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Running head: Correlates of pond species richness

Title: **Environmental correlates of plant and invertebrate species richness in ponds**

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ABSTRACT

Ponds (lentic water bodies <2ha) constitute a considerable biodiversity resource. Understanding the environmental factors that underlie this diversity is important in protecting and managing the habitat. We surveyed 425 ponds for biological and physical characteristics with 78 of those also surveyed for chemical characteristics. A total of 277 invertebrate species and 265 plant species were found. Species richness varied between 2 and 99 (mean 27.2 ± 0.6 SE) for invertebrates and 1 and 58 (mean 20.8 ± 0.4 SE) for plants. Generalised linear models were used to investigate variables that correlate with the species richness of plants and invertebrates, with additional models to investigate insect, Coleoptera, Odonata, Hemiptera, Trichoptera and Mollusca species richness. Models performed well for invertebrates in general (R^2=39.8%) but varied between lower-order invertebrate taxa (8.2-34.9%). Ponds with lower levels of shading and no history of drying contained higher numbers of species of plants and all invertebrate groups. Aquatic plant coverage positively correlated with species richness in all invertebrate groups apart from Trichoptera and the presence of fish was associated with high invertebrate species richness in all groups apart from Coleoptera. The addition of chemistry variables only increased the explanatory power of the model explaining plant species richness, for which phosphate was a highly significant factor. We demonstrate that the composition of biological communities varies along with their species richness and that less diverse ponds are more variable compared to more diverse ponds. Promoting a high landscape-level pond biodiversity will involve the management of a high diversity of pond types within that landscape.

KEYWORDS: species richness, invertebrates, plants, pond, shade, water permanence.

INTRODUCTION

The determinants of species richness at continental scales are still unclear. However, the *correlates* of species richness appear to centre around the twin concepts of water and energy (Field et al. 2009). At a local level, the problem becomes only slightly more tractable. Concepts such as niche overlap (Leibold and McPeek 2006), habitat heterogeneity (both temporal and spatial) (Tews et al. 2004) and area (Lomolino 2000) can be quantified and manipulated experimentally to investigate within and between habitat richness. One benefit of understanding the predictors of species richness is the potential for habitat management targeting those variables which enhance species richness of one or more taxa. Such informed management can ameliorate damage done either through passive damage and neglect or even through benign mismanagement based on unsound principles.

Ponds (defined as lentic water bodies under 2ha in area (De Meester et al. 2005)) represent a habitat that has traditionally been neglected in ecological studies (Céréghino et al. 2008). It is only recently that the value of ponds as a biodiversity resource (Williams et al. 2004), carbon sink (Downing et al. 2008), floodwater management tool and pollution filter (Fiener et al. 2005) has been recognised. Even when managed for mankind's use, ponds can still contribute to biodiversity, as has been shown for motorway stormwater retention ponds in France (Scher et al. 2004) and angling ponds in England (Wood et al. 2001). This combination of biodiversity and tangible ecosystem services make pond ecosystems excellent candidates for conservation. Previous studies have highlighted the biodiversity value of ponds in comparison to other aquatic habitats. Ponds in a lowland region of the UK were shown to contribute more species on a regional level than rivers, streams or ditches, although there was considerable variation in richness between individual ponds (Williams et al. 2004). The significant contribution made by ponds to the regional species pool – gamma diversity – has also been demonstrated across Europe (Davies et al. 2008). A number of studies have been published on pond species richness and its correlates, although no consensus has emerged on which variables best predict species richness. We briefly review a representative sample of these predictors below.

Physical correlates of pond species richness

The geographical location of ponds has been shown to influence communities and species richness, including the altitude of the pond (Hinden et al. 2005) and the location of the pond relative to other ponds (Briers and Biggs 2005). However, evidence for an effect of connectivity at smaller spatial scales is equivocal (Cottenie and De Meester 2003). In an analysis of climatic correlates of ponds varying in altitude, Rosset et al. (2010) found that environmental temperature explained a large proportion of the variance in species richness. Rosset et al. argue that there could be a 83% increase in species richness in lowland areas and a 150% increase in species richness in upland areas under projected climate warming. Studies involving pond area have yielded conflicting results, with some demonstrating strong influences on plants and invertebrates (Biggs et al. 2005) and others demonstrating weak (if any) effects on macroinvertebrate richness (Oertli et al. 2002; Søndergaard et al. 2005). This break from conventional species-area relationships may be due to second-order effects in the form of ecological interactions which vary between ponds of differing connectivity and dimensions (Scheffer et al. 2006). The relatively small size of ponds also renders them vulnerable to drying out, and drying has been shown to have an effect on alpha diversity of ponds (Biggs et al. 2005), with variations between the biological communities of temporary and permanent ponds (Collinson et al. 1995). Encroachment by terrestrial plants during succession leads to increased shading, which has been implicated in determining the abundance of aquatic macrophytes (Joye et al. 2006) and the structure of odonate communities (Suh and Samways 2005). Turbidity has been shown to influence zooplankton communities, which have a key ecological role (Cottenie and De Meester 2003).

Chemical correlations of pond species richness

pH has previously been shown to influence richness (Biggs et al. 2005; Hinden et al. 2005), with few species found <pH5.5 (Friday 1987). However, interactions between pH and other variables such as the presence of fish may produce the opposite pattern, where invertebrates are abundant in acidic lakes in which fish cannot persist (Bendell and McNicol 1987, 1995). Conductivity has been shown to correlate with macrophytes, odonates and beetles in alpine ponds, although this is not consistent with fundings from lowland areas (Hinden et al. 2005). The impacts of varying salinity on invertebrate communities have been demonstrated in the contexts of fresh-brackish-saline water communities (Williams 2003) and pollution caused by road salt (Williams et al. 2000). Oxygen demand and phosphate have been shown to influence invertebrate communities in rivers (Durance and Ormerod 2008) and lakes (Menetrey et al. 2005).

Biological correlates of pond species richness

Plant cover positively affects odonate communities (Carchini et al. 2005; Hinden et al. 2005), macrophyte richness (Hinden et al. 2005) and macroinvertebrate richness (Gee et al. 1997). The structural complexity of the plant community also plays a role in determining biomass of invertebrates, although not the species richness (McAbendroth et al. 2005). The presence of fish has strong effects on benthic invertebrate community structure (Gilliam et al. 1989), body size distributions (Blumenshine et al. 2000) and abundance (Bendell and McNicol 1995).

What is clear from these studies is that there is a large array of potential correlates of species richness (for a more comprehensive review of older studies, see Table 2 in Jeffries 1991). Few studies have combined biological, chemical and physical variables into an analysis of pond species richness over a large number of sites (cf. Biggs et al. 2005) and it may be this that has led to a lack of consensus concerning which variables correlate best with different aspects of species richness. We analyse the macrophyte and invertebrate species richness of 425 ponds in northern England in terms of physical and biological variables. We further analyse species richness of a subset of 78 ponds for biological, chemical and physical variables. These ponds are set in an agricultural landscape which is representative of much of lowland Europe.

METHODS

Pond survey methods

425 ponds in Cheshire, UK (Figure 1), were visited during the summer over a period of four years: between 25 May – 9 September 1995, 4 May – 25 August 1996, 27 April – 27 July 1997, and 1 July – 16 August 1998. Each pond was surveyed for physical and biological characteristics (Table 1) and one water chemistry sample was taken for each of a subset of 78 ponds from 1995 at the time of sampling. These water samples were sent to the National Rivers Association laboratory in Nottingham, UK, for analysis. Pond width and length were measured using measuring tape. Depth was ranked as either <0.5m, 0.5-1m, 1-1.5m, 1.5-2m or >2m. The proportion of the pond that was shaded ("% shade") was defined as the proportion of the water surface overhung by vegetation. The proportion of the pond covered by aquatic vegetation ("% plant cover") was estimated by eye. Landowners were asked whether the pond had ever been known to dry up to ascertain the permanence of water ("water permanence", 0=not known to dry up, 1=known to dry up). The presence of fish ("fish present") was evaluated both at the time of sampling using nets and by asking landowners. Turbidity of water ("turbidity") was defined as a binary variable, indicating whether the water appeared cloudy on the day of sampling. The drawdown of the pond ("drawdown") was defined as the vertical height between the normal winter mean water level and the height of the water at time of sampling. Summary statistics for these variables and chemical variables included in the analysis can be found in Table 2.

The presence or absence of invertebrate species was recorded using standardised sampling methods. Pond nets with 1mm mesh were used to collect invertebrates in the following microhabitats: (i) open water, (ii) over both sediment and bare substrate, and (iii) within the leaf litter. In addition, animals were collected through the scraping of rocks and logs that were either submerged or were found within the perimeter set by the maximum winter water level. Damp poolside areas were surveyed by creating a depression and netting the resulting puddles. The rationale behind the sampling was to continue surveying until no further species were found (Eyre et al. 1986). All plants present in the pond up to the winter high water level were recorded to species. Six species of amphibians were recorded during the surveys: *Triturus cristatus*, *T. vulgaris*, *T. helveticus*, *Bufo bufo*, *B. calamita* and *Rana temporaria*. Amphibian presence was confirmed at 297 of the 425 ponds. However, surveys were carried out across the amphibian breeding season and so it was not possible to verify whether a particular species was truly absent or simply not observed due to it not using the pond at the time of sampling. As such amphibian data are not included in this analysis.

Data analysis

Species richness of invertebrates, insects, Coleoptera, Hemiptera, Odonata, Trichoptera, Mollusca and plants were calculated from the aquatic sampling data. A Pearson correlation was used to assess the relationship between plant and invertebrate species richness. Cross-taxon congruence in species community similarity was investigated using non-parametric Mantel tests (Heino et al. 2009). Since water chemistry was only recorded for a subset of 78 ponds, two analyses were conducted. The first investigated plant and invertebrate richness in terms of the physical characteristics of the pond (n=425) and the second included both the physical characteristics and the chemical variables (n=78). Variables were assessed for normality and homoscedasticity using Shapiro-Wilk tests and by examining histograms, and transformations were applied where appropriate (Table 1). To reduce the number of variables, principal components analysis was used to summarise pond length, width and depth. The first component ("pond volume") explained 78.3% of the variance in these three measurements and is taken as a measure of pond volume. In the chemistry data, biochemical oxygen demand (BOD) and chemical oxygen demand (COD) were summarised using PCA into a principal component ("O_2 demand") which explained 90.1% of the variance in the two variables.

Patterns of species richness

Due to uncertainties over the shape of non-linear relationships in the data, generalised additive models were used to model patterns fo richness in terms of environmental predictors. In the first analysis (n=425 ponds), generalised additive mixed-effects models (GAMMs) were constructed using the nlme {Pinheiro, 2011 #1413} and mgcv {Wood, 2006 #1446} packages in R (R Development Core Team 2010). Pond volume (PC1 as described above), % plant cover, % shade, and ordinal date were included as smoothing functions, with water permanence and fish presence as parametric terms. The year of sampling was included as a random effect. The "gam" function in the mgcv library optimises smoothing during the fitting of the model, such that a prior estimation of polynomials is not required. Cubic regression spline smooth functions were used with shrinkage. This approach penalises poorly-fitting splines such that the smooth is reduced to zero when explanatory power is low, effectively removing that term from the model. The second analysis included only those ponds with chemistry data (n=78). All these ponds were all sampled in 1995 so there was no need for the inclusion of year as a random effect. Instead of GAMMs, generalised additive models (GAMs) were used for these analyses. For both analyses, models were used to explain species richness in each of the following groups: (i) invertebrates, (ii) insects, (iii) Coleoptera, (iv) Hemiptera, (v) Odonata, (vi) Trichoptera, (vii) Mollusca and (viii) plants.

Community variation

Conservation recommendations cannot be made solely on the basis of differences in species richness. For example, temporary ponds contain species which are largely restricted to intermittent hydroperiods and cannot persist in permanent ponds. These temporary waters also contain fewer species on average than permanent water bodies. Using only species richness as a measure of conservation value would involve removing temporary ponds and losing those species which are restricted to them. Therefore we analysed variations in community structure using models that were selected to describe species richness. Canonical correspondence analysis (CCA) was used in the vegan package in R to analyse each of the models and the significance of each term was calculated using the anova.cca function in vegan.

RESULTS

A total of 265 species of plants and 277 species of invertebrates were recorded during the surveys (see Appendix A and Appendix B, respectively, for species lists). Mean invertebrate species richness in each pond was 28.2 (± 0.6 SE) and mean plant species richness was 20.8 (± 0.4). There was a significant, though weak, correlation between plant and invertebrate species richness ($r=0.491$, $p<0.001$, $R^2=0.239$, Figure 2). When similarity matrices of the different groups were analysed, cross-taxon congruence was typically low between taxa that were independent of one another (Table 3).

Pond characteristics only (n=425)

Fitted relationships for parameters in this analysis can be seen in Appendix A and the related statistics are in Table 4. Pond volume has no relationship with species richness in any taxa and sampling date is related only to Trichoptera and plant richness (Table 4). The proportion of the pond that was shaded and a history of drying were both consistently significant across all taxa. In three taxa (Odonata, plants, Trichoptera), the relationship between shading and richness was approximately linear, corresponding to a progressive decline in species richness with increasing shading. However, in the remaining taxa (molluscs, Coleoptera, Hemiptera, insects generally and invertebrates generally) there was a non-linear response indicating that low levels of shading had no impact on richness but that higher levels of shading had strong negative effects on richness. Ponds that were known to have dried out contained significantly fewer species of all taxa. Plant cover was consistently positive and significant in all taxa apart from Trichoptera (although this approached significance, $p=0.089$). As with shading, relationships between plant cover and taxonomic richness. This was particularly evident with insect and invertebrate richness where increasing levels of plant cover had a positive effect where plant cover was sparse, but beyond a certain point (around 30% cover), there was no additional increase in species richness. Relationships between species richness and fish presence varied strongly between taxa, with significant positive relationships in the Odonata, Trichoptera and Mollusca but a significant negative relationship in the Coleoptera.

The explanatory power of models varied strongly between taxonomic groups between 10.3% (plants) and 31.4% (Hemiptera). The strongest term in the model explaining plant species richness was the percentage cover of aquatic plants. As this could be circular reasoning (more plants lead to more plants), we ran the same model excluding the plant coverage term. This reduced the adjusted-R^2 from 10.3% to 6.3%.

Pond characteristics and water chemistry (n=78)

Fitted relationships for parameters in this analysis can be seen in Appendix B and the related statistics are in Table 5. When chemistry data were included to analyse the subset of ponds the model fit (as measured by adjusted-R^2) was increased in models for all taxa apart from molluscs. However, the nature of the relationships between richness and predictors became extremely difficult to interpret with evidence of over-fitting of the splines to the data. This was particularly true for those taxa with relatively few species recorded (maximum species recorded in a single pond: Trichoptera=6, Mollusca=7, Hemiptera=7, Odonata=5, Coleoptera=32, insects=46, invertebrates=57, plants=43). For this reason, we limit our interpretation to the four richest groups: Coleoptera, insects, invertebrates and plants.

As with the first analysis, plant cover was positively related to richness in all four groups although this was not significant in the insects (p=0.093). Non-linearity in the relationship between invertebrate and insect richness and plant cover suggests that there is little variation in richness across intermediate levels of plant cover but a decline at low levels (<5%) and an increase in richness at higher levels (>30%). Also replicated in this analysis was the negative relationship between drying and species richness, although this was not a factor for the Coleoptera which was the only taxon negatively affected by fish presence. Pond volume was weakly (p=0.037) positively associated with plant richness. Higher species richness of plants, invertebrates and insects were associated with intermediate phosphate concentrations, while this was not a factor for Coleoptera. There is evidence for the opposite relationship with oxygen demand, where insect, invertebrate and plant richness is lowest at intermediate levels of oxgen demand.

Community variation

CCA demonstrated that there were a number of factors that influenced not only species richness but also community structure (Table 6). This means that speciose ponds tend to be associated with one extreme of a variable's range. This pattern can be seen for invertebrates (Figure 3A), where speciose ponds are clustered slightly above and to the left of the origin of the CCA plot, and plants (Figure 3B), where speciose ponds are clustered above and to the right of the origin. In both cases the less species rich ponds contain different and more-variable communities compared to the more species rich ponds.

DISCUSSION

General observations

We demonstrate that a reasonable proportion (26-30%) of the variance in the species richness of broad taxonomic groups such as invertebrates, insects and molluscs can be predicted with relatively few environmental variables. However, the predictive ability of models of species richness in lower-order taxonomic groups is more variable. While Hemiptera (31.4%) and Odonata (34.7%) were relatively well predicted, models explaining Coleoptera (12.7%) and Trichoptera (14.2%) species richness performed worse. Taxa responded uniformly with higher species richness in ponds that did not have a history of drying up and pond with lower amounts of shading. Pond volume never influenced species richness. Responses to turbidity and fish presence varied between groups. However, less species-rich ponds tend to contain different communities to more diverse ponds. The addition of water chemistry variables only seems to increase the predictive ability of models describing plant species richness, with phosphate concentration being a significant variable.

Physical correlates

Shading and drying exerted strong negative effects on the species richness of all taxa in the first analysis of only biological and physical pond characteristics. Shading has previously been suggested as having little effect on species richness (Biggs et al. 2005) but it is clearly a major factor affecting ponds in northern England and Switzerland (Joye et al. 2006). As mentioned earlier, permanent and temporary water bodies have different communities (Williams 1997), and while species richness is often lower in temporary water bodies these habitats may support more rare species (Collinson et al. 1995). Certainly fluctuating water levels and varying patterns of hydroperiodic fluctuation provide different habitats for species than permanent water bodies (Williams 1997) and occasional drying may benefit regional species richness when species vary in their ability to recolonise (Dorn 2008; Van De Meutter et al. 2006).

The only other study of this scale is described by Biggs et al. (2005), who list those environmental variables with which species richness was correlated. They find that only pond area and pH were significantly correlated with species richness in both macroinvertebrates and plants. Drying ("seasonality" in Biggs et al. 2005) negatively correlated with macroinvertebrate species richness and % cover vegetation positively correlated with plant species richness, as in our study. While vegetation abundance (% plant cover in this analysis) exhibited a significant relationship with species richness in our analysis, we can state categorically that there is no relationship between pond volume and species richness in our study system (in line with other studies Oertli et al. 2002; Søndergaard et al. 2005). Furthermore, Biggs et al. discount a range of variables as having an effect on species richness, including shade which was highly significant in this study. Thus, while there is agreement between the two studies that ponds constitute a considerable biodiversity resource, there is relatively little agreement on which environmental variables are influencing that species richness. However, it is worth noting that Biggs et al. do not include multiple regressions in their analysis, so it is not possible to draw direct parallels between their results and ours.

Chemical correlates

Water chemistry appeared not to significantly improve models with the exception that the addition of phosphate to the plant model leading to a 57% increase in explanatory power. Higher nutrient loading leads to a shift from vascular plants to an ecosystem dominated by algae (Genkai-Kato and Carpenter 2005), although this does not seem to have negatively influenced the faunal communities. Conductivity also featured in a number of models, although the effect was not so great. Conductivity has received attention in colder areas of the world where road salt has been implicated in increasing the lability of heavy metals in aquatic environments (Bauske and Goetz 1993). While chloride concentrations themselves have been shown to have little effect on macroinvertebrates (Benbow and Merritt 2004), amphibians are susceptible to levels of chloride produced by run-off from de-icing (Sanzo and Hecnar 2006).

Biological correlates

Fish have been shown to alter the composition of aquatic macroinvertebrate communities (Bendell and McNicol 1987), but it is clear that the effect is not uniform across invertebrate taxa. Our results agree with those of Hinden et al. (2005) who demonstrate positive relationships between fish presence and odonate species richness but negative relationships between fish presence and coleopteran species richness. We add to this pattern positive relationships with Hemiptera, Trichoptera and Mollusca. Schilling et al. (2009) have demonstrated that Coleoptera are less prevalent and occur at lower abundance in lakes containing fish than in lakes lacking fish (particularly Dystiscidae which were completely absent in fish-containing lakes). While they demonstrate similar patterns for Odonata and Hemiptera, Schilling et al. also find that (i) some Hemipteran groups are more prevalent and abundant in lakes containing fish and (ii) the percent occurrence of coenagrionid damselflies, one of the most common odonate groups in our sample, does not vary significantly between fish-containing and fishless lakes. Some coenagrionid damselflies are known to have adaptations which allow persistence with fish (McPeek 1990). Thus the variation between taxa in response to fish may stem from variation in susceptibility to fish predation, although Coleoptera have also been shown to avoid colonising sites containing fish (Resetarits 2001). Cloudy water is characteristic of algae-dominated systems with low macrophyte species richness, as we observed. The negative relationship between Coleoptera and Mollusca species richness and water turbidity may be an indirect effect of this relationship between turbidity and plant species richness. It is unclear as to why Hemiptera are more species rich in turbid ponds.

We have analysed a vast dataset of ponds over a relatively limited geographical scale, using consistent sampling methodology and measuring a wide array of biological, physical and chemical variables. With two exceptions (water permanence and shade), we have failed to find consistent predictors of species richness across aquatic taxa. Given such a result, possible explanations include that key predictor variables have been omitted from the analysis or that the relationship between predictors and response variables followed a non-linear pattern that was not characterised accurately by GLMs. However, an alternative explanation might involve the small island effect (SIE, Lomolino 2000; Lomolino and Weiser 2001) where species-area relationships break down at small island sizes. The SIE is thought to result from idiosyncratic processes that swamp the mechanisms that generate the species-area relationship in larger islands. Rather than only affecting the species-area relationship, such idiosyncratic processes may disrupt relationships between community structure, diversity and any number of environmental factors. In particular, the connectivity of the landscape and the resulting flow of propagules into a given pond can decouple environment-community relationships (Chase and Ryberg 2004; Cottenie et al. 2003). Plant communities inhabiting grassland habitat patches in agricultural landscapes such as those considered in this study are influenced by isolation (Bruun 2000). However, Bruun found no relationships between species' traits (e.g. dispersal mode, seed mass) and the extent to which they were affected by isolation. Note, however, that recent work has cast doubt on previous demonstrations and the very existence of the SIE (Dengler 2010; Tjørve and Tjørve in press). In phytoplankton communities of marine and freshwater habitats varying by >15 orders of magnitude in spatial extent, no evidence was seen for the SIE (Smith et al. 2005).

Should these idiosyncracies be present in the system, they render the conservation of ponds a complex task. We have demonstrated that community structure also varies along these environmental gradients. This community variation confounds conservation measures based on maximising alpha diversity, as diverse ponds may not contain some community elements that only occur in less diverse ponds. For example, rare species may be uncommon due to unusual habitat requirements which studies of broad taxonomic groups do not reveal. Temporary ponds and early succession ponds typically have lower species richness (Collinson et al. 1995), but a subset of species rely on these kinds of ponds and cannot persist without them (e.g. the endangered great crested newt, *Triturus cristatus*). Idiosyncratic relationships between individual variables and individual species have been demonstrated for pond crustaceans and beetles in UK ponds (Jeffries 2003). Counterintuitively, gamma diversity is thus maximised by conservation measures which reduce alpha diversity in a subset of individual ponds. In addition, the temporal dynamics of pond communities are rarely considered and even more rarely quantified (Jeffries 2005). This variability may mean that even if we could precisely define which variables correlated with species richness in ponds at the time of sampling, these relationships may not be stable in the longterm. Relationships may also be present between biological communities and the variability in a factor rather than absolute values of that factor, and this could occur over multiple timescales (Jackson et al. 2009). The small size of ponds makes them particularly susceptible to short-term fluctuations. For example, taxa inhabiting a pond may require tolerance to a range of chemical variables since water levels change and alter concentrations of chemicals in the water. Furthermore, viewing ponds as isolated habitats embedded within a terrestrial matrix may be misleading. The matrix between ponds is used extensively by amphibians (Semlitsch 1998) and the adults forms of semi-aquatic insects (Jackson and Resh 1989) and so the nature of this terrestrial habitat will also impact aquatic communities.

Ponds have been shown to provide a potential model system for a range of ecological and evolutionary investigations (De Meester et al. 2005) and where detailed knowledge about their history can be combined with small spatial scales they form a highly tractable model system. The role of ponds as a biodiversity resource is also now appreciated. However, while we now understand the extent of the biodiversity resource that we are protecting, there is still a long way to go before we are able to make the kind of evidence-based recommendations that are necessary for informed, practical conservation (Sutherland et al. 2004). We have demonstrated that the species richness of some broad aquatic groups (invertebrates, plants) can be predicted using environmental variables, although predictive power is reduced for narrower groups. However, we caution against the uncritical use of such relationships as justification for conservation measures, since promoting alpha diversity in individual ponds may not necessarily promote landscape level biodiversity.

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TABLES

Table 1 – Variables used in model selection procedures with definitions and transformations where deviations from normality were detected.

Variable	Definition
Year	Year of sampling (1995-98)
Date	Days since 1 January ("ordinal date")
Pond volume	First principal component of width, length and depth measures
% shade*	% area of pond shaded
% plant cover+	% area of pond covered by plants
Water permanence	Whether the pond is known to have dried up
Fish presence	Whether fish are present
pH	pH
Conductivity	Conductivity (µS/cm)
O_2 demand#	First principal component of biochemical oxygen demand and chemical oxygen demand
Chloride#	Chloride concentration (mg/l)
Orthophosphate#	Orthophosphate concentration (mg/l)

*=$^2\surd$ transform, +=$^3\surd$ transform, #=log-transform

Table 2 – Summary statistics for pond variables

Variable	Mean	S.E.	Median	Min	Max	N
Ordinal date	179	1.19	176.00	117	237	425
Width (m)	23.4	0.76	20	2	110	425
Length (m)	28.2	1.13	22	1.5	231	425
% total aquatic plant cover	12.9	1.08	1	0	95	425
% shading	22.9	1.37	10	0	100	425
Drawdown (cm)	7.16	0.62	5	0	150	425
Depth	<0.5m: n=109; 0.5-1m: n=99; 1-1.5m: n=76; 1.5-2m: n=122; >2m: n=17					425
Water permanence	96 (22.6%) ponds were known to dry up					425
Fish presence	149 (35.1%) ponds contain fish					425
Turbidity	115 (27.1%) ponds had cloudy water					425
pH	7.59	0.08	7.50	5.90	10.5	78
Conductivity (µS/cm)	537	29.9	470	111	1490	78
BOD (mg/l)	14.81	3.03	6.25	1.40	168	78
COD (mg/l)	261	111	97.0	25.0	8710	78
Cl (mg/l)	36.5	3.12	29.0	10.0	157	78
Orthophosphate (mg/l)	1.05	0.17	0.345	0.05	5.87	78

Table 3 – Results of Mantel tests on community similarity matrices to test cross-taxon congruence. Values are Spearman's rank correlations and are all significant at $p<0.01$. Values in *italics* indicate correlations between non-independent matrices.

	Invertebrates	Insects	Coleoptera	Hemiptera	Odonata	Mollusca
Invertebrates						
Insects	*0.918*					
Coleoptera	*0.759*	*0.847*				
Hemiptera	*0.467*	*0.497*	0.191			
Odonata	*0.370*	*0.367*	0.100	0.081		
Mollusca	*0.396*	0.135	0.070	0.089	0.132	
Plants	0.215	0.173	0.118	0.102	0.097	0.145

Table 4 – Results of generalised additive mixed models (GAMMs) describing the species richness of invertebrates and plants in 425 ponds in terms of biological and physical variables. All values are F-statistics apart from for parametric variables (drying and fish presence) which are t-statistics. Missing parameters indicate that that term was dropped from the models by shrinkage (see text for details). Fitted parameters can be seen in Appendix 1. **Bold** terms are significant at: ***=p<0.001, **=p<0.01, *=p<0.05.

	Invertebrates	Insects	Coleoptera	Hemiptera	Odonata	Trichoptera	Mollusca	Plants
Ordinal date	0.000	0.398	1.369	2.009	2.824	**8.937*****	0.406	**3.100***
Pond size	0.000	0.000	0.000	2.751	0.000	1.837	0.176	0.644
% TAC	**19.350*****	**17.737*****	**6.246****	**6.760****	**20.100*****	2.926	**10.157*****	**13.41*****
% shade	**26.440*****	**23.249*****	**13.372*****	**15.923*****	**18.617*****	**8.403****	**19.409*****	**7.064****
Drying	**-5.543*****	**-4.739*****	**-2.998****	**-6.214*****	**-5.192*****	**-3.208****	**-3.875*****	**-2.192***
Fish	0.544	-1.777	**-4.043*****	**2.705****	**3.485****	**2.216***	**4.856*****	1.437
R-squared	0.303	0.261	0.127	0.314	0.347	0.142	0.282	0.103

Table 5 – Results of generalised additive models (GAMs) describing the species richness of invertebrates and plants 78 ponds in terms of biological, physical and chemical variables. All values are F-statistics apart from for parametric variables (drying and fish presence) which are t-statistics. Missing parameters indicate that that term was dropped from the models by backwards model selection (see text for details). ***=p<0.001, **=p<0.01, *=p<0.05.

	Invertebrates	Insects	Coleoptera	Hemiptera	Odonata	Trichoptera	Mollusca	Plants
Pond size	0.856	0.886		**4.026***	1.167	3.296	1.492	**2.326***
% TAC	**2.591***	2.101	**4.606***	**4.547****	**2.847***	2.045		**5.265*****
% shade		0.571		0.619	**3.224****		1.723	
Ox Dem	**4.228****	**3.64****	1.581	**3.771****	**4.881****	1.959		**4.588****
Phosphate	**4.899****	**4.091***	1.440	**7.393*****	1.828	**2.602***		**4.944****
Cl	2.098	**2.184***		**5.997*****	**2.576***	**3.325****		
pH	**2.896***	2.689	1.919	**4.956*****	**3.813***			**3.174****
Cond	2.063	1.754	1.059	2.088	0.498	1.886	**4.871****	2.302
Drying	**-2.048***	**-2.266***	0.199	**-3.863****	-0.422	**-2.488***	0.165	**-2.076***
Fish	-1.625	-1.639	**-2.361***	-0.490	1.262	1.208	-1.080	0.910
R-squared	0.593	0.537	0.302	0.786	0.633	0.354	0.208	0.665

Table 6 – Results of canonical correspondence analysis (CCA) describing the variation in community structure of invertebrates and plants in 425 ponds based on models in Table 4. Missing parameters indicate that that term was dropped from the models by backwards model selection (see text for details). Values are F-statistics calculated using ANOVA with 999 permutations.

	Invertebrates	Insects	Coleoptera	Hemiptera	Odonata	Trichoptera	Mollusca	Plants
% plant cover	2.406^{***}	2.387^{***}	2.034^{***}	2.525^{**}	2.541^{**}		2.120^{**}	1.937^{***}
% shading	4.228^{***}	4.209^{***}	4.003^{***}	5.691^{***}	4.408^{**}	2.423^{**}	2.642^{***}	3.098^{***}
Water permanence	2.895^{***}	2.709^{***}	2.329^{***}	3.466^{***}	3.368^{***}	0.960	3.670^{***}	1.211^{*}
Fish presence			1.887^{***}	5.906^{***}	1.893^{*}	1.032	2.977^{***}	1.487^{***}
Turbidity			1.976^{***}	3.577^{***}			0.944	1.270^{**}

FIGURES

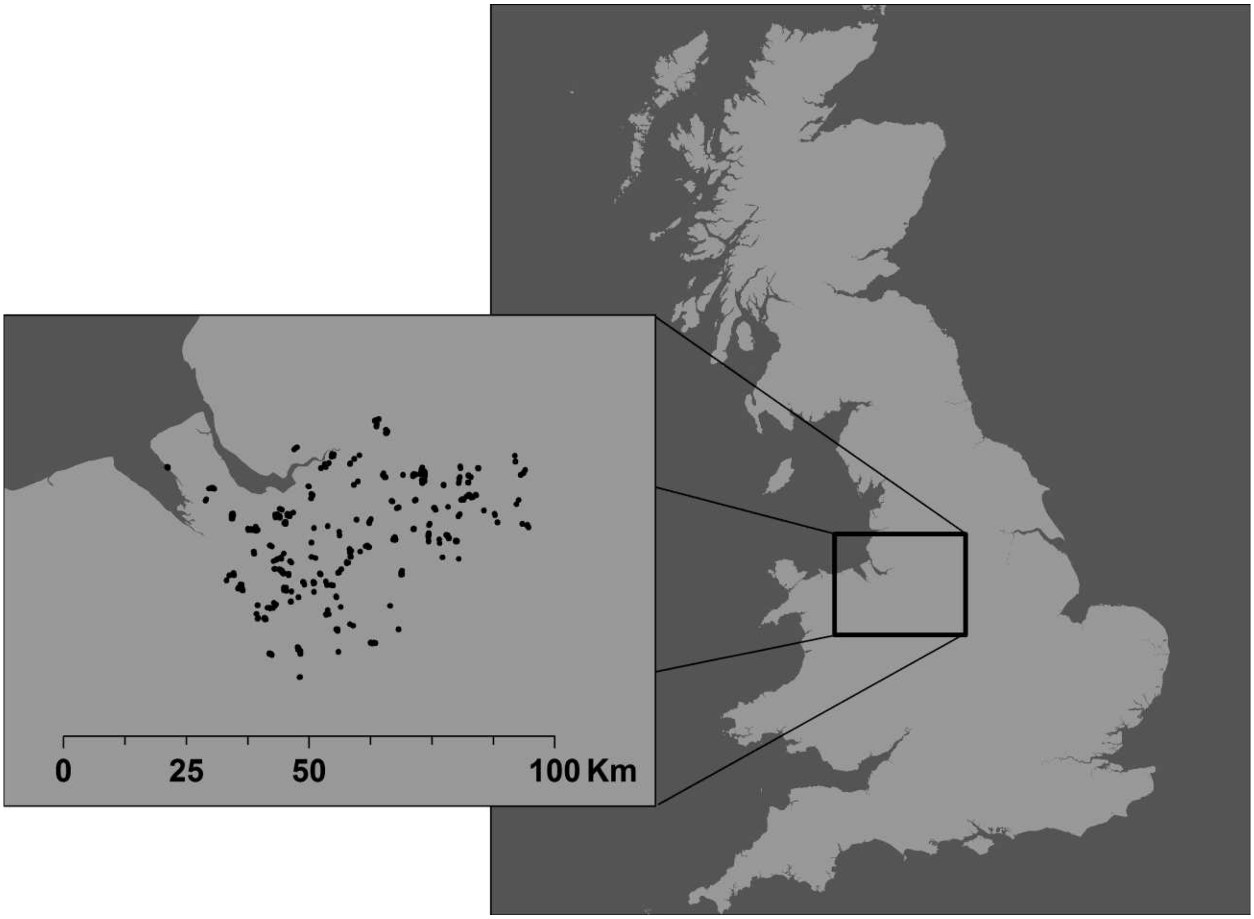

Figure 1 – Location of 425 ponds surveyed.

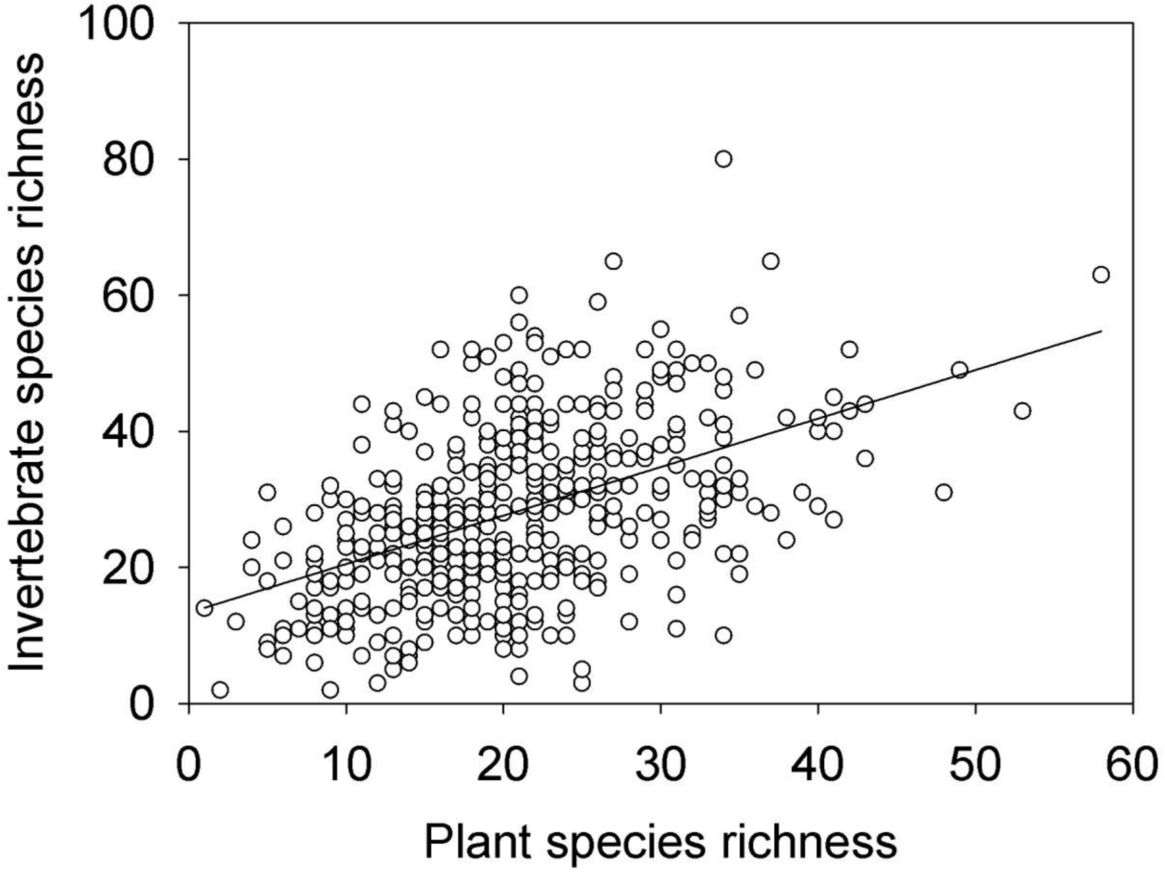

Figure 2 – Correlation between the number of invertebrate species and the number of plant species found in each pond (n=425, r=0.491, p<0.001).

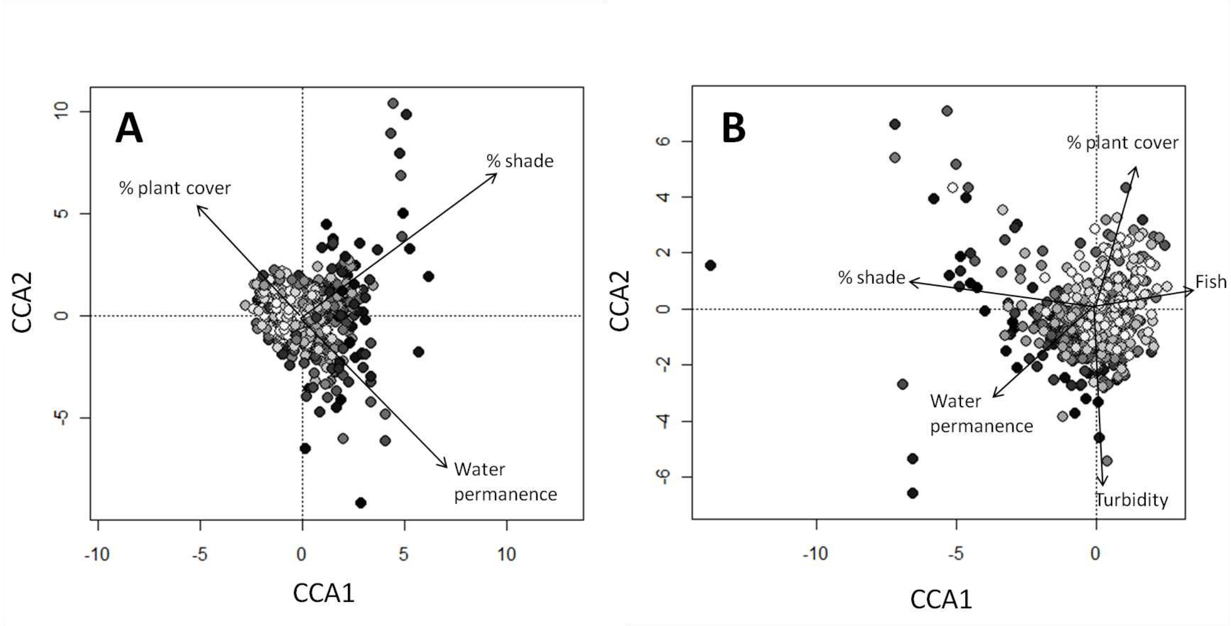

Figure 3 – Results of a canonical correspondance analysis describing community structure of (A) invertebrates and (B) plants in 425 ponds. See Table 6 for statistics. Symbols represent individual ponds and lighter symbols indicate more diverse ponds.