

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

3 Thornhill, I. A.<sup>1,2</sup>, Biggs, J.<sup>3</sup>, Hill, M. J.<sup>4</sup>, Briers, R.<sup>5</sup>, Gledhill, D.<sup>6</sup>, Wood, P. J.<sup>7</sup>, Gee, J. H.  
4 R.<sup>8</sup>, Ledger, M.<sup>1</sup> and Hassall, C.<sup>9</sup>.

5 <sup>1</sup> College of Liberal Arts, Bath Spa University, Newton St. Loe, Bath, BA2 9BN

6 <sup>2</sup> Geography, Earth and Environmental Science, University of Birmingham, Edgbaston,  
7 Birmingham, B15 2TT, UK

8 <sup>3</sup>Freshwater Habitats Trust, Bury Knowle House, Headington, Oxford, OX3 9HY

9 <sup>4</sup>Institute of Science and the Environment, University of Worcester, Henwick Grove,  
10 Worcester, WR2 6AJ, UK

11 <sup>5</sup>School of Applied Sciences, Edinburgh Napier University, Edinburgh, UK

12 <sup>6</sup>Research Institute for the Built and Human Environment, School of Environment and  
13 Life Sciences, Peel Building, University of Salford, Salford, Greater Manchester M5  
14 4WT, UK

15 <sup>7</sup>Centre for Hydrological and Ecosystem Science, Department of Geography,  
16 Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK

17 <sup>8</sup>IBERS (Institute of Biological, Environmental & Rural Sciences), Aberystwyth  
18 University, Penglais, Aberystwyth, SY23 3DA

19 <sup>9</sup>School of Biology, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK

20

21 **Corresponding author:** Ian Thornhill (ian.thornhill@live.co.uk, +44 (0) 7860 61 8575

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23 **Abstract**

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

32 In this study, a meta-analysis of seven separate pond studies from across England and Wales  
33 was carried out to explore the effect of urban and agricultural land-use gradients, shading,  
34 emergent vegetation, surface area and pH upon groups of functionally similar members of the  
35 macroinvertebrate fauna. Functional effect groups were first identified by carrying out a  
36 hierarchical cluster analysis using body size, voltinism and feeding habits (18 categories) that  
37 are closely related to biogeochemical processes (e.g. nutrient and carbon recycling).

38 Secondly, the influence of the gradients upon effect group membership (functional  
39 redundancy - FR) and the breadth of traits available to aid ecosystem recovery (response  
40 diversity) was assessed using species counts and functional dispersion (FDis) using 12  
41 response traits. The effect of land-use gradients was unpredictable, whilst there was a  
42 negative response in both FR and FDis to shading and positive responses to increases in  
43 emergent vegetation cover and surface area. An inconsistent association between FDis and  
44 FR suggested that arguments for taxonomic biodiversity conservation in order to augment  
45 ecosystem functioning are too simplistic. Thus, a deeper understanding of the response of  
46 functional diversity to disturbance could have greater impact with decision-makers who may

47 relate better to the loss of ecosystem function in response to environmental degradation than  
48 species loss alone.

#### 49 **Keywords**

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

52

#### 53 **Introduction**

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

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

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

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

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

95 the purpose of securing ecosystem service provision may not be appropriate (Lohbeck *et al.*  
96 2016)

97 Among the emerging anthropogenic stressors to which ecosystems are responding are  
98 changes in land-use patterns such as agricultural intensification and urbanisation, which are  
99 common causes of degradation and biodiversity loss (Sala *et al.* 2000; Mooney *et al.* 2009).

100 In addition, a number of pond studies have identified local environmental factors to have an  
101 impact upon biodiversity including shade (Hassall, Hollinshead & Hull 2011; Thornhill *et al.*  
102 2017a), surface area (Bronmark 1985; Heino 2000), emergent vegetation (Scheffer *et al.*  
103 1993; Declerck *et al.* 2005) and pH (Biggs *et al.* 2005), but no attempt has been made to  
104 directly consider response diversity along these gradients.

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

113 In the present study, we consider how six environmental gradients effect pond  
114 macroinvertebrate functional redundancy and response diversity through a meta-analysis of  
115 seven studies carried out across urban and rural landscapes of England and Wales, totalling  
116 387 sites and 463 taxa. The environmental gradients include two of land-use intensity  
117 (urbanisation and agriculture), three physical (degree of shading, emergent vegetation cover,  
118 surface area) and one chemical (pH). We follow a hierarchical effect-response functional trait

119 framework (Hooper *et al.* 2002; Laliberté *et al.* 2010) in order to measure response diversity  
120 based on the distinction between effect traits and response traits (Diaz & Cabido 2001).  
121 Species are classified across each study into functional effect groups, using three traits (17  
122 categories, Tachet *et al.* 2010) that affect the biogeochemical processes (e.g. nutrient and  
123 carbon cycling) which are critical to ecosystem service provision. The response diversity of  
124 each effect group is then quantified using a further nine traits that affect macroinvertebrate  
125 responses to disturbances. The aims of the meta-analyses were: (1) to estimate the mean  
126 effect of environmental gradients on response diversity and functional redundancy across all  
127 studies and (2) to test the null hypotheses that neither land-use nor environmental gradients  
128 have an effect on response diversity or functional redundancy within ponds. In so doing we  
129 are also able to consider whether the conservation of biodiversity is a useful objective for the  
130 maintenance of ecosystem services in ponds.

## 131 **Materials and methods**

### 132 **Macroinvertebrate sampling**

133 Data collection methodologies employed by all seven contributing studies (Table 1) broadly  
134 followed the standardized guidelines of the National Pond Survey (Biggs *et al.* 1998)  
135 including a three minute sweep sample divided between the mesohabitats present (Hill *et al.*  
136 2016). Water bodies included were mostly ponds (99%) with a surface area between 1m<sup>2</sup> and  
137 2ha that hold water for at least four months of the year (Biggs *et al.* 1998), with some (1%)  
138 larger in surface area, but shallow enough for the growth of rooted vegetation throughout  
139 (e.g. Morgan 1930). All studies used pooled data from sampling campaigns carried out during  
140 spring, summer and autumn months with the exception of those in the West Midlands which  
141 were only sampled during spring and summer. In all, samples from 387 sites in England and  
142 Wales were included in this study (Fig. 1), resulting in 463 taxa (see Table S1).

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

#### 145 **Environmental gradients**

146 Six environmental gradients were defined. Two anthropogenic land-use intensity gradients  
147 were based on the percentage coverage of agricultural and urban land within a 500m distance  
148 from the pond centroid. Studies were matched to either Land Cover Map 2000 (Fuller *et al.*  
149 2002) or 2007 (Morton *et al.* 2011); whichever was closest to the sampling periods. All seven  
150 studies recorded a variety of physical and chemical data, however, three physical and one  
151 chemical measure were consistently measured across all studies, with the exception of  
152 shading within that of West Yorkshire (Wood *et al.* 2001). Thus, environmental gradients  
153 were derived from measures of tree cover (i.e. percent shaded), the percentage coverage of  
154 emergent (e.g. *Typha* sp.) vegetation, surface area and pH. Covariance between the gradients  
155 was tested for statistical independence using Spearman's Rank (Supporting information Table  
156 S2), with all correlations less than  $\rho < 0.40$ .

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

#### 161 **Functional effect and response traits**

162 It is highly recommended in trait analyses to have all data at the same taxonomic level  
163 (Statzner, Bonada & Dolédec 2007) and our trait database predominately included species  
164 level information. In all we chose 12 traits comprising 72 categories (Table 2). The  
165 association between a taxon and a trait category was described using an affinity score based  
166 on a fuzzy coding technique (Chevenet, Doledec & Chessel 1994). The affinity of a taxon to

167 each category was coded from zero (no affinity) to three or ten (maximum affinity depending  
168 on the trait). Where affinity scores were not assigned an even weight was attributed across the  
169 trait categories. Affinity scores were standardized, so that their sum for a given taxon and a  
170 given trait was equal to one. This procedure ensured the same contribution of each trait to  
171 statistical analyses (Péru & Dolédec 2010).

172 Effect traits were defined as traits that influence biogeochemical processes, while response  
173 traits were primarily regenerative traits that influence how species respond to disturbances  
174 (Lavorel & Garnier 2002). Classifying traits into effect and response can be challenging and  
175 they can often be found to coincide (Diaz & Cabido 2001; Suding *et al.* 2008; Laliberté *et al.*  
176 2010). Three effect traits were selected in this study, which were also relevant as response  
177 traits. First, body mass is strongly correlated to metabolic rate in animals (Ehnes *et al.* 2014)  
178 which is directly related to several biological rates and processes such as predation and  
179 decomposition (Barnes *et al.* 2014; Mumme *et al.* 2015). Second, voltinism (the potential  
180 number of cycles within a year) may have important implications for temporal redistribution  
181 of nutrient processing (Merritt *et al.* 1996; Kovalenko *et al.* 2014). Finally, feeding habits  
182 have a clear and direct link to ecosystem processes such as leaf litter breakdown (Cummins  
183 1979; Lecerf *et al.* 2006). The remaining nine response traits are identified in Table 2.

#### 184 **Response diversity and functional redundancy**

185 The methodological approach to characterise response and functional diversity developed by  
186 Laliberté *et al.* (2010) was followed. For each dataset, we first computed a Gower  
187 dissimilarity matrix between all species using effect traits. Species were assigned to  
188 functional effect groups using Ward's minimum variance method, implementing Ward's  
189 clustering criterion (Murtagh & Legendre 2014). The number of effect groups was  
190 determined by visually inspecting the clustering dendrogram and setting cut-off levels in order



191 to retain a relatively consistent level of group membership. Effect groups were visualised  
192 using Non-Metric Multidimensional Scaling (NMDS) with the metaMDS function in the  
193 'vegan' package (Oksanen *et al.* 2017) and were accepted if they displayed statistically  
194 significant one-way analysis of similarity (ANOSIM, 9999 permutations) and clear visual  
195 separation. To facilitate group identification, mean trait values (and modes for categorical  
196 traits) for all effect groups are given in Table S4.

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

214 **Meta-analysis**

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

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

237 **Results**

238 The number of functional effect groups identified per study ranged from five (West  
239 Midlands, ROPA) to seven (Temporary Ponds, Wales) based on multivariate clustering  
240 analysis, which generated good separation in non-dimensional space and that had  
241 significantly more inter- than intra- group dissimilarity in all instances (ANOSIM  $r = 0.65 -$   
242  $0.76$ ,  $P < 0.001$ ). Effect group memberships averaged 32.6 species (SD 17.5, min. 8, max. 80)  
243 and typically related to body size and feeding habit, particularly shredders, predators and  
244 scrapers (Table S3).

245 The FDis metric is constructed so as to be independent of species richness (Laliberté &  
246 Legendre 2010). Despite this, the meta-analysis demonstrated the presence of a positive  
247 correlation between FDis and functional redundancy across all studies if the whole  
248 community is considered at each pond ( $\bar{Z}_r = 0.38$ ,  $P < 0.001$ , Fig. 2a). However, the strength  
249 of association varied between studies, and peaked within the urban studies of West Midlands  
250 ( $\rho=0.84$ ,  $P < 0.01$ ) and Leicestershire ( $\rho=0.80$ ,  $P < 0.01$ ), with the lowest correlation observed  
251 within the ROPA dataset ( $\rho=0.11$ ,  $P > 0.05$ ). When effect groups were considered the  
252 strength of association was much stronger owing to the prevalence of tied ranks ( $\bar{Z}_r = 0.78$ ,  $P$   
253  $< 0.001$ , Fig. 2b), although the pattern was comparable.

254 **Land-use intensity**

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

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

262 Agriculture displayed a positive effect on functional redundancy ( $\bar{Z}_r = 0.09$ ,  $P = 0.003$ ) and  
263 response diversity ( $\bar{Z}_r = 0.07$ ,  $P < 0.001$ ). The effect upon functional redundancy was positive  
264 and significantly different from zero for the National Pond Survey ( $Z_r = 0.08$ ,  $P \leq 0.05$ ),  
265 ROPA ( $Z_r = 0.11$ ,  $P \leq 0.05$ ), and West Midlands ( $Z_r = 0.36$ ,  $P \leq 0.05$ ) datasets (Fig. 3). Whilst  
266 the positive effect was more consistent across all datasets for response diversity, only the  
267 National Pond Survey was significantly, and positively different from zero ( $Z_r = 0.09$ ,  $P \leq$   
268  $0.05$ , Fig. 4).

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

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

279 For the most urban studies (West Midlands and Leicestershire) however, partial correlations  
280 revealed several interacting factors despite low level of pre-analysis covariance (Table S2).  
281 Here, the strength of relation between urbanisation and both functional redundancy, and to a  
282 lesser extent response diversity, increased once the effects of shade, emergent vegetation and

283 surface area were controlled for. The largest increase was observed in the West Midlands  
284 study when controlling for shade ( $\rho = -0.06$ ,  $P = 0.47$ , partial  $\rho = -0.20$ ,  $P = 0.01$ , Table S5).

### 285 **Physical factors**

286 On average the degree of shading had a negative effect upon both functional redundancy ( $\bar{Z}_r$   
287  $= -0.11$ ,  $P = 0.06$ ) and response diversity ( $\bar{Z}_r = -0.03$ ,  $P = 0.20$ ), however, the direction and  
288 shape of the effect differed markedly between studies such that neither were significant at the  
289 95% confidence interval. Two studies (Temporary Ponds, West Midlands) had significant  
290 negative functional redundancy effect values ( $P \leq 0.05$ , Fig. 3) whilst the effect of shading  
291 was less pronounced upon response diversity with only the West Midlands study significantly  
292 differing from zero ( $Z_r = 0.27$ ,  $P \leq 0.05$ , Fig. 4).

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

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

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

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

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

### 313 **Water chemistry**

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

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

327 **Discussion**

328 **Local environmental gradients had greater influence upon functional diversity**

329 Ponds are important for a range of ecosystem services, particularly flood management and  
330 water purification, as well as cultural services for example, by providing a sense of place or a  
331 positive impact upon human well-being (Briers 2014; Hassall 2014). To this end,  
332 conventional approaches to conservation have typically focused on the maintenance of  
333 biodiversity in order to ensure functional resilience. The meta-analysis revealed that of the  
334 gradients studied, local physical and chemical factors had a more consistent and stronger  
335 influence upon functional diversity than the land-use gradients considered. The degree of  
336 shading generally reduced both functional redundancy (the number of species within  
337 functional effect groups) and response diversity (the dispersion of traits amongst effect group  
338 members). Conversely, the amount of emergent vegetation and pH (except Leicestershire)  
339 had the opposite effect. Several studies have previously identified the dominant effect of local  
340 physical or chemical factors upon biodiversity compared to landscape scale factors (Thornhill  
341 *et al.* 2017a; Hill *et al.* 2017), whilst others have identified connectivity or proximity to other  
342 water bodies as being further significant factors (Gledhill, James & Davies 2008; Chester &  
343 Robson 2013; Simaika, Samways & Frenzel 2016). Given the importance of functional  
344 redundancy and response diversity to functional resilience (Elmqvist *et al.* 2003; Nyström  
345 2006; Mori, Furukawa & Sasaki 2013) these findings suggest that management at a local-  
346 scale such as encouraging emergent vegetation growth and limiting heavy shading can help to  
347 ensure the longer-term provision of pivotal ecosystem functions required to maintain  
348 particular ecosystem service provision (e.g., nutrient cycling) in the face of global  
349 environmental change.

350 Excessive shading has often been cited as having a negative effect upon the biodiversity of  
351 ponds (Gee *et al.* 1997; Sayer *et al.* 2012; Thornhill *et al.* 2017a). Although the presence of

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

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

370 Partial correlations revealed confounding effects of pH upon the relation between  
371 urbanisation and functional diversity within the National Pond Survey. With the effect of pH  
372 removed, only a weak effect of urbanisation upon functional diversity remained. Reduced  
373 invertebrate species richness in more acidic waters is generally expected (Feldman & Connor  
374 1992; Nicolet *et al.* 2004), however, the Leicestershire study was a marked contrast, indicated  
375 lower functional diversity with high pH. The Leicestershire study had a skewed prevalence of  
376 alkaline sites, with most (66%) having elevated pH (7.6 - 10.3, Table 1, Table S3).



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

379 **Land-use gradients had an inconsistent influence upon functional diversity**

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

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

395 Urbanisation and agriculture were significant, but weak correlates ( $\rho = -0.27$ ,  $P < 0.001$ ).

396 However, the inconsistent response to land-use gradients may suggest that the relative extent  
397 of urban versus agricultural land-use is important and may represent replacement of urban  
398 land-use with more semi-natural surroundings. Alternatively, the manner of response may  
399 reflect that some of the studies were more geographically isolated and offered a parochial  
400 view of the environment and were thus more context-dependent (Aiba *et al.* 2016) to which

401 variance in agricultural practices and urban form may contribute. Although we used a  
402 frequently cited buffer to characterise land-use influences (500m, Waterkeyn *et al.* 2008; Hill  
403 *et al.* 2016), characterising ponds is often challenging as their catchments are ill-defined and  
404 their origins varied and frequently anthropogenic (Hill *et al.* 2016; Thornhill *et al.* 2017b).

#### 405 **Biodiversity and ecosystem function**

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

#### 420 **Future research**

421 In the present study, we considered the effect of land-use intensity and environmental  
422 gradients upon as many as seven different effect groups per study and assigned all species to  
423 a functional effect group. However, future research could be focused upon particular trait  
424 clusters that relate more explicitly to combinations of traits that contribute to a desired

425 ecosystem service (de Bello *et al.* 2010). Indeed, response diversity varied within effect  
426 groups (e.g. scrapers) across the gradients studied suggesting that a generalised effect does  
427 not always apply. Nevertheless, a focus on individual processes in isolation is likely to  
428 underestimate levels of biodiversity required to maintain multifunctional ecosystems in which  
429 the same species can contribute to multiple services (Laliberté *et al.* 2010).

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

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

449 global environmental change (e.g. temperature, water availability) will help predict their  
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742 Table 1 Summary of contributing studies, local physical and chemical and landscape scale characteristics. Figures given are means  $\pm$ 1SD and  
 743 range in parentheses.

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

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

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 <i>et al.</i> 1997
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744 \*Freshwater Habitats Trust

745 Table 2 Selected invertebrate functional effect (E) and response (R) traits used in the analysis

746 (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

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748

749 **Figure captions**

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

751 Figure 2 Meta-analyses of the relationship between functional redundancy and response

752 diversity (FDis). Effect sizes  $Z_r$  are Z-transformed Pearson correlation coefficients ( $r$ )

753 between a) ranked functional redundancy and response diversity considering the whole

754 community and b) within each effect group, following the DerSimonian-Laird (DSL)

755 approach. A positive value of  $Z_r$  indicates correlation between the two measures of functional

756 diversity. Box size is proportional to the weight given to each study, based on sample size and

757 variance. Grey lines are 95% CI. The dashed grey line represents the null hypothesis. The

758 summary statistic (mean effect size  $\bar{Z}_r$ ) is represented by a black diamond whose width

759 corresponds to its 95% CI.

760 Figure 3 Meta-analyses of the effect of land-use intensity and environmental gradients on

761 functional redundancy across seven pond biodiversity studies. Effect sizes  $Z_r$  are Z-

762 transformed Pearson correlation coefficients ( $r$ ) between gradient category (four categories

763 within each gradient) and ranked within-group functional redundancy following the

764 DerSimonian-Laird (DSL) approach. A negative value of  $Z_r$  indicates a decrease in functional

765 redundancy as the independent parameter category increases. Box size is proportional to the

766 weight given to each study, based on sample size and variance. Grey lines are 95% CI. The

767 dashed grey line represents the null hypothesis. The summary statistic (mean effect size  $\bar{Z}_r$ ) is

768 represented by a black diamond whose width corresponds to its 95% CI. Shading data

769 unavailable for W. Yorks.

770 Figure 4 Meta-analyses of the effect of land-use intensity and environmental gradients on

771 response diversity across seven pond biodiversity studies. Effect sizes  $Z_r$  are Z-transformed

772 Pearson correlation coefficients ( $r$ ) between gradient category (four categories within each

773 gradient) and ranked within-group response diversity following the DerSimonian-Laird  
774 (DSL) approach. A negative value of  $Z_r$  indicates a decrease in functional diversity as the  
775 independent parameter category increases. Box size is proportional to the weight given to  
776 each study, based on sample size and variance. Grey lines are 95% CI. The dashed grey line  
777 represents the null hypothesis. The summary statistic (mean effect size  $\bar{Z}_r$ ) is represented by a  
778 black diamond whose width corresponds to its 95% CI. Shading data unavailable for  
779 W. Yorks.

780 Figure 5 Response diversity (FDis) of individual functional effect groups (EG, Table S3) in  
781 response to land-use intensity and environmental gradients for each of the seven studies. For  
782 clarity, individual data points are omitted and only loess-smoothed curves are shown (span =  
783 0.75). In each graph, curves of different colours represent different effect groups. FDis is  
784 ranked within each effect group (y-axis).  $Z_r$ , the effect size used in the meta-analysis, is the z-  
785 transformed Pearson correlation coefficient (r) between RD and land-use intensity or  
786 environmental gradient computed from all effect groups. a) National Pond Survey, b) ROPA,  
787 c) TP, d) W. Yorks, e) W. Midlands, f) Leicestershire, g) Wales. Shading data unavailable for  
788 W. Yorks.

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