeon simile	*36*	*Corixa panzeri*	*80*	*Hygrotus nigrolineatus*	*124*	Stratiomyidae	*168*
Caenis horaria	*37*	*Corixa punctata*	*81*	*Hygrotus versicolor*	*125*	Tipulidae	*169*
Caenis luctuosa	*38*	Corixidae nymph	*82*	*Hyphydrus ovatus*	*126*	Diptera Other	*170*
Caenis robusta	*39*	*Hesperocorixa linnaei*	*83*	*Ilybius fenestratus*	*127*	Hydrachnidiae	*171*
Cataclysta lemnata	*40*	*Hesperocorixa sahlbergi*	*84*	*Ilybius subaeneus*	*128*	Planariidae	*172*
Coenagrion puella	41	*Micronecta poweri*	*85*	*Laccophilus minutus*	*129*	Collembola	*173*
Erythromma najas	*42*	*Sigara concinnna*	86	*Rhantus frontalis*	*130*		
Ischnura elegans	*43*	*Sigara distincta*	*87*	*Rhantus suturalis*	131		
Pyrrhosoma nymphula	*44*	*Sigara dorsalis*	*88*	Elminthidae larvae	*132*		

Overall, spatial and physicochemical parameters explained 33.7% of the variance in macroinvertebrate communities from meadow ponds (Figure 7.9). Biological factors had no significant influence on macroinvertebrate community assemblage among meadow ponds. The majority of total variance was explained by the combination of physicochemical and spatial factors (P+SP), 14.4% (43% of explainable variance). Physicochemical factors (P|SP) could uniquely explain 14.1% and spatial parameters (SP|P) could alone explain 5.2% of the total variance in the faunal data. This indicates that whilst physicochemical factors had a significantly greater influence on macroinvertebrate community composition than spatial factors separately, the invertebrate communities were predominantly influenced by the combined effect of spatial and physicochemical parameters (Figure 7.9).

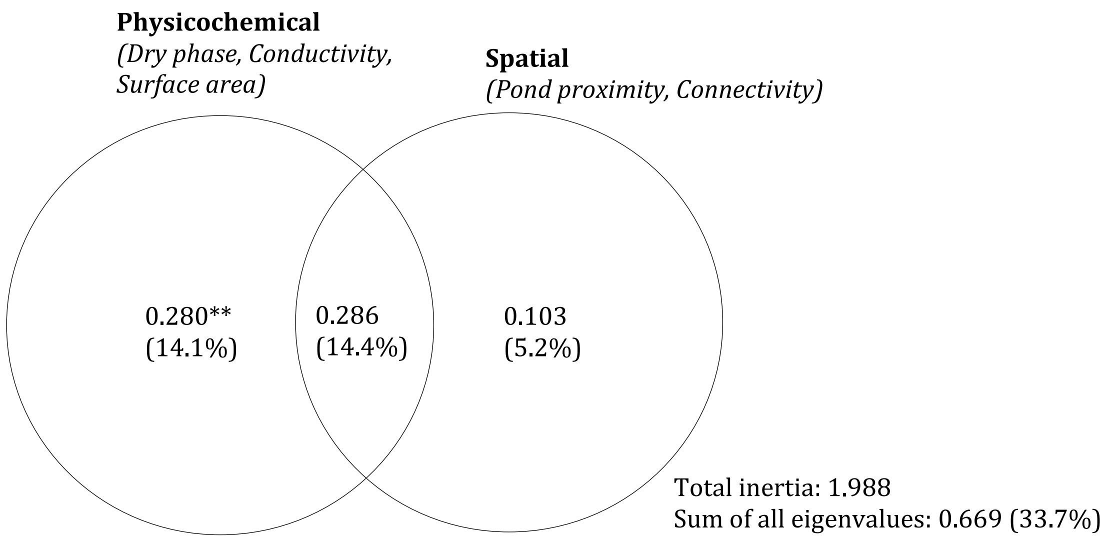

*Figure 7.9 - Variance partitioning of the relative influence of physicochemical and spatial variables on macroinvertebrate composition from meadow ponds. Values represent a proportion of the total variation (1.988). Percentage contributions of the total variance are presented in the parenthesis. ** = p<0.001.*

7.2.4 Influence of local and spatial parameters on macroinvertebrate assemblage among ephemeral ponds

A total of 27 ephemeral ponds (14 meadow, 6 urban, 4 forest and 3 agricultural) in Loughborough and the surrounding wider landscape were examined in this study. The canonical axes were highly significant (Monte Carlo significance test: $F=1.308$; $p<0.004$) and the first four canonical axes explained 25% of the species data (axis 1: 8.7%, axis 2: 6.9%, axis 3: 5.8%, axis 4: 3.6%). Axis 1 explained 34.8%, axis 2: 27.5%, axis 3: 23.5% and axis 4: 14.2% of the species-environment relationship. The dry phase (number of months pond basin was dry), pond proximity, pH and submerged macrophytes were identified to significantly influence the macroinvertebrate communities recorded from urban ponds (Table 7.7).

Table 7.7 - Significance of environmental parameters in explaining the variation in macroinvertebrate community composition from ephemeral pond habitats using forward selection Monte Carlo permutation tests (999) and Bonferroni correction

Physicochemical Characteristic	Environmental Group	Code in Figures 7.10 and 7.11	F. Ratio	P. Value
pH	Physicochemical	pH	1.66	0.014
Dry phase	Physicochemical	Dry phase	1.74	0.014
Pond proximity	Spatial	Pond Prox	1.59	0.020
Submerged macrophytes	Biological	SM	2.01	0.004

High community abundance was recorded from more isolated ponds and those with a lower proportion of pond covered with submerged macrophytes (Figure 7.10b). Conversely, greater taxon richness was associated with a shorter dry phase, a higher proportion of the pond covered by submerged macrophytes and greater pond proximity (Figure 7.10c). Ponds with lower taxon richness were associated with a longer dry phase and little submerged macrophyte coverage (Figure 7.10c). A greater proximity to other fresh waterbodies and a higher coverage of the pond by submerged macrophytes were associated with the greatest Shannon Wiener diversity scores. Although, high Shannon Wiener diversity index scores were also recorded from some ponds that were typically more isolated and with little submerged macrophyte coverage (Figure 7.10d). The lowest Shannon Wiener diversity scores were associated with ponds which demonstrated a long dry phase and higher pH levels (Figure 7.10d).

Several species of Coleoptera (e.g., *Agabus sturmii* (65), *Agabus bipustulatus* (63) *Hydroporus palustrus* (69) and *Colymbetes fuscus* (66)), Hirudinea (e.g., *Helobdella stagnalis* (19), *Erpobdella testacea* (17)), Odonata (e.g., Libellulidae 2 species (32, 33)) and the Diptera Dixidae (98) were associated with ponds which demonstrated a shorter dry phase (Figure 7.11). Whilst the Coleoptera *Hygrotus confluens* (commonly recorded from temporary waters: 71), the Hemiptera *Sigara lateralis* (55) and the Diptera Ceratopogonidae (94) were recorded in higher abundances from ponds with a longer dry period. Taxa corresponding to the numbers displayed on the species CCA output are presented in Table 7.8. A number of coleopteran species (e.g., *Acilus sulcatus* (62), *Helpohorus minutus* (87), *Hygrotus* - 2 species (72, 73)) Odonata (e.g., *Coenagrion puella* (27)) and hemipteran species (e.g., *Gerris lacustris* (57) *Notonecta glauca* (59) *Corixa punctata* (48)) were associated with ephemeral ponds with a greater proximity to other fresh waterbodies. Several species of Gastropoda (e.g., Planorbidae - 4 species (6, 7, 8, and 9)) were recorded in higher abundances from ponds with a greater proportion of submerged macrophytes covering the pond surface (Figure 7.11). A number of species were associated with ponds which had lower submerged macrophyte coverage and/or were more isolated including; the Diptera Chaoboridae (95); the Bilvalvia Pisidiidae (14); the Trichoptera *Limnephilus decipiens* (39) and *Limnephilus flavicornis* (40) and the Crustacea *Asellus aquaticus* (22). *Crangonyx pseudogracilis* (21) was located towards the middle of the ordination suggesting they were common and abundant in ephemeral ponds, are likely to have the prerequisite characteristics to survive in ephemeral ponds and/or that stochastic processes may play an important role in the distribution of Crustacea within ephemeral ponds.

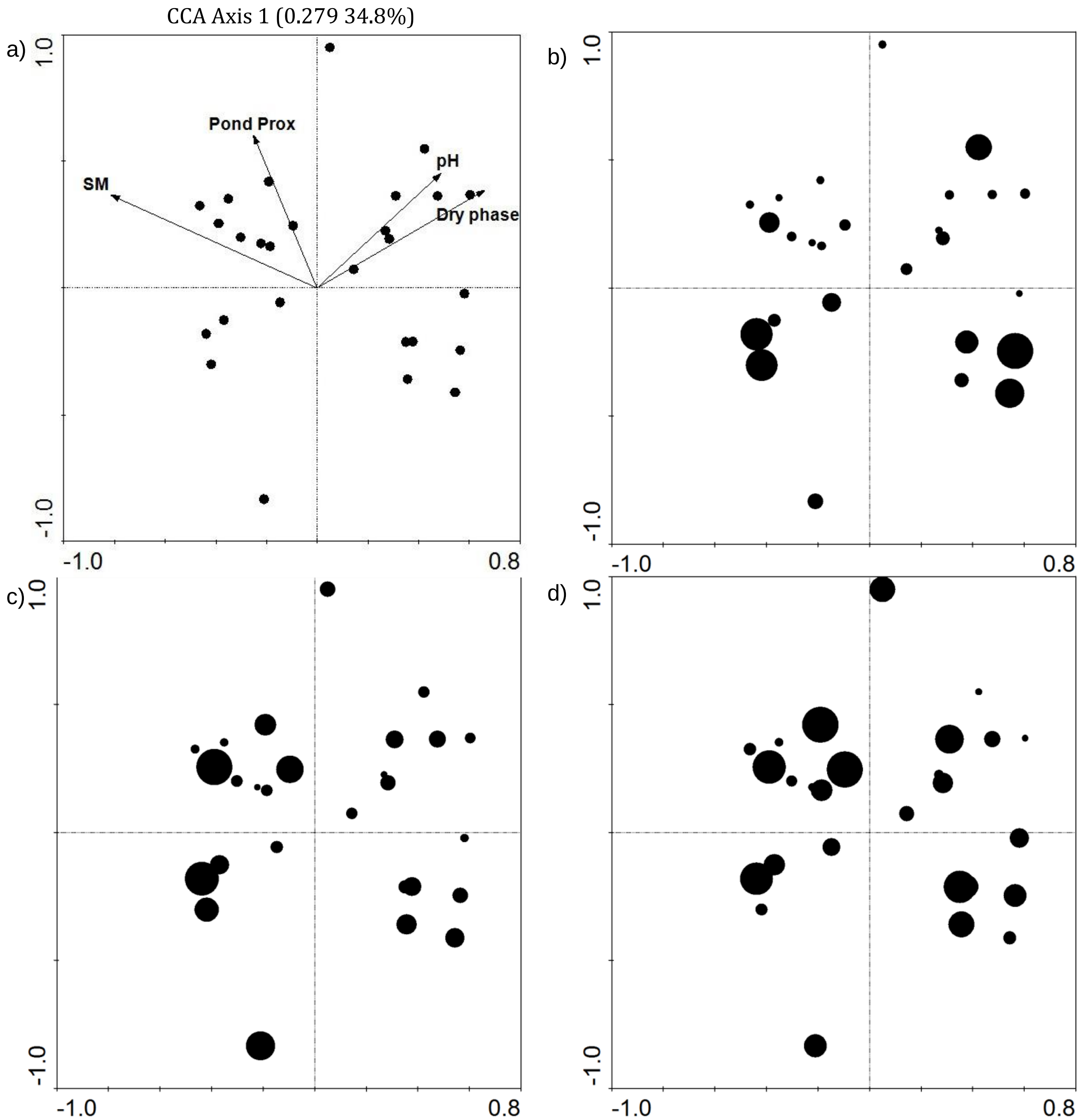

Figure 7.10 - Canonical Correspondence Analysis of ephemeral pond macroinvertebrate communities and; a) pond sites and significant environmental parameters (Pond Prox - pond proximity, SM - submerged macrophytes). Note - only significant environmental variables are presented; b) community abundance bubble plot; c) taxon number bubble plot and; d) Shannon Wiener diversity index bubble plot. The size of each bubble (pond site) is proportional to: b) community abundance, c) taxon richness and d) Shannon Wiener diversity index.

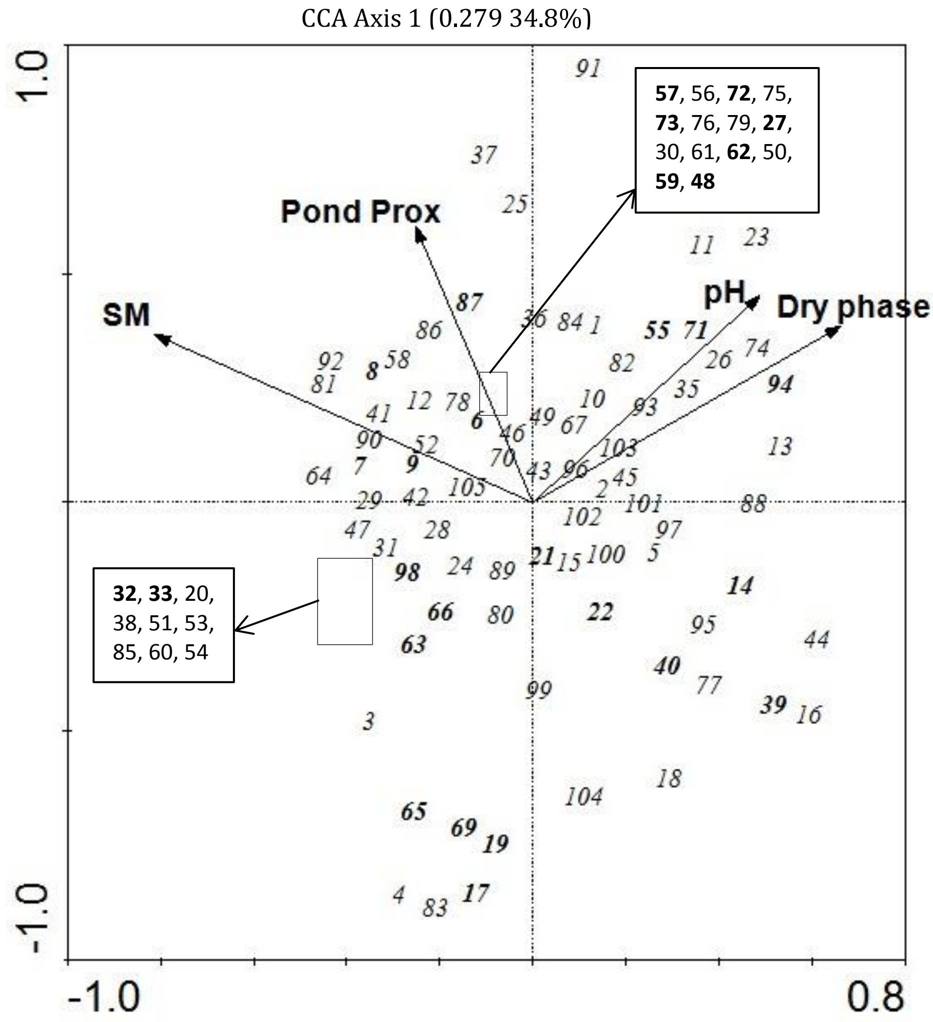

Figure 7.11 - CCA ordination of ephemeral pond macroinvertebrate taxa in relation to physicochemical, biological and spatial environmental parameters (Pond Prox - pond proximity, SM - submerged macrophytes). Note only significant environmental variables are presented in the final output. Macroinvertebrate taxa which correspond to the number displayed in the CCA output are presented in Table 7.8.

Table 7.8 - Ephemeral pond macroinvertebrate taxa and their representative number displayed in the CCA biplot

Taxa					
Lymnaea palustris	1	*Limnephilus binotatus*	37	*Hygrotus impressopunctatus*	73
Lymnaea peregra	2	*Limnephilus centralis*	38	*Hygrotus nigrolineatus*	74
Lymnaea stagnalis	3	*Limnephilus decipiens*	39	*Laccophilus minutus*	75
Lymnaea truncatula	4	*Limnephilus flavicornis*	40	*Rhantus frontalis*	76
Physidae	5	*Limnephilus griseus*	41	*Suphrodytes figuratus*	77
Gyraulus laevis	6	*Limnephilus incisus/affinis*	42	Elminthidae larvae	78
Anisus leucostoma	7	*Limnephilus lunatus*	43	*Hygrobia hermanni*	79
Planorbis planorbis	8	Limnephilus instar I+II	44	Haliplus Ruficollis Group	80
Anisus vortex	9	*Limnephilus marmoratus*	45	Haliplus larvae	81
Potamopyrgus antipodarum	10	*Limnephilus vittatus*	46	*Anacaena globulus*	82
Valvata cristata	11	*Callicorixa praeusta*	47	*Cercyon*	83
Valvata piscinalis	12	*Corixa punctata*	48	Helophorus terrestrial	84
Zonitidae	13	Corixidae nymph	49	*Helophorus dorsalis*	85
Pisidiidae	14	*Hesperocorixa sahlbergi*	50	*Helophorus (cf.) longitarsis*	86
Oligochaeta	15	*Micronecta poweri*	51	*Helophorus minutus*	87
Erpobdella octoculata	16	*Sigara dorsalis*	52	*Helophorus strigifrons*	88
Erpobdella testacea	17	*Sigara falleni*	53	*Hydrobius fuscipes*	89
Glossiphonia complanata	18	*Sigara fossarum*	54	Hydrophilidae larvae	90
Helobdella stagnalis	19	*Sigara lateralis*	55	*Laccobius biguttatus*	91
Theromyzon tessulatum	20	*Gerris gibbifer*	56	*Paracymus scutellaris*	92
Crangonyx pseudogracilis	21	*Gerris lacustris*	57	Scirtidae larvae	93
Asellus aquaticus	22	Gerridae nymph	58	Ceratopogonidae	94
Asellus meridianus	23	*Notonecta glauca*	59	Chaoboridae	95
Cloeon dipterum	24	Notonectidae nymph	60	Chironomidae	96
Caenis luctuosa	25	*Ilyocoris cimicoides*	61	Culicidae	97
Caenis robusta	26	*Acilius sulcatus*	62	Dixidae	98
Coenagrion puella	27	*Agabus bipustulatus*	63	Ephydridae	99
Ischnura elegans	28	*Agabus nebulosus*	64	Psychodidae	100
Coenagrionidae instar I+II	29	*Agabus sturmii*	65	Stratiomyidae	101
Aeshna instar I+II	30	*Colymbetes fuscus*	66	Tipulidae	102
Anax imperator	31	Dytiscidae larvae	67	Hydrachnidiae	103
Libellula depressa	32	*Hydroporus memnonius*	68	Planariidae	104
Libellula quadrimaculata	33	*Hydroporus palustris*	69	Collembola	105
Phryganea bipunctata	34	*Hydroporus pubescens*	70		
Grammotaulius nigropunctatus	35	*Hygrotus confluens*	71		
Limnephilus aricula	36	*Hygrotus inaequalis*	72		

The partitioning of variance highlighted the dominance of physicochemical factors on macroinvertebrate assemblages within the ephemeral ponds (Figure 7.12). Significant physicochemical, biological and spatial variables explained a total of 25% of the macroinvertebrate community variance. Physicochemical factors alone (P|B+SP) explained the highest proportion of total variance (12.3%), biological factors could uniquely (B|P+SP) explain 4.1% and spatial parameters could uniquely (SP|P+B) explain 4.7% of the total variation. A combination of physicochemical, biological and spatial (P+B+SP) could explain 1.8% of the total variance in macroinvertebrate assemblage (Figure 7.12). These results illustrate the importance of physicochemical factors in potentially driving ephemeral pond invertebrate communities.

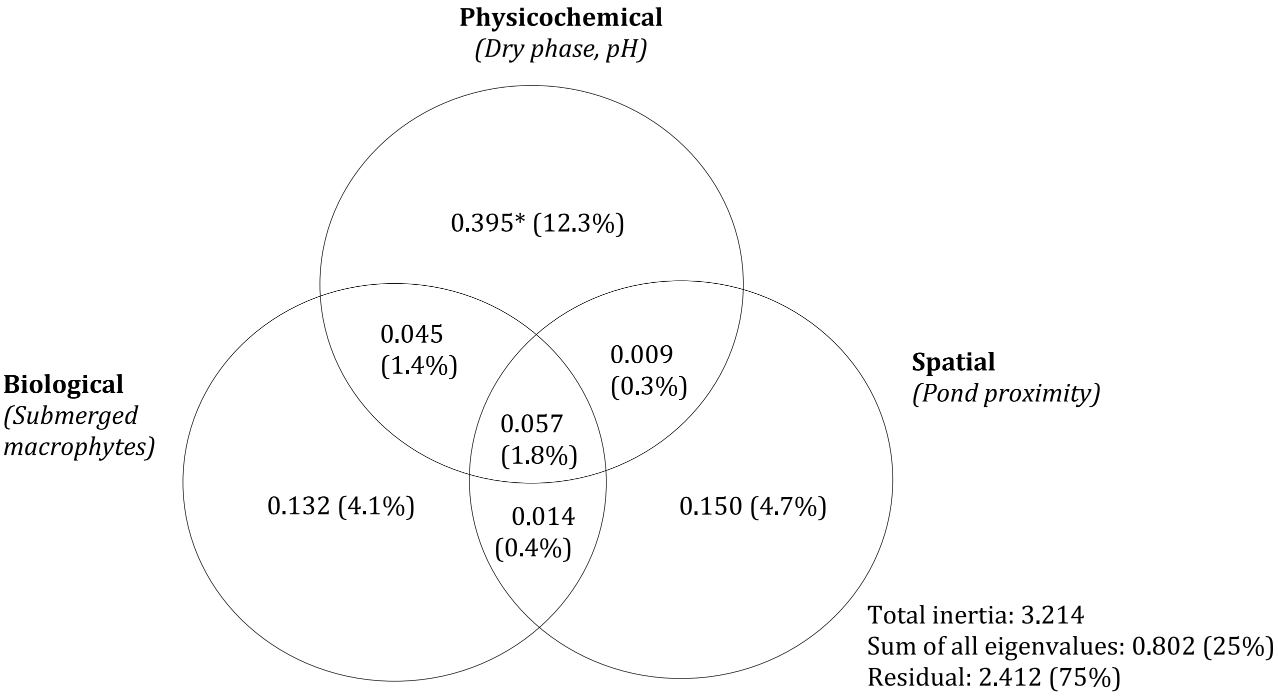

*Figure 7.12 - Variance partitioning of the relative influence of physicochemical, biological and spatial variables on macroinvertebrate composition among ephemeral pond communities. Values represent a proportion of the total variation (0.631). Percentage contribution of the total variance is presented in the parenthesis. * = p<0.05.*

7.2.5 Spatial patterns in macroinvertebrate assemblage dissimilarity

Non-parametric mantel type tests using Spearman's Rank correlation coefficients (in PRIMER 6) were used to examine the similarities between the spatial distance among ponds (SD), Euclidean environmental distance (E) and community dissimilarity (CD). A highly significant positive correlation between the spatial distance among pond sites and the macroinvertebrate community dissimilarity was recorded from all ponds across the region (*rho*=0.1, p<0.001) and among meadow pond sites (*rho*=0.507, p<0.001) (Table 7.9). However no significant correlation was recorded between spatial distance and community dissimilarity in urban and ephemeral pond habitats. Urban ponds, meadow ponds, ephemeral ponds and all pond sites across the region demonstrated a significant positive relationship between macroinvertebrate community dissimilarity and the Euclidean environmental distance (Table 7.9). A significant correlation between environmental distance and spatial distance was recorded among meadow and ephemeral pond sites while no significant relationship was found for urban pond sites and for all ponds across the region (Table 7.9).

Table 7.9 - Non-parametric Mantel type test results between macroinvertebrate community dissimilarity, Euclidean environmental distance and the spatial distance among ponds across the region (95 ponds), in the urban landscape (41 ponds), meadow landscape (35 ponds) and among ephemeral ponds (25 ponds). Rho represents the Spearman's Rank correlation coefficient between pairs of the three data matrices. P values were calculated through 999 permutations. CD = community dissimilarity; E = Euclidean environmental distance; SD = spatial distance between ponds. Significant variables (p≤0.05) are presented in bold

	Rho	P. Value
Regional Pond Community Assemblage		
CD x E	0.392	**0.001**
CD x SD	0.1	**0.013**
E x SD	0.015	0.34
Urban Pond Community Assemblage		
CD x E	0.4	**0.001**
CD x SD	0.042	0.319
E x SD	0.022	0.361
Meadow Pond Community Assemblage		
CD x E	0.586	**0.001**
CD x SD	0.507	**0.001**
E x SD	0.48	**0.001**
Ephemeral Pond Community Assemblage		
CD x E	0.149	**0.034**
CD x SD	-0.019	0.598
E x SD	0.137	**0.027**

7.3 Discussion

7.3.1 Environmental drivers of macroinvertebrate community assemblage

A primary interest of community ecology research is to determine the relative role and importance of local and spatial environmental processes driving macroinvertebrate community composition at different spatial scales (Pinel-Alloul *et al.,* 1995; Vanschoenwinkel *et al.,* 2007). At a regional scale, this study has demonstrated that a variety of physicochemical, biological and spatial variables influence pond macroinvertebrate communities providing evidence to accept the first hypothesis;

> *H_1: A combination of physicochemical, biological and spatial factors will influence communities at a regional scale.*

There have been few studies which have examined local and spatial influences on macroinvertebrate community assemblage at a regional scale. At smaller scales, studies which have addressed local (physicochemical/biological) and spatial (connectivity/pond proximity) factors have identified that a combination of local and spatial factors can best explain the variation in macroinvertebrate community composition (Cottenie *et al.,* 2005; Vanschoenwinkel *et al.,* 2007). The results of this study demonstrate that at a landscape-scale, different environmental factors influenced invertebrate communities in meadow (physicochemical and spatial) and urban (biological and physicochemical) environments (Table 7.10) and will be discussed in greater detail below. The results from this study (Figure 7.1, 7.4, 7.7) demonstrate that the greatest macroinvertebrate diversities within ponds at regional and landscape scales were associated with greater connectivity, proximity to other waterbodies, increased pond area and aquatic macrophyte cover, whilst the lowest diversities were associated with the drying of the pond basin) (Oertli *et al.,* 2002; Biggs *et al.,* 2005; Della Bella *et al.,* 2005; Williams *et al.,* 2008; Becerra-Jurado *et al.,* 2009; Bazzanti *et al.,* 2010).

Table 7.10 - Summary table of variance partitioning results for regional, urban, meadow and ephemeral ponds

	Regional	**Urban**	**Meadow**	**Ephemeral**
Number of ponds	95	41	34	27
Number of macroinvertebrate taxa	228	170	173	105
Significant environmental variables				
Physicochemical	*Dry phase, Surface area, pH, Dissolved oxygen*	*Dry phase, Surface area, pH*	*Dry phase, Conductivity, Surface area*	*Dry phase, pH*
Biological	*Fish presence, Submerged macrophytes, Emergent macrophytes*	*Submerged macrophytes, Emergent macrophytes*	*n/a*	*Submerged macrophytes*
Spatial	*Pond proximity, Connectivity*	*n/a*	*Pond proximity, Connectivity*	*Pond proximity*
% species variation explained by significant environmental variables	27.5	23.8	33.7	25
% Unique/combined variation explained				
P|B+SP (%)	9.2	9.4	14.1	12.3
B|P+SP (%)	4.9	5.8	n/a	4.1
SP|P+B (%)	3.2	n/a	5.2	4.7
P+SP|B (%)	4	n/a	14.4	0.3
P+B|SP (%)	4.4	8.7	n/a	1.4
SP+B|P (%)	1.9	n/a	n/a	0.4
P+B+SP (%)	0	n/a	n/a	1.8

7.3.1.1 Pond surface area

The influence of pond area (size) on invertebrate community composition has been widely debated (Oertli *et al.,* 2002; Rundle *et al.,* 2002; Céréghino *et al.,* 2008; Schriever and Williams, 2013). Biogeographical theory suggests that the larger the pond the greater the aquatic taxon richness, which has been recorded by several studies on pond macroinvertebrate communities (Brönmark, 1985; Spencer *et al.,* 1999; Biggs *et al.,* 2005; Bilton *et al.,* 2009). However, biogeographical theory does have limitations with regards to pond habitats as a number of studies have identified that pond area has a weak relationship with macroinvertebrate richness (Oertli *et al.,* 2002; Bazzanti *et al.,* 2003) and suggested that a series of smaller ponds of similar area to a single large pond can support greater taxon richness (Oertli *et al.,* 2002).

7.3.1.2 Connectivity (pond proximity)

The rapid colonization and establishment of diverse and rich invertebrate communities in new ponds in Pinkhill Meadow, on the upper River Thames floodplain, Oxfordshire, was attributed to their high connectivity and proximity to a large number of other fresh waterbodies (Williams *et al.,* 2008). Furthermore, a positive correlation between aquatic macrophyte species richness and the pond's proximity to other waterbodies has been recorded in ponds across the UK (Biggs *et al*., 2005). A greater connectivity between pond habitats can increase floral and faunal richness by facilitating and increasing the dispersal and colonization of aquatic macrophyte and macroinvertebrate taxa between ponds (Biggs *et al.,* 2005). In the present study, at a landscape-scale (urban/semi-natural meadows) the influence of spatial factors was mixed. Within the meadow landscape spatial variables were an important determinant of macroinvertebrate distribution and were associated with greater invertebrate diversity whilst connectivity did not significantly influence community composition among ponds in an urban landscape. This provides evidence to support the second hypothesis;

> *H_2: Spatial factors will exert a greater influence on meadow ponds than urban or ephemeral pond communities.*

The group of meadow ponds most strongly associated with connectivity (Figure 7.7) were located adjacent to the River Soar and inundated by floodwater at least twice during the sampling period. The river flood pulse theory has highlighted the importance of river flooding for the delivery of water and resources to floodplain habitats (Junk, 1989; Benke *et al.,* 2000*;* Middleton, 2002; Reckendorfer *et al.,* 2006). Previous research has demonstrated that floodplains are areas of rich faunal and floral biodiversity (Ward *et al.,* 1999; Helfield *et al.,* 2012). However, several studies have suggested that high connectivity and regular inundation by floodwater may act to constrain species richness on the floodplain (Bornette *et al.,* 1998; Reckendorfer *et al.,* 2006). The reduced species richness at sites of high connectivity with the river may reflect the large physical disturbance (high flow velocity of flood water) caused by river floodwater on floodplains (Ward *et al.,* 2002; Tockner *et al.,* 2010; Starr *et al.,* 2014). Notwithstanding this, the results of the current study indicate that high invertebrate richness was associated with highly connected ponds adjacent to the River Soar. Similarly, the highest diversity of macroinvertebrate communities on the River Sipsey floodplain, Alabama, USA, were recorded from sloughs (wetlands) with greatest connectivity to the main river channel (Starr *et al.,* 2014). In this study the River Soar floodplain has a number of lateral drainage ditches connected to the main channel which can reduce the floodwater velocity over the floodplain. The high species richness associated with high connectivity among ponds on the floodplain may reflect the replenishing effect that floodwater can have (when there is lower floodwater flow velocity), especially in lowland landscapes (Lake *et al.,* 2006) such as: re-filling the lentic habitats; re-initiating hydrological connections; facilitating macroinvertebrate dispersal and colonization between floodplain habitats; and the provision of nutrients and food (Starr *et al.,* 2014). Although high connectivity may increase alpha diversity, it has been found to reduce beta-diversity in some aquatic systems (Warren, 1996; Pedruski and Arnott, 2011). However, whilst high connectivity (increased dispersal) can have a homogenizing effect on aquatic communities, the high environmental heterogeneity demonstrated by ponds (Williams *et al.,* 2003) may act to sort and regulate macroinvertebrate communities and maintain beta-diversity (Cottenie *et al.,* 2003; Pedruski and Arnott, 2011).

The proximity of ponds (connectivity) was not identified as a significant influence on macroinvertebrate community composition in urban landscapes ($p>0.05$, Figure 7.4). Urban ponds, especially those in domestic gardens are often surrounded by walls, fences or buildings (barriers) typical of urban landscapes. These physical barriers may significantly reduce pond connectivity and the ability of invertebrate and amphibian taxa to disperse or colonize new habitats, even if they are geographically in close proximity (Lehtinen and Galatowitsch, 2001; Parris, 2006; Hamer and Parris, 2011; Noble and Hassall, 2014).

Pond density was found to be strongly correlated with macroinvertebrate richness in the administrative district of Halton, UK, with a greater urban pond density strongly correlated with higher taxon richness (Gledhill *et al.,* 2008). This suggests that despite the physical barriers that may be present in urban landscapes, if pond density/connectivity is at a sufficient level (suggested to be 4.5 ponds per km^2 (Gledhill *et al.,* 2008)) it could play an important role in the distribution and composition of taxa and increase richness to comparable levels of the wider landscape (Gledhill *et al.,* 2008; Hamer *et al.,* 2012).

7.3.1.3 Hydroperiodicity

The cyclical drying of the pond basin (hydroperiodicity) was a key factor influencing macroinvertebrate community composition within ephemeral ponds at a regional and landscape (urban/meadow) scale (Figure 7.1, 7.4, 7.7, Table 7.10). It has been well documented that pond drying can reduce macroinvertebrate richness and influence the distribution of aquatic macroinvertebrate taxa within ephemeral ponds (Collinson *et al.,* 1995; Nicolet, 2001; Rundle *et al.,* 2002; Della Bella *et al.,* 2005). Macroinvertebrate richness has been shown to increase linearly with increasing hydroperiod length as increased pond duration will prolong the time available for colonization by macroinvertebrate taxa (Bilton *et al.,* 2001; Tarr *et al.,* 2005) and allow the development of taxa to sexual maturity. Despite having a lower richness than their perennial counterparts in this study, there were a number of species only associated with ephemeral pond habitats including *Limnephilus binotatus* (Trichoptera: Limnephilidae), *Helophorus minutus* (Coleoptera: Helophoridae), *Anisus leucostoma* (Gastropoda: Planorbidae) and Scritidae larvae (Coleoptera) (Figure 7.2, 7.5, 7.8). In addition, a number of semi-aquatic species such as Collembola and terrestrial *Helophorus* beetles were associated with ephemeral ponds. These temporary environments provide a very important habitat for a number of specialist aquatic taxa (and also generalist aquatic taxa, see Chapter 6) that are often outcompeted/cannot survive in perennial ponds and contribute significantly to pond beta and gamma (regional) diversity (Williams, 1997; Nicolet, 2001; Nicolet *et al.,* 2004; Della Bella *et al.,* 2005).

7.3.1.4 Biological variables

Aquatic macrophytes were identified to significantly influence the distribution of macroinvertebrate taxa and were associated with higher taxon richness at a regional scale and especially within urban landscapes. Emergent and submerged macrophytes have been shown to increase invertebrate pond diversity and to support a greater faunal richness than open water and other mesohabitats (Brönmark, 1985; Parsons and Matthews, 1995; Bazzanti *et al.,* 2010; Florencio *et al.,* 2014). Aquatic macrophytes can provide a source of food, protection from fish predation, oxygenation and egg laying sites (Biggs *et al.,* 1994; Williams *et al.,* 1999). There was little variation in macrophyte cover in meadow ponds; almost all meadow ponds in this study had dense emergent and submerged macrophyte communities which may, in part, explain why this particular variable was not identified to be an important influence in the distribution of aquatic invertebrate taxa in meadow landscapes (Table 7.10).

Fish presence was associated with urban pond habitats, (which is unsurprising as many urban ponds, especially in domestic gardens, are built for ornamental fish communities), and greater invertebrate richness at a regional scale. A low fish density within ponds may promote a more diverse macroinvertebrate community through predation of invertebrate predators and larger invertebrate taxa (preferentially eaten by fish as they are more readily seen) (Chaichana *et al.,* 2011) which can reduce the competition for resources and lower invertebrate predation pressure. However, previous research has demonstrated that large predatory fish populations can have a negative effect on macroinvertebrate richness in urban and rural ponds (Diehl, 1992; Nyström *et al.,* 2001; Angélibert *et al.,* 2004; Foltz and Dodson, 2009). It should also be acknowledged that only two of the ponds in this study were stocked for angling purposes (which has been shown to greatly reduce open water macroinvertebrate abundance and diversity (Wood *et al.,* 2001)) and Koi carp and other common ornamental pond species in urban ponds were fed regularly potentially reducing predation on macroinvertebrate taxa. In addition, the fish recorded from rural ponds were typically small species such as sticklebacks.

7.3.2 Relative influence of physicochemical, biological and spatial variables

Physicochemical variables explained more of the variation in macroinvertebrate assemblage than biological and spatial factors at a regional and landscape (meadow/urban) scale (Figure 7.3, 7.6, 7.9), indicating that local physicochemical variables were the dominant influence on invertebrate composition over biological and spatial factors. This provided evidence to support the third hypothesis;

> *H_3: Physicochemical parameters will be the dominant influence on macroinvertebrate assemblage at a regional and landscape (ephemeral, meadow and urban) scale.*

These findings support the species sorting paradigm in metacommunity theory (see Chapter 2.5.1, Leibold *et al.,* 2004). Similar to the findings in this study, local environmental (physicochemical/biological) variables explained more of the variance in macroinvertebrate community composition than spatial factors (pond proximity/connectivity) among 36 ephemeral rock pools in South Africa (Vanschoenwinkel *et al.,* 2007) and 80 ponds in Donana National Park, Spain (Florencio *et al.,* 2014) further suggesting there is a strong species sorting influence on macroinvertebrate communities. Within a small, highly connected pondscape in Belgium, local environmental variables were identified as the most important determinant of pond cladoceran community composition, whilst spatial factors (connectivity/pond proximity) were identified to have only a secondary role, increasing species richness through increased dispersal potential (Cottenie *et al.,* 2003; Cottenie and De Meester, 2003). At a larger scale, physicochemical/biological factors explained more of the variation in zooplankton community assemblage than spatial variables within 54 lakes in Quebec, Canada (Pinel-Alloul *et al.,* 1995).

However, the influence of biological or spatial factors should not be underestimated. Biological variables explained a greater proportion of macroinvertebrate community variation than spatial factors in urban ponds, and aquatic macrophytes have been demonstrated in numerous other studies to have an important role in the distribution and diversity of macroinvertebrate taxa (Gee *et al.,* 1997; Bazzanti *et al.,* 2010; Florencio *et al.,* 2014). A significant amount of variation in macroinvertebrate community composition was explained by a combination of two groups of variables (e.g., physicochemical and biological explained 4.4% of the total variation at a regional scale), highlighting the importance of an interplay between environmental processes in driving community composition. In addition, among meadow ponds, the combination of physicochemical and spatial factors explained the greatest proportion of variance

(14.4%) in macroinvertebrate community composition. This further demonstrates the importance of the interaction between local and spatial variables at regional and landscape scales. Community dissimilarity was observed in this study to increase with geographical distance between ponds (and those ponds in close proximity had similar assemblages) in meadow landscapes and at a regional scale, although this pattern was not observed among urban ponds (Table 7.9). This suggests that mass effects may also have a significant role in determining macroinvertebrate community composition at a regional scale and in meadow landscapes. This provides evidence to accept the fourth hypothesis;

> *H_{4a}: Dissimilarity in community composition between pond sites will increase with geographic distance at a regional scale and among meadow and ephemeral ponds.*
>
> *H_{4b}: There will be no difference in community dissimilarity with geographic distance among urban ponds*

Cottenie *et al.* (2003) found direct connectivity between ponds had a homogenizing effect on zooplankton composition as they were able to disperse through the hydrological links. Thirty six rock pools in South Africa, in close proximity to each other, were recorded to have similar communities of passively dispersing invertebrate taxa but connectivity had no influence on actively dispersing taxa (Vanschoenwinkel *et al.,* 2007). In this study, actively dispersing taxa, especially Coleoptera, were associated with highly connected ponds (Figure 7.2). Most highly connected ponds (semi-natural meadow ponds - located in areas designated for nature conservation) had suitable physicochemical and biological conditions for Coleoptera and their close proximity promoted dispersal among the pond habitats, whereas passively dispersing invertebrates (a number of Gastropoda and Hirudinea taxa) were associated with larger pond areas (Figure 7.2, 7.5). The influence of pond area on Gastropoda was also noted by Brönmark, (1985) and Oertli *et al.* (2002), although Gastropoda abundance and richness, in this study and others, was additionally influenced by submerged macrophytes which can provide a source of food and refuge from predation (Brönmark, 1985). Taking a metacommunity approach, based on the results of this research (at a regional and landscape scale) and other studies, a combination of mass effects and species sorting (see Chapter 2.5.1, Leibold *et al.,* 2004) most effectively explains the variance among macroinvertebrate assemblages (Cottenie *et al.,* 2005; Vanschoenwinkel *et al.,* 2007; Ng *et al.,* 2009). Spatial factors (mass effects) promote the dispersal and colonization of invertebrates within a metacommunity but it is the variation in local (physicochemical/biological) factors (species sorting) that regulates and drives the variation (beta-diversity) in macroinvertebrate community composition (Cottenie *et al.*, 2003; Cottenie and De Meester, 2004). There is a need to improve connectivity in urban areas to facilitate the dispersal and colonization of macroinvertebrate taxa and to augment urban pond biodiversity.

The environmental variables measured explained less than 35% of the variance in pond macroinvertebrate communities at a regional and landscape scale (Table 7.10), indicating that there are other unquantified environmental variables and stochastic processes that have an important role in determining macroinvertebrate community assemblage (Pinel-Alloul *et al.,* 1995). Water chemistry data were limited in this study, which has been reported in other studies to be an important influence of pond macroinvertebrate community composition (Friday, 1987; Heino, 2000; Biggs *et al*., 2005; Williams *et al.,* 2006). This suggests that local physicochemical conditions may have been underestimated in this research and could exert even greater influence on macroinvertebrate community composition.

7.4 Summary

There are multiple interacting physicochemical, biological and spatial variables influencing macroinvertebrate community composition in ponds. Pond area and the drying of the pond basin were identified to significantly influence macroinvertebrate distribution across all spatial scales and environments. However, at a landscape-scale, meadow and urban ponds were influenced by different environmental variables. Spatial variables were not identified to influence significantly the distribution of macroinvertebrate taxa in urban areas, but were important in meadow landscapes. The physical barriers (buildings and fences) in urban environments may reduce the ability of taxa to disperse. Given the importance of connectivity in other landscapes and metacommunities, improving pond connectivity in urban areas will facilitate the dispersal and colonization of macroinvertebrate taxa and could augment urban biodiversity. Biological factors had no significant influence on invertebrate distribution in meadow ponds (which were all macrophyte rich) but were important in urban landscapes, offering protection from fish predation and a source of food. Physicochemical factors were the dominant influence on macroinvertebrate communities at a regional and landscape scale (urban/meadow) whilst biological and/or spatial factors had a lesser, but still important, influence on community composition. The interplay between physicochemical, biological and spatial factors also had an important role in driving the variation in macroinvertebrate assemblage at both a regional and landscape scale. In the framework of metacommunity theory, a combination of species sorting and mass effect best describes the distribution and variation in macroinvertebrate assemblage at a regional scale and in meadow landscapes, but within urban ponds species sorting alone best describes the variation in macroinvertebrate community composition. Through the consideration of all three groups of variables (physicochemical, biological and spatial) together, it increases the ability to predict and examine faunal communities (Pinel-Alloul *et al.,* 1995) and can provide greater detail and focus for management and conservation guidelines across larger spatial scales.

Chapter 8. Summary, key themes, future research and conclusions

8.1 Introduction

The principle aim of this thesis was to examine and quantify the aquatic macroinvertebrate biodiversity (alpha, beta and gamma) and conservation value of ponds over a range of spatial scales and landscapes (especially those that have been understudied in the published literature) that characterize the lowland environment of the UK. Specifically, this research has addressed the following objectives;

1. To quantify pond macroinvertebrate biodiversity and conservation value at a regional scale within a range of landscapes in Leicestershire, UK (see Chapter 4).
2. To examine the seasonal variability of aquatic macroinvertebrate communities associated with ponds (see Chapters 4, 5 & 6).
3. To characterise aquatic macroinvertebrate biodiversity within a range of ponds (garden, 'other' urban and park) in the urban landscape (see Chapter 5).
4. To quantify the macroinvertebrate biodiversity of perennial and ephemeral ponds in two floodplain meadow landscapes of the lower River Soar floodplain, UK (see Chapter 6).
5. To examine the physicochemical, biological and spatial (connectivity) characteristics influencing macroinvertebrate community composition within ponds at a range of spatial scales (see Chapter 7).

The data presented within the results chapters (4-7) examined the macroinvertebrate communities within ponds at a regional and landscape scale across urban and rural (perennial and ephemeral ponds) environments within Leicestershire, UK. The research undertaken fulfils all 5 of the thesis research objectives (see above). Each of these objectives will be examined in further detail in the following section. The results of this thesis potentially provide the basis for the development of a variety of practical management strategies to augment pond macroinvertebrate biodiversity in rural and anthropogenically disturbed landscapes/pondscapes. This chapter highlights the key findings from the results chapters, considers the key themes arising from the detailed examination of aquatic macroinvertebrate biodiversity that have emerged and suggests areas for future research.

8.2 Summary

The first investigation presented in this thesis **(Chapter 4)** aimed to quantify the aquatic macroinvertebrate biodiversity within ponds at a regional scale. Specifically, it provided a comparison of pond macroinvertebrate assemblages and diversity within a range of pond types (meadow, agricultural, forest, urban) typical of European lowland landscapes and specifically addressed the first objective of the thesis;

> *(1) To spatially quantify pond macroinvertebrate biodiversity and conservation value at a regional scale within a range of landscapes in Leicestershire, UK.*

Literature on aquatic macroinvertebrate biodiversity in ponds at a regional scale (incorporating a range of landscapes) is limited, underlining the need for further research at this spatial scale. At an alpha (site) diversity scale (using community abundance, taxon richness and a range of alpha diversity indices), meadow ponds (total taxa: 175, mean: 39) were identified as supporting the most diverse macroinvertebrate communities, whilst urban (total taxa: 170, mean: 21) and forest ponds (total taxa: 62, mean: 18) supported the lowest diversity (Figure 4.1, 4.2). Across the region, a significant proportion of the national species pool was represented within pond habitats (228 taxa). This finding was consistent with the wider literature highlighting the importance of pond habitats as sites of high biodiversity at larger spatial scales (Williams *et al*., 2003; Nicolet *et al*., 2004; Biggs *et al*., 2005; Davies *et al*., 2008b). Aquatic macroinvertebrate diversity was highest during the autumn season across all four landscapes (meadow, agricultural forest and urban) (Figure 4.3, 4.4); although most previous pond surveys have been restricted to a single season (Armitage *et al*., 2012) and this comparison is not always possible. Based on the results of this study, if pond invertebrate surveys can only be undertaken during a single season, an autumn survey likely provides the best representation of the macroinvertebrate diversity (although some taxa such as Trichoptera may be under-represented due to their life cycle) (Table 4.3). Detailed analysis indicated that there were strong seasonal differences in macroinvertebrate assemblages in meadow and agricultural ponds (Figure 4.7). In contrast, largely similar assemblages were recorded among urban and forest ponds throughout the three seasons, possibly reflecting the low connectivity (Gledhill *et al*., 2008; Noble and Hassall, 2014) (reduced dispersal potential) and high level of anthropogenic disturbance which could be limiting the natural turnover of macroinvertebrate taxa. This fulfils the second objective;

> *(2) To examine the seasonal variability of aquatic macroinvertebrate communities associated with ponds.*

In addition, emergent and submerged macrophyte mesohabitats supported the highest alpha diversity when compared with floating, overhanging trees and open water mesohabitats (Figure 4.5). This reinforced previous research that has indicated that aquatic macrophytes are important habitat for macroinvertebrate taxa as a source of food, sites for egg laying and protection from fish predation (Diehl *et al*., 1992; Biggs *et al*., 1994a).

Within Chapter 4, macroinvertebrate communities were demonstrated to be highly heterogeneous across the region (ANOSIM $p<0.01$, C_j: 0.19) and, specifically, urban pond macroinvertebrate assemblages were shown to be significantly different to meadow and agricultural pond communities (Table 4.8; Figure 4.6). This study revealed that, at a regional scale, ponds support significant macroinvertebrate diversity and have a high conservation value (Table 4.11) (supporting a number of rare and endemic taxa), adding further evidence to observations made in the wider literature (Nicolet *et al*., 2004; Davies *et al*., 2008b; Oertli *et al*., 2009; Gioria *et al*., 2010). Meadow ponds were identified to have the greatest conservation value whilst urban ponds recorded the lowest conservation value (based on the Community Conservation Index (Chad and Extence, 2004), most likely reflecting the high levels of anthropogenic disturbance.

The following two chapters (**Chapters 5 - 6)** examined and quantified the biodiversity of urban and meadow ponds in greater detail. **Chapter 5** examined the macroinvertebrate diversity of a range of pond types within urban landscapes, fulfilling the third objective of the thesis;

> *(3) To characterise aquatic macroinvertebrate biodiversity within a range of ponds (garden, 'other' urban and park) in the urban landscape.*

Analysis demonstrated alpha diversity indices were significantly higher among park ponds than garden or 'other' urban ponds (Figure 5.1, 5.2). The lowest alpha diversities were recorded among garden ponds (total taxa: 44, mean: 9). However, across the urban landscape, ponds were shown to support high macroinvertebrate biodiversity (total: 170), comparable to meadow (total: 175) and agricultural ponds (total: 126) in this study and higher than that recorded in previous urban pond biodiversity studies (Gledhill *et al*., 2008; Briers, 2014). However, at an individual scale, pond diversity varied from species poor (2 taxa) to taxon rich (61 taxa) ponds. These results support the findings of previous research which highlight the high variability in urban pond macroinvertebrate diversity (Gledhill *et al*., 2008; Briers, 2014; Hassall, 2014; Noble and Hassall, 2014). Further analysis identified significant differences in community assemblage between park and garden ponds (ANOSIM $p<0.001$, Figure 5.5). However, while the pond types supported different assemblages, there was a significant overlap of taxa within garden and park pond communities. 'Other' urban pond communities were highly heterogeneous (C_j: 0.19), which is likely to reflect the variable successional states and management strategies of this pond type. Conservation value was highly variable, but was highest in park ponds and lowest in garden ponds (Table 5.9); this bought into question the suitability of garden ponds to support high invertebrate richness and offset the negative impacts of urbanisation (Gledhill *et al*., 2008). Despite the variable conservation value, at the landscape scale, urban ponds supported a number of rare taxa (4 Coleoptera, 1 Zygoptera) and many had high taxon richness (particularly park ponds) indicating that with the appropriate management and conservation strategies, these small anthropogenic habitats could have a vital role to play in the preservation of urban biodiversity (Hassall, 2014).

Aquatic macroinvertebrate biodiversity within ephemeral and perennial floodplain meadow ponds was quantified in **Chapter 6** fulfilling the fourth objective of the thesis;

> *(4)* T*o quantify the macroinvertebrate biodiversity of perennial and ephemeral ponds in two meadow landscapes of the lower River Soar floodplain, UK*.

Alpha diversity was found to be significantly higher in perennial compared to ephemeral meadow ponds (Figure 6.2, 6.4). Reflecting the findings of the previous chapters, aquatic macrophyte mesohabitats were identified as supporting the greatest taxon richness in perennial and ephemeral floodplain meadow ponds. Despite regular inundation of ephemeral and perennial ponds by floodwater, examination of the invertebrate communities revealed that ephemeral pond communities were heterogeneous (high beta-diversity) when compared to perennial meadow ponds (ANOSIM $p<0.005$, Figure 6.6), supporting temporary water specialists such as *A. leucostoma* (Gastropoda: Planorbidae), *L. aricula* (Trichoptera: Limnephilidae) and *L. centralis* (Trichoptera: Limnephilidae). These findings are consistent with previous studies which identified that ephemeral ponds support lower taxon richness than their perennial counterparts but often host very different community assemblages (Collinson *et al*., 1995; Nicolet, 2001; Della Bella *et al*., 2005). Further analysis indicated that the proportion of the macroinvertebrate community that passively dispersed was similar in ephemeral ponds (34%) to perennial ponds (46%). This contradicts previous research (Nicolet, 2001, Nicolet *et al*., 2004) and it appears to suggest that the regular flooding (by the River Soar floodwater) and mixing of water can facilitate the passive dispersal of taxa between perennial waterbodies and ephemeral pond habitats in the current study. Analysis of meadow pond conservation value identified that perennial ponds supported a greater number of species of conservation interest but overall there was no significant difference in conservation value between ephemeral and perennial meadow ponds (both had a number of ponds of high conservation value) (Table 6.8).

Chapter 7 aimed to determine the relative influence of physicochemical, biological and spatial variables on aquatic macroinvertebrate distribution using a variance partitioning approach. The analyses undertaken fulfilled the final objective of the thesis;

> *(5) To examine the physicochemical, biological and spatial (connectivity) characteristics influencing macroinvertebrate community composition within ponds at a range of spatial scales.*

At a regional scale, a range of physicochemical, biological and spatial variables all influenced the distribution of aquatic macroinvertebrate taxa within pond habitats (Table 7.1, Figure 7.1). Although at the landscape-scale, different variables influenced pond communities in meadow and urban environments; meadow ponds were influenced by physicochemical and spatial variables, whilst urban ponds were most influenced by physicochemical and biological variables (Table 7.3, 7.5). The structure of the urban environment (characterised by walls, fences and buildings) may act as a physical barrier, reducing pond connectivity and the ability of macroinvertebrates to disperse to new habitats even when in relatively close geographical proximity. Analysis undertaken in this chapter identified pond area, connectivity, and aquatic macrophytes to be associated with the highest diversity, whilst drying of the pond basin was associated with the lowest. These findings widely agree with previous literature (Brönmark, 1985; Oertli *et al*., 2002; Rundle *et al*., 2002; Biggs *et al*., 2005; Della Bella *et al*., 2005; Gledhill *et al*., 2008). Variance partitioning clearly demonstrated the dominant influence of physicochemical factors (explained 9.2% of total variance at a regional scale; 9.4% in urban ponds, 14.1% in meadow ponds and 12.3% in ephemeral ponds) influencing the variation in macroinvertebrate taxa at the regional and landscape scale. However, the importance of biological and spatial factors should not be overlooked as further analysis identified that a combination of factors (e.g., spatial and physicochemical explained 4% at a regional scale and 14.4% among meadow landscapes) also described a large proportion of the variation in macroinvertebrate community composition. These results have been echoed in the wider academic literature which emphasises the dominance of local (physicochemical) factors and but also the importance of the interaction between environmental factors in influencing the variation in macroinvertebrate communities at a range of spatial scales (Pinel-Alloul *et al*., 1995; Cottenie *et al*., 2003; Cottenie and De Meester, 2003; Vanschoenwinkel *et al*., 2007). Taking a metacommunity approach (Leibold *et al*., 2004) the results from this study support and add weight to the findings of previous research which indicates that a combination of species sorting (local factors: physicochemical/biological) and mass effects (spatial: connectivity) can best describe the variation in macroinvertebrate community composition within a metacommunity (Cottenie, 2005; Vanschoenwinkel *et al*., 2007).

8.3 Key themes

Throughout the research undertaken in this thesis there were a number of recurring themes. These include, scale (spatial and temporal), the conservation of pond habitats/environments at the individual pond and landscape scale, and the wider management of small freshwater habitats.

8.3.1 Scale

The examination of aquatic macroinvertebrate biodiversity over a range of scales was a recurring theme throughout the research. Pond biodiversity studies have often focussed on a small number of ponds at limited spatial scales (Vanschoenwinkel *et al*., 2007; Armitage *et al*., 2012; Noble and Hassall, 2014). At a regional scale, addressing pond biodiversity at alpha, beta and gamma scales across a wide range of landscapes could provide information required to direct available funds for conservation to where it may be needed most. Alpha diversity could identify individual ponds which are of high conservation value or in need of restoration, whilst beta and gamma diversity can help inform conservation strategies at larger (landscape/regional) spatial scales. Through an examination of semi-natural landscapes alongside anthropogenic landscapes, macroinvertebrate biodiversity baseline/reference conditions for the anthropogenically dominated landscapes can be determined (Williams *et al*., 2003). Furthermore, research quantifying regional/landscape scale biodiversity may provide essential information for the development of more sophisticated strategies for a wide range of commercial and industrial processes (e.g., the ecologically sensitive application of agricultural fertiliser and urban runoff collection) that can help reduce the anthropogenic impact upon pond habitats by predicting which ponds are most likely to be susceptible to change or damage (Williams *et al*., 2003).

Ponds should not be considered as individual bodies of water independent of one another, but as a network of discrete aquatic habitats within a landscape (pondscape) (Boothby 1997a; Hassall *et al*., 2012). At a landscape-scale, pondscapes have been demonstrated to support greater macroinvertebrate biodiversity than rivers, lakes and streams (Biggs *et al*., 2005; Davies *et al*., 2008b). Consequently, landscape-scale studies are vitally important not only to provide greater detail and knowledge of the biodiversity of a pondscape within a particular landscape (e.g., urban, forest or agricultural) but also regarding their contribution to specific conservation and management strategies required within that landscape. Regional and landscape scale studies enable the examination of larger scale spatial environmental factors such as connectivity alongside local environmental factors (e.g., pond size and water chemistry) and may provide more accurate and realistic explanations of patterns of macroinvertebrate community composition. However, detailed analysis at an individual site scale can determine the affinities between particular mesohabitat types and macroinvertebrate taxa/diversity providing further information to potentially augment biodiversity within these small lentic systems via targeted habitat management (Bazzanti *et al*., 2010).

This thesis examined biodiversity over three seasons, but examining pond ecology over much longer time periods could provide another important scale of pond biodiversity research: temporal. Indeed, a number of studies have demonstrated that floral and faunal biodiversity and heterogeneity of invertebrate communities varies over time as well as space (Angélibert *et al*., 2004; Florencio *et al*., 2011; Jeffries, 2011; Hassall *et al*., 2012). Ecological patterns which are difficult to explain based on a single season or 1 year surveys may appear to be heavily influenced by stochastic processes but the patterns may instead be quite deterministic (e.g., historic effects) when examined over a longer temporal scale (Jeffries, 2008; Jeffries, 2011). Addressing the biodiversity of ponds habitats at a range of spatial and temporal scales is vital to increase the knowledge base of pond ecosystems and inform conservation and management practices at the correct spatial scale.

8.3.2 Conservation of small lentic freshwater habitats

Freshwater conservation effort in the UK and internationally has traditionally focussed on lotic systems and larger lentic waterbodies, whilst small waterbodies have been largely ignored (Williams *et al.,* 2003; Oertli *et al*., 2009). Another key focus of this thesis was the conservation value of a wide range of ponds. Europe's most important piece of water legislation, the Water Framework Directive (WFD), affords protection only to larger lentic systems (lakes >50ha) (Sayer, 2014). However, there has been increasing awareness of the conservation value of ponds and their contribution to aquatic biodiversity (Nicolet *et al*., 2007; Bilton *et al*., 2009; Oertli *et al.,* 2009). A very limited number of pond types (e.g., Mediterranean temporary ponds) are recognised under the EU Habitats Directive (Oertli *et al*., 2005) and pond habitats are considered a Habitat of Principle Importance under the Post-2010 Biodiversity Framework in the UK (BRIG, 2008). This study has demonstrated that ponds can provide habitats of high conservation value in all landscapes typical of European lowland regions which needs to be recognised in conservation policy and legislation.

Ponds clearly support substantial biodiversity and have a high conservation value in many landscapes including highly anthropogenic urban environments. Yet operationally pond conservation remains a significant issue across Europe as a result of the lack of legislative power to protect most pond habitats (Hassall *et al*., 2012). The scale at which the designation of ponds for conservation is applied is quite different to the scales which ponds contribute most towards aquatic biodiversity. Currently, conservation of ponds relies heavily on the presence of rare taxa (e.g., species under the Wildlife and Countryside Act 1981) or very high biodiversity in order to designate individual ponds as a Priority Habitat (under the Post-2010 Biodiversity Framework) or as a Site of Special Scientific interest (SSSI) (Hassall *et al*., 2012). The current system of individual designation of ponds for conservation is an important aspect of pond conservation as they can provide rich habitats and support rare taxa (and could be an important conservation method in some urban areas where ponds are currently poorly connected and tend to be isolated from other waterbodies).

However, pond biodiversity has been demonstrated to be exceptionally high at a landscape/regional scale in this study and others (as a result of their high physicochemical and biological heterogeneity) and pond conservation needs to be incorporated at this spatial scale (Boothby, 1999; Oertli *et al*., 2002; Williams *et al*., 2003; Davies *et al*., 2008a; Gioria *et al*., 2010; Sayer, 2014). Landscape-scale based conservation affords protection/consideration of the entire pond network and promotes high regional diversity (the scale which ponds contribute most to biodiversity). A focus on pond conservation at the landscape-scale is likely to be the most ecologically beneficial and sustainable way to conserve pond networks, promote regional biodiversity across rural and urban landscapes and increase the connectivity between ponds and other freshwater habitats (e.g., reconnect isolated ponds and green spaces in urban areas) (Sayer, 2014). In addition, ponds should be seen as part of an aquatic network incorporating rivers, lakes, streams, wetlands and other aquatic systems. Integrating multiple aquatic habitat types into landscape-scale conservation, will provide an efficient and sustainable way of conserving and enhancing floral and faunal diversity across a range of aquatic habitats (Sayer, 2014).

Temporal studies of pond biodiversity have demonstrated that the conservation value of individual ponds fluctuates through time as rare taxa that are present in a pond in one year may be absent in the next (Hassall *et al.,* 2012). This further suggests moving away from the designation of individual ponds for conservation towards the designation of pond clusters and the pondscape to provide the greatest long term conservation benefit for floral and faunal diversity (Hassall *et al.*, 2012). Nonetheless, it is clearly recognised there are difficulties surrounding landscape-scale conservation, most notably the diversity and potential conflict of interest/priorities and the politics associated with multiple land ownership (Sayer, 2014).

The ponds of greatest conservation value in this study were located in areas specifically designed for nature conservation (Cossington Meadow; see Chapter 4.2.6 and Chapter 6.2.6). In addition, these pond sites of high conservation value were located on the River Soar floodplain with high lateral connectivity to the river (regularly inundated with floodwater). Nature reserves inadvertently provide landscape-scale (pondscape) conservation and often provide a highly connected freshwater landscape (incorporating rivers, lakes, ponds and wetlands) which can allow for a wide dispersal and colonization of many aquatic taxa reliant on different aquatic habitats throughout their lifecycle (Cottenie, 2005; Williams *et al.*, 2008; Sayer, 2014). Outside of areas specifically designed for nature conservation, there is little pondscape conservation and many freshwater habitats have become isolated. In particular, rivers have been disconnected from their floodplains (and consequently from floodplain ponds) by levees and embankments (Sayer, 2014). However, landscape based conservation approaches are being undertaken outside of nature reserves in some parts of the UK. For example, the UK Wildlife Trust is incorporating a 'living landscape approach' which provides landscape-scale conservation (approx. 100 UK sites) to restore and reconnect large areas of terrestrial and aquatic habitat (rural and urban) to create ecological networks improving the conditions for wildlife outside of nature reserves (The Wildlife Trusts, 2014). In addition, the Wiltshire Wildlife Trust is restoring links and corridors between wildlife sites in urban and rural landscapes to reconnect large areas of land through the restoration of meadows, hedges and ponds at a landscape-scale to augment biodiversity and create a wildlife-friendly environment (The Wildlife Trusts, 2014).

Farmland ponds have been widely recognised to support considerable biodiversity on agricultural land (Céréghino *et al.*, 2008a; Ruggiero *et al.*, 2008; Gioria *et al.*, 2010; Sayer *et al.*, 2012). Agri-environment schemes (AES) may enable pond conservation at a pondscape scale as these schemes provide financial compensation to farmers who incur a loss in income associated with measures which promote and benefit biodiversity, including maintaining pond habitats on agricultural land (Kleijn and Sutherland, 2003; Davies *et al*., 2008a). Despite the financial compensation, farmland pond numbers continue to decline and many agricultural ponds are typically left unmanaged resulting in degraded ponds with poor water quality (accumulate sediment and nutrients from the surrounding agricultural land), which over time can become terrestrialized as a result of sedimentation (Sayer *et al*., 2012; Sayer, 2014). Active management is required in some agricultural and urban areas to improve the condition of agricultural ponds and ensure that a wide range of successional stages and environmental conditions are present across the landscape to promote biodiversity (Sayer *et al*., 2013). AES may also afford pond conservation at smaller spatial scales, providing conservation to 'clusters' of ponds on individual farms that have agreed to an AES. Currently, this may be more realistic than landscape-scale conservation in most agricultural landscapes because of difficulties surrounding the co-operation of farmers with different priorities and the costs surrounding co-ordinating conservation on multiple farms (Davies *et al*., 2008a).

8.3.3 Management of small lentic freshwater habitats

There has been wide debate surrounding the role of management of ponds and pondscapes to promote biodiversity (Biggs *et al*., 1994; Williams *et al*., 1999; Nicolet *et al*., 2004; Sayer *et al*., 2012; Sayer *et al*., 2013; Noble and Hassall, 2014). Currently, while pond conservation is focussed around the development of new ponds (e.g., the Million Ponds Project), management and restoration provides another conservation strategy to restore and improve the biodiversity of the existing pond resource (Sayer *et al*., 2013). Management should only be undertaken where necessary as many semi-natural and ephemeral ponds rarely require active management (Biggs *et al*., 1994; Nicolet *et al*., 2004). However, for ponds located within anthropogenic landscapes (urban and agricultural) active management is a necessary step to reduce the impact of anthropogenic disturbance and improve pond biodiversity in these human dominated landscapes (Sayer *et al*., 2012; Hassall, 2014). Prior to any management a pond survey should be undertaken (in particular to quantify the presence of uncommon/rare taxa) to assess their conservation value and determine if management is necessary (Nicolet *et al*., 2004).

The results of this study demonstrated that local (physicochemical and biological) factors were more influential in determining community composition than spatial factors at regional and landscape scales. Improving local conditions should therefore take priority over spatial factors in order to improve biodiversity potential. In particular, pond area was associated with the highest diversities and macroinvertebrate diversity was consistently higher among aquatic macrophyte mesohabitats than other mesohabitats across all landscapes. In anthropogenic landscapes (urban and agricultural) this research suggested that if ponds have good and stable physical (including chemical and biological) habitat, invertebrates will colonize and the pond will support diverse communities. Pond management should aim to ensure that there is sufficient coverage of aquatic macrophytes within ponds (in particular, ensure there is sufficient structural complexity of macrophytes in the littoral zone) and that a variety of emergent and submerged macrophytes are present to promote macroinvertebrate biodiversity (Biggs *et al*., 1994; Bazzanti *et al*., 2010); although other habitats including areas of open water should also be maintained to support open water specialist taxa.

However, the importance of connectivity should not be ignored; it was associated with very high diversity in semi-natural meadow ponds. Connectivity may greatly increase biodiversity potential in ponds (Gledhill *et al*., 2008; Williams *et al*., 2008; Noble and Hassall, 2014), especially in urban landscapes where currently there are numerous physical barriers reducing the connectivity. Wherever possible, physical barriers surrounding urban ponds should be removed and buffer zones could be incorporated around ponds to reduce the impact of anthropogenic disturbance. Maintaining urban connectivity is likely to become increasingly important in the near future as the need for urban land will increase in accordance with population growth (Noble and Hassall, 2014). Increased pond connectivity in urban and agricultural landscapes will promote the rapid (re)colonization of flora and fauna (many invertebrates are good dispersers e.g., Odonata (Angélibert and Giani, 2003) and Coleoptera (Lundkvist *et al*., 2002)) and may help improve the resilience of pond communities and the ability of pond sites to recover quickly from anthropogenic disturbance (Thornhill, 2012). Despite existing in a network, ponds are discrete habitats and disturbance in one pond is likely to have little impact on others in the connected network, whilst a single disturbance event in a river may impact a substantial stretch (Thornhill, 2012).

The building of new, high quality ponds should be actively encouraged in anthropogenic landscapes to offset pond loss and provide new high quality habitat for floral and faunal colonization (e.g., the Millions Ponds Project in the UK is a 50 year project which seeks to create a network of new, clean water ponds across the UK (Freshwater Habitats Trust, 2014). Given the importance of pond size and connectivity for biodiversity reported in this study it is suggested that wherever possible new ponds should be built within existing pond networks or as a network of new ponds and be as large as possible. In many instances the development of new garden ponds may be the only available option to compensate for the loss of urban ponds due to urban development (Gledhill *et al*., 2008). The development of new garden ponds will increase the density of the urban pondscape raising the biodiversity potential of urban ponds. However, if garden pond creation and management is to be promoted as a means to enhance current biodiversity, it is important that home-owners/gardeners are provided with guidance regarding how this potentially valuable resource can help support freshwater biodiversity into the future. In addition, management of floodplain meadows should encourage the development of ponds as they will increase floodplain biodiversity and hydrological connectivity between the floodplain and the river. New ponds on floodplain meadows are likely to be colonized quickly and have high biodiversity (similar to the established ponds) soon after development (Williams *et al*., 2008) which is most likely the result of the lateral connectivity to the river promoting colonization and providing nutrients for flora and fauna (Figure 8.1).

(a) (b)

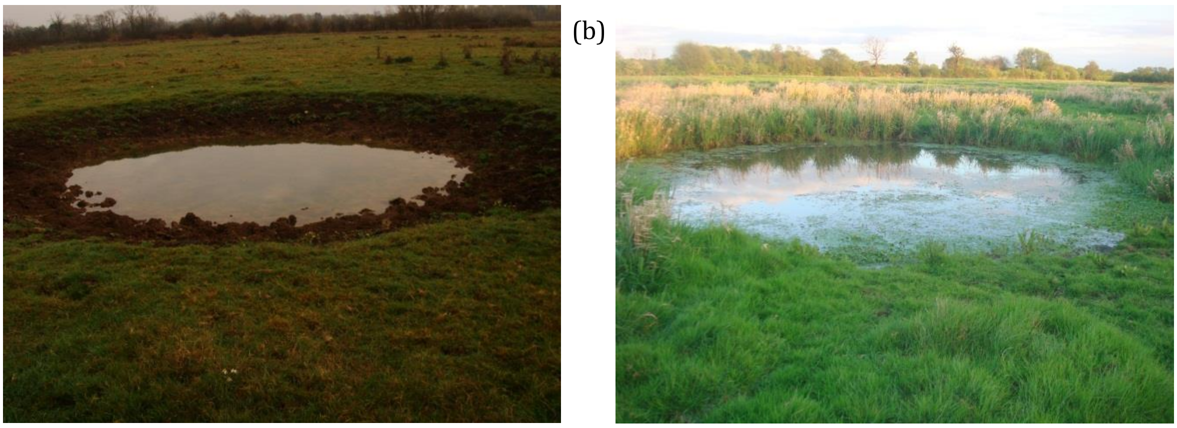

Figure 8.1 - (a) Newly dug pond (2011) on River Soar floodplain (Cossington meadow (M17) and (b) two years after being dug; established submerged and emergent macrophyte beds and high macroinvertebrate diversity (total taxa: 63). Photograph: Matthew Hill.

Often ponds in urban areas are not built for biodiversity but for other anthropogenic purposes (e.g., flood reduction and water quality improvement). Many of the 'other' urban ponds in this study were stormwater retention ponds. However, with the careful management of urban ponds including Sustainable Urban Drainage systems (SUDs) and stormwater retention ponds the maximum potential of these ponds for water quality control/flood reduction and biodiversity can be achieved (Briers, 2014; Pond Conservation Trust, 2003). Pond warden schemes should be promoted in towns and cities. These schemes could greatly increase the number of urban ponds monitored, their biodiversity and enhance public awareness of ponds (DCPWA, 2014; Footprint Trust, 2014). However, adequate training should be provided to ensure that the most appropriate conservation and management practices are being undertaken by volunteers.

At a landscape/regional scale, management should promote a wide range of pond types as different environmental conditions (e.g., hydroperiod, successional stage, water chemistry) support heterogeneous communities, thereby increasing regional diversity. In particular, the hydroperiod characteristics of ephemeral ponds should be maintained and protected as this study has demonstrated that these habitats support distinct communities to perennial ponds and contribute to high gamma diversity (Nicolet *et al*., 2004). Further, a large number of floral and faunal taxa are commonly associated with particular pond successional stages (e.g., ponds in a late successional stage are likely to support taxa not recorded from ponds at an early to mid-successional stage; Hassall *et al*., 2012). Maintaining a range of pond successional stages in rural and anthropogenically (urban/agricultural) dominated landscapes will promote high regional (gamma) diversity ensuring a wide range of habitats are available for aquatic flora and fauna (Hassall *et al*., 2012; Sayer *et al*., 2013).

8.4 Future research

This thesis provides one of the first studies to address aquatic macroinvertebrate biodiversity within ponds at a regional scale, across a range of landscapes typical of European lowland environments. In addition, this thesis has contributed to the understanding of macroinvertebrate diversity within pond habitats in lesser studied environments through a detailed examination of different scales (alpha, beta and gamma) of macroinvertebrate diversity. In particular, the study of a range of pond types in urban landscapes provides a greater understanding of the aquatic macroinvertebrate diversity and the environmental variables driving the community composition which have provided information for the development of practical management strategies that may augment urban pond biodiversity. The following section provides further research that would advance understanding of the biodiversity within ephemeral and perennial ponds.

- The urban pond study in this thesis provides a basis from which future research could be undertaken. This study and others has highlighted the importance of connectivity for the diversity and richness of pond communities in the wider landscape (Biggs *et al*., 2005; Vanschoenwinkel *et al*., 2007; Williams *et al*., 2008). Although not identified as important in this study, pond connectivity in urban areas needs to be further examined across a range of urban environments with variable pond densities to determine its influence and importance for aquatic biodiversity (Gledhill *et al*., 2008; Noble and Hassall, 2014).
- Further examination of garden pond ecology and their management strategies is required as they have largely been ignored in academic research. It has been estimated that 2.5 - 3.5 million garden ponds exist in the UK (Davies *et al*., 2009b). Given the large number of garden ponds that exist, they could have an important role in sustaining aquatic biodiversity in the future (with the correct management) and acting as refugia in anthropogenically disturbed landscapes.
- Ephemeral ponds remain one of the most understudied freshwater habitats in European lowland landscapes. While this study has provided a greater understanding of invertebrate taxa within floodplain meadow ephemeral ponds, further research is necessary to ascertain ephemeral biodiversity (particularly hyporheic taxa) in other lowland landscapes, and also to understand the response of ephemeral pond communities to the colonization of non-native taxa.
- This thesis has identified the macroinvertebrate biodiversity over a range of spatial scales, but there is a paucity of research addressing temporal biodiversity variability within ponds. There is a need for future research to undertake longer-term temporal studies within pond habitats, to examine the fluctuation and temporal heterogeneity of pond invertebrate communities and the response of communities to temporal fluctuations of environmental variables (Florencio *et*

al., 2009; Jeffries, 2011; Hassall *et al.,* 2012). A greater monitoring and understanding of the temporal dynamics of pond ecology and hydrology will provide long term data sets for the development of sustainable conservation and management strategies.

- Further research is required to increase the pond research base more generally. Freshwater ecological research has historically been focussed towards rivers and lakes (Oertli *et al*., 2009). Even though there has been a significant increase in interest in pond biodiversity in recent years, when comparing pond biodiversity research with that of rivers, lakes and streams (using the Thomson Reuters ISI Web of Knowledge database), pond publications between 1991-2008 contributed less than 10% of the total (Oertli *et al*., 2009). Further, between 2009 and 2013 (following on the methodology employed by Oertli *et al*., (2009)) pond biodiversity publications continued to contribute less than 10% of the total freshwater publications (Figure 8.2). Increasing the pond biodiversity research base will enhance our understanding of these small lentic systems, raise their profile and could inform specific conservation legislation and management strategies targeted towards ponds.

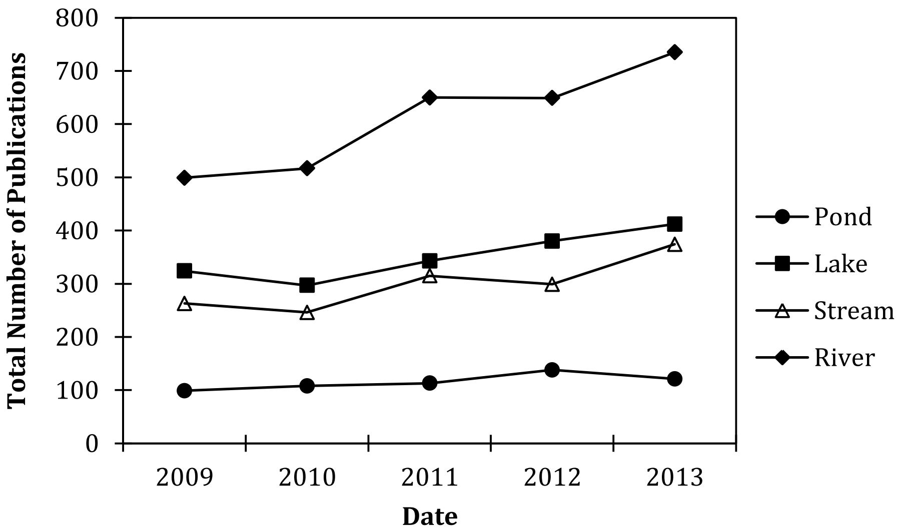

Figure 8.2 - Total number of peer reviewed publications (based on the search topic "biodiversity" and one of the 4 freshwater systems: ponds, lakes, rivers and streams) between 2009-2013 using the ISI Web of Knowledge data base

8.5 Conclusion

Ponds are common and abundant features in European lowland landscapes yet they have been relatively understudied compared to other freshwater habitats (rivers, lakes and streams). This thesis has highlighted the need for a greater understanding and quantification of pond biodiversity, especially urban and ephemeral pond biodiversity which has been largely neglected to date. Through undertaking a comparative analysis of aquatic macroinvertebrate biodiversity within ponds over multiple landscapes and spatial scales, this thesis has consistently demonstrated the ecological importance and conservation value of small lentic waterbodies in rural and urban landscapes. The results have highlighted the large contribution of many ponds to urban biodiversity and the distinct macroinvertebrate communities within ephemeral ponds compared to their perennial counterparts in meadow landscapes. In addition, this thesis has demonstrated the importance of a combination of local and spatial environmental factors (although local factors were dominant) in driving the macroinvertebrate community assemblage within ponds at a regional and landscape scale. This study has underlined a need for greater conservation attention centred on pond habitats because of their considerable contribution to local and regional freshwater biodiversity. In particular, focussing more conservation effort towards urban ponds may help raise urban pond biodiversity to the levels recorded in the wider landscape and is vital for the ongoing protection of pond sites and biota from further habitat fragmentation in urban landscapes. Increased understanding of pond biodiversity and the environmental processes which drive community composition across a range of environments (especially urban) will provide vital information for the future regional and landscape conservation practices of these small but fascinating lentic waterbodies.

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Appendicies

Appendix 1

Site characteristics for the 95 pond sites in north Leicestershire

Site Name	Location	Pond Type	Surrounding Land-use	Construction	Permanence
			Urban		
UP1	Loughborough University	Urban	Urban Development	Man-made	Permanent
UP2	Loughborough University	Urban	Urban Development	Man-made	Permanent
UP3	Loughborough University	Urban	Urban Development	Man-made	Permanent
UP4	Loughborough University	Urban	Urban Development	Man-made	Ephemeral
UP5	Loughborough University	Urban	Urban Development	Man-made	Permanent
UP6	Loughborough University	Urban	Urban Development	Man-made	Permanent
UP7	Loughborough University	Urban	Grassland/Urban Development	Man-made	Ephemeral
UP8	Loughborough University	Urban	Urban Development	Man-made	Permanent
UP9	Loughborough University	Urban	Urban Development	Man-made	Ephemeral
UP10	Loughborough University	Urban	Urban Development	Man-made	Permanent
UP11	Loughborough University	Urban	Urban Development	Man-made	Permanent
UP12	Loughborough University	Urban	Urban Development	Man-made	Ephemeral
UP13	Loughborough Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP14	Loughborough Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP15	Loughborough Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP16	Loughborough Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP17	Loughborough Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP18	Loughborough Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP19	Loughborough Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP20	Mountsorrel Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP21	School	Urban	Urban Development	Man-made	Permanent
UP22	School	Urban	Urban Development	Man-made	Permanent
UP23	School	Urban	Urban Development	Man-made	Permanent
UP24	School	Urban	Urban Development	Man-made	Permanent
UP25	Garden	Urban	Residential	Man-made	Permanent
UP26	Garden	Urban	Residential	Man-made	Permanent
UP27	Garden	Urban	Residential	Man-made	Permanent
UP28	Garden	Urban	Residential	Man-made	Permanent
UP29	Garden	Urban	Residential	Man-made	Permanent
UP30	Garden	Urban	Residential	Man-made	Permanent
UP31	Garden	Urban	Residential	Man-made	Permanent
UP32	Garden	Urban	Residential	Man-made	Permanent
UP33	Garden	Urban	Residential	Man-made	Permanent
UP34	Garden	Urban	Residential	Man-made	Permanent
UP35	Garden	Urban	Residential	Man-made	Permanent

Site Name	Location	Pond Type	Surrounding Land-use	Construction	Permanence
UP36	Garden	Urban	Residential	Man-made	Permanent
UP37	Garden	Urban	Residential	Man-made	Permanent
UP20	Loughborough Urban Park	Urban	Grass/Urban Development	Man-made	Permanent
UP38	Golf Course	Urban	Managed Grass	Man-made	Permanent
UP39	Golf Course	Urban	Managed Grass	Man-made	Permanent
UP40	Golf Course	Urban	Managed Grass	Man-made	Permanent
UP41	Residential	Urban	Grass/Urban Development	Man-made	Ephemeral
			Meadow		
M1	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M2	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M3	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Ephemeral
M4	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M5	Nature Reserve (CM)	Meadow	Floodplain Meadow	Natural	Ephemeral
M6	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M7	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M8	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M9	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Ephemeral
M10	Nature Reserve (CM)	Meadow	Floodplain Meadow	Natural	Ephemeral
M11	Nature Reserve (CM)	Meadow	Floodplain Meadow	Natural	Ephemeral
M12	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M13	Nature Reserve (CM)	Meadow	Floodplain Meadow	Natural	Ephemeral
M14	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M15	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M16	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M17	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M18	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M19	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M20	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M21	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M22	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M23	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent

Site Name	Location	Pond Type	Surrounding Land-use	Construction	Permanence
M24	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M25	Nature Reserve (CM)	Meadow	Floodplain Meadow	Man-made	Permanent
M26	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Ephemeral
M27	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Ephemeral
M28	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Ephemeral
M29	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Ephemeral
M30	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Ephemeral
M31	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Permanent
M32	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Ephemeral
M33	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Ephemeral
M34	SSSI site (LBM)	Meadow	Lammas Meadow (Floodplain)	Natural	Ephemeral
M35	Country Park	Meadow	Grassland	Man-made	Permanent
			Forest		
FP1	Woodland	Forest	Rock Outcrop/Woodland	Man-made	Permanent
FP2	Woodland	Forest	Deciduous Woodland/Agricultural crop	Man-made	Permanent
FP3	Woodland	Forest	Deciduous Woodland	Natural	Ephemeral
FP4	Woodland	Forest	Deciduous Woodland	Natural	Ephemeral
FP5	Country Park	Forest	Mixed Deciduous Woodland	Man-made	Permanent
FP6	Country Park	Forest	Mixed Deciduous Woodland/Grassland	Man-made	Ephemeral
FP7	Forest	Forest	Mixed Deciduous Woodland	Natural	Ephemeral
			Agricultural		
AP1	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Permanent
AP2	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Permanent
AP3	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Permanent
AP4	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Permanent
AP5	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Permanent
AP6	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Ephemeral
AP7	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Permanent
AP8	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Ephemeral
AP9	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Ephemeral
AP10	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Permanent
AP11	Agricultural Land	Agricultural	Agricultural Crop	Man-made	Permanent
AP12	Agricultural Land	Agricultural	Pasture	Man-made	Permanent

Appendix 2

Selected site photographs of ponds in meadow, agricultural, forest and urban landscapes. See Appendix 1 for pond site characteristics.

Meadow: a) M35 b) M6 c) M7 d) M8 e) M11 f) M14 g) M15 h)M20 i) M24 j) M32 k)M28 l) M33

a) M35

b) M6

c) M7

d) M8

e) M11

f) M14

Meadow ponds continued


g) M15


h) M20


i) M24


j) M32


k) M28


l) M33

Agricultural: a) AP1 b) AP2 c) AP4 d) AP12 e) AP5 f) AP6 g) AP7 h) AP8 i) AP9 j) AP11


a) AP1


b) AP2


c) AP4


d) AP12


e) AP5


f) AP6

Agricultural ponds continued

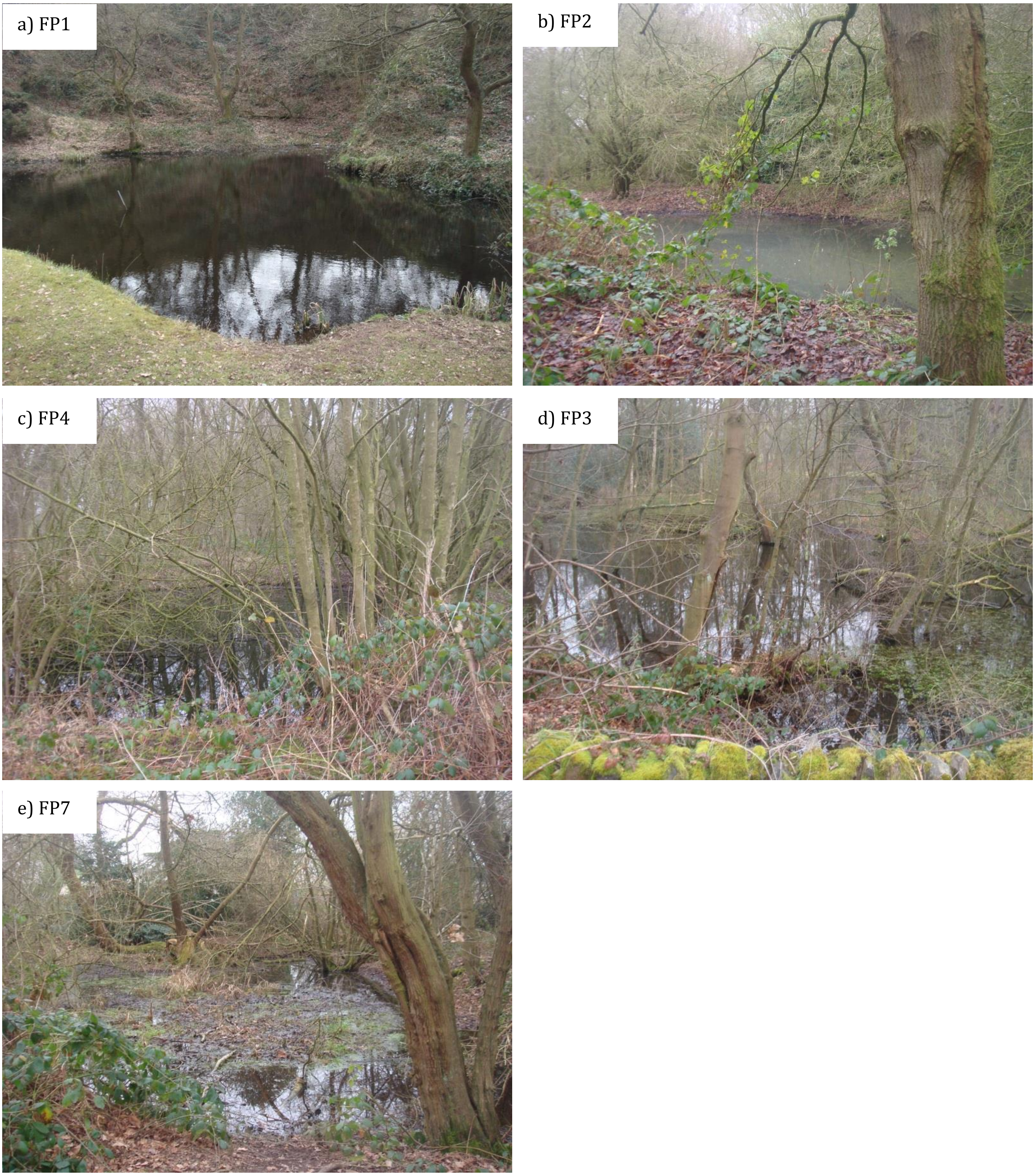
g) AP7

h) AP8

i) AP9

j) AP11

Forest: a) FP1 b) FP2 c) FP4 d) FP3 e) FP7



Urban: A) UP20) b) UP36 c) UP13 d) UP19 e) UP40 f) UP1 g) UP33 h) UP16 i) UP17 j) UP6 k) UP11 l) UP9


a) UP20


b) UP36


c) UP13


d) UP19


e) UP40


f) UP1

Urban ponds continued


g) UP33


h) UP16


i) UP17


j) UP6


k) UP11


l) UP9

Appendix 3

Pond data recording sheet (modified version of the National Pond Survey recording sheet (Biggs *et al.*, 1998))

Recording Sheet

Site name: ________________ Survey No: ____________ Grid Reference: _________

Date: ________________ Surveyor: ____________ Spatial/temporal:_________

Location: _________________ Pond Dried: _____________

Brief description of the pond: ____

____

Pond size

Pond Area [   ] Pond Depth [cm] Pond age (if Known) [   ]

Origin___________

Seasonal water level fluctuation and permanence

Drawdown height [cm] (The height difference between maximum and current water levels)

Permanence [   ] (1 = pond never dries, 2 = rarely dries, 3 = sometimes dries, 4 = dries annually)

Overhanging trees and shrub

Water overhung [%] Pond margin overhung [%]

Is the pond dry? [   ] If yes, hard base [%] soft sediment [%]

Surrounding land-use (% estimate in three land use zones)

Land-use	**<5m**	**0-100m**	**Surface Water Catchment**
Deciduous tree & woodland			
Coniferous tree & woodland			
Garden			
Car park			
Meadow			
Moor/Lowland Heath			
Scrub/Hedge			
Park			
Roads			
Arable			
Streams, ditches			
Buildings and concrete			
Rank vegetation			
Unimproved grassland			
Rock, stone gravel			
Ponds and lakes			
Semi-improved grass			
Paths and tracks			

Is the pond located in an area protected for nature conservation? [ ]

TYPE:

Pond successional stage

Early [ ] Intermediate [ ] Late [ ] Other ________________

Other adjacent wetlands and water bodies

Are there any other wetlands within 1km distance from the pond? [ ]

If yes, fill in below

Wetland	0-5m (No.)	0-100m (No.)	0-500m (No.)	0-1km (No.)
Pond				
Lake				
Ditch/Stream				
River (>4m wide)				
Fen/Marsh				
Bog				
Wet grassland				
Other______				

Is the pond located on or near to a stream or river floodplain? Rank 1-3 [ ]
(1 - very near stream/floodplain, 3 - Very far from stream/floodplain)

Is the pond located in a traditionally watery or wetland area? Rank 1-3 [ ]
(1 – Located on a wetland/ watery area, 3- on land not traditionally watery)

How isolated is the pond? Rank 1-5 [ ]

Water source (estimate importance of following water sources)

Water source	%	Water source	%	Water source	%
Groundwater	______	Runoff	______	Direct Precipitation	_______
Flood water	______	Flush	______	Stream or Ditch	_______
Spring	______	Other	______________________________		

Nature of pond base

Substratum	%	Substratum	%
Clay/Silt		Butyl/synthetic	
Peat		Decomposing leaves and twigs	
Sand		Gravel	
Lined (bin liner)		Coarse organic debris	
Gravel		Concrete	
Pebbles and rocks		Organic ooze	

Bank type

	%		%
Natural earth		Wood	
Lined		Metal piling	
Concrete		Stone	
Other_______________		Bare ground	

Pond management Is there evidence of pond management? [ ] If yes, fill in below

	% Pond Area
Overhanging trees cut back	
Pond dredged (suction/vegetation)	
Emergent/submerged plants cut back	
Surrounding vegetation strimmed/cut	
Edges mowed	
Pond widened	
Pond deepened	
Concreted bottom/banks	

Livestock grazing Is the pond grazed by livestock? [ ]

If yes, which animal/s? Cows [ ] Sheep [ ] Horses [ ] Other [ ]

% Pond grazed [%] % Margin Grazed [%]

Rank Grazing Intensity (1 = minimal, 2 = light, 3 = moderate, 4 = heavy, 5 = very heavy)

Grazing Intensity ____________

Duck and wildfowl grazing Is there evidence of duck and wildfowl grazing? [ ]

If yes, what is the grazing intensity? (Same scale as livestock) _____________

Which duck and wildfowl graze the pond? ________________________________ How many? ______

Other grazing Is the pond grazed by other animals? [ ] Species ___________________

If yes, what is the grazing intensity? (Same scale as the livestock grazing intensity) ______________

% pond grazed [ ] %margin grazed [ ]

Fish Are fish present in the pond? [ ] Species ________________________________

If yes, rank fish impact for the whole pond (same scale as livestock grazing intensity) _____________

Macrophyte cover % of pond area covered by emergent macrophyte [%]
submerged macrophyte [%] floating macrophyte [%]

Water quality

pH [ ] Conductivity [ ] Temperature [ ]

Dissolved Oxygen [ ]

Turbidity [cm] Water Colour____________ Probable source of colour ________________

Nitrogen [ ] Phosphorous [ ]

Pollution Is there any evidence of rubbish or other pollutants? [ ]

Type of pollutant____

Rank overall pond degradation (0=none, 10 most degraded possible) [ ]

Are there any mitigating factors? ____

Discrete mesohabitats for invertebrates

List all discrete pond mesohabitats

____________________ ____________________ ____________________
____________________ ____________________ ____________________

Has a photograph been taken? [ ]

Additional comments ____
____
____
____

Appendix 4

Community Conservation Index (CCI) conservation scores for UK aquatic invertebrates from Chad and Extence (2004: 614-624)

TRICLADIDA
Planariidae:

Planaria torva 6	*Polycelis nigra 1*	*Polycelis tenuis 1*
Polycelis felina 3	*Phagocata vitta 3*	*Crenobia alpina 2*

Dugesiidae:

Dugesia lugubris 2	*Dugesia tigrina 3*	*Dugesia polychroa 2*

Dendrocoelidae:

Dendrocoelum lacteum 2 *Bdellocephala punctata 7*

GASTROPODA
Neritidae:
Theodoxus fluviatilis 3
Viviparidae:

Viviparus viviparus 3	*Viviparus contectus 5*

Valvatidae:

Valvata cristata 2	*Valvata macrostoma 9*	*Valvata piscinalis 1*

Hydrobiidae:

Hydrobia ventrosa 4	*Hydrobia neglecta 6*	*Hydrobia ulvae 1*
Mercuria confusa 10	*Marstoniopsis scholtzi 8*	*Potamopyrgus antipodarum 1*

Truncatella subcylindrica 8
Bithyniidae:

Bithynia tentaculata 1	*Bithynia leachii 5*

Assimineidae:

Assiminea grayana 2	*Paludinella littorina 8*

Lymnaeidae:

Lymnaea truncatula 3	*Lymnaea glabra 9*	*Lymnaea palustris 2*
Lymnaea stagnalis 1	*Lymnaea auricularia 2*	*Lymnaea peregra 1*

Myxas glutinosa 10
Physidae:

Aplexa hypnorum 5	*Physa fontinalis 1*

Planorbidae:

Planorbarius corneus 4	*Menetus dilatatus 7*	*Planorbis carinatus 1*
Planorbis planorbis 1	*Anisus vorticulus 9*	*Anisus vortex 1*
Anisus leucostoma 5	*Gyraulus laevis 6*	*Gyraulus albus 1*
Gyraulus acronicus 9	*Armiger crista 2*	*Bathyomphalus contortus 2*

Hippeutis complanatus 3 *Segmentina nitida 10*
Acroloxidae:
Acroloxus lacustris 2
Ancylidae:
Ancylus fluviatilis 1
Succineidae:

Succinea oblonga 8	*Succinea putris 1*	*Succinea pfeifferi 1*
Succinea elegans 6	*Catinella arenaria 10*	

Vertiginidae:

Vertigo antivertigo 3	*Vertigo moulinsiana 8*	*Vertigo lilljeborgi 8*

Vertigo angustior 10
Zonitidae:
Zonitoides nitidus 4

BIVALVIA
Margaritiferidae:
Margaritifera margaritifera 7
Unionidae:

Unio pictorum 3	*Unio tumidus 5*	*Anodonta cygnaea 2*
Anodonta anatina 3	*Pseudanodonta complanata 7*	

Sphaeriidae:

Sphaerium rivicola 3	*Sphaerium corneum 1*	*Sphaerium solidum 10*
Musculium lacustre 3	*Pisidium amnicum 3*	*Musculium transversum 5*
Pisidium casertanum 1	*Pisidium conventus 7*	*Pisidium personatum 3*

Pisidium obtusale 4 *Pisidium milium 4* *Pisidium pseudosphaerium 8*
Pisidium supinum 5 *Pisidium subtruncatum 1* *Pisidium henslowanum 4*
Pisidium lilljeborgii 5 *Pisidium hibernicum 4* *Pisidium nitidum 3*
Pisidium pulchellum 5 *Pisidium tenuilineatum 8* *Pisidium moitessierianum 4*
Dreissenidae:
Dreissena polymorpha 2

HIRUDINEA
Piscicolidae:
Piscicola geometra 2
Glossiphoniidae:
Theromyzon tessulatum 2 *Hemiclepis marginata 4* *Glossiphonia heteroclita 4*
Glossiphonia complanata 1 *Boreobdella verrucata 7* *Haementeria costata 7*
Batracobdella paludosa 7 *Helobdella stagnalis 1*
Hirudinidae:
Hirudo medicinalis 8 *Haemopis sanguisuga 5*
Erpobdellidae:
Erpobdella testacea 5 *Erpobdella octoculata 1* *Dina lineata 6*
Trocheta subviridis 4 *Trocheta bykowskii 5*

ARANEAE
Argyroneta aquatica 3

ANOSTRACA
Artemia salina 10 Chirocephalus diaphanus 9

NOTOSTRACA
Triops cancriformis 10

MALACOSTRACA
Bathynellacea:
Bathynella natans 7 *Bathynella stammeri 7*
Mysidacae:
Mysis relicta 10 Neomysis integer 1
Isopoda:
Asellus aquaticus 1 *Asellus cavaticus 7* *Asellus communis 7*
Asellus meridianus 3 *Sphaeroma hookeri 2* *Sphaeroma rugicauda 2*
Jaera nordmanni 2
Amphipoda:
Corophiidae:
Corophium curvispinum 3 *Corophium arenarium 5* *Corophium insidiosum 7*
Corophium lacustre 8 *Corophium multisetosum 2* *Corophium volutator 3*
Crangonyctidae:
Crangonyx pseudogracilis 1 *Crangonyx subterraneus 7*
Melitidae:
Allomelita pellucida 7
Gammaridae:
Gammarus duebeni 4 *Gammarus lacustris 5* *Gammarus pulex 1*
Gammarus tigrinus 1 *Gammarus zaddachi 1* *Gammarus insensibilis 8*
Echinogammarus berilloni 7
Niphargidae:
Niphargus glenniei 7 *Niphargus aquilex 6* *Niphargus fontanus 7*
Niphargus kochianus s.l. 7
Talitridae:
Orchestia cavimana 5
Palaeomonidae:
Palaemonetes varians 1 *Palaemon longirostris 5*
Astacidae:
Austropotamobius pallipes 7

EPHEMEROPTERA

Siphlonuridae:

Siphlonurus armatus 6 *Siphlonurus lacustris 4* *Siphlonurus alternatus 6*
Ameletus inopinatus 5

Baetidae:

Baetis buceratus 6 *Baetis fuscatus 4* *Baetis rhodani 1*
Baetis scambus 4 *Baetis vernus 3* *Alainites (Baetis) muticus 2*
Labiobaetis (Baetis) atrebatinus 6 *Nigrobaetis (Baetis) digitatus 5*
Nigrobaetis (Baetis) niger 4 *Centroptilum luteolum 4*
Cloeon dipterum 1 *Cloeon simile 2* *Procloeon bifidum 6*
Procloeon pennulatum 5

Heptageniidae:

Rhithrogena germanica 5 *Rhithrogena semicolorata 2*
Kageronia (Heptagenia) fuscogrisea 7 *Electrogena (Heptagenia) lateralis 2*
Heptagenia longicauda 10 *Heptagenia sulphurea 4*
Ecdyonurus dispar 2 *Ecdyonurus insignis 5* *Ecdyonurus torrentis 2*
Ecdyonurus venosus 2 *Arthroplea congener 10*

Leptophlebiidae:

Leptophlebia marginata 3 *Leptophlebia vespertina 3*
Paraleptophlebia cincta 3 *Paraleptophlebia submarginata 2*
Paraleptophlebia werneri 8 *Habrophlebia fusca 2*

Ephemerellidae:

Ephemerella notata 6 *Serratella (Ephemerella) ignita 1*

Potamanthidae:

Potamanthus luteus 9

Ephemeridae:

Ephemera danica 1 *Ephemera lineata 9* *Ephemera vulgata 4*

Caenidae:

Brachycercus harrisellus 6 *Caenis beskidensis 7* *Caenis horaria 1*
Caenis luctuosa 1 *Caenis macrura 4* *Caenis pseudorivulorum 6*
Caenis pusilla 6 *Caenis rivulorum 3* *Caenis robusta 5*

PLECOPTERA

Taeniopterygidae:

Taeniopteryx nebulosa 4 *Rhabdiopteryx acuminata 7*
Brachyptera putata 7 *Brachyptera risi 3*

Nemouridae:

Protonemura praecox 5 *Protonemura montana 6* *Protonemura meyeri 6*
Amphinemura standfussi 6 *Amphinemura sulcicollis 2*
Nemurella picteti 2 *Nemoura cinerea 1* *Nemoura dubitans 7*
Nemoura avicularis 4 *Nemoura cambrica 2* *Nemoura erratica 5*

Leuctridae:

Leuctra geniculata 4 *Leuctra inermis 1* *Leuctra hippopus 3*
Leuctra nigra 4 *Leuctra fusca 1* *Leuctra moselyi 6*

Capniidae:

Capnia bifrons 6 *Capnia atra 5* *Capnia vidua 7*

Perlodidae:

Isogenus nubecula 9 *Perlodes microcephala 3* *Diura bicaudata 3*
Isoperla grammatica 2 *Isoperla obscura 10*

Perlidae:

Dinocras cephalotes 4 *Perla bipunctata 3*

Chloroperlidae:

Chloroperla torrentium 1 *Chloroperla tripunctata 4* *Chloroperla apicalis 10a*

ODONATA

Platycnemididae:

Platycnemis pennipes 5

Coenagriidae:

Pyrrhosoma nymphula 3 *Ischnura elegans 1* *Ischnura pumilio 7*
Enallagma cyathigerum 2 *Coenagrion armatum 10*

Coenagrion hastulatum 9 *Coenagrion mercuriale 8*
Coenagrion puella 2 *Coenagrion pulchellum 5* *Coenagrion scitulum 10*
Ceriagrion tenellum 6 *Erythromma najas 4*
Lestidae:
Lestes dryas 9 *Lestes sponsa 4*
Calopterigidae:
Calopteryx splendens 2 *Calopteryx virgo 5*
Gomphidae:
Gomphus vulgatissimus 7
Cordulegasteridae:
Cordulegaster boltonii 4
Aeshnidae:
Brachytron pratense 5 *Aeshna caerulea 7* *Aeshna cyanea 2*
Aeshna grandis 2 *Aeshna isosceles 10* *Aeshna juncea 4*
Aeshna mixta 3 *Anax imperator 5*
Corduliidae:
Cordulia aenea 6 *Somatochlora arctica 8* *Somatochlora metallica 7*
Oxygastra curtisii 10
Libellulidae:
Orthetrum cancellatum 5 *Orthetrum coerulescens 5*
Libellula depressa 5 *Libellula fulva 8* *Libellula quadrimaculata 4*
Sympetrum flaveolum 7 *Sympetrum fonscolombii 7*
Sympetrum nigrescens 7 *Sympetrum sanguineum 5*
Sympetrum danae 5 *Sympetrum striolatum 1* *Sympetrum vulgatum 7*
Leucorrhinia dubia 7

HEMIPTERA
Mesoveliidae:
Mesovelia furcata 6
Hebridae:
Hebrus pusillus 7 *Hebrus ruficeps 5*
Hydrometridae:
Hydrometra gracilenta 8 *Hydrometra stagnorum 2*
Veliidae:
Velia caprai 2 *Velia saulii 5* *Microvelia pygmaea 7*
Microvelia reticulata 5 *Microvelia buenoi 8*
Gerridae:
Gerris costae 4 *Gerris lateralis 5* *Gerris thoracicus 4*
Gerris gibbifer 4 *Gerris argentatus 5* *Gerris lacustris 1*
Gerris odontogaster 2 *Aquarius (Gerris) najas 5* *Aquarius (Gerris) paludum 7*
Limnoporus rufoscutellatus 6
Nepidae:
Nepa cinerea 3 *Ranatra linearis 5*
Naucoridae:
Ilyocoris cimicoides 4
Aphelocheiridae:
Aphelocheirus aestivalis 5
Notonectidae:
Notonecta glauca 1 *Notonecta viridis 5* *Notonecta obliqua 5*
Notonecta maculata 5
Pleidae:
Plea minutissima 4
Corixidae:
Micronecta scholtzi 6 *Micronecta minutissima 8* *Micronecta poweri 4*
Cymatia bonsdorffi 4 *Cymatia coleoptrata 4* *Glaenocorisa propinqua 5*
Callicorixa praeusta 3 *Callicorixa wollastoni 5* *Corixa dentipes 5*
Corixa punctata 1 *Corixa affinis 6* *Corixa panzeri 5*
Corixa iberica 7 *Hesperocorixa linnei 4* *Hesperocorixa sahlbergi 2*
Hesperocorixa castanea 4 *Hesperocorixa moesta 6* *Arctocorisa carinata 6*

Arctocorisa germari 5 *Sigara dorsalis 1* *Sigara striata 7*
Sigara distincta 3 *Sigara falleni 1* *Sigara fallenoidea 6 b*
Sigara fossarum 3 *Sigara scotti 5* *Sigara lateralis 2*
Sigara nigrolineata 2 *Sigara concinna 5* *Sigara limitata 5*
Sigara semistriata 5 *Sigara venusta 4* *Sigara selecta 6*
Sigara stagnalis 5

COLEOPTERA
Haliplidae:
Brychius elevatus 3 *Peltodytes caesus 7* *Haliplus apicalis 7*
Haliplus confinis 2 *Haliplus flavicollis 4* *Haliplus fluviatilis 2*
Haliplus fulvus 4 *Haliplus furcatus 10* *Haliplus heydeni 7*
Haliplus immaculatus 4 *Haliplus laminatus 7* *Haliplus lineatocollis 1*
Haliplus lineolatus 4 *Haliplus mucronatus 8* *Haliplus obliquus 4*
Haliplus ruficollis 1 *Haliplus variegatus 8* *Haliplus varius 8*
Haliplus wehnckei 3
Hygrobiidae:
Hygrobia hermanni 4
Noteridae:
Noterus clavicornis 2 *Noterus crassicornis 7*
Dytiscidae:
Laccophilus hyalinus 1 *Laccophilus minutus 2* *Laccophilus obsoletus 9*
Hydrovatus clypealis 8 *Hyphydrus ovatus 2* *Hydroglyphus geminus 7*
Bidessus minutissimus 8 *Bidessus unistriatus 10* *Hygrotus decoratus 7*
Hygrotus inaequalis 2 *Hygrotus quinquelineatus 7*
Hygrotus versicolor 5 *Coelambus confluens 7* *Coelambus impressopunctatus 5*
Coelambus nigrolineatus 8 *Coelambus novemlineatus 7*
Coelambus parallelogrammus 7 *Hydroporus angustatus 2*
Hydroporus discretus 3 *Hydroporus elongatulus 8* *Hydroporus erythrocephalus 3*
Hydroporus ferrugineus 7 *Hydroporus glabriusculus 8* *Hydroporus gyllenhalii 2*
Hydroporus incognitus 3 *Hydroporus longicornis 7* *Hydroporus longulus 5*
Hydroporus marginatus 7 *Hydroporus melanarius 5* *Hydroporus memnonius 4*
Hydroporus morio 6 *Hydroporus neglectus 7* *Hydroporus nigrita 3*
Hydroporus obscurus 5 *Hydroporus obsoletus 7* *Hydroporus palustris 1*
Hydroporus planus 2 *Hydroporus pubescens 2* *Hydroporus rufifrons 9*
Hydroporus scalesianus 9 *Hydroporus striola 2* *Hydroporus tessellatus 2*
Hydroporus tristis 5 *Hydroporus umbrosus 4* *Suphrodytes dorsalis 5*
Stictonectes lepidus 7 *Graptodytes bilineatus 8* *Graptodytes flavipes 9*
Graptodytes granularis 7 *Graptodytes pictus 3* *Porhydrus lineatus 6*
Deronectes latus 7 *Nebrioporus assimilis 5* *Nebrioporus depressus 7*
Nebrioporus griseostriatus 7 *Nebrioporus elegans 1*
Stictotarsus duodecimpustulatus 2 *Oreodytes alpinus 8*
Oreodytes davisii 6 *Oreodytes sanmarkii 2* *Oreodytes septentrionalis 3*
Scarodytes halensis 7 *Laccornis oblongus 7* *Platambus maculatus 2*
Copelatus haemorrhoidalis 3 *Agabus affinis 4*
Agabus arcticus 6 *Agabus biguttatus 7* *Agabus bipustulatus 1*
Agabus brunneus 9 *Agabus chalconatus 7* *Agabus congener 5*
Agabus conspersus 7 *Agabus didymus 1* *Agabus guttatus 5*
Agabus labiatus 7 *Agabus melanarius 7* *Agabus melanocornis 5*
Agabus nebulosus 1 *Agabus paludosus 1* *Agabus striolatus 9*
Agabus sturmii 1 *Agabus uliginosus 7* *Agabus undulatus 9*
Agabus unguicularis 7 *Ilybius aenescens 7* *Ilybius ater 3*
Ilybius fenestratus 7 *Ilybius fuliginosus 1* *Ilybius guttiger 7*
Ilybius quadriguttatus 5 *Ilybius subaeneus 7* *Rhantus aberratus 10*
Rhantus bistriatus 6 *Rhantus exsoletus 5* *Rhantus frontalis 7*
Rhantus grapii 7 *Rhantus suturalis 7* *Colymbetes fuscus 1*
Hydaticus seminiger 7 *Hydaticus transversalis 7* *Acilius canaliculatus 7*
Acilius sulcatus 5 *Graphoderus bilineatus 10* *Graphoderus cinereus 8*
Graphoderus zonatus 10 *Dytiscus circumcinctus 7* *Dytiscus circumflexus 7*

Dytiscus dimidiatus 7	*Dytiscus lapponicus 7*	*Dytiscus marginalis 1*
Dytiscus semisulcatus 4		

Gyrinidae:

Gyrinus aeratus 7	*Gyrinus caspius 3*	*Gyrinus distinctus 7*
Gyrinus marinus 2	*Gyrinus minutus 7*	*Gyrinus opacus 7*
Gyrinus paykulli 7	*Gyrinus substriatus 1*	*Gyrinus suffriani 7*
Gyrinus urinator 7	*Orectochilus villosus 3*	

Hydrophilidae:

Georissus crenulatus 7	*Spercheus emarginatus 10*	*Hydrochus angustatus 7*
Hydrochus brevis 8	*Hydrochus carinatus 8*	*Hydrochus elongatus 8*
Hydrochus ignicollis 8	*Hydrochus megaphallus 8*	*Hydrochus nitidicollis 8*
Helophorus aequalis 1	*Helophorus alternans 7*	*Helophorus arvernicus 7*
Helophorus brevipalpis 1	*Helophorus dorsalis 8*	*Helophorus flavipes 2*
Helophorus fulgidicollis 7	*Helophorus grandis 2*	*Helophorus granularis 5*
Helophorus griseus 7	*Helophorus laticollis 9*	*Helophorus longitarsis 8*
Helophorus minutus 3	*Helophorus nanus 7*	*Helophorus nubilus 4*
Helophorus obscurus 3	*Helophorus strigifrons 7*	*Helophorus tuberculatus 8*
Coelostoma orbiculare 6	*Cercyon bifenestratus 8*	*Cercyon convexiusculus 7*
Cercyon depressus 7	*Cercyon granarius 8*	*Cercyon impressus 1*
Cercyon lateralis 3	*Cercyon littoralis 3*	*Cercyon lugubris 7*
Cercyon marinus 3	*Cercyon melanocephalus 2*	*Cercyon sternalis 7*
Cercyon tristis 7	*Cercyon ustulatus 7*	*Paracymus aeneus 10*
Paracymus scutellaris 7	*Hydrobius fuscipes 1*	*Limnoxenus niger 7*
Anacaena bipustulata 7	*Anacaena globulus 1*	*Anacaena limbata 1*
Anacaena lutescens 3	*Laccobius atratus 7*	*Laccobius atrocephalus 7*
Laccobius biguttatus 5	*Laccobius bipunctatus 2*	*Laccobius minutus 2*
Laccobius obscuratus 10	*Laccobius simulator 8*	*Laccobius sinuatus 7*
Laccobius striatulus 2	*Helochares lividus 7*	*Helochares obscurus 8*
Helochares punctatus 7	*Enochrus affinis 7*	*Enochrus bicolor 7*
Enochrus coarctatus 7	*Enochrus fuscipennis 5*	*Enochrus halophilus 7*
Enochrus isotae 8	*Enochrus melanocephalus 7*	*Enochrus ochropterus 7*
Enochrus quadripunctatus 7		*Enochrus testaceus 3*
Cymbiodyta marginella 5	*Chaetarthria seminulum 7*	*Hydrochara caraboides 10*
Hydrophilus piceus 8	*Berosus affinis 7*	*Berosus luridus 7*
Berosus signaticollis 7	*Berosus spinosus 8*	

Hydraenidae:

Ochthebius aeneus 10	*Ochthebius auriculatus 7*	*Ochthebius bicolon 7*
Ochthebius dilatatus 3	*Ochthebius exsculptus 7*	*Ochthebius lenensis 9*
Ochthebius marinus 7	*Ochthebius minimus 1*	*Ochthebius nanus 7*
Ochthebius poweri 8	*Ochthebius punctatus 7*	*Ochthebius pusillus 7*
Ochthebius subinteger 7	*Ochthebius viridis 7*	*Hydraena britteni 5*
Hydraena gracilis 1	*Hydraena minutissima 7*	*Hydraena nigrita 7*
Hydraena palustris 9	*Hydraena pulchella 7*	*Hydraena pygmaea 8*
Hydraena riparia 1	*Hydraena rufipes 7*	*Hydraena testacea 7*
Limnebius aluta 7	*Limnebius crinifer 8*	*Limnebius nitidus 7*
Limnebius papposus 7	*Limnebius truncatellus 1*	

Elmidae:

Elmis aenea 1	*Esolus parallelepipedus 4*	*Limnius volckmari 2*
Macronychus quadrituberculatus 8		*Normandia nitens 9*
Oulimnius major 8	*Oulimnius rivularis 7*	*Oulimnius troglodytes 7*
Oulimnius tuberculatus 2	*Riolus cupreus 7*	*Riolus subviolaceus 7*
Stenelmis canaliculata 9		

Dryopidae:

Helichus substriatus 7	*Dryops anglicanus 8*	*Dryops auriculatus 7*
Dryops ernesti 3	*Dryops griseus 8*	*Dryops luridus 1*
Dryops nitidulus 7	*Dryops similaris 7*	*Dryops striatellus 7*

Heteroceridae:

Heterocerus fenestratus 3		*Heterocerus flexuosus 5*
Heterocerus hispidulus 8		*Heterocerus obsoletus 3*

Chrysomelidae:
Donacia aquatica 7 *Donacia bicolora 7* *Donacia cinerea 7*
Donacia clavipes 7 *Donacia crassipes 7* *Donacia dentata 7*
Donacia impressa 7 *Donacia marginata 4* *Donacia obscura 9*
Donacia semicuprea 5 *Donacia simplex 5* *Donacia sparganii 7*
Donacia thalassina 7 *Donacia versicolorea 5* *Donacia vulgaris 5*
Plateumaris affinis 7 *Plateumaris braccata 7* *Plateumaris discolor 5*
Plateumaris sericea 3
Curculionidae:
Prasocuris phellandrii 3 *Prasocuris junci 5* *Tanysphyrus lemnae 5*
Eubrychius velutus 7 *Litodactylus leucogaster 7* *Phytobius canaliculatus 7*
Phytobius quadricornis 7 *Phytobius quadrinodosus 8* *Phytobius quadrituberculatus 5*
Gymnetron beccabungae 7 *Gymnetron veronicae 7* *Poophagus sisymbrii 5*
Bagous (Hydronomus) alismatis 7
Scirtidae:
Elodes elongata 8 *Cyphon pubescens 8* *Prionocyphon serricornis 8*
Scirtes orbicularis 8

MEGALOPTERA
Sialidae:
Sialis lutaria 1 *Sialis fuliginosa 5* *Sialis nigripes 7*

NEUROPTERA
Osmylidae:
Osmylus fulvicephalus 5
Sisyridae:
Sisyra fuscata 5 *Sisyra dalii 7* *Sisyra terminalis 5*

TRICHOPTERA
Rhyacophilidae:
Rhyacophila dorsalis 1 *Rhyacophila septentrionis 7* *Rhyacophila obliterata 4*
Rhyacophila munda 3
Glossosomatidae:
Glossosoma conformis 4 *Glossosoma boltoni 3* *Glossosoma intermedium 8*
Agapetus fuscipes 1 *Agapetus ochripes 3* *Agapetus delicatulus 3*
Philopotamidae:
Philopotamus montanus 2 *Wormaldia occipitalis 2* *Wormaldia mediana 5*
Wormaldia subnigra 5 *Chimarra marginata 7*
Polycentropodidae:
Neureclipsis bimaculata 3 *Plectrocnemia conspersa 2* *Plectrocnemia geniculata 3*
Plectrocnemia brevis 8 *Polycentropus flavomaculatus 2* *Polycentropus irroratus 5*
Polycentropus kingi 5 *Holocentropus dubius 4* *Holocentropus picicornis 3*
Holocentropus stagnalis 4 *Cyrnus trimaculatus 3* *Cyrnus insolutus 10*
Cyrnus flavidus 5
Economidae:
Ecnomus tenellus 5
Psychomyiidae:
Tinodes waeneri 1 *Tinodes maclachlani 4* *Tinodes assimilis 5*
Tinodes pallidulus 9 *Tinodes maculicornis 7* *Tinodes unicolor 7*
Tinodes rostocki 7 *Tinodes dives 7* *Lype phaeopa 4*
Lype reducta 3 *Metalype fragilis 7* *Psychomyia pusilla 4*
Hydropsychidae:
Hydropsyche pellucidula 2 *Hydropsyche angustipennis 1* *Hydropsyche siltalai 1*
Hydropsyche saxonica 10 *Hydropsyche contubernalis 4* *Hydropsyche bulgaromanorum 10*
Hydropsyche instabilis 4 *Hydropsyche fulvipes 7* *Hydropsyche exocellata 10*
Cheumatopsyche lepida 4 *Diplectrona felix 4*
Hydroptilidae:
Agraylea multipunctata 1 *Agraylea sexmaculata 5* *Allotrichia pallicornis 5*
Hydroptila sparsa 4 *Hydroptila simulans 3* *Hydroptila cornuta 7*

Hydroptila lotensis 9 *Hydroptila angulata 5* *Hydroptila sylvestris 7*
Hydroptila martini 6 *Hydroptila occulta 5* *Hydroptila tineoides 2*
Hydroptila pulchricornis 6 *Hydroptila forcipata 3* *Hydroptila vectis 2*
Hydroptila tigurina 10 *Hydroptila valesiaca 7* *Ithytrichia lamellaris 4*
Ithytrichia clavata 8 *Orthotrichia angustella 5* *Orthotrichia tragetti 10*
Orthotrichia costalis 5 *Oxyethira flavicornis 3* *Oxyethira tristella 10d*
Oxyethira simplex 6 *Oxyethira falcata 3* *Oxyethira frici 4*
Oxyethira distinctella 10 *Oxyethira sagittifera 8* *Oxyethira mirabilis 8*
Tricholeiochiton fagesii 8

Phryganeidae:

Hagenella clathrata 10 Phryganea grandis 5 Phryganea bipunctata 2
Oligotricha striata 4 Agrypnia varia 3 Agrypnia obsoleta 5
Agrypnia picta 10e Agrypnia pagetana 5 Agrypnia crassicornis 10
Trichostegia minor 5

Limnephilidae:

Ironoquia dubia 9 *Apatania wallengreni 5* *Apatania auricula 7*
Apatania muliebris 5 *Drusus annulatus 1* *Ecclisopteryx guttulata 4*
Limnephilus rhombicus 3 *Limnephilus flavicornis 2* *Limnephilus subcentralis 7*
Limnephilus borealis 7 *Limnephilus marmoratus 3* *Limnephilus politus 4*
Limnephilus tauricus 9 *Limnephilus pati 10* *Limnephilus stigma 4*
Limnephilus binotatus 5 *Limnephilus decipiens 5* *Limnephilus lunatus 1*
Limnephilus luridus 2 *Limnephilus ignavus 6* *Limnephilus fuscinervis 7*
Limnephilus elegans 7 *Limnephilus griseus 4* *Limnephilus bipunctatus 5*
Limnephilus affinis 3 *Limnephilus incisus 3* *Limnephilus hirsutus 4*
Limnephilus centralis 3 *Limnephilus sparsus 2* *Limnephilus auricula 3*
Limnephilus vittatus 3 *Limnephilus nigriceps 6* *Limnephilus extricatus 2*
Limnephilus fuscicornis 5 *Limnephilus coenosus 4* *Grammotaulius nitidus 10*
Grammotaulius nigropunctatus 4 *Glyphotaelius pellucidus 3*
Nemotaulius punctatolineatus 8 *Anabolia nervosa 2*
Phacopteryx brevipennis 7 *Rhadicoleptus alpestris 5*
Potamophylax latipennis 2 *Potamophylax cingulatus 2*
Potamophylax rotundipennis 6 *Halesus radiatus 2*
Halesus digitatus 3 *Melampophylax mucoreus 5*
Stenophylax permistus 3 *Stenophylax vibex 5* *Micropterna lateralis 2*
Micropterna sequax 1 *Mesophylax impunctatus 5* *Mesophylax aspersus 8*
Allogamus auricollis 4 *Hydatophylax infumatus 5* *Chaetopteryx villosa 3*

Molannidae:

Molanna angustata 2 *Molanna albicans 5*

Beraeidae:

Beraea pullata 4 *Beraea maurus 3* *Ernodes articularis 8*
Beraeodes minutus 5

Odontoceridae:

Odontocerum albicorne 3

Leptoceridae:

Ceraclea albimacula 5 *Ceraclea nigronervosa 4* *Ceraclea fulva 5*
Ceraclea senilis 7 *Ceraclea annulicornis 4* *Ceraclea dissimilis 3*
Athripsodes aterrimus 1 *Athripsodes cinereus 1* *Athripsodes albifrons 4*
Athripsodes bilineatus 5 *Athripsodes commutatus 6* *Mystacides nigra 6*
Mystacides azurea 2 *Mystacides longicornis 1* *Triaenodes bicolor 2*
Ylodes conspersus 7 *Ylodes simulans 8* *Ylodes reuteri 8*
Erotesis baltica 8 *Adicella reducta 3* *Adicella filicornis 8*
Oecetis ochracea 2 *Oecetis furva 5* *Oecetis lacustris 3*
Oecetis notata 8 *Oecetis testacea 4* *Leptocerus tineiformis 5*
Leptocerus lusitanicus 9 *Leptocerus interruptus 8* *Setodes punctatus 8*
Setodes argentipunctellus 8

Goeridae:

Goera pilosa 3 *Silo pallipes 2* *Silo nigricornis 5*

Lepidostomatidae:

Crunoecia irrorata 3 *Lepidostoma hirtum 2* *Lasiocephala basalis 6*

Brachycentridae:
Brachycentrus subnubilus 6
Sericostomatidae:
Sericostoma personatum 1 Notidobia ciliaris 6

DIPTERA
Tipulidae/Tipulidae/Limoniidae/Cylindrotomidae
Arctoconopa melampodia 9 Cheilotrichia imbuta 7 Dactylolabis sexmaculata 7
Dactylolabis transversa 7 Dicranota gracilipes 7 Dicranota guerini 7
Dicranota robusta 7 Dicranota simulans 8 Elliptera omissa 10
Erioptera bivittata 9 Erioptera limbata 9 Erioptera meigeni 8
Erioptera meijeri 9 Erioptera neilseni 7 Erioptera nigripalpis 8
Erioptera pusilla 10 Erioptera sordida 8 Gonomyia abbreviata 8
Gonomyia alboscutellata 10 Gonomyia bifida 7 Gonomyia bradleyi 9
Gonomyia connexa 10 Gonomyia conoviensis 7 Gonomyia sexguttata 10
Helius pallirostris 7 Limnophila abdominalis 7 Limnophila apicata 7
Limnophila fasciata 10 Limnophila glabricula 7 Limnophila heterogyna 10
Limnophila mundata 7 Limnophila pictipennis 9 Limnophila pulchella 7
Limnophila trimaculata 7 Limnophila verralli 7 Limonia aperta 10
Limonia aquosa 7 Limonia bezzii 9 Limonia caledonica 7
Limonia complicata 7 Limonia consimilis 8 Limonia danica 8
Limonia distendens 7 Limonia goritiensis 8 Limonia halterella 7
Limonia lucida 7 Limonia occidua 7 Limonia omissinervis 9
Limonia ornata 7 Limonia rufiventris 8 Limonia stigmatica 7
Limonia stylifera 9 Limonia ventralis 7 Molophilus bihamatus 7
Molophilus corniger 7 Molophilus czizeki 8 Molophilus lackschewitzianus 8
Molophilus niger 7 Molophilus propinquus 7 Neolimnophila carteri 7
Neolimnophila placida 7 Nephrotoma crocata 8 Orimarga juvenilis 7
Orimarga virgo 8 Ormosia aciculata 9 Ormosia bicornis 9
Ormosia staegeriana 7 Paradelphomyia ecalcarata 9 Paradelphomyia fuscula 7
Paradelphomyia nielseni 7 Pedicia lucidipennis 7 Pedicia unicolor 7
Phalacrocera replicata 7 Pilaria fuscipennis 7 Pilaria meridiana 7
Pilaria scutellata 7 Prionocera pubescens 9 Prionocera subserricornis 9
Rhabdomastix hilaris 8 Rhabdomastix inclinata 9 Scleroprocta pentagonalis 8
Scleroprocta sororcula 7 Tasiocera collini 10 Tasiocera fuscescens 10
Tasiocera jenkinsoni 10 Tasiocera laminata 7 Thaumasoptera calceata 7
Tipula bistilata 9 Tipula cheethami 7 Tipula coerulescens 8
Tipula gimmerthali 8 Tipula grisescens 8 Tipula limbata 8
Tipula marginata 8 Tipula serrulifera 10 Tipula siebkei 10
Tipula truncorum 7 Triogma trisulcata 8
Dixidae:
Dixa dilatata 5 Dixa maculata 7 Dixa nebulosa 4
Dixa nubilipennis 5 Dixa puberula 5 Dixa submaculata 4
Dixella aestivalis 4 Dixella amphibia 4 Dixella attica 7
Dixella autumnalis 3 Dixella filicornis 7 Dixella graeca 9
Dixella martinii 4 Dixella obscura 7 Dixella serotina 7
Culicidae:
Aedes communis 10 Aedes dorsalis 8 Aedes flavescens 9
Aedes leucomelas 10 Aedes stictus 8 Anopheles algeriensis 10
Culiseta longiareolata 10 Orthopodomyia pulcripalpis 8
Thaumaleidae:
Thaumalea testacea 6 Thaumalea truncata 8 Thaumalea verralli 6
Ceratopogonidae:
Dasyhelea lithotelmatica 9
Simuliidae:
Prosimulium hirtipes 5 Prosimulium latimucro 7 Prosimulium tomosvaryi 7
Metacnephia amphora 7 Simulium latipes 6 Simulium angustitarse 6
Simulium lundstromi 4 Simulium armoricanum 5 Simulium cryophilum 4
Simulium juxtacrenobium 6 Simulium urbanum 7 Simulium dunfellense 5

Simulium costatum 5 *Simulium angustipes 4* *Simulium velutinum 4*
Simulium aureum 5 *Simulium lineatum 3* *Simulium pseudequinum 5*
Simulium equinum 2 *Simulium erythrocephalum 3* *Simulium ornatum 1*
Simulium intermedium 5 *Simulium trifasciatum 5* *Simulium argyreatum 3*
Simulium variegatum 4 *Simulium tuberosum (sp. complex) 4* *Simulium rostratum 6*
Simulium morsitans 7 *Simulium posticatum 5* *Simulium reptans 5*
Simulium noelleri 3
Stratiomyidae:
Beris clavipes 7 *Beris fuscipes 7* *Odontomyia angulata 10*
Odontomyia argentata 9 *Odontomyia hydroleon 10* *Odontomyia ornata 9*
Odontomyia tigrina 7 *Oxycera analis 9* *Oxycera dives 8*
Oxycera leonina 10 *Oxycera morrisii 7* *Oxycera pardalina 7*
Oxycera pygmaea 7 *Oxycera terminata 9* *Stratiomys chamaeleon 10*
Stratiomys longicornis 9 *Stratiomys potamida 7* *Vanoyia tenuicornis 7*
Rhagionidae:
Atrichops crassipes 8
Tabanidae:
Atylotus plebeius 10 *Chrysops sepulcralis 9* *Haematopota grandis 8*
Tabanus cordiger 7 *Tabanus glaucopis 8*
Empididae:
Chelifera angusta 7 *Chelifera aperticauda 7* *Chelifera astigma 10*
Chelifera concinnicauda 7 *Chelifera monostigma 7* *Chelifera subangusta 7*
Clinocera nivalis 8 *Clinocera tenella 8* *Clinocera wesmaelii 7*
Dolichocephala ocellata 8 *Dryodromia testacea 7* *Hemerodromia adulatoria 7*
Hemerodromia laudatoria 7 *Hemerodromia melangyna 9* *Stilpon lunata 7*
Stilpon sublunata 7 *Weidemannia impudica 10* *Weidemannia lamellata 10*
Weidemannia lota 7 *Weidemannia phantasma 8*
Dolichopodidae:
Acropsilus niger 10 *Aphrosylus mitis 8* *Campsicnemus compeditus 7*
Campsicnemus magius 8 *Campsicnemus marginatus 7* *Campsicnemus pectinulatus 7*
Campsicnemus pusillus 7 *Chrysotus monochaetus 7* *Chrysotus suavis 7*
Dolichopus arbustorum 8 *Dolichopus cilifemoratus 9* *Hydrophorus viridis 8*
Rhaphium fractum 7 *Syntormon macula 8* *Syntormon filiger 7*
Syntormon mikii 9 *Syntormon zelleri 7* *Systenus bipartitus 8*
Systenus leucurus 7 *Systenus pallipes 7* *Systenus scholtzii 7*
Systenus tener 8 *Telmaturgus tumidulus 8*
Syrphidae:
Anasimyia interpuncta 8 *Anasimyia lunulata 7* *Chrysogaster macquarti 7*
Eristalis cryptarum 9 *Eristalis rupium 7* *Helophilus groenlandicus 9*
Lejogaster splendida 7 *Lejops vittata 9* *Mallota cimbiciformis 7*
Orthonevra brevicornis 7 *Orthonevra geniculata 7* *Parhelophilus consimilis 9*
Sciomyzidae:
Antichaeta analis 8 *Antichaeta brevipennis 9* *Colobaea bifasciella 7*
Colobaea distincta 7 *Colobaea pectoralis 9* *Colobaea punctata 7*
Dictya umbrarum 7 *Pherbellia argyra 9* *Pherbellia brunnipes 7*
Pherbellia griseola 7 *Pherbellia grisescens 7* *Pherbellia nana 7*
Psacadina vittegera 9 *Psacadina zernyi 9* *Pteromicra glabricula 7*
Pteromicra leucopeza 9 *Pteromicra pectorosa 9* *Renocera striata 7*
Sciomyza dryomyzina 9 *Sciomyza simplex 7* *Tetanocera freyi 8*
Scathophagidae:
Acanthocnema glaucescens 7 *Acanthocnema nigrimana 8*
Muscidae:
Lispe caesia 7 *Lispe consanguinea 9* *Lispe uliginosa 7* *Phaonia exoleta 8*

Appendix 5

Pooled total aquatic (spring, summer and autumn samples combined) aquatic macroinvertebrate taxa list from meadow, agricultural forest and urban pond sites

Symbols represent proportional abundance: ◦ <1% • 1-10% ○ >10-25% ● >25% blank - not present

Appendix presented on a CD

Appendix 6

Pond site and mean value of abundance, taxa and diversity indices (SWD - Shannon Wiener diversity index; BPDI - Berger Parker Dominance index; SD - Simpsons diversity index; MD - Margalef diversity index; McD - McIntosh diversity index and; FD - Fisher's alpha)

Site	Abundance	Taxa	SWD	BPDI	SD	MD	McD	FA
				Meadow				
M1	1810	48	1.95	0.37	4.13	6.27	0.52	9.06
M2	5571	73	2.20	0.44	4.28	8.35	0.52	11.87
M3	351	8	0.56	0.85	1.36	1.19	0.15	1.46
M4	2478	43	1.83	0.44	3.83	5.37	0.50	7.40
M5	152	22	2.45	0.20	9.02	4.18	0.72	7.06
M6	3379	58	2.27	0.42	4.66	7.12	0.55	10.11
M7	3098	61	2.63	0.20	9.01	7.46	0.68	10.78
M8	4219	66	2.65	0.20	9.33	7.79	0.68	11.12
M9	277	16	1.17	0.68	2.05	2.67	0.32	3.70
M10	466	29	2.44	0.23	7.86	4.56	0.67	6.86
M11	1277	40	2.27	0.34	5.59	5.45	0.59	7.85
M12	2099	65	2.35	0.25	5.93	8.37	0.60	12.73
M13	169	14	1.78	0.46	3.87	2.53	0.53	3.63
M14	2507	54	2.36	0.32	5.81	6.77	0.60	9.73
M15	2541	61	2.68	0.24	9.42	7.65	0.69	11.25
M16	4125	62	2.92	0.20	11.76	7.33	0.72	10.36
M17	5661	63	2.18	0.45	4.31	7.18	0.53	9.93
M18	3228	46	2.29	0.38	5.41	5.57	0.58	7.60
M19	1770	45	2.76	0.21	10.68	5.88	0.71	8.41
M20	3758	47	2.15	0.37	5.23	5.59	0.57	7.57
M21	5344	40	1.91	0.41	3.99	4.54	0.51	5.87
M22	1966	45	2.47	0.20	7.90	5.80	0.66	8.22
M23	2928	53	2.79	0.19	11.66	6.52	0.72	9.20
M24	2488	64	2.76	0.31	7.86	8.06	0.66	11.99
M25	3232	49	2.04	0.53	3.38	5.94	0.46	8.20
M26	85	5	0.68	0.81	1.49	0.90	0.20	1.16
M27	197	6	0.91	0.56	2.17	0.95	0.34	1.17
M28	2296	37	2.21	0.33	5.61	4.65	0.59	6.27
M29	2253	25	0.90	0.80	1.54	3.11	0.20	3.94
M30	835	31	1.59	0.64	2.37	4.46	0.36	6.35
M31	891	20	1.69	0.37	4.27	2.80	0.53	3.64
M32	219	9	1.52	0.45	3.48	1.48	0.49	1.89
M33	316	9	0.83	0.80	1.55	1.39	0.21	1.73
M34	497	9	1.10	0.47	2.51	1.29	0.39	1.56
M35	3532	49	1.78	0.42	3.92	5.88	0.50	8.06
				Agricultural				
AP1	1974	29	1.26	0.67	2.09	3.69	0.32	4.82
AP2	968	34	2.44	0.29	7.20	4.80	0.65	6.87
AP3	2114	44	2.35	0.28	6.07	5.62	0.61	7.87
AP4	1762	47	2.62	0.25	8.41	6.16	0.67	8.88
AP5	3078	39	2.19	0.27	6.22	4.73	0.61	6.30
AP6	1496	18	1.60	0.48	3.30	2.33	0.46	2.88
AP7	1003	50	2.65	0.24	8.74	7.09	0.68	11.08
AP8	41	11	2.20	0.20	9.54	2.69	0.76	4.93
AP9	1769	9	0.56	0.84	1.38	1.07	0.15	1.21
AP10	633	34	1.77	0.58	2.81	5.12	0.42	7.70
AP11	5576	44	1.00	0.79	1.60	4.99	0.21	6.52
AP12	2614	51	1.58	0.64	2.34	6.35	0.35	8.99

Site	Abundance	Taxa	SWD	BPDI	SD	MD	McD	FA
				Forest				
FP1	2206	22	1.54	0.49	3.25	2.73	0.45	3.40
FP2	1737	12	1.53	0.32	4.05	1.48	0.52	1.73
FP3	710	20	1.79	0.31	4.61	2.89	0.55	3.83
FP4	2023	19	0.97	0.68	1.91	2.37	0.28	2.90
FP5	633	27	1.59	0.59	2.63	4.03	0.40	5.73
FP6	565	19	1.52	0.47	3.05	2.84	0.44	3.80
FP7	1110	10	1.28	0.45	3.04	1.28	0.44	1.52
				Urban				
UP1	4801	22	1.31	0.58	2.54	2.48	0.38	2.87
UP2	1756	9	1.33	0.37	3.37	1.07	0.47	1.21
UP3	2644	14	1.59	0.44	3.77	1.65	0.49	1.89
UP4	93	3	0.74	0.74	1.72	0.44	0.26	0.59
UP5	2090	26	1.99	0.34	5.25	3.27	0.58	4.19
UP6	2222	34	1.44	0.44	2.80	4.28	0.41	5.70
UP7	670	14	1.44	0.57	2.73	2.00	0.41	2.51
UP8	1978	39	1.99	0.26	5.30	5.01	0.58	6.89
UP9	265	17	1.97	0.32	5.00	2.87	0.59	4.06
UP10	1335	20	1.56	0.41	3.61	2.64	0.49	3.34
UP11	2972	42	2.41	0.35	6.16	5.13	0.61	6.93
UP12	39	5	1.38	0.38	3.82	1.09	0.56	1.52
UP13	1520	47	2.17	0.34	5.47	6.28	0.59	9.20
UP14	2530	59	2.33	0.27	5.87	7.40	0.60	10.81
UP15	1198	41	2.47	0.31	6.65	5.64	0.63	8.23
UP16	1968	50	2.08	0.38	4.64	6.46	0.55	9.34
UP17	1691	61	2.33	0.33	5.37	8.07	0.58	12.40
UP18	6628	29	1.36	0.50	2.82	3.18	0.41	4.07
UP19	1116	43	2.06	0.46	4.04	5.99	0.52	8.89
UP20	303	4	0.50	0.83	1.40	0.53	0.16	0.65
UP21	3744	20	1.61	0.45	3.57	2.31	0.48	2.71
UP22	1945	13	1.05	0.60	2.20	1.59	0.33	1.86
UP23	1025	11	0.74	0.82	1.47	1.44	0.18	1.72
UP24	6766	21	1.40	0.57	2.75	2.27	0.40	2.79
UP25	45	2	0.30	0.91	1.20	0.26	0.10	0.43
UP26	728	12	0.84	0.78	1.61	1.67	0.22	2.04
UP27	670	8	1.19	0.46	2.71	1.08	0.41	1.28
UP28	1265	14	0.97	0.73	1.80	1.82	0.26	2.21
UP29	1111	8	1.07	0.68	2.01	1.00	0.30	1.17
UP30	210	12	1.06	0.74	1.79	2.06	0.27	2.77
UP31	900	11	0.79	0.81	1.51	1.47	0.19	1.77
UP32	112	3	0.39	0.88	1.26	0.42	0.12	0.57
UP33	237	6	0.43	0.91	1.20	0.91	0.09	1.12
UP34	1034	4	0.93	0.69	1.96	0.43	0.29	0.55
UP35	977	6	1.21	0.47	2.89	0.73	0.43	0.84
UP36	2379	24	1.37	0.48	2.96	2.96	0.43	3.72
UP37	1550	5	0.95	0.64	2.13	0.54	0.32	0.67
UP38	3998	40	1.78	0.31	4.46	4.70	0.53	6.18
UP39	6006	45	1.22	0.71	1.90	5.06	0.28	6.61
UP40	4470	42	2.03	0.28	5.51	4.88	0.58	6.42
UP41	85	3	0.62	0.74	1.65	0.45	0.25	0.61

Appendix 7

Summary table of mean environmental characteristics for pond sites (SWS: surface water shaded, PMS: pond margin shaded, EM: emergent macrophytes, SM: submerged macrophytes, FM: floating macrophytes, Cond: conductivity, DO: dissolved oxygen, FP: fish presence.

Site Name	Area (m^2)	Depth (cm)	SWS (%)	PMS (%)	EM (%)	SM (%)	FM (%)	pH	Cond	DO (%)	FP
Meadow											
M1	12.5	53.3	0.3	0.3	3.3	59	30.3	7.9	957.3	63.1	Yes
M2	548.3	84.3	3.7	30	45	41.7	0	8.1	484	83.1	Yes
M3	29.5	9.1	0	0	14	0	0	8.7	353.5	98	No
M4	38	37.3	68.3	46.7	45	33.7	5.3	7.5	1494	28.3	Yes
M5	315.2	8	0	0	25	72.5	0	8.6	486.5	119.5	No
M6	1074.2	78.7	2	20	21.7	73	0.3	7.7	1382	85.8	Yes
M7	535.1	26.5	0	0	30	20	16.7	7.9	693	86.9	Yes
M8	1225	100	6.7	0.3	10	16.7	0	8.3	778.7	90.9	Yes
M9	23.9	9.5	0	0	0	0	0	8.4	417.5	102	No
M10	114.5	13.3	0	0	30	26.7	3.3	8.5	499	81.7	No
M11	54.2	22	10	16.7	66.7	19.3	0.7	7.8	521.3	78.5	No
M12	5256	200	0	0	16.7	10	1.7	8.3	607.3	111.9	Yes
M13	11.9	9.5	0	0	36.5	60	0	8.4	371	105.5	No
M14	108.1	81	0	0	2	38	0	9.1	569.3	89.9	No
M15	107.3	87.3	0	0	2	17	0	8.5	656.7	89.7	No
M16	91.1	58	0	0	3	12	0	8.5	694	93.9	No
M17	97.4	61	0	0	1.7	11	0	8.4	660.3	96.5	No
M18	97.6	59	0	0	1.7	21	0	8.5	705.3	95	No
M19	88.5	52.2	0	0	1.3	87	0	8.3	708	99	No
M20	91.6	53.8	0	0	2.3	8.7	0	8.6	822	92.6	No
M21	88.6	45.7	0	0	1	8.3	0	8.4	864.3	97.6	No
M22	90.6	38.5	0	0	2.2	3.7	0	8.3	814.3	96.6	No
M23	81.1	46.3	0	0	4.3	14.7	0	8.5	744	96.4	No
M24	101.5	89.3	0	0	1.3	23.3	0	8.5	700.3	101.5	No
M25	94.5	91	0	0	1.7	13.7	3.3	9	700.7	95.5	No
M26	496.9	44	0	0	0	100	0	7	461	71	No
M27	457.6	19	0	0	2	98	0	6.7	80	71	No
M28	177.6	20.3	0	0	45	52	0	7.1	237	57.2	No
M29	121.6	31.5	0	0	48	36.5	0	6.9	240	55.5	No
M30	24.8	16.7	0	0	86.7	5	0	7.2	396.3	71.5	No
M31	40	53.3	93.3	96.7	23.3	56.7	1.7	7.2	422.3	64.5	No
M32	10.3	15	0	0	80	10	0	6.6	344	60	No
M33	118.8	39	0	0	80	15	0	6.4	460	57	No
M34	1258	100	30	85	5	5	0	7.2	987	63	No
M35	107.9	83	0	0	15	26.7	8.3	7.9	167.7	78.4	No
Agricultural											
AP1	92.9	55.7	4.7	23.7	86.7	3.3	5	7.9	723	67.6	No
AP2	106.1	77	0	0	20.3	28.3	12.7	7.6	885	56.4	No
AP3	146.9	78.3	6.7	9	20	25	3.3	7.9	588.7	81.5	No
AP4	92	93.3	5	12.3	45	12.3	5	8	476.3	81.5	No
AP5	108.7	26.3	8.3	46.7	63.3	26.7	1.7	7.7	1251.3	49.4	No
AP6	93.5	34	40	71.7	48.3	2	9.7	7.7	1326.7	43.3	No
AP7	113.7	31.7	0	0	25.7	23.3	28.3	7.9	744	131.6	No
AP8	185.5	26	100	100	5	0	0	7.6	782	26.5	No
AP9	24.4	12	0	0	80	15	4	8.3	745	76	No
AP10	160.3	66	13.3	21.7	30	37.3	8.3	8.1	758.7	93	No
AP11	328.5	100	0	0	8.3	21.7	16.7	8.2	575	75.5	No
AP12	4566	200	4.3	63.3	5	5	2	8.2	524	88.2	Yes

Site Name	Area (m^2)	Depth (cm)	SWS (%)	PMS (%)	EM (%)	SM (%)	FM (%)	pH	Cond	DO (%)	FP
Forest											
FP1	171	200	23.3	40	1.3	4	0	7.4	205	42.2	Yes
FP2	166.7	51.3	36.7	68.3	1.7	2	55	7.8	347	38.3	No
FP3	472.7	31	55	53	3.3	0.3	1.7	7.4	345	55.1	No
FP4	131.8	22.3	93.3	98.3	0	1.3	0	7.8	993	55.1	No
FP5	102.8	35	5.3	36.7	3.7	32.7	0	6.9	204.3	98.1	No
FP6	88.6	14.3	4.3	5	57.7	41.3	0.3	6.2	104.3	113.1	No
FP7	144	13	95	95	40	25	0	6.8	267	29	No
Urban											
UP1	93.1	82.7	41.7	48.3	32.7	6.7	2	7.4	606	54.6	No
UP2	21.2	5.33	33.3	33.3	6.7	1.7	0	7.7	974	71.4	No
UP3	10.9	8	65	65	2.3	0.3	0	7.6	792.7	54.1	No
UP4	5.5	11.5	0	0	77.5	15	0	7.5	249.5	37	No
UP5	276.5	57.8	0	0	41.7	48.3	1	8	299.7	63.3	Yes
UP6	2030	200	0.7	0.67	21.7	5.67		8.5	630	107.5	Yes
UP7	231.6	36.5	47.5	37.5	55	10.5	32.5	8.2	222.5	83	No
UP8	1407	7	15.3	25	95.7	3.7	0.67	7.5	724	55	No
UP9	17.9	6.5	0	0	87.5	12.5	0	7.8	479.5	96.5	No
UP10	9.2	4.2	93.3	98.3	94.3	3	0	7.5	866	59.7	No
UP11	186.9	79	6.7	31	20	31.7	5	8.4	411.7	105.2	Yes
UP12	37.8	4	0	0	100	0	0	7.7	1322	73	No
UP13	6837	200	5.3	85	2.3	20	1.83	8.2	611.7	89.1	Yes
UP14	9309	200	3.4	33.3	8.3	11.7	0	8	638	66.4	Yes
UP15	4802	200	5.3	75	2	7.3	0.33	8.5	887	65.5	Yes
UP16	683	200	3.7	55	18.3	13.3	0	7.7	755	73.3	Yes
UP17	2659	200	2	77.7	10.7	23.7	0	7.9	420.7	93.2	Yes
UP18	1728	200	9	99	4.3	10.3	3	7.9	1024	83.7	Yes
UP19	236.2	36.7	0	0	43.3	11.7	0	7.9	511	91.2	No
UP20	691	40	10	46.7	0.3	0.3	0	8.1	611.7	77.3	Yes
UP21	16.3	47.7	0	0	2	32.3	96.67	7	89.7	17.4	No
UP22	16.5	62.9	0	0	0	50	23.33	7.9	379	95.6	No
UP23	11.7	41	80	81.7	5	31.7	5	7.6	493.3	61.9	No
UP24	51.6	57.6	0.7	0.7	8.3	75	38	7.5	244	71.6	No
UP25	7.12	42.8	0	0	0	0	0	9.8	219.7	77.7	Yes
UP26	4.51	60	0	0	20	11.7	47.67	7.9	365.3	88.6	Yes
UP27	1.9	35.5	11.7	28.3	13.7	48.3	26.67	7.9	216.7	71.2	No
UP28	2.7	56.3	0	0	18.3	68.3	19.33	7.6	456	75.1	Yes
UP29	3.9	17.2	0	0	50	43.3	0.83	7.5	104.7	51.4	No
UP30	4.8	35.5	0	0	0	5	6.7	8.3	356	118	Yes
UP31	10.9	37.3	0	0	15	31.7	18.3	8.3	415.3	86.2	Yes
UP32	3.4	16.5	0	0	3.7	0	96.7	7.2	357.7	13.1	No
UP33	3.9	70.4	0	0	6.7	11.7	10	8.1	355.7	104	Yes
UP34	0.8	27.3	33.3	33.3	5	0.3	86.7	7.6	624	25.6	Yes
UP35	2.9	39.3	50	46.7	1.7	0.7	45	7.7	739.3	28.4	No
UP36	86.5	47.3	76.7	58.3	2.7	9.3	32	8.2	465.3	102.5	Yes
UP37	6.8	14.5	100	100	2.3	1.7	30	7.5	784	55.5	No
UP38	154.1	100	20	25	8.3	58.3	15	7.3	98.7	55.9	Yes
UP39	159.2	60.5	2	0.7	28.7	53.3	0	6.8	63.7	80.7	No
UP40	168.2	100	0.7	1	18.3	6	3.7	6.9	276	105.5	No
UP41	3	17	0	0	10	90	0	6.3	414	34	No