Macroinvertebrate community composition and diversity in ephemeral and perennial ponds on unregulated floodplain meadows in the UK

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Abstract

Ponds are common and abundant landscape features in temperate environments, particularly on floodplains where lateral connectivity with riverine systems persists. Despite their widespread occurrence and importance to regional diversity, research on the ecology and hydrology of temperate ephemeral and perennial floodplain ponds lags behind that of other shallow waterbodies. This study examines the aquatic macroinvertebrate diversity of 34 ponds (20 perennial and 14 ephemeral) on two unregulated riverine floodplain meadows in Leicestershire, UK. Perennial ponds supported nearly twice the diversity of ephemeral ponds. Despite frequent inundation of floodwater and connectivity with other floodplain waterbodies, ephemeral ponds supported distinct invertebrate communities when compared to perennial ponds. When the relative importance of physical and chemical, biological and spatial characteristics was examined, physical and chemical characteristics were found to account for more variation in community composition than biological or spatial variables. The results suggest that niche characteristics rather than neutral colonisation processes dominate the structure of invertebrate communities of floodplain ponds. The maintenance of pond networks with varying hydroperiod lengths and environmental characteristics should be encouraged as part of conservation management strategies to provide heterogeneous environmental conditions to support and enhance aquatic biodiversity at a landscape scale.

Key Words: community composition, community heterogeneity, connectivity, dry phase duration, hydroperiod, invertebrate, species richness

Introduction

Floodplain landscapes are sites of exceptionally high aquatic, semi-aquatic and terrestrial diversity (Ward et al. 1999; Helfield et al. 2012) which may be strongly influenced by lateral connectivity to lotic ecosystems (Tockner et al. 2000; Starr et al. 2014). The flooding of riverine landscapes creates and maintains a variety of aquatic habitats and typically results in a network of hydrologically connected perennial and ephemeral waterbodies at a range of successional stages (Paillex et al. 2013). However, due to anthropogenic flow regulation, embankment and channelization to reduce flood risk and to protect infrastructure and agricultural activities on the floodplain, many rivers are hydrologically disconnected from their floodplain along most of their course (Nilsson et al. 2005; Paillex et al. 2013). This has resulted in a long term trend of terrestrialization of floodplain habitats compounded by agricultural expansion and urbanisation leading to a reduction in freshwater biodiversity and habitat (Tockner & Stanford 2002; Reckendorfer et al. 2006).

Ponds located on traditionally managed floodplains can provide important habitats for a wide range of unique flora and fauna (Shiel, et al. 1998; Williams et al. 2008). Floodplain ponds support diverse aquatic habitats and often represent locations of high alpha (site), beta (between ponds) and gamma (regional) diversity (Gergel 2002). They are common and abundant aquatic habitats globally (Williams 1997; Boix et al. 2016) often occurring in pond networks but they have been poorly studied in most regions compared to other freshwater habitats (Gergel 2002; Williams 2006). Many floodplain ponds are ephemeral (they experience recurrent drying; Williams et al. 2001), and are often characterised by a gradient of permanence (hydroperiod), from those containing water for a few months through to those with perennial surface water. Floodplain ponds therefore have the potential to be strongly controlled by colonisation dynamics, but may equally be driven by local habitat conditions, particularly if some ponds dry while others remain wet.

The physical and chemical conditions of ephemeral ponds are demanding for biota and often become extreme as the pond dries and aquatic habitat is lost (Williams 1996; Williams 2006; Bagella et al. 2010). Due to the potentially wide range of conditions they experience, ephemeral ponds have been shown to be important habitats for a diverse range of macroinvertebrate taxa adapted to and able to exploit the conditions they offer (Bazzanti et al. 2010). Although ephemeral ponds often support a lower taxonomic richness than perennial ponds, they may support a high richness of ‘rare’ and endemic taxa (Nicolet et al. 2004; Armitage et al. 2012) and in some cases support a greater number and proportion of rare taxa than perennial ponds in close geographical proximity (Collinson et al. 1995; Della Bella et al. 2005). Fish typically occur in low abundances or are absent from ephemeral ponds as they cannot withstand desiccation which may greatly reduce predation pressure on invertebrates (although high predation pressure may still occur from other vertebrates and invertebrates e.g., Amphibia, Coleoptera and Crustacea; Brendonck et al. 2002). The absence of fish may also increase the abundance/richness of open water taxa and other fauna that may be outcompeted in perennial ponds (Bronmark & Hansson 2005; De Meester et al. 2005).

There has been a recent drive to re-connect rivers with their floodplains and to rehabilitate and restore aquatic habitats on the floodplain to support faunal and floral diversity (Buijse et al. 2002; Reckendorfer et al. 2006; Paillex et al. 2015). However, debate surrounds the relative importance of local habitat (referring to the physical, chemical and biological characteristics of individual ponds) and regional (connectivity/isolation: the spatial configuration of ponds) variables in determining pond community composition (Vanschoenwinkel et al. 2007). Although the physical and chemical characteristics of ponds have been considered in some detail (Hinden et al. 2005; Hassall et al. 2011), most have largely ignored the relative role of regional variables in influencing community composition (Van de Meutter et al. 2007; Heino et al. 2014). Metacommunity theory provides a theoretical framework to partition the mechanisms that may underlie biological distributions in a pond network (Leibold et al. 2004; Vanschoenwinkel et al. 2007). A metacommunity is defined as ‘a set of local communities that are linked by dispersal of multiple potentially interacting species’ (Leibold et al. 2004: 602) where communities are located on a continuum from those dominated entirely by regional colonisation dynamics, to those where niche differentiation based on local habitat conditions dominate. Four general community types can therefore be recognised; 1) p*atch dynamics* - numerous homogenous patches are present in which the driving force of community structure is a trade-off between competitive ability and dispersal (Leibold et al. 2004); 2) *species sorting* - species distribute amongst heterogeneous patches based on their ability to specialize within particular abiotic niches (Cottenie et al. 2003; Vanschoenwinkel et al. 2007); 3) *mass effects* - dispersal drives community composition. Different patches experience different conditions at a given time and dispersal of individuals between patches is frequent, creating source-sink relationships. Local extinctions of individual species can be prevented by dispersal from patches where they are good competitors (Heino et al. 2014); and 4) *the neutral view* - which assumes species are functionally equivalent and distribute amongst patches at random (Leibold et al. 2004).

To investigate the potential local and regional drivers of pond community composition and diversity we quantified the macroinvertebrate diversity and community structure of ephemeral and perennial ponds located in largely unregulated floodplain meadows. We examined whether spatial proximity (neutral processes) or local environmental variables (niche processes) dominated macroinvertebrate community composition among the ephemeral and perennial ponds.

Methods

Study area and sites

Ponds are defined here as small lentic water bodies between 25 m^2 and 2 ha in area, frequently less than 2 m deep, which normally hold water for at least 4 months of the year (Williams et al. 2010). A comprehensive examination of 34 ponds was undertaken on two largely unregulated floodplain meadows adjacent to the River Soar, Leicestershire, UK: Cossington Meadow (25 ponds, ~86 ha, lat: 52.715621 long: -1.116947) and Loughborough Big Meadow (9 ponds, ~60 ha, lat: 52.789178 long: -1.116947). Both meadows are located in nature conservation areas and are naturally inundated by water from the River Soar during the winter and early spring each year. Fluvial gravel and sand were historically quarried from Cossington Meadow, but since 2004 it has been a protected 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. The majority of the larger ponds and lakes are of anthropogenic origin (relicts of quarrying) but since their creation, limited direct management has been undertaken and they are minimally affected by low density pastoral agriculture associated with traditional floodplain meadow systems. Loughborough Big Meadow is part of a Site of Special Scientific Interest and is one of the few remaining traditional floodplain Lammas meadows in the UK. Lammas refers to a particular type of land tenure. During the crop-raising period (February to August) the land owners divide the meadow into sections and sell the rights to the hay crop to local farmers. Once the hay crop has been gathered the land becomes subject to the rights of common grazing (mid-August - February). The study took place during 2012 and was characterised by drought conditions at the start followed by a period of sustained high rainfall (Marsh et al., 2013). In some regions of the UK this resulted in significant variability in water levels and wetting and drying of temporary ponds (Jeffries 2015). However, the lowland location of the ponds in this study meant that at the start of the sampling programme the majority of pond basins were wet and although water levels were highly variable, the total number of inundation events (floods) and duration that the basins were dry (hydroperiod) was comparable to average conditions.

Aquatic macroinvertebrate sampling

The ponds studied comprised two groups: (i) 20 perennial ponds - water bodies which contained water all year round and; (ii) 14 ephemeral ponds - ponds which became dry (dry phase varied from 3-6 months) at least once during the study period (Jan 2012 - Dec 2012). Floodwater recharge from the River Soar was the primary driver of hydroperiodicity for the ephemeral ponds studied. Aquatic macroinvertebrate samples were collected on three occasions from each pond corresponding to spring, summer and autumn seasons. The total number of samples taken was 87 (perennial n=60, ephemeral n=27). All temporary ponds dried at least once during the sampling period and were not sampled during the dry phase. In this study the sampling strategy of fixed timed macroinvertebrate collections was deemed not suitable to examine diversity within the small and ephemeral ponds where the wetted area varies seasonally (Armitage et al. 2012). The strategy was therefore modified to obtain representative samples from all sites whilst ensuring that the small freshwater habitats/communities were not adversely affected by the sampling (Armitage et al. 2012). The sampling time allocated to each pond was proportional to its surface area up to a maximum of 3 minutes (Biggs et al. 1998). The maximum sampling time of 3 minutes was used for ponds with a surface area >50 m^2; for smaller ponds 30 seconds of sampling for every 10 m^2 surface area was employed. A standard pond net (mesh size, 1 mm) was used to sample aquatic macroinvertebrate taxa. The total sampling time designated to each individual pond was divided equally between the mesohabitats present (open water, emergent macrophytes and submerged macrophytes). If one mesohabitat dominated the pond, sampling time was further divided to reflect this; for example, in a pond with 3 mesohabitats sampling time was divided by 4 – one from each mesohabitat with an additional sample from the dominant mesohabitat (Biggs et al. 1998). In addition, an inspection of hard surfaces or larger substrate (e.g., rocks and large floating leaves) for aquatic macroinvertebrates was undertaken for 1 minute at each site. In the laboratory, aquatic macroinvertebrate samples from each habitat were processed and preserved in 70% industrial methylated spirits prior to identification. Taxa were identified to species level except, Diptera larvae, Planariidae, and Hydrachnidiae which were identified to order or family level and Oligochaeta and Collembola were recorded as such. The macroinvertebrate taxa with UK conservation designations were identified using the extensive list provided by the JNCC (JNCC 2015).

Environmental data collection

The following local environmental parameters were measured at each site prior to macroinvertebrate sampling: surface area (wetted area: m^2), mean water depth (cm), the percentage of the pond margin and pond surface shaded by overhanging vegetation, the presence of fish (0/1 as a dummy variable); and dry phase length (duration in months between Jan-Dec 2012 that the pond was dry). Conductivity ($\mu S\ cm^{-1}$), pH (Hanna Instruments - HI198311 and HI98127) and dissolved oxygen (DO $mg\ l^{-1}$) (Mettler Toledo DO Meter SG6) were measured at the margin of each site using portable meters. The occurrence and proportion (% of surface area) of mesohabitats within each pond was recorded. Regional environmental variables; Pond connectivity - number of waterbodies hydrologically connected to a sample site (e.g., through rivulets or overland flooding) and pond proximity - the number of other fresh waterbodies within 500 m (Vanschoenwinkel et al. 2007; Waterkeyn et al.

2008), were recorded through visual inspection (walking extensively around each site during each season to identify nearby perennial and ephemeral ponds and through the use of aerial imagery provided by Google Earth Software (Goole Earth 2015). Every attempt was made to record all waterbodies within 500 m of each meadow pond site, however, small temporary ponds can be difficult to identify through visual inspection and aerial images and it is therefore acknowledged that a small number of temporary ponds may have been overlooked.

Statistical analyses

Aquatic macroinvertebrate diversity was examined across the floodplain meadow landscape (gamma diversity) and for individual ephemeral and perennial ponds (alpha diversity). Macroinvertebrate abundance and taxon richness were calculated for each mesohabitat and pond site (mesohabitat and seasonal data for each pond site were combined to provide a total measure of diversity for each study site) using PRIMER 6 (Clarke and Gorley 2006). Ecological diversity is heavily affected by the sample size and sampling procedures (McCabe & Gotelli 2000). As a result, rarefaction (Hulbert 1971) was undertaken in PRIMER 6 to estimate species richness for each mesohabitat and pond site for a given number of individuals drawn randomly from a sample (McCabe & Gotelli 2000). The least abundant sample had 28 individuals; as a result, 28 individuals were randomly sampled from each mesohabitat and pond site and the rarefied species richness was recorded.

The statistical significance of differences in faunal diversity among the ephemeral and perennial pond types and mesohabitats (open water, emergent and submerged macrophytes) were examined using a nested analysis of variance (nested ANOVA) with Bonferonni *post hoc* tests. Pond type and mesohabitat were included as fixed effects and site was nested within pond type as a random effect. Differences in the dispersal characteristics and functional feeding groups of macroinvertebrate communities between ephemeral and perennial ponds were examined using a non-parametric ANOVA (Kruskal-Wallis test). Dispersal and functional feeding traits assigned to individual macroinvertebrate taxa follow the classification of Tachet et al. (2003) and Merritt and Cummins (1996). Variability in physical and chemical parameters between pond sites were examined using oneway analysis of variance (ANOVA). The data were examined to ensure they complied with the underlying assumptions of parametric statistical tests (e.g., normal distributions) and abundance data were $\log_{10}$ transformed where required. All univariate analyses were undertaken in IBM SPSS Statistics (version 21, IBM Corporation, New York). The Waikato Environment for Knowledge Analysis (WEKA) machine learning software (version 3.6.1) was used to construct regression trees to predict taxa richness of the ponds from the collected environmental data (Witten et al. 2011). A regression tree was generated with the M5P option and 10% cross validation in WEKA (Quinlan 1993; Witten & Frank 2000).

The variability of macroinvertebrate communities was described using MVDISP in PRIMER 6 (Clarke & Gorley 2006) to compare the multivariate dispersion (compositional variability) of communities in ephemeral and perennial ponds. Community heterogeneity between ephemeral and perennial pond sites was statistically examined using Analysis of Similarity (ANOSIM) in PRIMER 6 (Clarke & Gorley 2006). Prior to ANOSIM analysis, faunal-abundance data were log (X+1) transformed. The PRIMER 6 program RELATE (a mantel-type test) was used to examine the relationship between the aquatic macroinvertebrate community dissimilarity and spatial distance (meters) and environmental distance (Euclidean). RELATE tests the significance of a Spearman's rank correlation between two distance matrices (Bray-Curtis community dissimilarity and geographic distance between study pond sites). To test the association between macroinvertebrate taxa and pond type and identify indicator taxa of ephemeral and perennial ponds Indicator Value analysis (IndVal) (Dufrêne & Legendre 1997) was undertaken in R (R Development Core Team 2013).

The associations between macroinvertebrate community composition and environmental variables (local and regional) were assessed using Redundancy Analysis (RDA) implemented in the programme CANOCO (Version 4.5; ter Braak & Šmilauer 2002). Due to natural variability in macroinvertebrate community assemblages, seasonal faunal data from individual pond sites were combined and mean values of environmental variables calculated. Prior to analysis, environmental parameters were $\log_{10}$ transformed (except for pH) to reduce the influence of skew in the data set and overcome the effect of their physical units (Legendre & Birks 2012). Faunal-abundance data were Hellinger transformed prior to analysis (Legendre & Gallagher 2001). A forward selection procedure, using a random Monte-Carlo permutations test (999 random permutations) with Bonferroni correction was employed to determine the significance of the relationship between the environmental variables and macroinvertebrate composition. Only physical and chemical parameters significantly influencing the faunal data ($p<0.05$ before Bonferroni correction) were included in the final model.

Variance partitioning analysis was used undertaken using CANOCO 4.5 to examine the amount of variation in macroinvertebrate community assemblage that can be explained by local (physical and chemical or biological) and regional (spatial) variables (Borcard et al. 1992). Only environmental parameters from the RDA identified to significantly influence macroinvertebrate community composition were used in the variance partitioning analysis. The total percentage of variance explained by the RDA was partitioned into unique contribution (percentage of variance explained by each individual group of environmental variables), and common contributions (variation explained by a combination of groups of environmental variables) using partial RDAs (Borcard et al. 1992; Vanschoenwinkel et al. 2007).

Results

Environmental characteristics

Environmental conditions recorded among ephemeral and perennial ponds from the two meadow sites were highly variable (Table 1). Perennial ponds were on average twice as deep (ANOVA $F_{1, 33} = 37.65$, $p<0.001$), had higher pH (ANOVA $F_{1, 33} = 11.12$, $p<0.002$) and conductivity (ANOVA $F_{1, 33} = 18.28$, $p<0.001$) than ephemeral ponds. The proportion (%) of the pond covered by emergent macrophytes was nearly four times greater for ephemeral ponds compared to perennial ponds (ANOVA $F_{1, 33} = 5.52$, $p<0.025$) (Table 1). Surface area, surface water shaded, pond margin shaded, submerged macrophyte cover and dissolved oxygen did not differ significantly between ephemeral and perennial ponds ($p>0.05$). Fish were present in 19 perennial ponds but were absent from all ephemeral ponds.

Macroinvertebrate diversity

Across the two floodplain meadows, a total of 173 taxa were recorded within 16 orders and 56 families from the ephemeral (93 taxa) and perennial ponds (164 taxa; see Supplementary Material Appendix 1 and Appendix 2 for full list of taxa). Macroinvertebrate taxon richness varied widely among pond sites ranging from 5 (ephemeral pond) to 73 (perennial pond) taxa. Macroinvertebrate assemblages within ephemeral and perennial ponds were dominated taxonomically by Coleoptera (Fig. 1). On average, hemipteran taxa constituted a much higher proportion of the species richness recorded in perennial ponds (>21%) than ephemeral ponds (<10%). In contrast, Diptera and Crustacea taxa formed, on average, a greater proportion of the taxa richness in ephemeral than perennial ponds (Fig. 1). The taxa most widely distributed across the meadow pond sites were Chironomidae larvae (32 ponds), Oligochaeta (30 ponds) and *Crangonyx pseudogracilis* (28 ponds). A total of 9 macroinvertebrate taxa were only recorded in the ephemeral ponds (*Galba trunculata, Libellula quadrimaculata, Limnephilus auricula, Limnephilus centralis, Limnephilus griseus, Gerris gibbifer,* Elmidae larvae, *Helophorous dorsalis* and *Paracymus scutellaris*).

Perennial ponds supported nearly three times the mean taxon richness (ANOVA $F_{1, 105} = 21.75$; $p<0.001$) and twice the rarefied taxon richness (ANOVA $F_{1, 81} = 11.20$; $p<0.001$) compared to ephemeral ponds (Table 2). Mean macroinvertebrate abundance (ANOVA $F_{1, 129} = 5.49$; $p<0.05$) in ephemeral ponds was 20% of that in perennial ponds (Table 2). A significant difference in the number of taxa (ANOVA $F_{2, 109} = 9.77$; $p<0.001$), rarefied taxa richness (ANOVA $F_{2, 109} = 3.08$; $p<0.05$) and marginally significant difference in abundance (ANOVA $F_{2, 109} = 3.07$; $p<0.051$) was observed among the meadow ponds when individual mesohabitat units were considered. Macroinvertebrate abundance was typically greater amongst emergent macrophytes (Fig. 2a). Macroinvertebrate richness and rarefied richness were higher within submerged macrophytes and emergent macrophytes than open water for all ponds (Fig. 2b; 2c). The regression tree analysis yielded a single regression equation: *Taxa number = 6.312 * Log area + 7.6575 * pH - 43.2272 *Log Hydroperiod dry months + 7.1705 * Log emergent macrophytes - 29.4961.* The cross validated correlation coefficient of 0.86, indicating that the regression equation was a good predictor of taxa number.

When functional feeding groups were examined, a greater proportion of the macroinvertebrate community were scrapers and deposit feeders in ephemeral ponds, whilst piercers constituted a greater proportion of the communities recorded in perennial ponds (Fig. 3a). There were a greater proportion of non-predatory taxa recorded in ephemeral ponds (mean: 73%) than perennial ponds (mean: 58% Kruskal-Wallis $p<0.05$). The proportion of passively and actively dispersing taxa did not differ statistically between the two pond types ($p>0.05$) (Fig. 3b).

Macroinvertebrate community composition was significantly different for ephemeral and perennial ponds (ANOSIM $R=0.581$, $p<0.005$). Ephemeral meadow ponds had a higher multivariate dispersion (1.56) than perennial ponds (0.73) indicating that ephemeral ponds displayed greater community heterogeneity than those of perennial ponds (Table 2; Fig. 4). Macroinvertebrate taxa identified as indicator species for ephemeral and perennial meadow ponds are presented in Table 3.

Macroinvertebrate - environment associations

RDA indicated that five environmental variables (connectivity, pond proximity, pond surface area, submerged macrophyte coverage and the dry phase duration) had a significant influence on community composition (Fig. 4; Monte Carlo Tests $F=3.33$ $p<0.005$) with all axes explaining 45.8% of the assemblage variance. A clear distinction between ephemeral (towards the bottom right) and perennial ponds (far left and top) was apparent in the RDA biplot (Fig. 4). A cluster of 12 perennial ponds directly connected to each other and the River Soar plotted on the far left of axis 1 (Fig. 4a). These ponds were inundated twice by floodwater from the River Soar during the sampling period. The other perennial meadow ponds typically had larger surface areas (Fig. 4a). The seasonal drying of the pond basin ($F=3.77$ $p<0.01$) was identified to be a key parameter structuring macroinvertebrate composition among ephemeral meadow ponds (Fig. 4a). In addition, ephemeral ponds were associated with reduced pond proximity. The highest taxon richness was typically associated with greater surface area ($F=2.3$ $p<0.01$), pond connectivity and pond proximity to other waterbodies ($F=4.12$ $p<0.01$) whilst the lowest richness was associated with longer dry phases (Fig. 4b).

Local and regional environmental factors

Variance partitioning indicated a greater influence of local physical and chemical variables on community composition (10.8% of total variance) compared to spatial (4.5%) or biological variables (4.1%; Fig. 5) among the meadow ponds studied. A combination of physical, chemical and spatial variables provided the greatest explanation of community composition (11.8%) among the meadow ponds. Community composition was more different between ponds that were further apart (*rho:* 0.507 $p<0.001$) or that differed in local habitat conditions (*rho:* 0.586 $p<0.001$).

Discussion

Macroinvertebrate diversity

Perennial meadow ponds supported nearly twice the number of macroinvertebrate taxa compared to ephemeral ponds, based on rarefied taxa richness. Several other studies have reported perennial ponds support significantly greater richness than ephemeral ponds in both Temperate and Mediterranean landscapes (Collinson et al. 1995; Nicolet 2001; Della Bella et al. 2005). However, in contrast to the meadow ponds in this study, previous studies have reported more actively dispersing taxa in ephemeral than perennial ponds (Nicolet 2001; Nicolet et al. 2004). The greater proportion of less-mobile taxa in these UK ephemeral ponds may reflect the frequent floodplain inundation, and mixing of water across the floodplain (high connectivity), which would facilitate the migration of passively dispersing taxa from perennial to ephemeral pond habitats (Nicolet et al. 2004). The greater proportion of non-predatory macroinvertebrate fauna recorded from ephemeral ponds most likely reflects the short hydroperiod (typically 6 months). This probably reduced the colonisation potential and occurrence of some larger, longer-lived predators (e.g., Coleoptera, Odonata, fish) which typically have generation times greater than the hydroperiod of the ephemeral ponds (Bilton et al. 2001; De Meester et al. 2005; Williams 2006). However, other studies have demonstrated that highly mobile aquatic predators will commonly colonize temporary ponds in spring and disperse to perennial ponds during the summer, with some Coleoptera remaining in damp patches within temporary pond basins after open water has receded and may only disperse more widely when the basin has dried completely (Davy-Bowker et al. 2002).

When placed in a national context, the average richness of ephemeral meadow ponds in this study (19 taxa) was lower than that recorded in a UK wide study of temporary ponds (25 taxa: Nicolet et al. 2004) and elsewhere in the UK (Bilton et al. 2009; Armitage et al. 2012). However, direct comparison is not straightforward as taxonomic resolution, habitat quality and sampling strategies differ between the studies. Macroinvertebrate diversity of ponds in this study is almost certainly significantly higher since Diptera were only resolved to family level. In addition, semi-aquatic and terrestrial riparian fauna (Carabidae and Staphylinidae) that frequently utilise pond basins during the dry phase (Lott 2001) were not recorded here or in other studies of ephemeral ponds (Della Bella et al. 2005; Dell et al. 2014) and clearly represents an underestimation of their contribution to biodiversity (Collinson et al. 1995; Drake, 2001).

Several gastropod taxa (*L. palustris, R. balthica* and Physidae) and the juvenile life stages of Dytiscidae (Coleoptera) and Corixidae were identified as indicator taxa of perennial ponds in this study. The Gastropoda, *L. palustris, R. balthica* and Physidae, were widely distributed in perennial ponds, but occurred infrequently in ephemeral ponds as they cannot withstand prolonged desiccation (Nicolet 2001; Della Bella et al. 2005). In contrast, the gastropod *A. leucostoma* was common in ephemeral ponds and can survive desiccation by burrowing into sediments and entering a state of diapause (Bratton 1990). Similarly, the larvae of Dytiscidae and Corixidae were largely confined to perennial ponds since they are unlikely to survive the dry phase within ephemeral pond basins. Although not exclusive to the ephemeral ponds, *Hesperocorixa sahlberghi* was also identified as an indicator of ephemeral ponds. *H. sahlberghi* frequently colonises densely vegetated habitats (emergent macrophyte coverage was greater in ephemeral ponds) and may have also benefited from the absence of predatory fish (Savage 1989).

Macroinvertebrate community composition

Community composition was strongly associated with habitat characteristics (45.8% of variance was explained); although the strength was lower than for other studies of small pond or rock-pool communities (e.g., Vanschoenwinkel et al. 2007), reflecting the effect of local (e.g. physical and chemical factors) and regional (i.e. connectivity / proximity) parameters in the analysis (Florencio et al. 2014). The community composition recorded in this study was more strongly linked with the physical and chemical characteristics of the pond rather than biological or regional drivers. Local environmental variables also explained more of the variance in macroinvertebrate community composition for ephemeral ponds than how the ponds were distributed in space in South Africa (Vanschoenwinkel et al. 2007) and Donana National Park, Spain (Florencio et al. 2014). Connectivity between ponds can have a homogenizing effect on community structure, increasing diversity as taxa are able to disperse more freely (Cottenie et al. 2003), although other studies have shown this effect to be stronger for passively dispersing taxa than for active dispersers (Vanschoenwinkel et al. 2007). In the current study, more distant ponds did have more dissimilar communities, but spatial factors were of secondary importance to the local habitat (Cottenie et al. 2003; Cottenie & De Meester 2003).

If these ponds were placed into the metacommunity framework, the heterogeneity of the habitats and macroinvertebrate communities violate the key assumptions for patch dynamics to apply (assumes that habitat patches are identical; Vanschoenwinkel et al. 2007). A combination of mass effects (connectivity and pond proximity) and species sorting (physical, chemical and biological; Leibold et al. 2004) would probably most effectively explain the 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 the metacommunity but it is the variation in local physical and chemical factors (species sorting) that regulates and controls community composition (Cottenie et al. 2003; Cottenie & De Meester 2003).

The greater importance of local variables over regional variables may explain the high community heterogeneity recorded between ephemeral and perennial ponds (Collinson et al. 1995; Della Bella et al. 2005). While high connectivity (floodwater inundation) promotes the dispersal of invertebrates between ephemeral and perennial ponds, it is the local pond conditions (e.g., hydroperiod, wetted area, depth, emergent macrophyte coverage) which sorts and structures the communities. However, the results of this study also indicates many taxa from ephemeral ponds also occur in perennial ponds (Bazzanti et al. 2003; Nicolet et al. 2004; Bilton et al. 2009). Many taxa common to both pond types were generalists, including several Diptera families (Culicidae and Tipulidae spp.) which have the prerequisite traits for successful colonisation and development in ephemeral waterbodies including; rapid development, rapid recolonization via aerial dispersal and the ability of some larvae to persist in damp sediments (Drake 2001).The high density and hydrological connectivity (regular inundation) of ephemeral and perennial ponds on the floodplains would have increased the opportunity for passive dispersal events and allowed many perennial pond taxa to colonise the ephemeral ponds on the floodplain (Nicolet et al. 2004).

High connectivity between the river and floodplain can lead to short-term reductions in species richness in systems where large floods disturb the wetland habitats and reset successional trajectories (Bornette et al. 1998; Reckendorfer et al. 2006; Tockner et al. 2010). The floodplain meadows in the current study were not subject to any high magnitude floods during the study period and the high species richness and community heterogeneity among ponds reflects the range of successional stages present, and the gradual re-filling and re-wetting of the lentic (and potentially hyporheic) habitats which facilitate the dispersal of macroinvertebrates and resources (Lake et al. 2006; Starr et al. 2014; Paillex et al. 2015). The absence of erosive floodwaters was also important in structuring the macrophytes within both the perennial and ephemeral ponds. Aquatic macrophytes were found to be important determinants of assemblage and diversity in this and in other studies (Bazzanti et al. 2010; Florencio et al. 2014). This reflects the importance of macrophytes as structurally diverse and complex habitats with abundant niches for aquatic invertebrates, their capacity to serve as refugia from predation, provide sites for oviposition and provide an abundance of trophic resources (Bazzanti et al. 2010).

Conservation of floodplain meadow ponds

Perennial and ephemeral floodplain meadow ponds provide a valuable and important habitat for aquatic macroinvertebrates, supporting a wide diversity of fauna at an alpha and gamma scale and a number of taxa of conservation interest (Armitage et al. 2012). Despite this, there is limited formal or direct legislative protection (e.g., from the Water Framework Directive or the Habitats Directive, Hassall et al. 2016) of ephemeral ponds in temperate regions at a European scale (Williams et al. 2001; Nicolet et al. 2004). However, it is important to recognise that at a national scale in the UK, ephemeral and perennial ponds may be protected via designation as a priority habitat (BRIG 2008). In addition, the meadow ponds in this study were located in established nature reserves which indirectly provided protection for the ponds and help maintained a high density of ephemeral and perennial pond habitats (and high macroinvertebrate diversity).

Natural inundation of the floodplain and riparian meadows would have historically been typical of many temperate zone lowland systems prior to land drainage, agricultural improvement and river regulation. Reconnecting the river with its floodplain will provide significant opportunities to re-naturalize floodplains (Reckendorfer et al. 2006; Castella et al. 2015), however many temperate rivers have poor water quality and polluted floodwater may significantly reduce taxonomic diversity of freshwater bodies on the floodplain (Tockner & Stanford 2002). Strategies to improve river water quality should be implemented alongside river-floodplain reconnection to take advantage of the bioremediation (nutrient storage and processing) potential of floodplain water bodies. However, care is also required to ensure that floodplain wetland and pond restoration is not compromised or prevented due to pre-existing poor river water quality. The reconnection of the channel to the floodplain is will also provide additional refuge habitat for many floral and faunal taxa, potentially increasing ecosystem resilience and the long-term sustainable management of floodplain waterbodies.

Results of this study indicate that pond biodiversity conservation on floodplains should primarily focus on improving local habitat quality and diversity. For example, management practices should aim to maintain a diverse array of ephemeral and perennial ponds on floodplains (encompassing the full hydrosere successional sequence) with varying hydroperiod lengths and environmental conditions (Biggs et al. 1994; Williams et al. 2003; Bilton et al. 2009) in order to provide a wide range of niches for invertebrate taxa to utilise. However, wherever possible pond connectivity should be increased on floodplains to provide greater opportunities for macroinvertebrate dispersal and colonisation (Williams et al. 2008). The creation of new ephemeral and perennial pond basins on the floodplain will increase connectivity and dispersal potential between the river and existing floodplain waterbodies (including ponds) and will also provide new high quality sites for macroinvertebrate taxa to utilise. Further, where appropriate the excavation of small rivulets (channels) may increase connectivity between individual ponds and enhance dispersal potential. Quantifying aquatic macroinvertebrate diversity and distribution on unregulated (semi)natural floodplain meadows (across all waterbody types) potentially provides important information regarding the reference conditions for these increasingly rare systems. This is an essential pre-requisite for the ongoing conservation of existing sites and the future restoration and, where both socially acceptable and possible, the re-connection of rivers to their floodplains.

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Tables

Table 1 - Summary table of measured environmental variables for ephemeral and perennial ponds across the floodplain meadow sites; SWS: pond surface area shaded, PMS: pond margin shaded, EM: emergent macrophytes, SM: submerged macrophytes, COND: conductivity, DO: dissolved oxygen.

	Perennial (n = 20)				**Ephemeral (n = 14)**			
	Mean	Std.Error	Min	Max	Mean	Std.Error	Min	Max
Area (m^2)	828	589	13	11923	230	90	10	1258
Depth (cm)	65	5	27	>100	26	7	8	>100
SWS (%)	9	6	0	93	2.9	2	0	30
PMS (%)	10	5	0	97	7.3	6	0	85
EM (%)	11	3	1	45	37	8	0	87
SM (%)	25	4	4	73	36	9	0	100
pH	8.3	0.1	7.2	9.1	7.5	0.2	6.4	8.7
COND ($\mu S\ cm^{-1}$)	773	59	422	1494	418	55	80	987
DO (%)	89	4	28	112	78	6	55	120

Table 2 - Summary table (±SE) of macroinvertebrate diversity within the ephemeral and perennial floodplain meadow pond sites. * indicates statistically significant difference ($p<0.05$) between ephemeral and perennial ponds.

	Perennial meadow ponds	**Ephemeral meadow ponds**	**All ponds**
Total taxon	164	93	173
Mean taxa *	53 (±2.71)	19 (±3.21)	39 (±3.60)
Rarefied taxa richness*	23	14	19
Mean abundance *	3155 (±292.64)	671 (±200)	2132 (±284)
Multivariate dispersion (MVDISP)	0.73	1.564	n/a
Total number of ponds supporting at least one taxa with a conservation designation	8	5	13
Taxa with a conservation designation	*Berosus luridus, Ilybius subaeneus, Agabus conspersus, Hygrotus nigrolineatus, Rhantus frontalis*	*Helophorus dorsalis, Paracymus scutellaris, Hygrotus nigrolineatus, Rhantus frontalis*	

Table 3 - Top 6 aquatic macroinvertebrate taxa identified as indicator species for ephemeral or perennial ponds. * = p<0.05, ** = P<0.01.

Ephemeral ponds	Stat	**Perennial ponds**	Stat
Collembola**	0.93	Dytiscidae larvae**	0.97
*Hesperocorixa sahlberghi**	0.66	*Crangonyx pseudogracilis***	0.95
		*Stagnicola palustris***	0.95
		Corixidae nymph**	0.92
		Physidae**	0.90
		*Radix Balthica***	0.89

Figure Captions

Figure 1 Mean percentage of taxonomic orders recorded within the perennial and ephemeral floodplain meadow ponds in this study for selected macroinvertebrate groups.

Figure 2 Macroinvertebrate abundance (a), taxonomic richness (b) and rarefied taxonomic richness (based on 30 individuals drawn randomly from a sample) recorded within different mesohabitat units within perennial and ephemeral 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, ***** = outlier defined on the basis of being >3 times the interquartile range from the rest of the scores.

Figure 3 Proportion (mean %) of functional feeding group (a) and dispersal type (b) among ephemeral and perennial pond communities.

Figure 4 RDA ordination of site plots for perennial and ephemeral floodplain meadow pond Hellinger transformed macroinvertebrate assemblages: (a) site plot with significant environmental parameters shown and (b) taxon richness bubble plot. Empty circles = perennial ponds, filled circles = ephemeral ponds. Note **-** the size of each bubble is proportional to the absolute taxonomic richness.

Figure 5 The unique and combined influence of physical and chemical, biological and spatial variables on macroinvertebrate composition. Values represent the proportion of the total variation (1.00). Percentage contribution of the total variance is presented in parenthesis.

Figure 1

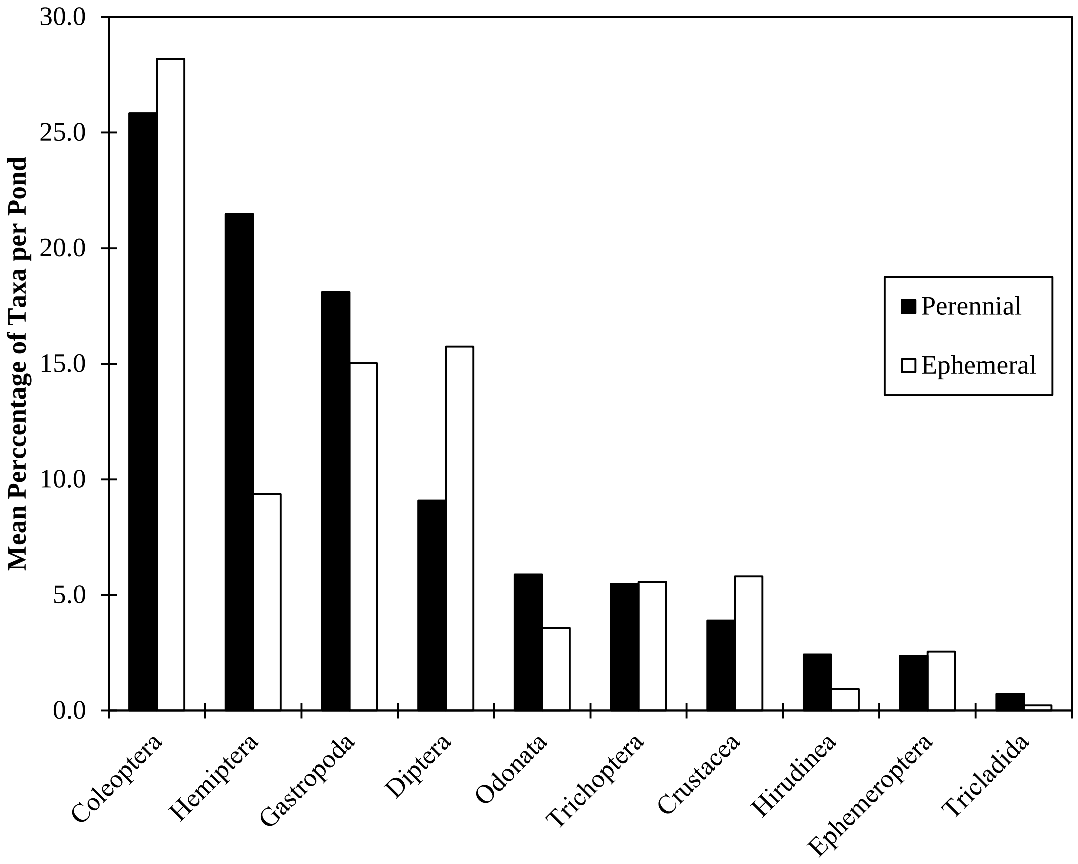
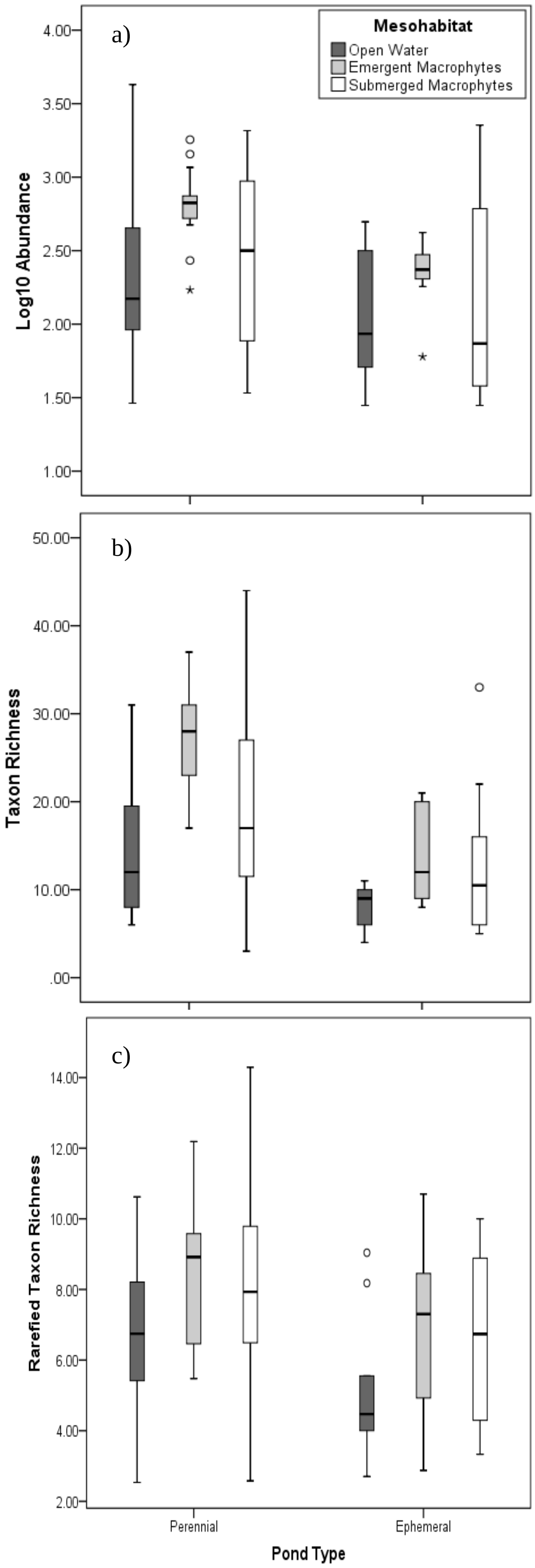

Mean Perccentage of Taxa per Pond
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Perennial
Ephemeral
Coleoptera
Hemiptera
Gastropoda
Diptera
Odonata
Trichoptera
Crustacea
Hirudinea
Ephemeroptera
Tricladida

Figure 2



a)
Mesohabitat
Open Water
Emergent Macrophytes
Submerged Macrophytes
Log10 Abundance
4.00
3.50
3.00
2.50
2.00
1.50
1.00
b)
Taxon Richness
50.00
40.00
30.00
20.00
10.00
.00
c)
Rarefied Taxon Richness
14.00
12.00
10.00
8.00
6.00
4.00
2.00
Perennial
Ephemeral
Pond Type

Figure 3

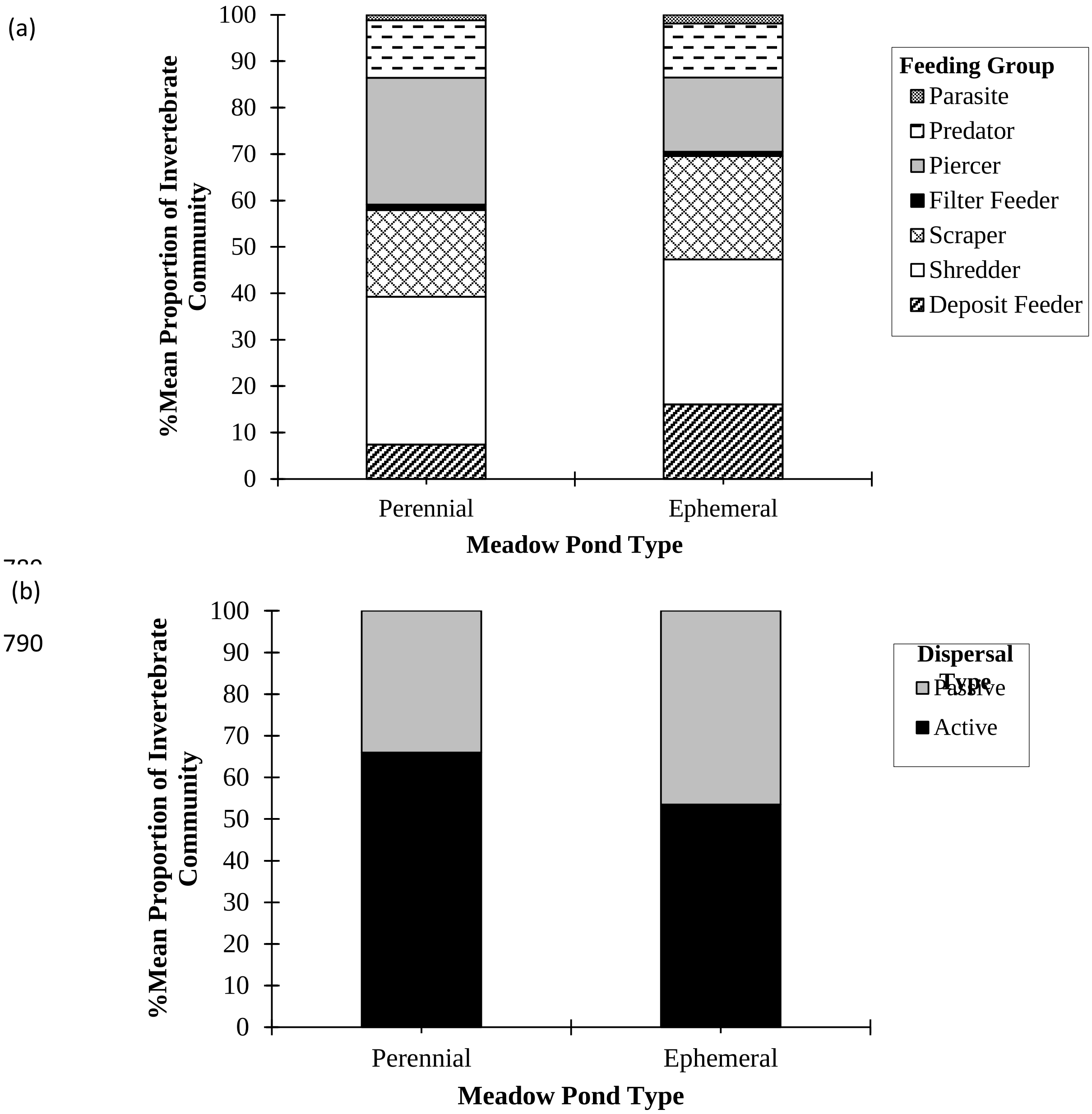
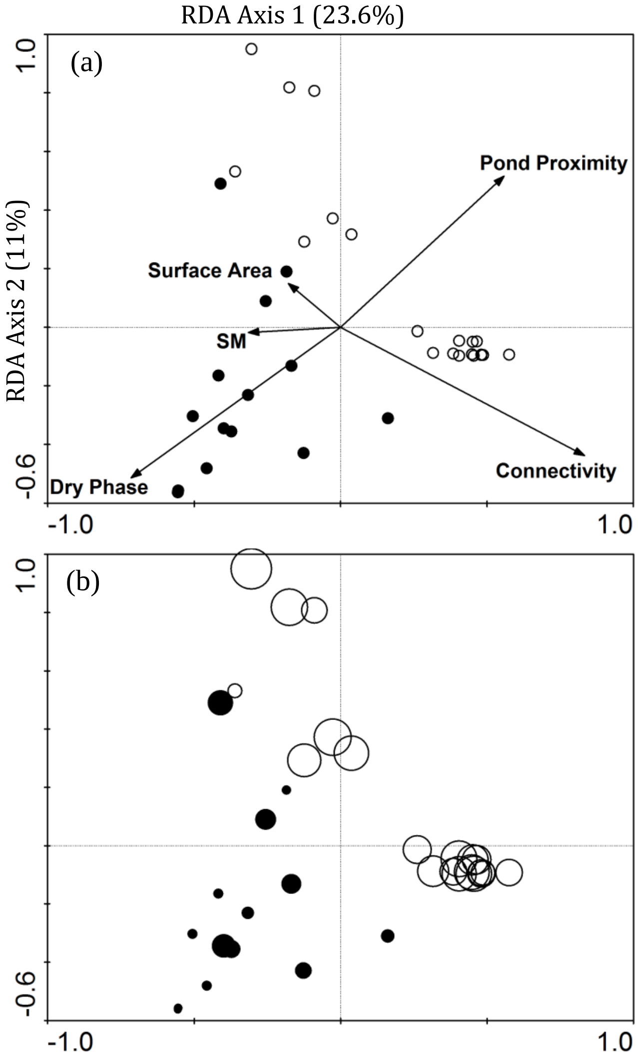
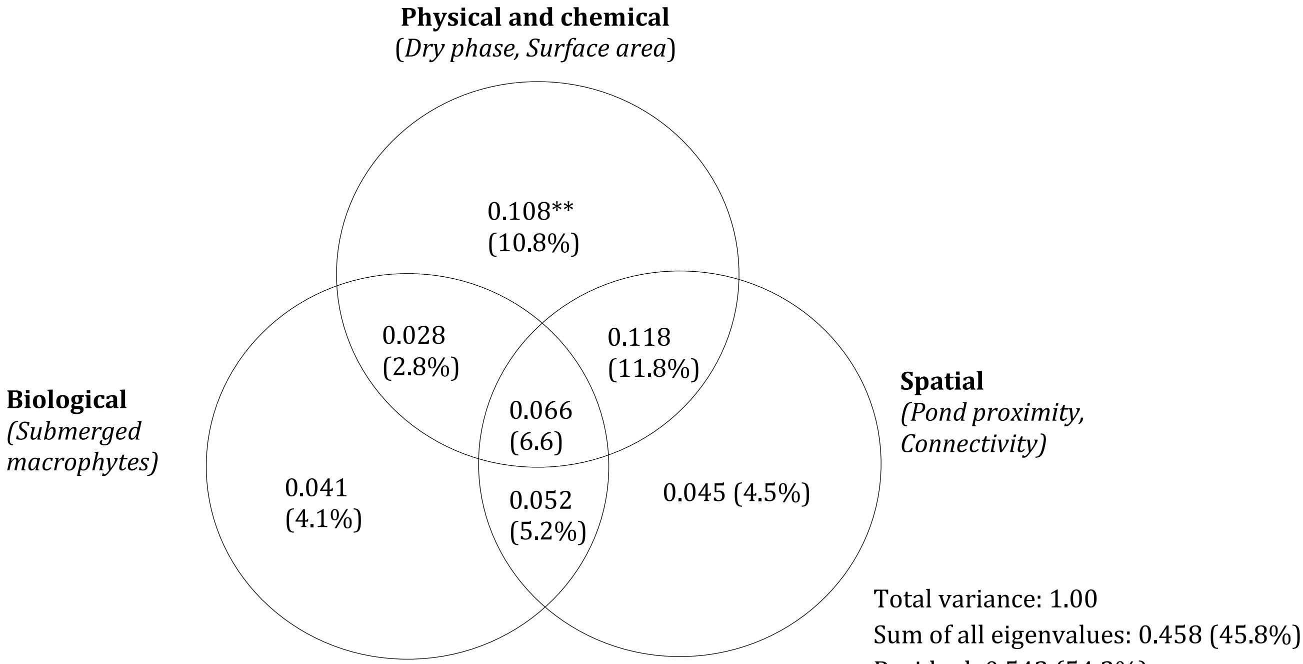

(a)
%Mean Proportion of Invertebrate Community
100
90
80
70
60
50
40
30
20
10
0
Perennial
Ephemeral
Meadow Pond Type
Feeding Group
Parasite
Predator
Piercer
Filter Feeder
Scraper
Shredder
Deposit Feeder
(b)
%Mean Proportion of Invertebrate Community
100
90
80
70
60
50
40
30
20
10
0
Perennial
Ephemeral
Meadow Pond Type
Dispersal Type
Passive
Active

Figure 4



RDA Axis 1 (23.6%)
RDA Axis 2 (11%)
(a)
Pond Proximity
Surface Area
SM
Dry Phase
Connectivity
1.0
-0.6
-1.0
1.0
(b)
1.0
-0.6
-1.0
1.0

Figure 5



Physical and chemical
(Dry phase, Surface area)
0.108**
(10.8%)
0.028
(2.8%)
0.118
(11.8%)
0.066
(6.6)
Biological
(Submerged macrophytes)
0.041
(4.1%)
0.052
(5.2%)
0.045 (4.5%)
Spatial
(Pond proximity, Connectivity)
Total variance: 1.00
Sum of all eigenvalues: 0.458 (45.8%)
Residual: 0.542 (54.2%)