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Title: Temporal dynamics of aquatic communities and implications for pond conservation

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ABSTRACT

Conservation through the protection of particular habitats is predicated on the assumption that the conservation value of those habitats is stable. We test this assumption for ponds by investigating temporal variation in macroinvertebrate and macrophyte communities over a 10-year period in northwest England. We surveyed 51 ponds in northern England in 1995/6 and again in 2006, identifying all macrophytes (167 species) and all macroinvertebrates (221 species, excluding Diptera) to species. The alpha-diversity, beta-diversity and conservation value of these ponds were compared between surveys. We find that invertebrate species richness increased from an average of 29.5 species to 39.8 species between surveys. Invertebrate gamma-diversity also increased between the two surveys from 181 species to 201 species. However, this increase in diversity was accompanied by a decrease in beta-diversity. Plant alpha-, beta- and gamma-diversity remained approximately constant between the two periods. However, increased proportions of grass species and a complete loss of charophytes suggests that the communities are undergoing succession. Conservation value was not correlated between sampling periods in either plants or invertebrates. This was confirmed by comparing ponds that had been disturbed with those that had no history of disturbance to demonstrate that levels of correlation between surveys were approximately equal in each group of ponds. This study has three important conservation implications: (i) a pond with high diversity or high conservation value may not remain that way and so it is unwise to base pond conservation measures upon protecting currently-speciose habitats; (ii) maximising pond gamma-diversity requires a combination of late and early succession ponds, especially for invertebrates; and (iii) invertebrate and plant communities in ponds may require different management strategies if succession occurs at varying rates in the two groups.

Keywords: biodiversity, conservation, invertebrates, plants, pond, succession, temporal

INTRODUCTION

Moss (1998, pp 473-4) gives five root causes for the vulnerability of freshwaters to damage by humankind: (i) negative associations on the part of the public, (ii) the use of freshwaters as receptors or transporters of waste, (iii) replacement of natural wetlands by artificial reservoirs to store valuable water, (iv) the value to be gained in terms of additional fertile land by draining, and (v) mismanagement. While progress has been made in communicating the value of natural wetlands, ponds suffer from the additional problem of perceived insignificance based on the small physical dimensions and apparently limited biodiversity. Research over the past 20 years has sought to overturn this perception by highlighting the high biodiversity, landscape ecological role and ecosystem services that ponds provide.

Ponds have been shown to contain a greater proportion of the regional biodiversity than other types of wetlands including lakes, ditches, rivers and streams (Biggs et al. 2005; Williams et al. 2004) and this pattern has been shown to hold for agricultural landscapes across Europe (Davies et al. 2008). As well as having a greater diversity of flora and fauna, ponds also contain a greater proportion of rare species (Williams et al. 2004) and a greater proportion of unique species (Davies et al. 2008) than other freshwater bodies. Ponds in the landscape cannot truly be considered independent of one another, as they function as a network of habitats. The term “pondscape” has been coined to describe this meta-habitat (Boothby 1997). This degree of connectivity in the pondscape acts in three complementary ways to facilitate metapopulation persistence. First, ponds act as “stepping stone” habitats (Fortuna et al. 2006), and are explicitly recognised as such in Article 10 of the EU Habitats Directive. Such stepping stone habitats help to improve the permeability of the landscape for aquatic and semi-aquatic organisms. Second, the semi-independent nature of individual ponds means that environmental perturbations such as pollution and disease are restricted in effect compared to freshwaters with larger catchments such as rivers (Biggs et al. 2005). Third, ponds act as refugia for biodiversity such that, should a population of a given species in one pond become extinct, there are more populations close at hand to recolonise that habitat (Sherratt et al. 1999). This network of ponds contributes substantially to ecosystems services, including the retention of floodwater (Wanielista and Yousef 1993), the deposition of organic pollutants (Hawkins and Schofield 2003) and the sequestration of carbon (Downing et al. 2008).

Attempts at conserving ponds have focused on rare types of ponds covered under Annex I of the EU Habitats Directive, on specific components of the aquatic flora and fauna, or on “ecological quality”. This last category has received a great deal of attention and has spawned a number of metrics (for an overview, see Indermuehle et al. 2004) including the Predictive System of Multimetrics (PSYM, Biggs et al. 2005), the Community Conservation Index (CCI, Chadd and Extence 2004), invertebrate and amphibian richness metrics to assess trophic state (Menetrey et al. 2005), an assessment of species richness designed to be compatible with the Water Framework Directive (PLOCH, Oertli et al. 2005), and the Pond Biodiversity Index (IBEM, Angélibert et al. 2010; Indermuehle et al. 2010), a modification of PLOCH which reduces costs and taxonomic skills required to carry out the surveys. In addition, ponds are known to be dynamic habitats, prone to rapid and uneven rates of successional change and vulnerable to mismanagement (Boothby and Hull 1997). However, there has been little investigation of the ways in which the communities inhabiting ponds change over time.

Previous studies of turnover in ponds have tended to focus on a relatively small number of taxa. Briers and Warren (2000) studied two *Notonecta* sp. (Hemiptera) at 68 ponds over 3 consecutive years and found variability in habitat quality affected patch occupancy. Moore (1991) studied the pattern of community assembly by observing breeding behaviour by adult Odonata (which may not be an accurate method of predicting the aquatic residents (Raebel et al. 2010)) at 20 newly-created woodland ponds over 27 years, describing a transition between pioneer and climax odonate communities. Cottenie and De Meester (2003) investigated zooplankton communities in a very highly connected cluster of 34 ponds over 3 consecutive years, and found that environmental variables, particularly turbidity, varied between years and influenced diversity. The same link between biotic diversity and environmental variables was seen in a survey of seasonal variation in three French ponds (Angélibert et al. 2004). The composition of beetle communities at 18 ponds was shown to vary between years, with the age of the pond exerting the largest influence on community variability (Fairchild et al. 2000). Where the full invertebrate community has been studied, this has sometimes been only within a limited number of habitats, such as Macan's (1977) study of the invertebrate fauna of a single pond over 20 years.

However, a small number of recent studies have considered entire communities across a number of habitats. Jeffries (1994) studied the effects of drought on a system of 29 temporary ponds, each with an area of 1m², by comparing invertebrate community data before the drought with data from after the drought. Jeffries found that patch extinction rates were high in all species, but that temporary pond species colonised faster than permanent pond species. These studies suggest that inter-annual variations in the environment can cause substantial variations in community structure. In a later study, Jeffries surveyed annually the invertebrate (Jeffries 2011) and plant (Jeffries 2008) communities in a series of 30 small (1m²), newly-created, temporary ponds over a very small area (<500m²) for 10 years. Both invertebrate and plant metacommunities were influenced deterministically by patterns of inundation, leading to large variations between ponds even over such a small spatial scale. Chase (2007) created 20 mesocosms varying in volume between 20 litres and 1,140 litres. These showed considerable variation in amphibian, macroinvertebrate and plant communities, even across a small spatial scale. When a drought treatment was applied to half of the mesocosms, community structure showed convergence which Chase attributed to the filtering out of those species that could not tolerate drought conditions.

Previous studies, therefore, have focused either on a narrow range of taxa, a small number of habitats or a specific type of habitat (temporary ponds or mesocosms). Few studies of changing pond communities have considered side-by-side the plant and invertebrate communities of permanent ponds. The relative abundances of taxa within these communities have a strong bearing on the potential application of conservation measures which are largely based on the presence of rare species or diverse communities. Thus the temporal dynamics of pond communities may alter the conservation value of a habitat. We surveyed 51 ponds 10 years apart and identified all plants and macroinvertebrates (excluding Diptera) to species. Thirty-six of these ponds are thought to be 18th Century marl pits. We provide a comparison of alpha-, beta- and gamma-diversity between periods as well as quantifying changes in "conservation value" defined using existing metrics. More importantly, however, we provide a comparison of spatial and temporal beta-diversity. These data are used to examine the implications of this temporal variation in beta-diversity for pond

conservation strategies at pond and pondscape levels. We discuss our findings in light of attempts to conserve ponds and their communities.

METHODS

Field surveys

The faunal and floral communities of 51 ponds in northern England were characterised (Figure 1, see Table 1 for a summary of pond characteristics for 44 of those ponds for which physical parameters were measured). We provide further details of the pondscape elsewhere (Hassall et al. 2011). This region is low-lying and used extensively for agriculture with relatively low levels of human habitation. Cheshire (2,343 Km²) contains 20,546 mapped lentic water bodies of less than 2ha, though in some areas, up to 30% of ponds present may be unmapped (Hollinshead, unpublished data). The number of ponds holding standing water is estimated to be well in excess of 17,500 (Boothby 1997). The county overlies a glacial outwash plain of boulder clays, separating the hills of North Wales to the west from the Peak District of Derbyshire to the east, and is predominantly rural. Pastoral agriculture dominates, resulting in a mosaic of mainly small fields, hedgerows and patchy woodland. Pond density aside, the area may be considered representative of North West European pastoral lowlands. The vast majority of ponds in the Cheshire landscape are anthropogenic in origin, with the most numerous being marl pit ponds. Marl pits persisted in the landscape in the period before the advent of piped water in fields as watering holes for stock. This was a secondary benefit, their primary purpose being the extraction of marl, a base rich glacial clay deposit. The practice in Cheshire dates back to the medieval period occurring with varying intensity, but particularly during the 1790s under the spur of increases in food crop prices. By the 1840s the practice was in rapid decline due to cheaper alternatives and increasing labour costs. The marl pit ponds included in the 2006 re-survey can be identified with confidence in the early editions of the Ordnance Survey County Series 1:10560 map (available as GeoTIFF image files, Landmark Information Group Limited, 2010).

Each of the 51 ponds was surveyed in 1995 or 1996 and again in 2006 for both invertebrates and plants. Twenty-eight ponds were surveyed between 25 May and 22 July 1995, with 23 more ponds surveyed between 26 May and 19 July 1996. All ponds were then resurveyed between 15 May and 24 June 2006. Benthic substrate was either clay (n=23) or silt/soil (n=28). All ponds were within 500m of neighbouring ponds or wetlands. Fourteen ponds were confirmed to contain fish and six were known to have dried up at least once in the past. Water chemistry measurements, including pH, conductivity and nitrogen concentrations, were taken for all ponds during the second survey.

Recent pond histories were sought from land managers/owners. Seven of the 51 ponds were recently created in 1995/6 (within the previous 5-6 years), including 4 as mitigation against *Triturus cristatus* breeding pond loss due to road construction in 1993. The remaining 44 ponds originated as marl pit ponds and were created in the late 18th Century. Six of the 44 marl pit ponds had been substantially dredged, and 3 others had undergone less extensive dredging or bank re-grading prior to survey (see Table 2a for ponds that were modified between surveys and Table 2b for details of pond history and modification prior to the surveys). During the period between the initial survey and re-survey in 2006 two were drained and in-filled to a substantial degree, and one in-filled completely, all three being marl pits in origin. Four were subject to dredging, two with re-grading of

banks. According to consultations with land owners, no other management of the ponds themselves took place, though management of the immediately surrounding terrestrial landscape has changed considerably in some cases.

The presence and absence of invertebrate species was recorded using standardised sampling methods. Pond nets with 1mm mesh were used to collect invertebrates using travelling kick-sweeps within the main water body. Kick sweeps were carried out in all identified microhabitats, usually over bare substrate, within the leaf litter and in submerged vegetation. Only larger macroinvertebrates that can be caught by a 1mm mesh net were included in the study (a species list of plants and invertebrates can be found in Appendices A and B). 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. The data used in this study were the presence or absence of each species during the surveys. The same methods were employed by the same surveyor in all surveys to account as far as possible for variations in recording.

Data analysis

Alpha-diversity (species richness) was calculated separately for invertebrates and plants for each of the ponds. Beta-diversity was calculated for each of the ponds in the initial survey using the β_{sim} method as recommended by Koleff et al. (2003; see that paper for a review of beta-diversity metrics). This value was the mean β_{sim} for each pond compared with each other pond. Beta-diversity was also calculated between time periods for the same ponds. Gamma-diversity was calculated for the invertebrates and plants separately. The Community Conservation Index (CCI, Chadd and Extence 2004), was used to assess the conservation value of the invertebrate communities, and Species Rarity Index (SRI, based on methods in Williams et al. 2004) was calculated as an equivalent measure for plants. The CCI involves the assignment of a Conservation Score to a range of species based on their relative rarity (see Appendix 2 in Chadd and Extence 2004). These scores are averaged for each site and then multiplied by a Community Score which is based either on the greatest CS (the method used in this analysis) or Biological Monitoring Working Party (BMWP) scores for that site. SRI uses a similar method to allocate Species Rarity Scores to each species which are then averaged for each site to give the SRI.

Due to issues with non-normality of the data, non-parametric statistics were used. Alpha-diversity, beta-diversity, and conservation value (CCI or SRI) were compared between surveys using paired Wilcoxon signed-rank tests. The spatial and temporal beta-diversity were also compared using paired Wilcoxon signed-rank tests. Spearman's rank correlations were employed to test for consistency in alpha-diversity, beta-diversity and conservation value (CCI or SRI) between surveys. To evaluate the contributions of disturbances between surveys (see Table 2a) compared to the natural evolution of the ponds communities in the absence of disturbance, these analyses were carried out on both the total pond dataset (n=51) and the subset of ponds for which there was no evidence of disturbance (n=36). To evaluate the contributions made by different taxa to the observed variations in community structure, the losses and gains of species across the entire surveys

within each order of plants and invertebrates were tallied. All analyses were carried out using R (R Development Core Team 2006) and the R package “vegan” (Oksanen et al. 2007). The statistical significance of the results should be interpreted in light of the number of tests performed. We performed 22 statistical tests and a conservative correction for this would involve multiplying the p-values by 22. Significance is therefore unequivocal when $p < 0.0023$. We also present test statistics for all tests so that effect sizes are clear in all cases.

RESULTS

General results

The two surveys recorded 167 species of plants and 221 species of invertebrates. Plant gamma-diversity was 149 in 1995/6 and 142 in 2006, while invertebrate gamma-diversity was 181 in 1995/6 and 201 in 2006 (Figure 2C). The distribution of these species across taxonomic groups can be seen in Figure 3. The results of Wilcoxon signed-ranks tests and Spearman's rank correlations did not differ qualitatively between the full dataset and the subset of undisturbed ponds (Table 3) so only the full dataset is discussed.

Plant communities

Alpha-diversity in plant communities was strongly correlated between the two sampling periods (Figure 4A), although there is only a weak correlation between the two surveys in beta-diversity (Figure 4C, statistics are in Table 3). The species rarity index (SRI) for the first survey was not significantly correlated with that of the second (Figure 4E). Paired Wilcoxon signed-ranks tests showed that there was no significant difference between ponds in alpha-diversity, beta-diversity or SRI between the two surveys. Mean species richness was 23.5 (± 1.3 SE) in 1995/6 and 22.3 (± 1.3) in 2006. However, these measures of overall species richness disguise the fact that there were community changes between surveys (Figure 3A). Most notably, all three charophytes (*Chara vulgaris* var. *papillata*, *Chara vulgaris* var. *vulgaris* and *Nitella flexilis*), plants of conservation importance in the UK, were lost from the four ponds in which they were found in the first survey. This loss was accompanied by a net loss in Asteridae, including three of four *Callitriche* sp. and both *Bidens* sp. This decline was balanced in terms of species numbers by an increase in the number of grass (Poales) species. The beta-diversity between surveys of the same ponds was significantly lower than the spatial beta-diversity within either of the two surveys (first survey: $V=1325$, $p < 0.001$, second survey: $V=1316$, $p < 0.001$; Figure 2B). Nine species of plants that are considered alien to the region were identified (Table 4). There was no general trend in the occupancy of these species, although *Epilobium ciliatum* and *Lemna minuta* colonised 12 and 9 ponds, respectively, in between surveys.

Invertebrate communities

Invertebrate communities showed a contrasting pattern to that seen in plants. There were no significant correlations between alpha-diversity, beta-diversity or CCI between the two surveys (Table 3, Figure 4B, D, F). Alpha-diversity increased significantly between surveys from an average of 29.5 (± 1.5 SE) in 1995/6 to 39.8 (± 1.7) in 2006, and beta-diversity decreased significantly (Figure 2A,B). Both patterns were significant even after conservative control for multiple tests. CCI showed no significant difference between surveys, but a small number of ponds changed CCI value markedly, as can be seen from the outliers in Figure 4F. When the communities were analysed in greater detail, two patterns were evident: 7 out of 22 orders which were identified from the surveys

increased in diversity without losing any species (Figure 3B). In addition, there was a high degree of turnover with a net increase in species richness in insect orders, particularly the Coleoptera, Hemiptera, Odonata and Trichoptera. As with the botanical data, the beta-diversity between surveys of the same ponds was significantly lower than the spatial beta-diversity within either of the two surveys (first survey: $V=1254$, $p<0.001$, second survey: $V=1076$, $p<0.001$; Figure 2B). Temporal beta-diversity was significantly higher in invertebrates than in plants ($V=208$, $p<0.001$).

DISCUSSION

We provide a detailed comparison of invertebrate and plant communities sampled 10 years apart which sheds light on the temporal dynamics of a pond landscape. In particular we highlight contrasting patterns between the invertebrate and botanical communities of the ponds that were studied (summarised in Figure 4). Botanical communities appear to be relatively stable, with ponds that were recorded as more diverse in the first survey tending to remain more diverse in the second. Plant gamma-diversity shows a marginal decrease between the two periods. Alpha-diversity of invertebrates, on the other hand, is weakly correlated between time periods and shows a marked rise between surveys. This corresponds to a higher temporal beta-diversity than in plants and an increase in gamma-diversity. However, accompanying this rise in diversity is a decline in beta-diversity suggesting that the ponds are becoming more similar across the landscape. These patterns hold both for older marl pit ponds that have existed since the late 18th Century and that might be expected to have stable communities, as well as for ponds created since 1990.

The lack of clear variation between plant communities in the two surveys may be due to either (i) a slower pattern of succession towards a climax community, or (ii) the presence of a stable, climax community prior to the first survey. Rates of initial colonisation can be very quick (Barnes 1983) so we may already have observed a climax community in the first survey, although few studies have followed large numbers of ponds for any length of time. However, one piece of evidence against this is the presence (and subsequent loss) of charophytes, of which *Nitella flexilis* is rated as Nationally Scarce, from four survey ponds. These species readily colonise early successional ponds but may be excluded by competition as succession continues (Wade 1990). The increase in grasses (Poales) suggests succession towards terrestrial habitats in these wetlands is still underway.

The majority of the increase in gamma-diversity in invertebrates was due to the immigration of active dispersers such as beetles, damselflies, dragonflies and true bugs (Figure 3B). This pattern suggests that the species pool contained within the network of ponds that were the focus of this study (our gamma diversity) is more susceptible to colonisation by winged, mobile species from the regional species pool. Diptera, which were not included in this analysis due to issues with identification of larvae, often also feature as early colonisers (Barnes 1983). Relatively few of the species that colonised between surveys were passive dispersers, although freshwater snails comprise 20 out of 45 non-insect species that were found across the two surveys. The most notable invertebrate species found during the surveys was *Hydrocara caraboides*, the lesser silver water beetle, which is protected in the UK under Schedule 5 of the Wildlife and Countryside Act 1981. The presence of such a species immediately qualifies a site for consideration as a "site of special scientific interest" (SSSI) in the UK. However, it is worth pointing out that while this beetle increased its presence from two ponds in 1995/6 to three ponds in 2006, it was not found at the two original sites in 2006 and the three sites from the second survey represent new records. Thus SSSI designation on

the basis of the presence of *H. caraboides* could, in this case at least, result in wasted conservation resources.

Variability between pond communities tends to be higher than for other water body types (Davies et al. 2008; Williams et al. 2004). We provide the first quantification of variation in both plant and invertebrate communities within individual ponds over time, which provides an additional dimension to pond diversity. The issue of succession is of particular importance in dynamic habitats of limited area such as ponds, where natural succession may be rapid and conspicuous. Succession rate is determined by the rate of autochthonous production and the rate of input and deposition of allochthonous material. Ponds are among the most productive habitat on earth, as demonstrated by their high rates of carbon sequestration (Downing et al. 2008). This makes them particularly vulnerable to loss through succession, which results from what has been termed "benign neglect" on the part of landowners and managers (Boothby and Hull 1997). The turnover that we observed suggests that some groups of species (e.g. grasses) become more prevalent at later stages of succession but that this comes at the cost of other species (e.g. charophytes). The replacement of one group by another leads to a stable diversity with higher species turnover. Late-succession ponds likely contain species that are not present in mid- or early-succession ponds, as demonstrated by the turnover in species. As a result, the maintenance of ponds through dredging of sediment, cropping of vegetation or fencing of banks may not benefit landscape-level biodiversity. Instead, to manage for maximal gamma-diversity ponds should be permitted to undergo succession to grassland, but new ponds must be created to maintain the continuum of successional states. Recent successes with pond creation schemes are beginning to inform this practice (Williams et al. 2008), where earlier efforts were largely without a rigorous scientific basis (Williams et al. 1999).

While individual ponds interact strongly at a local level with surrounding terrestrial habitat, the catchments of these water bodies tend to be relatively small. This has two implications for the physicochemical characteristics of the water body. First, a disturbance (e.g. pollution, invasive species) event of a given size occurring within the catchment will have a greater effect within smaller catchments as there will be less additional input to buffer against the change. Second, the probability of such an event falling within a smaller catchment is lower than within a larger catchment. Therefore, when a pond is damaged it is badly damaged, but damage is localised and ponds which have suffered little if any negative anthropogenic impacts are also relatively common (Biggs et al. 2005). It is likely that this contributes to the wide range in alpha-diversity that is seen in surveys of ponds within regions (Williams et al. 2004). As well as this susceptibility of ponds to environmental perturbation, the stochasticity of occupancy of particular species makes conservation difficult. Conservation of ponds tends to rely on the presence of high biodiversity or rare species (e.g. in the UK to designate a site as a "Site of Special Scientific Interest", SSSI). However, we note that conservation value of plant and invertebrate communities and the presence of particular species (e.g. *Hydrochara caraboides*, as mentioned above) which would guarantee legislative protection are highly variable in time. The dynamic nature of the pond community therefore reduces the applicability of the only current legislative protection for this habitat. Our results lend yet more support to a shift in focus from statutory designation of individual ponds for conservation, to pond clusters and the pondscape at wider landscape scales.

Pond conservation is a major issue across Europe due to the lack of legislative protection afforded to this neglected habitat (Céréghino et al. 2008). We highlight the value of a well-studied pondscape in northern England which may be considered representative of much of pastoral lowland Europe. Previous studies have highlighted the contribution that ponds make to landscape biodiversity but have largely neglected temporal variation (Jeffries 2005). We provide a comprehensive description of invertebrate and plant communities sampled 10 years apart and demonstrate that biodiversity and conservation value are not consistent over time, whether or not there is disturbance. It is intended that the recurrent re-survey of the 51 ponds continue forming the basis of an on-going longitudinal study of temporal and spatial variation in of biodiversity. Furthermore, the extent of this temporal variation in communities varies between plants and invertebrates. If the goal in pond conservation is to maximise gamma-diversity, this can only be achieved by taking into account the constantly changing nature of the pondscape.

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TABLES

Table 1 – Summary statistics for 44 ponds.

	Mean	Median	SE	Range
Altitude (m)	49.3	50	4.9	10-125
Area (m ²)	2154	1508	338	101-9425
% shaded by tree	10.7	5	2.6	80
pH	7.62	7.80	0.09	6.50-8.60
Conductivity (mS)	0.72	0.68	0.04	0.38-1.69
Total ammonia nitrogen (mg.l ⁻¹)	0.81	0.14	0.22	0.00-6.45
Depth classes (n): 1m (n=5), 2m (n=10), 3m (n=11), 4m (n=12), 5m (n=6)				

Table 2a – Details of ponds modified between surveys

Pond ID code	Notes
CH95/014	Created 1990, fish introduced since 1995
CH95/021	Some in-filled
CH95/026	Recent signs of dredging, similar successional stage to 1995 when kept open as watering point
CH95/039	Dredged and enlarged slightly
CH95/043	New lobe dredged in 2000 to create habitat for <i>Hydrochara caraboides</i> , now deteriorated
CH95/072	Drain installed to regulate size
CH95/099	Land drains directed into pond increased depth substantially
CH96/018	Partly in-filled
CH96/035	Bank re-grade, possibly dredged since 1996
CH96/044	Was subject to pollution incident some years before 2006 survey, banks may have been re-graded.
CH96/049	Marginal scrub clearance and bank re-grade 2005/6.
CH96/058	Drained and partly in-filled
CH96/059	Partly dredged 1996, since extensively modified and dredged
CH96/077	Dredged completely in 1994, fish being introduced shortly after
CH95/073	Created 1989, by amalgamation of two marl pits, partially drained

Table 2b – Details of ponds unmodified between surveys

Pond ID code	Notes
CH95/032	Recently dredged in 1995, apparently not since
CH95/044	Shallow dredge before 1995 survey, none since
CH95/045	Shallow dredge before 1995 survey, none since
CH95/076	Cleared in 1992, nothing since
CH95/091	Dredged 2-5 years ago
CH95/094	Dredged 2-5 years ago
CH95/113	Believed to have been dredged some years prior to 1995 survey, nothing since
CH96/028	New mitigation pond created 1993, no management, angling a problem
CH96/031	New mitigation pond created 1993, no management, angling a problem
CH96/032	New mitigation pond created 1993, no management, angling a problem
CH96/033	New mitigation pond created 1993, no management
CH96/043	Newly restored rubble filled marl pit in 1996, no management since
CH96/061	Dredged and landscaped shortly before the survey in 1996

Table 3 – Results of statistical analysis (Spearman rank correlations and paired Wilcoxon signed rank tests) investigating variation in diversity between 51 ponds across two sampling periods (1995/6 and 2006). ^{NS} indicates non-significant statistical test results at a reduced α -level to account for multiple tests ($\alpha=0.0023$). Values for the subset of undisturbed ponds (n=36) are given in square brackets.

		Invertebrates	Plants
Correlations	Alpha-diversity	$\rho=0.355, p=0.011$ ^{NS} [$\rho=0.280, p=0.098$ ^{NS}]	$\rho=0.639, p<0.001$ [$\rho=0.691, p<0.001$]
	Beta-diversity	$\rho=0.297, p=0.030$ ^{NS} [$\rho=0.276, p=0.104$ ^{NS}]	$\rho=0.428, p=0.002$ [$\rho=0.503, p=0.002$]
	CCI/SRI	$\rho=-0.100, p=0.486$ ^{NS} [$\rho=-0.219, p=0.199$ ^{NS}]	$\rho=0.259, p=0.066$ ^{NS} [$\rho=0.250, p=0.142$ ^{NS}]
Differences	Alpha-diversity	$V=133.5, p<0.001$ [$V=363.5, p=0.001$]	$V=731, p=0.369$ ^{NS} [$V=656, p=0.933$ ^{NS}]
	Beta-diversity	$V=1192, p<0.001$ [$V=1007, p<0.001$]	$V=497, p=0.121$ ^{NS} [$V=512, p=0.128$ ^{NS}]
	CCI/SRI	$V=554, p=0.309$ ^{NS} [$V=601.5, p=0.604$ ^{NS}]	$V=618, p=0.677$ ^{NS} [$V=574.5, p=0.411$ ^{NS}]

Table 4 – Change in occurrence between surveys in nine alien plant species.

Species	Survey 1 occupancy	Survey 2 occupancy	Extinctions	Colonisations
<i>Acorus calamus</i>	1	1	0	0
<i>Crassula helmsii</i>	1	2	1	2
<i>Elodea canadensis</i>	5	2	3	0
<i>Elodea nuttallii</i>	4	5	2	3
<i>Epilobium ciliatum</i>	10	17	5	12
<i>Iris pseudacorus</i>	17	19	2	4
<i>Lagarosiphon major</i>	0	1	0	1
<i>Lemna minuta</i>	1	9	1	9
<i>Nymphaea alba</i>	1	1	1	1

Figures

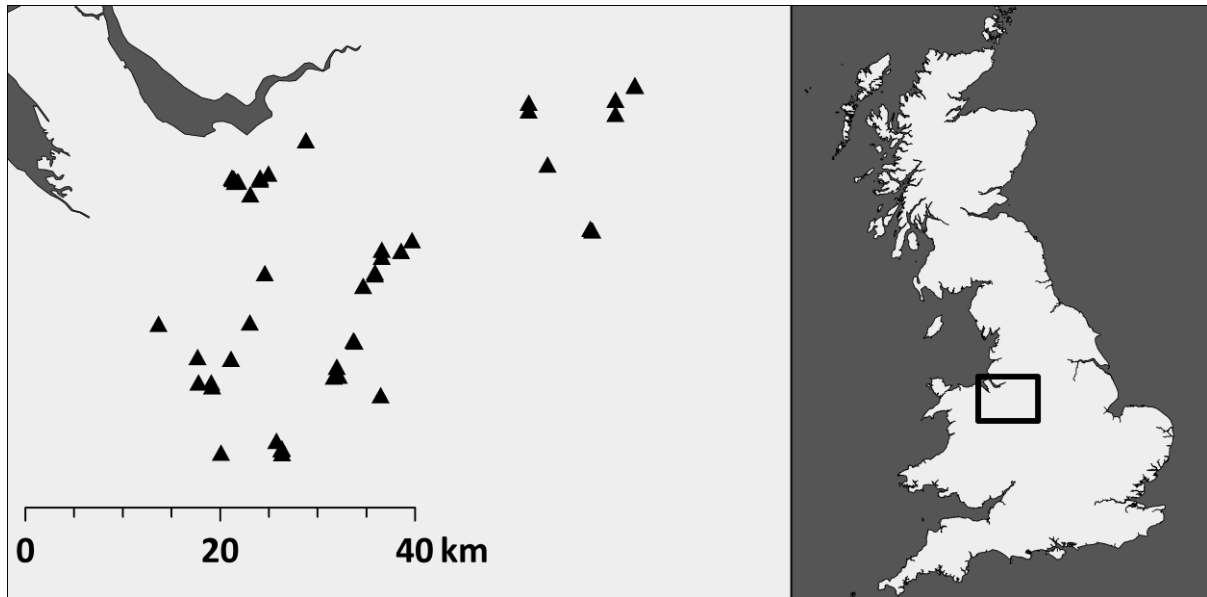


Figure 1 – Map of northwest England showing the locations of surveyed ponds.

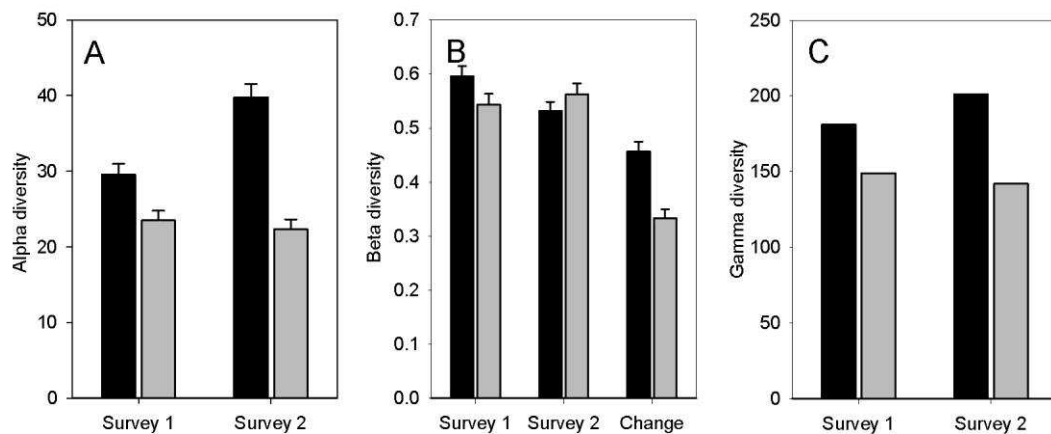
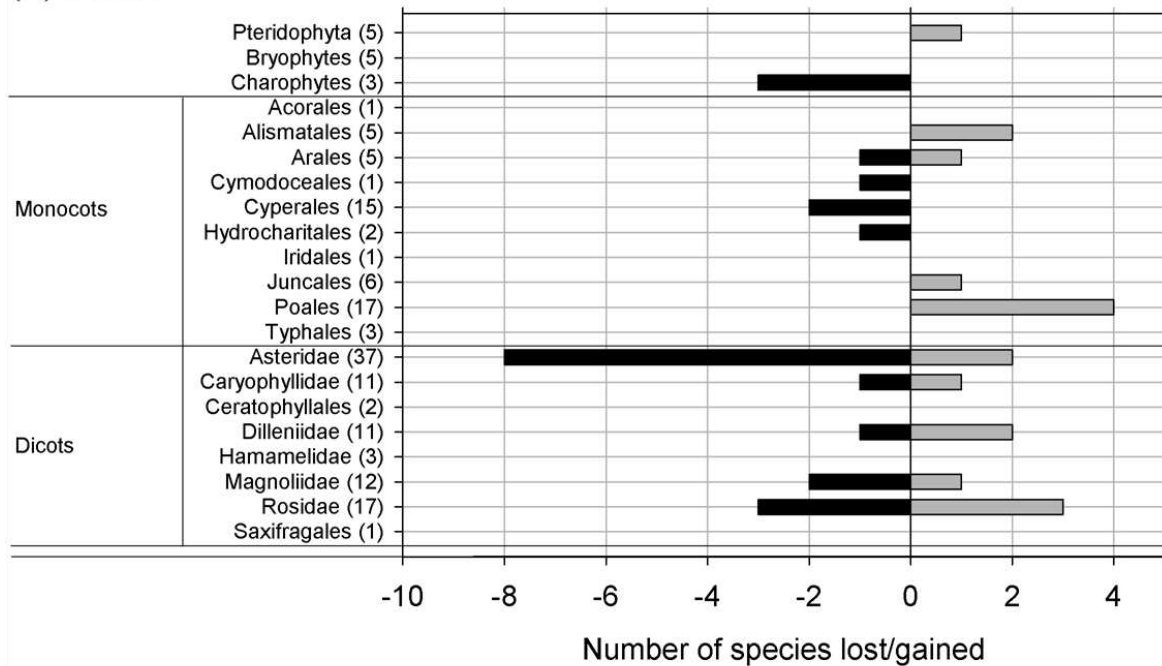


Figure 2 – Variation in (A) alpha-, (B) beta- and (C) gamma-diversity of invertebrates (black bars) and plants (grey bars) between two surveys carried out on the same 51 ponds in 1995/6 (“Survey 1”) and 2006 (“Survey 2”). Beta-diversity marked "change" is the sample of pairwise comparisons between the same 51 ponds at the two sampling periods. Error bars are 1SE.

(A) Plants



(B) Invertebrates

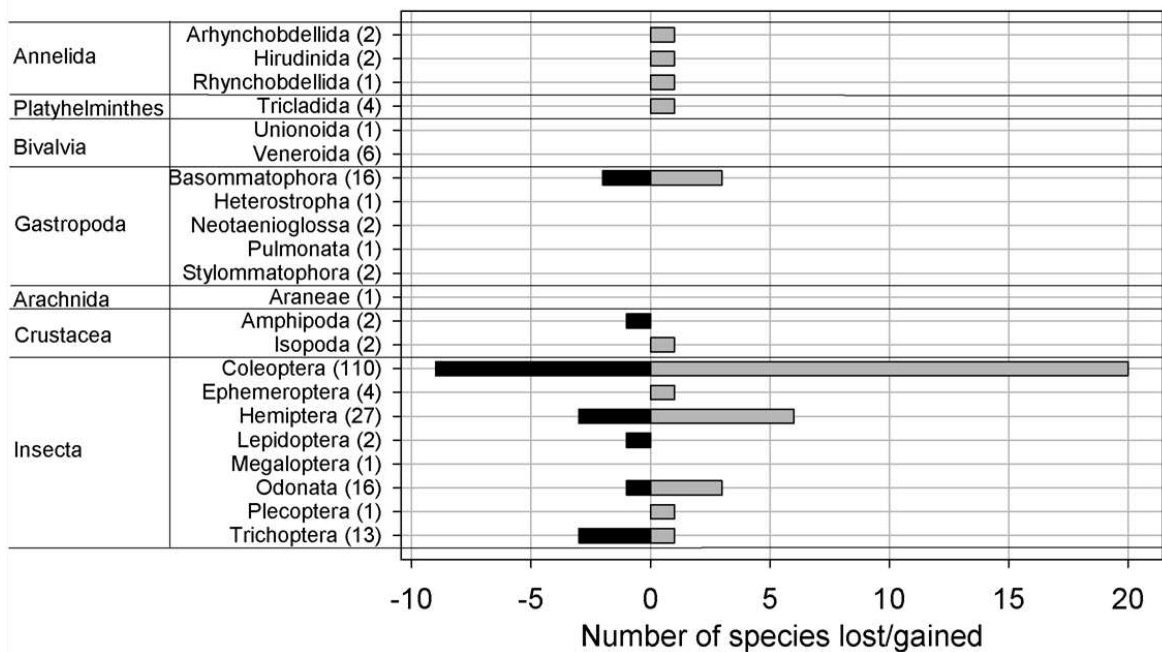


Figure 3 – Patterns of species gain (grey bars) and loss (black bars) in (A) plant and (B) invertebrate taxa between two surveys carried out on the same 51 ponds in 1995/6 and 2006. Species loss corresponds to species that were recorded in the first survey but not in the second, while gains are species that were not recorded in the first survey but were recorded in the second. Numbers in brackets represent the number of species in each taxon found across the two surveys.

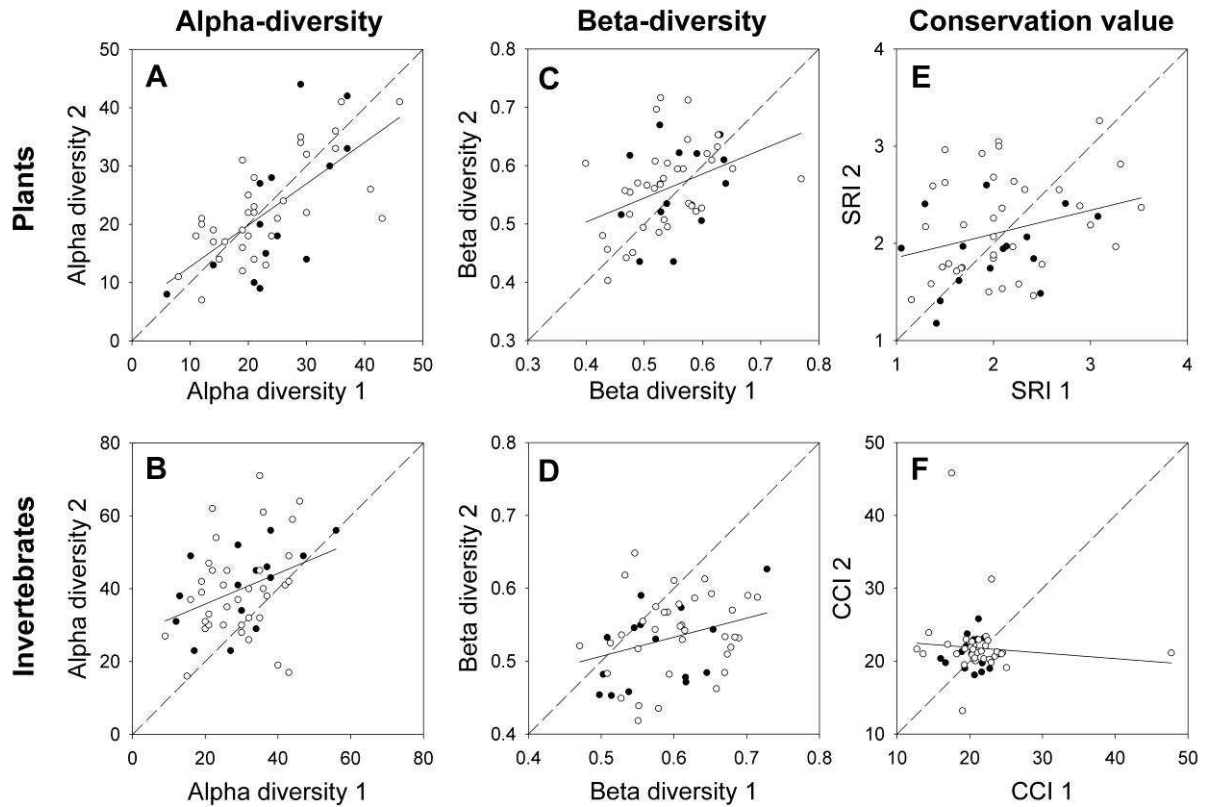


Figure 4 – Variation in (A,B) alpha-diversity, (C,D) beta-diversity and (E,F) conservation value (species rarity index (SRI) for plants, or community conservation index (CCI) for invertebrates) between two surveys carried out on the same 51 ponds in 1995/6 (x-axis, denoted "1") and 2006 (y-axis, denoted "2"). Dashed lines denote 1:1 relationships and solid lines are linear regressions. Open symbols are undisturbed ponds and closed symbols are disturbed (dredged, in-filled or fish introduced) ponds.