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The functional response and resilience in small waterbodies along land-use and environmental gradients

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Response diversity and functional resilience in ponds (Ian Thornhill ian.thornhill@live.co.uk)

Abstract

There is growing recognition of the essential services provided to humanity by functionally intact ecosystems. Freshwater ecosystems are found throughout agricultural and urban landscapes and provide a wide range of ecosystem services, but globally they are also amongst the most vulnerable. In particular, ponds (lentic waters typically less than 2ha), provide natural flood management, sequester carbon and hold significant cultural value. However, to inform their management it is important to understand a) how functional diversity varies in response to disturbance and b) the link between biodiversity conservation and ecosystem function.

In this study, a meta-analysis of seven separate pond studies from across England and Wales was carried out to explore the effect of urban and agricultural land-use gradients, shading, emergent vegetation, surface area and pH upon groups of functionally similar members of the macroinvertebrate fauna. Functional effect groups were first identified by carrying out a hierarchical cluster analysis using body size, voltinism and feeding habits (18 categories) that are closely related to biogeochemical processes (e.g. nutrient and carbon recycling). Secondly, the influence of the gradients upon effect group membership (functional redundancy - FR) and the breadth of traits available to aid ecosystem recovery (response diversity) was assessed using species counts and functional dispersion (FDis) using 12 response traits. The effect of land-use gradients was unpredictable, whilst there was a negative response in both FR and FDis to shading and positive responses to increases in emergent vegetation cover and surface area. An inconsistent association between FDis and FR suggested that arguments for taxonomic biodiversity conservation in order to augment ecosystem functioning are too simplistic. Thus, a deeper understanding of the response of functional diversity to disturbance could have greater impact with decision-makers who may relate better to the loss of ecosystem function in response to environmental degradation than species loss alone.

Keywords

Ecosystem functioning, nutrient recycling, response diversity, ponds, ecosystem services, functional resilience

Introduction

Global biodiversity loss continues at an unprecedented rate (Butchart *et al.* 2010) and declines in freshwater biodiversity are greater than those observed in terrestrial systems (Sala *et al.* 2000; Vörösmarty *et al.* 2010). Among the most vulnerable of freshwater habitats are ponds (natural, semi-natural and artificial, defined here as lentic waterbodies, typically less than 2ha, which provide a wealth of ecosystem services and can be found throughout agricultural and urban landscapes (e.g. Williams *et al.* 2004; Jeffries 2012; Hill *et al.* 2016). The implications of such biodiversity loss is of significant concern for the wider functioning of freshwater systems and their resilience in the face of global environmental change, as well as local stochastic events (Chapin *et al.* 2000; Gerisch 2014).

There has been growing recognition of the essential services provided to human populations by functionally intact ecosystems (Kremen & Ostfeld 2005; Balvanera *et al.* 2006), with conservation ecology often focused on the maintenance of biodiversity to secure ecosystem function (Brophy *et al.* 2017). Pond habitats can provide water storage, purify drainage, sequester carbon and provide significant recreational and cultural value (Bolund & Hunhammar 1999; Zedler & Kercher 2005). However, many ponds are in a neglected state (Williams *et al.* 2010; Hassall, Hollinshead & Hull 2012), with minimal management intervention in anthropogenically dominated landscapes likely causing ecological impairment

(Sayer *et al.* 2012). To date, the functional diversity of ponds has received little research focus, with more attention paid to their value as biodiversity hotspots than ecosystem service providers (Hassall 2014). However, a better understanding of how functional diversity responds to environmental change (i.e. functional resilience) would aid ecosystem-based management aimed at retaining or enhancing ecosystem services (Kremen 2005; Lapointe *et al.* 2014).

Functional diversity is defined as the diversity of functional characteristics within an ecological community based on morphological, behavioural, or life-history traits (Petchey & Gaston 2006). For ecosystems to be functionally resilient it is important to understand how functional diversity varies in response to disturbance, particularly amongst those species that share similar functional traits (Chapin *et al.* 1997; Moore & Olden 2017). For ponds, this 'response diversity' is yet to be explored, but is considered essential for ecosystem recovery following disturbances and thus pivotal to the long-term, sustainable provision of ecosystem services (Elmqvist *et al.* 2003; Folke *et al.* 2004; Bruno *et al.* 2016).

Within an ecosystem, sets of co-existing species whose functional effects overlap may be classified into 'functional effect groups', based on the traits which determine these effects (Hooper *et al.* 2002; Lavorel & Garnier 2002). For example, large-bodied invertebrate shredders may form one effect group, predators another. A higher number of species within a given effect group suggests greater functional redundancy, and thus a greater resilience against the removal of any one species whose functional loss can be compensated by other species within that effect group (Naeem 1998). However, should species within a given effect group differ in their response to environmental change or disturbance, then a linear relationship between species richness and functional resilience cannot be assumed (Elmqvist *et al.* 2003). Under such circumstances, the argument for the conservation of biodiversity for the purpose of securing ecosystem service provision may not be appropriate (Lohbeck *et al.* 2016)

Among the emerging anthropogenic stressors to which ecosystems are responding are changes in land-use patterns such as agricultural intensification and urbanisation, which are common causes of degradation and biodiversity loss (Sala *et al.* 2000; Mooney *et al.* 2009). In addition, a number of pond studies have identified local environmental factors to have an impact upon biodiversity including shade (Hassall, Hollinshead & Hull 2011; Thornhill *et al.* 2017a), surface area (Bronmark 1985; Heino 2000), emergent vegetation (Scheffer *et al.* 1993; Declerck *et al.* 2005) and pH (Biggs *et al.* 2005), but no attempt has been made to directly consider response diversity along these gradients.

Consideration of response diversity in freshwater systems, however, has been restricted to rivers and lakes (Elmqvist *et al.* 2003; Durance *et al.* 2016). Within these systems, response diversity is important for the maintenance of leaf litter breakdown rates (Jonsson *et al.* 2002) and in mitigating the effect of toxic chemical stress, acidification and extreme events (Carpenter & Cottingham 1997; Woodward *et al.* 2015). The study of response diversity in freshwaters has been bolstered by a robust and growing body of work on functional traits in freshwater invertebrates (e.g. Merritt & Cummins 1996; Tachet *et al.* 2010), thus facilitating further study of response diversity.

In the present study, we consider how six environmental gradients effect pond macroinvertebrate functional redundancy and response diversity through a meta-analysis of seven studies carried out across urban and rural landscapes of England and Wales, totalling 387 sites and 463 taxa. The environmental gradients include two of land-use intensity (urbanisation and agriculture), three physical (degree of shading, emergent vegetation cover, surface area) and one chemical (pH). We follow a hierarchical effect-response functional trait framework (Hooper *et al.* 2002; Laliberté *et al.* 2010) in order to measure response diversity based on the distinction between effect traits and response traits (Diaz & Cabido 2001). Species are classified across each study into functional effect groups, using three traits (17 categories, Tachet *et al.* 2010) that affect the biogeochemical processes (e.g. nutrient and carbon cycling) which are critical to ecosystem service provision. The response diversity of each effect group is then quantified using a further nine traits that affect macroinvertebrate responses to disturbances. The aims of the meta-analyses were: (1) to estimate the mean effect of environmental gradients on response diversity and functional redundancy across all studies and (2) to test the null hypotheses that neither land-use nor environmental gradients have an effect on response diversity or functional redundancy within ponds. In so doing we are also able to consider whether the conservation of biodiversity is a useful objective for the maintenance of ecosystem services in ponds.

Materials and methods

Macroinvertebrate sampling

Data collection methodologies employed by all seven contributing studies (Table 1) broadly followed the standardized guidelines of the National Pond Survey (Biggs *et al.* 1998) including a three minute sweep sample divided between the mesohabitats present (Hill *et al.* 2016). Water bodies included were mostly ponds (99%) with a surface area between 1m^2 and 2ha that hold water for at least four months of the year (Biggs *et al.* 1998), with some (1%) larger in surface area, but shallow enough for the growth of rooted vegetation throughout (e.g. Morgan 1930). All studies used pooled data from sampling campaigns carried out during spring, summer and autumn months with the exception of those in the West Midlands which were only sampled during spring and summer. In all, samples from 387 sites in England and Wales were included in this study (Fig. 1), resulting in 463 taxa (see Table S1).

Macroinvertebrate identification was typically to species level with the exception of Oligochaeta, Diptera and small bivalves.

Environmental gradients

Six environmental gradients were defined. Two anthropogenic land-use intensity gradients were based on the percentage coverage of agricultural and urban land within a 500m distance from the pond centroid. Studies were matched to either Land Cover Map 2000 (Fuller *et al.* 2002) or 2007 (Morton *et al.* 2011); whichever was closest to the sampling periods. All seven studies recorded a variety of physical and chemical data, however, three physical and one chemical measure were consistently measured across all studies, with the exception of shading within that of West Yorkshire (Wood *et al.* 2001). Thus, environmental gradients were derived from measures of tree cover (i.e. percent shaded), the percentage coverage of emergent (e.g. *Typha* sp.) vegetation, surface area and pH. Covariance between the gradients was tested for statistical independence using Spearman's Rank (Supporting information Table S2), with all correlations less than $\rho<0.40$.

To facilitate comparison across studies, four standardised classes were calculated for each gradient using quartiles based on data pooled from across all seven studies. As a consequence of this approach, not all studies had sites represented across all classes, in particular the most urban of studies (Hill, Mathers & Wood 2015; Thornhill *et al.* 2017, Table S3).

Functional effect and response traits

It is highly recommended in trait analyses to have all data at the same taxonomic level (Statzner, Bonada & Dolédec 2007) and our trait database predominately included species level information. In all we chose 12 traits comprising 72 categories (Table 2). The association between a taxon and a trait category was described using an affinity score based on a fuzzy coding technique (Chevenet, Doledec & Chessel 1994). The affinity of a taxon to each category was coded from zero (no affinity) to three or ten (maximum affinity depending on the trait). Where affinity scores were not assigned an even weight was attributed across the trait categories. Affinity scores were standardized, so that their sum for a given taxon and a given trait was equal to one. This procedure ensured the same contribution of each trait to statistical analyses (Péru & Dolédec 2010).

Effect traits were defined as traits that influence biogeochemical processes, while response traits were primarily regenerative traits that influence how species respond to disturbances (Lavorel & Garnier 2002). Classifying traits into effect and response can be challenging and they can often be found to coincide (Diaz & Cabido 2001; Suding *et al.* 2008; Laliberté *et al.* 2010). Three effect traits were selected in this study, which were also relevant as response traits. First, body mass is strongly correlated to metabolic rate in animals (Ehnes *et al.* 2014) which is directly related to several biological rates and processes such as predation and decomposition (Barnes *et al.* 2014; Mumme *et al.* 2015). Second, voltinism (the potential number of cycles within a year) may have important implications for temporal redistribution of nutrient processing (Merritt *et al.* 1996; Kovalenko *et al.* 2014). Finally, feeding habits have a clear and direct link to ecosystem processes such as leaf litter breakdown (Cummins 1979; Lecerf *et al.* 2006). The remaining nine response traits are identified in Table 2.

Response diversity and functional redundancy

The methodological approach to characterise response and functional diversity developed by Laliberté *et al.* (2010) was followed. For each dataset, we first computed a Gower dissimilarity matrix between all species using effect traits. Species were assigned to functional effect groups using Ward's minimum variance method, implementing Ward's clustering criterion (Murtagh & Legendre 2014). The number of effect groups was determined by visually inspecting the clustering dendogram and setting cut-off levels in order to retain a relatively consistent level of group membership. Effect groups were visualised using Non-Metric Multidimensional Scaling (NMDS) with the metaMDS function in the 'vegan' package (Oksanen *et al.* 2017) and were accepted if they displayed statistically significant one-way analysis of similarity (ANOSIM, 9999 permutations) and clear visual separation. To facilitate group identification, mean trait values (and modes for categorical traits) for all effect groups are given in Table S4.

For each site, functional redundancy was quantified as the number of species within an effect group, whilst response diversity of each effect group was quantified by measuring the multivariate functional dispersion based on a Gower dissimilarity matrix of species response traits (FDis, Laliberté & Legendre 2010). Gower dissimilarity was chosen because it allows mixed variable types (e.g. categorical and binary), as well as missing values (Legendre & Legendre 1998). The FDis metric is the average distance of individual species to their group centroid in response trait space and is minimally influenced by species number. Therefore, the use of FDis was aimed to ensure that response diversity was statistically independent of functional redundancy. We weighted response diversity by relative abundances as ecosystem function is often closer related to species dominance rather than diversity (Oliver *et al.* 2015), particularly in human-modified environments (Lohbeck *et al.* 2016). A decrease in multivariate dispersion in response trait space (i.e. a loss of response diversity) for a given effect indicates that its composition has shifted towards species that are more similar to each other in how they respond to disturbance, thereby indicating a loss of resilience. If, in a given site, an effect group contained no species or only one species (in which case no multivariate dispersion can be computed), it was assigned a response diversity value of zero (Laliberté *et al.* 2010).

Meta-analysis

For each of the seven study datasets (Table 1) we used all effect groups from all sites as individual observations. Therefore, the total number of observations is equal to the number of effect groups multiplied by the total number of sites, each site representing an independent measurement (where ties were present, observations were assigned equal ranks). First, response diversity and functional redundancy were ranked between sites and within each effect group to control for intergroup differences (Laliberté *et al.* 2010). Second, Pearson correlation coefficients were calculated between environmental gradient category (ordinal variable with four classes for each gradient studied) and either ranked within-group response diversity or ranked within-group functional redundancy. Thus, a rank correlation was generated that is conceptually equivalent to using the Spearman rank correlation with the exception that ranking occurs within each group and not across all groups. We used correlation coefficients as effect sizes in a formal meta-analysis across all datasets using the random effect DerSimonian-Laird (DSL) approach (Schulze 2004).

In the DSL approach, correlations are first transformed using Fisher's Z transformation. The asymptotic variance of $Z_r$is calculated as $V_z = 1/(n-3)$, where n is the sample size (number of effect groups × number of sites. Unlike r which is bounded between -1 and 1, Z_r ranges from $-\infty$ to $+\infty$. Negative values of Z_r indicate a negative association between response diversity (or functional redundancy) and the environmental gradient. The mean effect size $\bar{Z}_r$ represents the average relationship between the environmental gradient and the response diversity or functional redundancy of all effect groups from all seven studies. Z_r and 95% confidence intervals were computed as described by Schulze (2004). The package 'metacor' was used to perform the meta-analysis (Laliberté 2009).

Results

The number of functional effect groups identified per study ranged from five (West Midlands, ROPA) to seven (Temporary Ponds, Wales) based on multivariate clustering analysis, which generated good separation in non-dimensional space and that had significantly more inter- than intra- group dissimilarity in all instances (ANOSIM $r = 0.65$ - 0.76, $P < 0.001$). Effect group memberships averaged 32.6 species (SD 17.5, min. 8, max. 80) and typically related to body size and feeding habit, particularly shredders, predators and scrapers (Table S3).

The FDis metric is constructed so as to be independent of species richness (Laliberté & Legendre 2010). Despite this, the meta-analysis demonstrated the presence of a positive correlation between FDis and functional redundancy across all studies if the whole community is considered at each pond ($\bar{Z}_r = 0.38$, $P < 0.001$, Fig. 2a). However, the strength of association varied between studies, and peaked within the urban studies of West Midlands ($\rho=0.84$, $P < 0.01$) and Leicestershire ($\rho=0.80$, $P < 0.01$), with the lowest correlation observed within the ROPA dataset ($\rho=0.11$, $P > 0.05$). When effect groups were considered the strength of association was much stronger owing to the prevalence of tied ranks ($\bar{Z}_r = 0.78$, $P < 0.001$, Fig. 2b), although the pattern was comparable.

Land-use intensity

The degree of urbanisation within 500m of the pond edge had no clear overall influence on functional redundancy ($\bar{Z}_r = 0.02$, $P = 0.31$) but had an overall significant, positive effect on response diversity ($\bar{Z}_r = 0.05$, $P = 0.03$). For functional redundancy, only the National Pond Survey study was significantly different from zero with a positive response to increasing urbanisation ($Z_r = 0.18$, $P \leq 0.05$, Fig. 3). Both the National Pond Survey ($Z_r = 0.13$, $P \leq 0.05$,

Fig. 4) and ROPA ($Z_r = 0.11$, $P \leq 0.05$) had significant and positive responses in response diversity to urbanisation.

Agriculture displayed a positive effect on functional redundancy ($\bar{Z}_r = 0.09$, $P = 0.003$) and response diversity ($\bar{Z}_r = 0.07$, $P < 0.001$). The effect upon functional redundancy was positive and significantly different from zero for the National Pond Survey ($Z_r = 0.08$, $P \leq 0.05$), ROPA ($Z_r = 0.11$, $P \leq 0.05$), and West Midlands ($Z_r = 0.36$, $P \leq 0.05$) datasets (Fig. 3). Whilst the positive effect was more consistent across all datasets for response diversity, only the National Pond Survey was significantly, and positively different from zero ($Z_r = 0.09$, $P \leq 0.05$, Fig. 4).

A notable variation across effect groups was apparent in the West Midlands, where the response diversity of small scrapers (EG1) decreased with increasing agricultural land-use while all other effect groups increased (Fig. 5e, Table S3).

Partial correlations were ran in order to evaluate whether the effects of land-use remained unaltered when controlling for the effects of local environmental variables (Tables S5 - S8). In most instances there was little deviation from the zero-order correlations. However, with pH as the controlling variable, the strength of correlation between urbanisation and both functional redundancy ($\rho = 0.18$, $P < 0.001$, partial $\rho = 0.10$, $P = 0.01$) and response diversity ($\rho = 0.13$, $P < 0.001$, partial $\rho = 0.06$, $P = 0.10$) was reduced. A similar, but weaker effect was also observed when considering agricultural land-use.

For the most urban studies (West Midlands and Leicestershire) however, partial correlations revealed several interacting factors despite low level of pre-analysis covariance (Table S2). Here, the strength of relation between urbanisation and both functional redundancy, and to a lesser extent response diversity, increased once the effects of shade, emergent vegetation and surface area were controlled for. The largest increase was observed in the West Midlands study when controlling for shade ($\rho = -0.06$, $P = 0.47$, partial $\rho = -0.20$, $P = 0.01$, Table S5).

Physical factors

On average the degree of shading had a negative effect upon both functional redundancy ($\bar{Z}_r = -0.11$, $P = 0.06$) and response diversity ($\bar{Z}_r = -0.03$, $P = 0.20$), however, the direction and shape of the effect differed markedly between studies such that neither were significant at the 95% confidence interval. Two studies (Temporary Ponds, West Midlands) had significant negative functional redundancy effect values ($P \leq 0.05$, Fig. 3) whilst the effect of shading was less pronounced upon response diversity with only the West Midlands study significantly differing from zero ($Z_r = 0.27$, $P \leq 0.05$, Fig. 4).

A non-linear relationship was apparent between increasing shading and response diversity within effect groups (Fig. 5) with three studies (National Pond Survey, Temporary Ponds, Leicestershire) suggesting peaks in the response diversity of most effect groups at intermediate levels of shading.

Coverage of emergent vegetation had an overall positive effect upon functional redundancy ($\bar{Z}_r = 0.15$, $P < 0.001$) and response diversity ($\bar{Z}_r = 0.09$, $P = 0.005$). Four of the seven studies (National Pond Survey, Temporary Ponds, West Midlands, Leicestershire) showed a significant positive effect upon functional redundancy with emergent vegetation ($P \leq 0.05$, Fig. 3), whilst Temporary Ponds, West Yorkshire and Leicestershire showed a positive effect of emergent vegetation coverage for response diversity ($P \leq 0.05$, Fig. 4).

The average effect of surface area upon functional redundancy ($\bar{Z}_r = 0.10$, $P = 0.10$) and response diversity ($\bar{Z}_r = 0.10$, $P = 0.01$) was positive and statistically significant. The strongest responses in functional redundancy were observed within the National Pond

Survey, ROPA, West Midlands and Wales studies (Fig. 3) which extended to the Temporary Ponds dataset when response diversity was considered (Fig. 4).

Changes in response diversity between effect groups contrasted markedly with surface area in Leicestershire ponds with two each showing null (EG 3 and 4, larger shredders and scrapers, filterers), unimodal (EG 1 and 6, medium sized shredders, scrapers and deposit feeders) and positive (EG 2 and 5, large scrapers, filterers and parasites) responses in response diversity (Fig. 5f).

Water chemistry

Overall, no significant effect was observed upon functional redundancy (0.06, $P = 0.27$), or response diversity ($\bar{Z}_r = 0.12$, $P = 0.15$) by pH. Four from the seven studies (National Pond Survey, Temporary Ponds, Wet Midlands, Wales) exhibited a positive response in functional redundancy, significantly different to zero (Fig. 3). However, three were negative and one (Leicestershire) significantly so ($Z_r = -0.33$, $P \leq 0.05$). A more consistent and positive response was apparent in response diversity across all studies, however only the National Pond Survey and West Midlands studies demonstrated a positive effect that significantly differed from ($P \leq 0.05$, Fig. 4).

Patterns in response diversity across different effect groups in individual studies showed some variation with positive, negative and non-linear relationships apparent (Fig. 5). For example, the effect of pH upon response diversity in the National Pond Survey was consistent and positive. However, this consistency of relationship across effect groups was the exception rather than the norm.

Discussion

Local environmental gradients had greater influence upon functional diversity

Ponds are important for a range of ecosystem services, particularly flood management and water purification, as well as cultural services for example, by providing a sense of place or a positive impact upon human well-being (Briers 2014; Hassall 2014). To this end, conventional approaches to conservation have typically focused on the maintenance of biodiversity in order to ensure functional resilience. The meta-analysis revealed that of the gradients studied, local physical and chemical factors had a more consistent and stronger influence upon functional diversity than the land-use gradients considered. The degree of shading generally reduced both functional redundancy (the number of species within functional effect groups) and response diversity (the dispersion of traits amongst effect group members). Conversely, the amount of emergent vegetation and pH (except Leicestershire) had the opposite effect. Several studies have previously identified the dominant effect of local physical or chemical factors upon biodiversity compared to landscape scale factors (Thornhill *et al.* 2017a; Hill *et al.* 2017), whilst others have identified connectivity or proximity to other water bodies as being further significant factors (Gledhill, James & Davies 2008; Chester & Robson 2013; Simaika, Samways & Frenzel 2016). Given the importance of functional redundancy and response diversity to functional resilience (Elmqvist *et al.* 2003; Nyström 2006; Mori, Furukawa & Sasaki 2013) these findings suggest that management at a local-scale such as encouraging emergent vegetation growth and limiting heavy shading can help to ensure the longer-term provision of pivotal ecosystem functions required to maintain particular ecosystem service provision (e.g., nutrient cycling) in the face of global environmental change.

Excessive shading has often been cited as having a negative effect upon the biodiversity of ponds (Gee *et al.* 1997; Sayer *et al.* 2012; Thornhill *et al.* 2017a). Although the presence of some heavily shaded ponds in the pond network is likely to benefit a small number of species (Lundkvist, Landin & Karlsson 2002), the results suggest that excessive shading is to the detriment of functional redundancy and response diversity. However, several of the independent studies incorporated into the meta-analysis exhibited intermediate peaks in both FR and FDis in response to shading reflecting the findings of earlier studies of pond biodiversity (Gee *et al.* 1997; Thornhill *et al.* 2017a). In contrast, emergent vegetation had a positive effect on functional redundancy and response diversity. Macrophyte stands are integral to nutrient recycling, being both a source and a sink of nutrients (Brönmark & Hansson 2008) and are well known to provide refugia, feeding and foraging opportunities for a wide range of invertebrate species (Lillie & Budd 1992; Gee *et al.* 1997).

Overall, increased surface area improved functional redundancy and response diversity in ponds. A similar pattern is well documented between surface area and biodiversity (Søndergaard et al. 2005; Biggs et al. 2005; Ruggiero et al. 2008). However for macroinvertebrates, some studies suggest small patch size and isolation can promote species richness (Scheffer et al. 2006; Nakanishi et al. 2014). Indeed, null or contrasting changes in response diversity between effect groups were occasionally observed here (e.g. West Yorkshire, Leicestershire), suggesting agreement with Oertli et al. (2002) that the effect of pond area can vary between macroinvertebrate groups.

Partial correlations revealed confounding effects of pH upon the relation between urbanisation and functional diversity within the National Pond Survey. With the effect of pH removed, only a weak effect of urbanisation upon functional diversity remained. Reduced invertebrate species richness in more acidic waters is generally expected (Feldman & Connor 1992; Nicolet *et al.* 2004), however, the Leicestershire study was a marked contrast, indicated lower functional diversity with high pH. The Leicestershire study had a skewed prevalence of alkaline sites, with most (66%) having elevated pH (7.6 - 10.3, Table 1, Table S3).

Consequently, the contrast may be due to a low representation of sites with lower pH, or the influence of highly alkaline ponds in a eutrophic state (Interagency Freshwater Group 2015).

Land-use gradients had an inconsistent influence upon functional diversity

There was a weak, but significant effect of both land-use gradients (urbanisation and agriculture) upon response diversity and increasing proportional cover of agricultural land-use appeared to particularly improve functional redundancy in some studies. For example, the most urban study in the West Midlands exhibited a significant improvement in functional redundancy to increasing agriculture. However, this response was only weakly followed in the second most urban study in Leicestershire and both had markedly reduced response diversity effects.

When controlling for the effect of local environmental variables (shade, surface area and emergent vegetation) a stronger, negative effect of increased urbanisation upon both functional redundancy and response diversity was revealed in the West Midlands and Leicestershire studies. In both of these studies larger ponds were retained in more urban areas (e.g. Thornhill *et al.* 2017b), thus suggesting the presence of larger ponds in the most highly urbanised landscapes might support higher levels of functional resilience, as these sites are also likely to be less shaded and support complex macrophyte stands (Hamer & Parris 2011; Hassall *et al.* 2011; Thornhill *et al.* 2017a).

Urbanisation and agriculture were significant, but weak correlates ($\rho = -0.27$, $P < 0.001$). However, the inconsistent response to land-use gradients may suggest that the relative extent of urban versus agricultural land-use is important and may represent replacement of urban land-use with more semi-natural surroundings. Alternatively, the manner of response may reflect that some of the studies were more geographically isolated and offered a parochial view of the environment and were thus more context-dependent (Aiba *et al.* 2016) to which variance in agricultural practices and urban form may contribute. Although we used a frequently cited buffer to characterise land-use influences (500m, Waterkeyn *et al.* 2008; Hill *et al.* 2016), characterising ponds is often challenging as their catchments are ill-defined and their origins varied and frequently anthropogenic (Hill *et al.* 2016; Thornhill *et al.* 2017b).

Biodiversity and ecosystem function

Response diversity, as indicated by the FDis metric is constructed so as to be independent of functional redundancy (Laliberté & Legendre 2010). However, some association was evident between the two across all seven studies. Despite this, the strength of association varied considerably. In addition, one occurrence (from 41) indicated maintenance of response diversity despite significant decreases in functional redundancy (Temporary Ponds and shading) and five indicated significant increases in functional redundancy not matched by response diversity (Fig. 3, Fig. 4). Thus, in agreement with Laliberté *et al.* (2010), response diversity could be little influenced or even increase with concurrent losses in functional redundancy. These findings suggest that the link between ecosystem function and biodiversity in small waterbodies is not clear and the use of ecosystem functioning as a basis for biodiversity conservation should be carefully considered (Srivastava & Vellend 2005; Dee *et al.* 2017). However, given the large degree of turnover between ponds and concomitant changes in species dominance (Hill *et al.* 2017), the maintenance of biodiversity likely remains critical for functional resilience (Lohbeck *et al.* 2016).

Future research

In the present study, we considered the effect of land-use intensity and environmental gradients upon as many as seven different effect groups per study and assigned all species to a functional effect group. However, future research could be focused upon particular trait clusters that relate more explicitly to combinations of traits that contribute to a desired ecosystem service (de Bello *et al.* 2010). Indeed, response diversity varied within effect groups (e.g. scrapers) across the gradients studied suggesting that a generalised effect does not always apply. Nevertheless, a focus on individual processes in isolation is likely to underestimate levels of biodiversity required to maintain multifunctional ecosystems in which the same species can contribute to multiple services (Laliberté *et al.* 2010).

This study incorporated three effect traits that relate predominantly to the recycling and redistribution of nutrients through feeding habits. However, traits could be added for the exploration of other ecosystem service traits such as those that relate to public perceptions of aquatic biodiversity (Hassall 2014). Such traits might be positively (e.g. colour) or negatively (e.g. disease vectors, invasiveness) associated with aesthetic or cultural ecosystem services, which may not align with biochemical processing but could promote the adoption of ponds by local communities.

In conclusion, there is an urgent need for human society to better manage freshwater resources to sustain or enhance the multiplicity of ecosystem services they provide (Durance *et al.* 2016). Until recently, the value of ponds for their biodiversity has been largely overlooked in comparison with larger systems (Williams *et al.* 2004) and scant attention has been paid to their ecosystem functioning. This study identifies key local environmental gradients (e.g. shading, emergent vegetation cover) that influence functional resilience, which could inform tractable management advice. However, the response of individual functional effect groups varied within studies, as did the strength and direction of relationships between studies. For conservation initiatives, the findings suggest that the link between ecosystem function and biodiversity is not clear and the use of ecosystem functioning as a basis for biodiversity conservation should be carefully considered. These differences highlight future areas for research, whilst consideration of additional factors more aligned to anticipated global environmental change (e.g. temperature, water availability) will help predict their influence upon functional resilience in pond ecosystems.

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Table 1 Summary of contributing studies, local physical and chemical and landscape scale characteristics. Figures given are means ±1SD and range in parentheses.

Study ref.	Geography	n	Urb.	Agri.	Shade.	pH.	Emerge.	Area (sq. m)	Reference
NPS	England & Wales	119	10.7±19.0 (0.0 - 79.5)	40.4±28.5 (0.0 - 92.1)	17.8±23.2 (0.0 - 100)	6.6±1.0 (3.8 - 8.6)	30.4±22.8 (0.1 - 90.0)	2162±3782 (8.0 - 20650)	Biggs et al., 1998
ROPA	England & Wales	34	8.4±15.2 (0.0 - 80.8)	67.1±26.9 (2.6 - 97.1)	11.0±14.4 (0.0 - 65.0)	7.2±1.2 (3.3 - 8.7)	25.8±23.5 (0.1 - 80.3)	1399±1890 (26 - 8200)	FHT Realising Our Potential Award dataset (unpub.)
TP	England & Wales	76	17.5±23.2 (0.0 - 91.9)	46.6±26.6 (0.0 - 96.2)	21.0±28.1 (0.0 - 90.0)	6.9±1.2 (2.5 - 9.5)	50.9±31.5 (0.0 - 100)	1060±1704 (25 - 10000)	FHT* Temporary Ponds dataset (unpub.)
W.Yorks	West Yorkshire	36	15.6±18.0 (0.6 - 86.1)	29.7±11.1 (2.5 - 57.4)	n/a	6.9±0.6 (5.2 - 8.0)	18.3±18.0 (0.0 - 60.0)	2845±3726 (50 - 16000)	Wood et al., 2001
W.Midlands	West Midlands	30	67.7±28.4 (6.0 - 96.8)	26.7±24.3 (0.5 - 75.6)	30.1±31.4 (0.0 - 100)	7.7±0.5 (6.7 - 9.1)	12.6±13.2 (0.0 - 41.4)	3597±4053 (299 - 14967)	Thornhill et al., 2017
Leic.	Leicestershire	41	51.6±31.7 (0.4 - 94.6)	41.1±26.9 (5.5 - 96.2)	17.5±28.4 (0.0 - 100)	7.8±0.6 (6.3 - 9.8)	23.0±29.3 (0.0 - 100)	780±1929 (1.0 - 9309)	Hill et al., 2015

Wales	Wales	51	1.8±2.6 (0.0 - 12.3)	55.6±30.3 (0.0 - 94.0)	41.8±15.3 (9 - 68)	7.1±0.9 (5.0 - 10.2)	11.8±20.9 (0.0 - 98)	4476±10309 (100 - 62000)	Gee *et al.* 1997

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Table 2 Selected invertebrate functional effect (E) and response (R) traits used in the analysis (after Tachet *et al.* 2010)

Functional trait	E/R	No. categories
Maximum body size	E/R	7
Life cycle duration	R	2
Voltinism	E/R	3
Aquatic stage	R	4
Reproduction	R	8
Dispersal	R	4
Resistance forms	R	5
Respiration	R	5
Locomotion and substrate relation	R	8
Substrate (preferendum)	R	9
Food	R	9
Feeding habits	E/R	8

Figure captions

Figure 1 Distribution of sites within seven contributing studies across England and Wales

Figure 2 Meta-analyses of the relationship between functional redundancy and response diversity (FDis). Effect sizes Z_r are Z-transformed Pearson correlation coefficients (r) between a) ranked functional redundancy and response diversity considering the whole community and b) within each effect group, following the DerSimonian-Laird (DSL) approach. A positive value of Z_r indicates correlation between the two measures of functional diversity. Box size is proportional to the weight given to each study, based on sample size and variance. Grey lines are 95% CI. The dashed grey line represents the null hypothesis. The summary statistic (mean effect size $\bar{Z}_r$) is represented by a black diamond whose width corresponds to its 95% CI.

Figure 3 Meta-analyses of the effect of land-use intensity and environmental gradients on functional redundancy across seven pond biodiversity studies. Effect sizes Z_r are Z-transformed Pearson correlation coefficients (r) between gradient category (four categories within each gradient) and ranked within-group functional redundancy following the DerSimonian-Laird (DSL) approach. A negative value of Z_r indicates a decrease in functional redundancy as the independent parameter category increases. Box size is proportional to the weight given to each study, based on sample size and variance. Grey lines are 95% CI. The dashed grey line represents the null hypothesis. The summary statistic (mean effect size $\bar{Z}_r$) is represented by a black diamond whose width corresponds to its 95% CI. Shading data unavailable for W. Yorks.

Figure 4 Meta-analyses of the effect of land-use intensity and environmental gradients on response diversity across seven pond biodiversity studies. Effect sizes Z_r are Z-transformed Pearson correlation coefficients (r) between gradient category (four categories within each gradient) and ranked within-group response diversity following the DerSimonian-Laird (DSL) approach. A negative value of Z_r indicates a decrease in functional diversity as the independent parameter category increases. Box size is proportional to the weight given to each study, based on sample size and variance. Grey lines are 95% CI. The dashed grey line represents the null hypothesis. The summary statistic (mean effect size $\bar{Z}_r$) is represented by a black diamond whose width corresponds to its 95% CI. Shading data unavailable for W.Yorks.

Figure 5 Response diversity (FDis) of individual functional effect groups (EG, Table S3) in response to land-use intensity and environmental gradients for each of the seven studies. For clarity, individual data points are omitted and only loess-smoothed curves are shown (span = 0.75). In each graph, curves of different colours represent different effect groups. FDis is ranked within each effect group (*y*-axis). Z_r, the effect size used in the meta-analysis, is the z-transformed Pearson correlation coefficient (r) between RD and land-use intensity or environmental gradient computed from all effect groups. a) National Pond Survey, b) ROPA, c) TP, d) W. Yorks, e) W. Midlands, f) Leicestershire, g) Wales. Shading data unavailable for W. Yorks.

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Author contribution statement

Ian A. Thornhill conceived of the presented study, carried out the statistical analysis and drafted the manuscript in collaboration with all other authors who each provided critical feedback through various media. Ian A. Thornhill also carried out field and laboratory work for the West Midlands dataset included within the study.

Jeremy Biggs provided early insight into the concept here presented and oversaw collection of several of the studied datasets in his capacity as Director of the Freshwater Habitats Trust. These datatsets were the National Pond Survey, ROPA and Temporary Ponds as well as provided useful edits and suggestions in the finalisation of the presented manuscript.

Matthew J. Hill provided invaluable intellectual input into the conceptualisation and interpretation of the presented manuscript and was central to the dataset collected in Leicestershire (with support from Paul J. Wood), carrying out field collection and laboratory analysis.

Paul J. Wood carried out the sampling and analysis of the West Yorkshire (Loughborough) dataset and provided important comments and edits throughout the draft stages.

Rob Briers was pivotal to the scope of the analysis here presented, making early recommendations to improve the robustness of the analytical approach - specifically regarding land-use. Rob Briers was also an important conduit for expanding the analysis from six to seven datasets through his liaison with John Gee. He also make valuable comments and suggestions regarding the methodological approach here applied.

Dave Gledhill, Paul J. Wood and Mark Ledger helped shape the manuscript, providing useful comments on the findings in relation to the wider literature on urban freshwater research and functional resilience. Paul J. Wood and Mark Ledger were also pivotal to data collection in the Leicestershire and West Midlands datasets respectively.

John Gee contributed the most rural datasets here considered (Wales) and made insightful comments on the analytical approach and interpretation of the findings. In addition he made notable contributions to the general layout and flow of the manuscript.

Chris Hassall facilitated the initial collation of the datasets here included and gave early intellectual advice on the concept applied and importance of the study. He also provided valuable comment at the draft stages which have helped improve the relevance of the manuscript to the wider research community.