

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

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

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

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

8 ³Freshwater Habitats Trust, Bury Knowle House, Headington, Oxford, OX3 9HY

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

11 ⁵School of Applied Sciences, Edinburgh Napier University, Edinburgh, UK

12 ⁶Research 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 ⁷Centre for Hydrological and Ecosystem Science, Department of Geography,
16 Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK

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

19 ⁹School 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

22 **Paper type:** Original research

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 1m² 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
450 influence upon functional resilience in pond ecosystems.

451 **Acknowledgements**

452 The authors would like to thank the various organizations who provided resources for the
453 datasets included in this study: IT is grateful for the support from the Natural Environment
454 Research Council, The James Hutton Institute and various private landowners. JB is thankful
455 to the EU Life Program who funded the PondLife Project. MH would like to acknowledge
456 Leicestershire County Council and the private landowners that granted access to their land.
457 DG would like to thank Halton Borough Council for support and access to pond sites and JG
458 would like to thank Natural Resource for Wales, Dyfed and Powys County Councils, Welsh
459 National Parks and the Environment Agency. CH is grateful for support from a Marie Curie
460 International Incoming Fellowship within the 7th European Community Framework
461 Programme.

462 **References**

- 463 Aiba, M., Kurokawa, H., Onoda, Y., Oguro, M., Nakashizuka, T. & Masaki, T. (2016)
464 Context-dependent changes in the functional composition of tree communities along
465 successional gradients after land-use change. *Journal of Ecology*, **104**, 1347–1356.
- 466 Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. &
467 Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem
468 functioning and services. *Ecology letters*, **9**, 1146–56.
- 469 Barnes, A.D., Jochum, M., Mumme, S., Haneda, N.F., Farajallah, A., Widarto, T.H. & Brose,
470 U. (2014) Consequences of tropical land use for multitrophic biodiversity and ecosystem
471 functioning. *Nature Communications*, **5**, 5351.

- 472 de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg,
473 M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins da Silva, P., Potts, S.G., Sandin, L.,
474 Sousa, J.P., Storkey, J., Wardle, D.A. & Harrison, P.A. (2010) Towards an assessment
475 of multiple ecosystem processes and services via functional traits. *Biodiversity and*
476 *Conservation*, **19**, 2873–2893.
- 477 Biggs, J., Fox, G., Nicolet, P., Walker, D., Whitfield, M. & Williams, P. (1998) *A Guide to*
478 *the Methods of the National Pond Survey*.
- 479 Biggs, J., Williams, P., Whitfield, M., Nicolet, P. & Weatherby, A. (2005) 15 years of pond
480 assessment in Britain: results and lessons learned from the work of Pond Conservation.
481 *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 693–714.
- 482 Bolund, P. & Hunhammar, S. (1999) Ecosystem services in urban areas. *Ecological*
483 *Economics*, **29**, 293–301.
- 484 Briers, R. a. (2014) Invertebrate communities and environmental conditions in a series of
485 urban drainage ponds in eastern Scotland: Implications for biodiversity and conservation
486 value of SUDS. *Clean - Soil, Air, Water*, **42**, 193–200.
- 487 Bronmark, C. (1985) Freshwater snail diversity: effects of pond area , habitat heterogeneity
488 and isolation. *Oecologia*, **67**, 127–131.
- 489 Brönmark, C. & Hansson, L.-A. (2008) *The Biology of Lakes and Ponds*. Oxford University
490 Press, Oxford, UK.
- 491 Brophy, C., Dooley, Á., Kirwan, L., Finn, J.A., McDonnell, J., Bell, T., Cadotte, M.W. &
492 Connolly, J. (2017) Biodiversity and ecosystem function: making sense of numerous
493 species interactions in multi-species communities. *Ecology*, **98**, 1771–1778.
- 494 Bruno, D., Gutiérrez-Cánovas, C., Sánchez-Fernández, D., Velasco, J. & Nilsson, C. (2016)

- 495 Impacts of environmental filters on functional redundancy in riparian vegetation.
496 *Journal of Applied Ecology*, **53**, 846–855.
- 497 Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond,
498 R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M.,
499 Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli,
500 A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque,
501 J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo,
502 M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B.,
503 Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié,
504 J.-C. & Watson, R. (2010) Global Biodiversity: Indicators of Recent Declines. *Science*,
505 **328**.
- 506 Carpenter, S.R. & Cottingham, K.L. (1997) Resilience and Restoration of Lakes.
507 *Conservation Ecology*, **1**, 2.
- 508 Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. & Tilman,
509 D. (1997) Biotic Control over the Functioning of Ecosystems. *Science*, **277**, 500–504.
- 510 Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L.,
511 Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Díaz, S. (2000)
512 Consequences of changing biodiversity. *Nature*, **405**, 234–42.
- 513 Chester, E.T. & Robson, B.J. (2013) Anthropogenic refuges for freshwater biodiversity:
514 Their ecological characteristics and management. *Biological Conservation*, **166**, 64–75.
- 515 Chevenet, F., Doledec, S. & Chessel, D. (1994) A fuzzy coding approach for the analysis of
516 long-term ecological data. *Freshwater Biology*, **31**, 295–309.
- 517 Cummins, K.W. (1979) Feeding ecology of stream invertebrates. *Annual Review of Ecology*

518 *and Systematics*, **10**, 147–172.

519 Declerck, S., Vandekerkhove, J., Johansson, L., Muylaert, K., Conde-Porcuna, J.M., Van der
520 Gucht, K., Perez-Martinez, C., Lauridsen, T., Schwenk, K., Zwart, G., Rommens, W.,
521 Lopez-Ramos, J., Jeppesen, E., Vyverman, W., Brendonck, L. & De Meester, L. (2005)
522 Multi-group biodiversity in shallow lakes along gradients of phosphorus and water plant
523 cover. *Ecology*, **86**, 1905–1915.

524 Dee, L.E., De Lara, M., Costello, C. & Gaines, S.D. (2017) To what extent can ecosystem
525 services motivate protecting biodiversity? *Ecology Letters*, **20**, 935–946.

526 Diaz, S. & Cabido, M. (2001) Vive la difference: Plant functional diversity matters to
527 ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646–655.

528 Durance, I., Bruford, M.W., Chalmers, R., Chappell, N.A., Christie, M., Cosby, B.J., Noble,
529 D., Ormerod, S.J., Prosser, H. & Weightman, A. (2016) Chapter Three – The Challenges
530 of Linking Ecosystem Services to Biodiversity: Lessons from a Large-Scale Freshwater
531 Study. *Advances in Ecological Research*, pp. 87–134.

532 Ehnes, R.B., Pollierer, M.M., Erdmann, G., Klarner, B., Eitzinger, B., Digel, C., Ott, D.,
533 Maraun, M., Scheu, S. & Brose, U. (2014) Lack of energetic equivalence in forest soil
534 invertebrates. *Ecology*, **95**, 527–537.

535 Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J.
536 (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and*
537 *the Environment*, **1**, 488–494.

538 Feldman, R.S. & Connor, E.F. (1992) The relationship between pH and community structure
539 of invertebrates in streams of the Shenandoah National Park, Virginia, U.S.A.
540 *Freshwater Biology*, **27**, 261–276.

- 541 Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling,
542 C.S. (2004) Regime Shifts, Resilience, and Biodiversity in Ecosystem Management.
543 *Annual Review of Ecology, Evolution, and Systematics*, **35**, 557–581.
- 544 Fuller, R.M., Smith, G.M., Sanderson, J.M., Hill, R. a., Thomson, A.G., Cox, R., Brown,
545 N.J., Clarke, R.T., Rothery, P. & Gerard, F.F. (2002) *Countryside Survey 2000 Module 7*
546 *Land Cover Map 2000*. Dorchester.
- 547 Gee, J.H.R., Smith, B.D. & Lee, K.M. (1997) The ecological basis of freshwater pond
548 management for biodiversity. *Aquatic Conservation: Marine and Freshwater*
549 *Ecosystems*, **7**, 91–104.
- 550 Gerisch, M. (2014) Non-random patterns of functional redundancy revealed in ground beetle
551 communities facing an extreme flood event (ed J Harwood). *Functional Ecology*, **28**,
552 1504–1512.
- 553 Gledhill, D.G., James, P. & Davies, D.H. (2008) Pond density as a determinant of aquatic
554 species richness in an urban landscape. *Landscape Ecology*, **23**, 1219–1230.
- 555 Hamer, A.J. & Parris, K.M. (2011) Local and landscape determinants of amphibian
556 communities in urban ponds. *Ecological Applications*, **21**, 378–390.
- 557 Hassall, C. (2014) The ecology and biodiversity of urban ponds. *Wiley Interdisciplinary*
558 *Reviews: Water*, **1**, 187–206.
- 559 Hassall, C., Hollinshead, J. & Hull, A. (2011) Environmental correlates of plant and
560 invertebrate species richness in ponds. *Biodiversity and Conservation*, **20**, 3189–3222.
- 561 Hassall, C., Hollinshead, J. & Hull, A. (2012) Temporal dynamics of aquatic communities
562 and implications for pond conservation. *Biodiversity and Conservation*, **21**, 829–852.
- 563 Heino, J. (2000) Lentic macroinvertebrate assemblage structure along gradients in spatial

- 564 heterogeneity , habitat size and water chemistry. *Hydrobiologia*, **418**, 229–242.
- 565 Hill, M.J., Biggs, J., Thornhill, I., Briers, R.A., Gledhill, D.G., White, J.C., Wood, P.J. &
566 Hassall, C. (2016) Urban ponds as an aquatic biodiversity resource in modified
567 landscapes. *Global Change Biology*, **23**, 986–999.
- 568 Hill, M.J., Heino, J., Thornhill, I., Ryves, D.B. & Wood, P.J. (2017) Effects of dispersal
569 mode on the environmental and spatial correlates of nestedness and species turnover in
570 pond communities. *Oikos*, **126**, 1575–1585.
- 571 Hill, M.J., Mathers, K.L. & Wood, P.J. (2015) The aquatic macroinvertebrate biodiversity of
572 urban ponds in a medium-sized European town (Loughborough, UK). *Hydrobiologia*,
573 **760**, 225–238.
- 574 Hooper, D.U., Solan, M., Symstad, A.J., Diaz, S., Gessner, M.O. & Buchmann, N. (2002)
575 Biodiversity and ecosystem functioning: synthesis and perspectives. *Biodiversity and*
576 *Ecosystem Functioning: Synthesis and Perspectives* (eds M. Loreau, S. Naeem & P.
577 Inchausti), pp. 195–208. Oxford University Press, Oxford.
- 578 Interagency Freshwater Group. (2015) *Common Standards Monitoring Guidance for*
579 *Freshwater Lakes*. Peterborough.
- 580 Jeffries, M.J. (2012) Ponds and the importance of their history: an audit of pond numbers,
581 turnover and the relationship between the origins of ponds and their contemporary plant
582 communities in south-east Northumberland, UK. *Hydrobiologia*, **689**, 11–21.
- 583 Jonsson, M., Dangles, O., Malmqvist, B. & Gueerold, F. (2002) Simulating species loss
584 following perturbation: assessing the effects on process rates. *Proceedings of the Royal*
585 *Society B: Biological Sciences*, **269**, 1047–1052.
- 586 Kovalenko, K.E., Brady, V.J., Ciborowski, J.J.H., Ilyushkin, S. & Johnson, L.B. (2014)

- 587 Functional Changes in Littoral Macroinvertebrate Communities in Response to
588 Watershed-Level Anthropogenic Stress (ed CJ Salice). *PLoS ONE*, **9**, e101499.
- 589 Kremen, C. (2005) Managing ecosystem services: what do we need to know about their
590 ecology? *Ecology Letters*, **8**, 468–479.
- 591 Kremen, C. & Ostfeld, R.S. (2005) A call to ecologists: measuring, analyzing, and managing
592 ecosystem services. *Frontiers in Ecology and the Environment*, **3**, 540–548.
- 593 Laliberté, E. (2009) metacor: Meta-Analysis with Correlation Coefficients as Effect Sizes. R
594 package version 1.0-2.
- 595 Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional
596 diversity from multiple traits. *Ecology*, **91**, 299–305.
- 597 Laliberté, E., Wells, J.A., Declerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I.,
598 Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S.,
599 Vesk, P.A. & Mayfield, M.M. (2010) Land-use intensification reduces functional
600 redundancy and response diversity in plant communities. *Ecology Letters*, **13**, 76–86.
- 601 Lapointe, N.W.R., Cooke, S.J., Imhof, J.G., Boisclair, D., Casselman, J.M., Curry, R.A.,
602 Langer, O.E., McLaughlin, R.L., Minns, C.K., Post, J.R., Power, M., Rasmussen, J.B.,
603 Reynolds, J.D., Richardson, J.S. & Tonn, W.M. (2014) Principles for ensuring healthy
604 and productive freshwater ecosystems that support sustainable fisheries. *Environmental*
605 *Reviews*, **22**, 110–134.
- 606 Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and
607 ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*,
608 **16**, 545–556.
- 609 Lecerf, A., Usseglio-Polatera, P., Charcosset, J.-Y., Lambrigot, D., Bracht, B. & Chauvet, E.

- 610 (2006) Assessment of functional integrity of eutrophic streams using litter breakdown
611 and benthic macroinvertebrates. *Archiv für Hydrobiologie*, **165**, 105–126.
- 612 Legendre, P. & Legendre, L. (1998) Numerical ecology: second English edition.
613 Developments in environmental modelling. *Developments in Ecological Modelling*, **20**,
614 853.
- 615 Lillie, R.A. & Budd, J. (1992) Habitat Architecture of *Myriophyllum spicatum* L. as an
616 Index to Habitat Quality for Fish and Macroinvertebrates. *Journal of Freshwater*
617 *Ecology*, **7**, 113–125.
- 618 Lohbeck, M., Bongers, F., Martinez-Ramos, M. & Poorter, L. (2016) The importance of
619 biodiversity and dominance for multiple ecosystem functions in a human-modified
620 tropical landscape. *Ecology*, **97**, 2772–2779.
- 621 Lundkvist, E., Landin, J. & Karlsson, F. (2002) Dispersing diving beetles (Dytiscidae) in
622 agricultural and urban landscapes in. *Annales Zoologici Fennici*, **39**, 109–123.
- 623 Merritt, R.W. & Cummins, K.W. (1996) *An Introduction to the Aquatic Insects of North*
624 *America*, 3rd ed. Kendall/Hunt, Dubuque, Iowa.
- 625 Merritt, R.W., Wallace, J.R., Higgins, M.J., Alexander, M.K., Berg, M.B., Morgan, W.T.,
626 Cummins, K.W. & Vandeneden, B. (1996) Procedures for the functional analysis of
627 invertebrate communities of the Kissimmee River-floodplain ecosystem. *Florida*
628 *Scientist*, **59**, 216–274.
- 629 Mooney, H., Larigauderie, A., Cesario, M., Elmquist, T., Hoegh-Guldberg, O., Lavorel, S.,
630 Mace, G.M., Palmer, M., Scholes, R. & Yahara, T. (2009) Biodiversity, climate change,
631 and ecosystem services. *Current Opinion in Environmental Sustainability*, **1**, 46–54.
- 632 Moore, J.W. & Olden, J.D. (2017) Response diversity, nonnative species, and disassembly

633 rules buffer freshwater ecosystem processes from anthropogenic change. *Global Change*
634 *Biology*, **23**, 1871–1880.

635 Morgan, A.H. (1930) *Field Book of Ponds and Streams, an Introduction to the Life of Fresh*
636 *Water*. Putnam, London.

637 Mori, A.S., Furukawa, T. & Sasaki, T. (2013) Response diversity determines the resilience of
638 ecosystems to environmental change. *Biological Reviews*, **88**, 349–364.

639 Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G. & Simpson, I.C.
640 (2011) *Final Report for LCM2007 – the New UK Land Cover Map. CS Technical Report*
641 *No 11/07 NERC/Centre for Ecology & Hydrology 112pp. (CEH Project Number:*
642 *C03259)*.

643 Mumme, S., Jochum, M., Brose, U., Haneda, N.F. & Barnes, A.D. (2015) Functional
644 diversity and stability of litter-invertebrate communities following land-use change in
645 Sumatra, Indonesia. *Biological Conservation*, **191**, 750–758.

646 Murtagh, F. & Legendre, P. (2014) Ward's Hierarchical Agglomerative Clustering Method:
647 Which Algorithms Implement Ward's Criterion? *Journal of Classification*, **31**, 274–295.

648 Naeem, S. (1998) Species Redundancy and Ecosystem Reliability. *Conservation Biology*, **12**,
649 39–45.

650 Nakanishi, K., Nishida, T., Kon, M. & Sawada, H. (2014) Effects of environmental factors on
651 the species composition of aquatic insects in irrigation ponds. *Entomological Science*,
652 **17**, 251–261.

653 Nicolet, P., Biggs, J., Fox, G., Hodson, M.J. & Reynolds, C. (2004) The wetland plant and
654 macroinvertebrate assemblages of temporary ponds in England and Wales. , **120**, 261–
655 278.

- 656 Nyström, M. (2006) Redundancy and Response Diversity of Functional Groups: Implications
657 for the Resilience of Coral Reefs. *AMBIO: A Journal of the Human Environment*, **35**,
658 30–35.
- 659 Oertli, B., Joye, D.A., Castella, E., Juge, R., Cambin, D. & Lachavanne, J.-B. (2002) Does
660 size matter? The relationship between pond area and biodiversity. *Biological*
661 *Conservation*, **104**, 59–70.
- 662 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson,
663 G.L., Solymos, P., Henry, M., Stevens, H. & Wagner, H. (2017) vegan: Community
664 Ecology Package. R package version 2.4-3.
- 665 Oliver, T.H., Isaac, N.J.B., August, T.A., Woodcock, B.A., Roy, D.B. & Bullock, J.M. (2015)
666 Declining resilience of ecosystem functions under biodiversity loss. *Nature*
667 *Communications*, **6**, 10122.
- 668 Péru, N. & Dolédec, S. (2010) From compositional to functional biodiversity metrics in
669 bioassessment: A case study using stream macroinvertebrate communities. *Ecological*
670 *Indicators*, **10**, 1025–1036.
- 671 Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking
672 forward. *Ecology Letters*, **9**, 741–758.
- 673 Ruggiero, A., Céréghino, R., Figuerola, J., Marty, P. & Angélibert, S. (2008) Farm ponds
674 make a contribution to the biodiversity of aquatic insects in a French agricultural
675 landscape. *Comptes rendus biologies*, **331**, 298–308.
- 676 Sala, O.E., Chapin Iii, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-
677 Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M.,
678 Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. &

- 679 Wall, D.H. (2000) Global Biodiversity Scenarios for the Year 2100. *Science*, **287**, 1770–
680 1774.
- 681 Sayer, C., Andrews, K., Shilland, E., Edmonds, N., Edmonds-Brown, R., Patmore, I., Emson,
682 D. & Axmacher, J. (2012) The role of pond management for biodiversity conservation in
683 an agricultural landscape. *Aquatic Conservation: Marine and Freshwater Ecosystems*,
684 **22**, 626–638.
- 685 Scheffer, M., Van Geest, G.J., Zimmer, K., Jeppesen, E., Sondergaard, M., Butler, M.G.,
686 Hanson, M.A., Declerck, S. & De Meester, L. (2006) Small habitat size and isolation
687 can promote species richness: second-order effects on biodiversity in shallow lakes and
688 ponds. *Oikos*, **112**, 227–231.
- 689 Scheffer, M., Houser, S.H., Meijer, M.L., Moss, B. & Jeppesen, E. (1993) Alternative
690 equilibria in shallow lakes. *Trends in ecology & evolution*, **8**, 275–9.
- 691 Schulze, R. (2004) *Meta-Analysis: A Comparison of Approaches*. Hogrefe & Huber,
692 Göttingen, Germany.
- 693 Simaika, J.P., Samways, M.J. & Frenzel, P.P. (2016) Artificial ponds increase local dragonfly
694 diversity in a global biodiversity hotspot. *Biodiversity and Conservation*, **25**, 1921–
695 1935.
- 696 Søndergaard, M., Jeppesen, E., Jensen, J.P.J.-P.J.P.J.-P., Søndergaard, M., Jeppesen, E. &
697 Jensen, J.P.J.-P.J.P.J.-P. (2005) Pond or lake: does it make any difference? *Archiv für*
698 *Hydrobiologie*, **162**, 143–165.
- 699 Srivastava, D.S. & Vellend, M. (2005) Biodiversity-Ecosystem Function Research: Is It
700 Relevant to Conservation? *Annual Review of Ecology, Evolution, and Systematics*, **36**,
701 267–294.

- 702 Statzner, B., Bonada, N. & Dolédec, S. (2007) Conservation of taxonomic and biological trait
703 diversity of European stream macroinvertebrate communities: a case for a collective
704 public database. *Biodiversity and Conservation in Europe*, pp. 367–390. Springer
705 Netherlands, Dordrecht.
- 706 Suding, K., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., G, E., Goldberg, D.,
707 Hooper, D.U., Jackson, S.T. & Navas, M.-L. (2008) Scaling environmental change
708 through the community-level: a trait-based response-and-effect framework for plants.
709 *Global Change Biology*, **14**, 1125–1140.
- 710 Tachet, H., Richoux, P., Bournard, M. & Usseglio-polatera, P. (2010) *Invertébrés D'eau*
711 *Douce: Systématique, Biologie, Écologie*, 2nd ed. Centre National de la Recherche
712 Scientifique Editions, Paris, France.
- 713 Thornhill, I., Batty, L., Death, R.G.R.G., Friberg, N.R.N.R. & Ledger, M.E.M.E. (2017a)
714 Local and landscape scale determinants of macroinvertebrate assemblages and their
715 conservation value in ponds across an urban land-use gradient. *Biodiversity and*
716 *Conservation*, **26**, 1065–1086.
- 717 Thornhill, I., Batty, L., Hewitt, M., Friberg, N.R. & Ledger, M.E. (2017b) The application of
718 graph theory and percolation analysis for assessing change in the spatial configuration of
719 pond networks. *Urban Ecosystems*, 1–13.
- 720 Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P.,
721 Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M. (2010) Global
722 threats to human water security and river biodiversity. *Nature*, **468**, 334–334.
- 723 Waterkeyn, A., Grillas, P., Vanschoenwinkel, B. & Brendonck, L. (2008) Invertebrate
724 community patterns in Mediterranean temporary wetlands along hydroperiod and
725 salinity gradients. *Freshwater Biology*, **53**, 1808–1822.

726 Williams, P.J., Biggs, J., Crowe, A., Murphy, J., Nicolet, P., Weatherby, A. & Dunbar, M.

727 (2010) *CS Technical Report No. 7/07 Countryside Survey: Ponds Report from 2007.*

728 Lancaster.

729 Williams, P., Whitfielda, M., Biggs, J., Bray, S., Fox, G., Nicolet, P. & Sear, D. (2004)

730 Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural

731 landscape in Southern England. *Biological Conservation*, **115**, 329–341.

732 Wood, P.J., Greenwood, M.T., Barker, S.A. & Gunn, J. (2001) The effects of amenity

733 management for angling on the conservation value of aquatic invertebrate communities

734 in old industrial ponds. *Biological Conservation*, **102**, 17–29.

735 Woodward, G., Bonada, N., Feeley, H.B. & Giller, P.S. (2015) Resilience of a stream

736 community to extreme climatic events and long-term recovery from a catastrophic flood.

737 *Freshwater Biology*, **60**, 2497–2510.

738 Zedler, J.B. & Kercher, S. (2005) Wetland Resources: Status, Trends, Ecosystem Services,

739 and Restorability. *Annual Review of Environment and Resources*, **30**, 39–74.

740

741

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
-------	-------	----	-------------------------	---------------------------	-----------------------	-------------------------	-------------------------	-----------------------------	------------------------

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

747

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.

789