

1                   **Urban ponds as an aquatic biodiversity resource in modified landscapes**

2   Running head: Macroinvertebrate biodiversity in urban aquatic ecosystems

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27 **Abstract**

28 Urbanization is a global process contributing to the loss and fragmentation of natural habitats.  
29 Many studies have focused on the biological response of terrestrial taxa and habitats to  
30 urbanization. However, little is known regarding the consequences of urbanization on freshwater  
31 habitats, especially small lentic systems. In this study we examined aquatic macroinvertebrate  
32 diversity (family and species level) and variation in community composition between 240 urban  
33 and 782 non-urban ponds distributed across the UK. Contrary to predictions, urban ponds  
34 supported similar numbers of invertebrate species and families compared to non-urban ponds.  
35 Similar gamma diversity was found between the two groups at both family and species  
36 taxonomic levels. The biological communities of urban ponds were markedly different to those  
37 of non-urban ponds and the variability in urban pond community composition was greater than  
38 that in non-urban ponds, contrary to previous work showing homogenisation of communities in  
39 urban areas. Positive spatial autocorrelation was recorded for urban and non-urban ponds at 0-50  
40 km (distance between pond study sites) and negative spatial autocorrelation was observed at 100-  
41 150 km, and was stronger in urban ponds in both cases. Ponds do not follow the same ecological  
42 patterns as terrestrial and lotic habitats (reduced taxonomic richness) in urban environments; in  
43 contrast they support high taxonomic richness and contribute significantly to regional faunal  
44 diversity. Individual cities are complex structural mosaics which evolve over long periods of  
45 time and are managed in diverse ways, promoting the development of a wide-range of  
46 environmental conditions and habitat niches in urban ponds which can promote greater  
47 heterogeneity between pond communities at larger scales. Ponds provide an opportunity for  
48 managers and environmental regulators to conserve and enhance freshwater biodiversity in

49 urbanized landscapes whilst also facilitating key ecosystem services including storm water  
50 storage and water treatment.

## 51 **Introduction**

52 Land use change has been predicted to be the greatest driver of biodiversity change in the 21<sup>st</sup>  
53 century (Sala *et al.*, 2000). The conversion of natural landscapes to urban areas represents a  
54 common land use transition, and is a significant process contributing to the loss of freshwater  
55 habitats and the degradation of those that remain, placing considerable pressure on native flora  
56 and fauna (McKinney, 2002). The fragmentation of natural habitats and development of uniform  
57 landscapes in urban areas has been demonstrated to cause the biotic homogenization of flora and  
58 fauna through the decline and exclusion of native species by land use modification (and  
59 associated anthropogenic pressures) and the establishment and spread of non-native invasive  
60 species through habitat disturbance and human introductions (McKinney, 2006; Grimm *et al.*,  
61 2008; Shochat *et al.*, 2010). Previous research has demonstrated that high levels of urbanization  
62 reduce macroinvertebrate and macrophyte species richness (e.g. in urban streams, Roy *et al.*,  
63 2003; Walsh *et al.*, 2005) to the point where urban environments are viewed as ‘ecological  
64 deserts’; although at moderate levels of urbanization greater diversity has been recorded for plant  
65 communities (McKinney *et al.*, 2008). In recent decades, significant improvements to the  
66 physical, chemical and ecological quality of urban freshwater ecosystems have been made in  
67 economically developed nations reflecting the decline in industrial developments, improved  
68 waste water treatment, and more effective environmental legislation (e.g., *The Water Framework*  
69 *Directive* in Europe; EC, 2000 and *The Water Act 2007* in Australia; Commonwealth of  
70 Australia, 2007). Although there have been significant improvements to the quality of many  
71 urban aquatic habitats, the number of water bodies in urban areas has declined over the past  
72 century (Wood *et al.*, 2003; Vaughan & Ormerod, 2012; Thornhill, 2013). Commercial and  
73 residential developments are expanding in urban areas to keep pace with population growth (66%

74 of global urban population are predicted to live in urban areas by 2050; United Nations, 2014) at  
75 the expense of urban green spaces (Dallimer *et al.*, 2011). Such losses of green/blue space are  
76 likely to place significant pressure on remaining urban freshwaters to support native flora and  
77 fauna and may lead to substantial shifts in the diversity and composition of species in urban areas  
78 (Fitzhugh & Richter, 2004; McKinney, 2006).

79

80 Ponds are ubiquitous habitat features in both urban and non-urban landscapes. In non-urban  
81 landscapes ponds have been demonstrated to support greater regional diversity of flora and fauna  
82 compared to rivers and lakes (Davies *et al.*, 2008). This biodiversity value may result from  
83 spatial and temporal diversity in pond environmental variables (Hassall *et al.*, 2011; Hassall *et*  
84 *al.*, 2012), which create a highly heterogeneous “pondscape” of habitats that provide a diverse  
85 array of ecological niches. Ponds have been acknowledged as providing important network  
86 connectivity across landscapes, acting as “stepping stones” that facilitate dispersal (Pereira *et al.*,  
87 2011). Within urban areas, ponds provide a diverse array of habitats and occur in a wide range of  
88 forms including garden ponds (Hill & Wood, 2014), sustainable urban drainage systems (SUDS;  
89 Briers, 2014; Hassall & Anderson, 2015), industrial, ornamental and park ponds (Gledhill *et al.*,  
90 2008; Hill *et al.*, 2015), recreation and angling ponds (Wood *et al.*, 2001), and nature reserve  
91 ponds (Hassall, 2014) which typically display heterogeneous physicochemical conditions (Hill *et*  
92 *al.*, 2015). Urban ponds are almost always of anthropogenic origin and often demonstrate  
93 different environmental characteristics to non-urban (semi-natural/agricultural) ponds; urban  
94 ponds commonly have concrete margins, a synthetic base, reduced vegetation cover, lower  
95 connectivity to other waterbodies, and are subject to run off from residential and industrial  
96 developments which can greatly increase the concentration of contaminants (Hassall, 2014).

97 While the definition of a “pond” versus a “lake” is still very much debated, a general rule is that  
98 ponds are standing water bodies <2ha in size. Urban waterbodies are frequently much smaller  
99 (closer to 1-5m<sup>2</sup> for garden ponds) but show a large variation in size (>10ha for park lakes). For  
100 a discussion of the definitions of ponds and lakes, we refer the reader elsewhere (Hassall, 2014;  
101 Appendix 1 in Biggs et al., 2005). Despite the considerable anthropogenic pressures on urban  
102 ponds, recent studies have demonstrated that ponds located within an urban matrix can provide  
103 important habitats for a wide range of taxa including macroinvertebrates (Hassall, 2014;  
104 Goertzen & Suhling, 2015; Hill *et al.*, 2015) and amphibians (Hamer *et al.*, 2012). In addition,  
105 many support comparable diversity to surrounding non-urban ponds (Hassall & Anderson, 2015)  
106 and also provide a wide range of ecosystems services in urban areas to offset the negative  
107 impacts of urbanization (Hassall, 2014). However, these patterns are inconsistent, and other  
108 studies have reported a lower diversity of macroinvertebrate and floral taxa in urban ponds  
109 reflecting the greater isolation of pond habitats (Hitchings & Beebee, 1997) and management  
110 practices designed for purposes other than biodiversity (e.g., emergent vegetation removal,  
111 Noble & Hassall, 2014).

112

113 While there has been increasing research interest in the biodiversity and ecosystem services of  
114 urban ponds across Europe (Hassall, 2014; Jeanmougin *et al.*, 2014; Goertzen & Suhling, 2015),  
115 the question remains as to whether urban ponds can provide similar levels of biodiversity to that  
116 recorded in ponds in the wider landscape. Few studies have compared urban pond faunal  
117 communities with non-urban pond communities (see Hassall & Anderson, 2015) and no known  
118 studies have examined urban pond macroinvertebrate diversity at a national scale. Furthermore,  
119 there are a series of ecological patterns within cities (e.g., reduced taxonomic diversity, biotic

120 homogenization, increase in non-native and invasive taxa) that have been described in terrestrial  
121 systems (particularly birds, butterflies, and plants: McKinney, 2008) but these have not been  
122 tested in aquatic ecosystems. This study provides a comparative analysis of environmental  
123 characteristics and macroinvertebrate communities contained within >1000 UK ponds, including  
124 ponds located in a number of cities and towns across the UK and non-urban ponds that cover a  
125 wide range of non-urban habitats including; nature reserves, agricultural land (pasture and crop),  
126 meadows, woodland and other wetlands. We test the following hypotheses (i) urban ponds  
127 support lower macroinvertebrate richness and diversity (family and species level) than non-urban  
128 ponds, as would be predicted from the greater anthropogenic stressors in urban areas; (ii) urban  
129 macroinvertebrate communities would be more homogeneous than non-urban communities at a  
130 family and species scale, due to the greater similarity of urban habitats as has been reported for  
131 terrestrial taxa; and (iii) urban pond communities demonstrate stronger spatial structuring at  
132 smaller scales than non-urban communities, through reduced connectivity, dispersal and gene  
133 flow.

134

## 135 **Materials and Methods**

### 136 *Data Management*

137 The UK covers a total area of 242,495 km<sup>2</sup> and has a population of approximately 64.6 million  
138 inhabitants. Over 6.8% of the UK land mass is classified as urban and approximately 80% of the  
139 population resides in urban areas (defined as areas >20ha containing >20,000 people, UKNEA,  
140 2011). Aquatic macroinvertebrate community data from 230 urban and 607 non-urban ponds and  
141 environmental data from 240 urban ponds and 782 non-urban ponds in the UK were collated



142 from 12 previous studies (Table 1). The spatial distribution of the studied urban and non-urban  
143 ponds is displayed in Figure 1.

144

145 Data collection methodologies employed by the majority of contributing studies (Table 1)  
146 broadly followed the standardized guidelines of the National Pond Survey (Biggs *et al.*, 1998)  
147 including a 3 minute sweep sample divided between the mesohabitats present (Studies 1, 2, 3, 4,  
148 5, 6, 9, 10, 11 and 12; Table 1). The other studies also sampled for aquatic macroinvertebrate  
149 taxa in all available mesohabitats, but sampling was undertaken until no new species were  
150 recorded (studies 7 and 8). The majority of studies were sampled across two or three seasons  
151 (studies 1, 3, 4, 6, 7, 10 and 11; Table 1) although five studies were only sampled during the  
152 summer months (studies 2, 5, 8, 9 and 12; Table 1). Environmental data recorded from pond sites  
153 varied between studies, but always included a common core of variables that were used in the  
154 comparative analysis: pond area, pH, percentage coverage of emergent macrophytes, percentage  
155 pond shading, and altitude. Ponds were categorized as urban or non-urban based on whether they  
156 were located within developed land use areas (DLUAs) – a landscape designation used by the  
157 UK-based Ordnance Survey to delineate urban and non-urban sites. We provide a comparison  
158 between our binary categorisation and two other measures of ‘urbanness’ (proportion of urban  
159 land use in a 1km buffer, and distance from urban land use areas) in the Supplementary  
160 Information (Part 1). We acknowledge that the definition of an urban pond is complex. Indeed, a  
161 previous attempt to define a typology of urban ponds concluded that these sites comprise a  
162 diverse array of different habitat types (Hassall, 2014). However, the intention with this study is  
163 to evaluate the aquatic biodiversity in urban areas, and to establish whether those urban sites are  
164 deserving of protection, value, and enhancement. Hence, rather than attempting to define the  
165 precise characteristics of an “urban pond”, we are focusing on the much more tractable issue of  
166 “ponds in urban areas”. Similarly, the definition of a “non-urban pond” for our purposes simply

167 includes ponds outside of urban areas. Our non-urban pond dataset is concentrated in agricultural  
168 landscapes which in the UK are typically characterised by low tree cover and low surrounding  
169 botanical diversity, along with high inputs of nutrients and agricultural effluents. These ponds  
170 are likely to be subject to “benign neglect” (i.e. limited management) but this will vary across the  
171 ponds in the study. Urban ponds in this study encompass a broad spectrum of urban areas, from  
172 their location in densely populated cities (e.g., Birmingham: population >1million) to smaller  
173 towns (e.g., Loughborough: estimated population of 60000). The urban ponds chosen for  
174 investigation included ponds in domestic gardens, industrial ponds (old mill ponds), ornamental  
175 ponds located in urban parks and drainage ponds (e.g., sustainable urban drainage systems /  
176 stormwater retention ponds; see Hassall, 2014). The issue of the representative nature of UK  
177 cities compared to cities elsewhere (in Europe or the wider world) is less clear for ponds, since  
178 there has been limited study of these habitats using standardised methods (see Hassall, 2014, for  
179 a discussion and a range of biodiversity studies). It is likely that the range of urbanised areas  
180 incorporated in our study covers the range of different urban landscapes that are found in  
181 European cities, from millennia-old cities with an evolving land use pattern (e.g. London), to  
182 centuries-old industrial towns (e.g. Leeds, Manchester), to 20<sup>th</sup> century towns which have been  
183 designed and built *de novo* (e.g. Milton Keynes).

184

185 The faunal dataset was converted into a presence-absence matrix to ensure data provided by the  
186 12 constituent studies were comparable and that any sampling bias was reduced. Abundance data  
187 may yield additional insights into variation in biomass and evenness among ponds, and we might  
188 expect greater biomass and evenness in non-urban sites where stressors are reduced and nutrient  
189 supply is greater. However, our primary goal within the present study is to investigate variation

190 in taxonomic richness across the pond types. Two key methodological differences exist in the 12  
191 studies. First, although most of the corresponding studies identified the majority of  
192 macroinvertebrate taxa to species level, each study also identified selected taxa (e.g., Diptera,  
193 Oligochaeta, Copepoda and Ostracoda) at higher taxonomic levels (Table 1). The influence of a  
194 higher taxonomic resolution of identification for aquatic macroinvertebrates has been examined,  
195 primarily within lotic habitats (Monk *et al.*, 2012; Heino, 2014). However, identification of  
196 macroinvertebrate taxa at family level has been shown to be appropriate to examine alpha, beta  
197 and gamma diversity in lentic systems (Le Viol *et al.*, 2009; Mueller *et al.*, 2013; Hassall &  
198 Anderson, 2015; Vilmi *et al.*, 2016) and is the resolution used by a range of environmental  
199 monitoring indices (e.g., biological monitoring working party [BMWP] and predictive system for  
200 multimetrics [PSYM] scores; Environment Agency & Pond Conservation Trust, 2002) and  
201 legislation (e.g., The Water Framework Directive; EC, 2000) across Europe. However, to assess  
202 the sensitivity of results to taxonomic resolution we performed all analyses at two taxonomic  
203 levels: first, to incorporate as many sites as possible and to ensure faunal data was comparable  
204 across all studies, aquatic macroinvertebrate data were reclassified to family level and analysis  
205 was undertaken at this higher taxonomic resolution. Second, statistical analysis was also  
206 undertaken on a subset of urban (207 ponds) and non-urban ponds (578 ponds) where species  
207 level data was available.

208

209 The second methodological variation was in the amount of sampling effort applied to the sites:  
210 sampling effort was limited to 3 minutes in 10 of the studies (following standard UK sampling  
211 protocols) but two studies used exhaustive sampling until no more species were found. A  
212 preliminary analysis showed that, in fact, the sites sampled for 3 minutes found more taxa

213 (average of  $14.7 \pm 0.4$  SE families,  $n=392$  sites; average of  $30.0 \pm 0.9$  species,  $n=340$ ) than sites  
214 sampled exhaustively (average of  $13.6 \pm 0.3$  SE families,  $n=518$  sites; average of  $26.8 \pm 0.6$   
215 species,  $n=518$ ). However, this lower number of species in exhaustive samples is likely to result  
216 from those sites occurring in the north of England where the regional species pool may be  
217 smaller. As a result, we find no evidence of bias between the exhaustive and time-limited  
218 samples. Finally, to provide the strongest possible test of the biodiversity value of urban ponds,  
219 urban pond communities (at a family and species level) were compared to a subset of the non-  
220 urban ponds with degraded sites excluded (leaving  $n=571$  non-urban ponds with family level  
221 data and 542 with species level data).

222

### 223 *Statistical Analysis*

224 Differences in environmental characteristics (pond area, percentage coverage of emergent  
225 macrophytes, pH, percentage pond shading and altitude) and aquatic macroinvertebrate  
226 communities at a family and species level between urban and non-urban ponds were examined.  
227 All analyses were carried out in the R environment (R Development Core Team, 2013). Prior to  
228 statistical analysis the data was screened to remove any missing values. Estimated gamma  
229 diversity was calculated using Chao2 estimator in the vegan package in R (Oksanen *et al.*, 2015).  
230 Mann-Whitney U tests were used to test for differences in alpha diversity (family and species  
231 richness) between urban and non-urban ponds. To account for the fact that there were different  
232 numbers of urban and non-urban sites, taxon accumulation curves were constructed by  
233 randomized resampling of sites without replacement using the *specaccum* function in vegan with  
234 1,000 permutations per sample size. From these curves the mean number of families and species  
235 in each simulated group of sites and the standard error were calculated. Variability between

236 urban and non-urban ponds in the environmental variables was tested using Mann-Whitney U  
237 tests. Differences between environmental variables and faunal community composition in urban  
238 and non-urban ponds were visualized using Non-Metric Multidimensional Scaling (NMDS) with  
239 the *metaMDS* function in the *vegan* package and were examined statistically using a  
240 ‘Permutational Analysis of Variance’ (PERMANOVA). Bray–Curtis dissimilarity was used to  
241 analyse the macroinvertebrate data and Euclidean distance used for the environmental data.  
242 Homogeneity of multivariate dispersions between the environmental data and macroinvertebrate  
243 communities from urban and non-urban ponds were calculated using the *betadisper* function in  
244 *vegan* and compared using an ANOVA. To identify indicator taxa of ephemeral and perennial ponds  
245 Indicator Value analysis (IndVal: Dufrêne & Legendre 1997) was undertaken. To test the spatial  
246 patterns of community structure in urban and non-urban ponds, a Mantel correlogram was  
247 constructed between the aquatic macroinvertebrate distance matrix (Euclidean) and the  
248 geographical distance for urban and non-urban ponds using the *mantel.correlog* function in the  
249 *vegan* package in R. Breaks among distance classes in the Mantel correlogram were defined in  
250 50km intervals. The Mantel correlogram enables the identification of changes in the strength of  
251 correlation between faunal distance matrices and geographic distance matrices at different spatial  
252 scales (Rangel *et al.*, 2010).

253

254 The relationship between macroinvertebrate assemblages and environmental variables (pH,  
255 percentage coverage of emergent macrophytes, percentage pond shading, altitude, location  
256 within urban area, and pond area) was examined using redundancy analysis (RDA) in the *vegan*  
257 package. A stepwise selection procedure (forward and backward selection) was employed to  
258 select the best model and environmental variables that significantly ( $p < 0.05$ ) explained the

259 variance in pond macroinvertebrate assemblages using the *ordistep* function in vegan, which  
260 uses permutation-based significance tests (999 permutations).

261

## 262 **Results**

### 263 *Urban and non-urban pond environmental characteristics*

264 Comparisons between specific environmental variables in urban and non-urban ponds that are  
265 thought to influence diversity and composition showed that altitude ( $W=108179.5$   $p<0.01$ ;  
266 Figure 2A) and pond shading ( $W=92965.5$   $p<0.01$ ; Figure 2B) were significantly higher for  
267 urban ponds (mean altitude:  $85.9 \pm 3.7$  masl; mean shading  $22.89 \pm 1.84$  %) than non-urban  
268 ponds (mean altitude:  $78.2 \pm 2.8$  masl; mean shading  $19.61 \pm 0.95$  %), but the absolute  
269 differences between the pond types are small enough that they may be biologically insignificant .  
270 pH was significantly higher for urban ponds (mean  $7.44 \pm 0.06SE$ ) compared to non-urban ponds  
271 ( $7.37 \pm 0.16$ ;  $W=37024$   $p<0.05$ ; Figure 2C) although in both pond types pH was close to neutral.  
272 Non-urban ponds demonstrated a greater variability in pH compared to urban ponds. A total of  
273 13% of non-urban ponds (66 ponds) recorded a pH  $<6.5$ , whilst only 4% of urban ponds (10  
274 urban ponds) recorded a pH  $<6.5$ . In addition, pond area was on average 43% larger in non-urban  
275 ponds ( $2207 \pm 139m^2$ ) compared to urban ponds ( $1546 \pm 171m^2$ ;  $W=75154.5$   $p<0.01$ ; Figure 2D).  
276 Emergent macrophyte coverage was significantly higher in non-urban ponds ( $33.10 \pm 1.08\%$ )  
277 compared to urban ponds ( $27.77 \pm 1.87\%$ ;  $W=81695$   $p<0.01$ ; Figure 2E) although the mean  
278 difference was  $<5\%$ .

279

### 280 *Aquatic macroinvertebrate diversity*

281 Family-level gamma diversity was similar between urban (observed 96 families, Figure 3A) and  
282 non-urban ponds (observed 103 families, Figure 3B), and the Chao2 estimator produced results  
283 taking into account sample size that were not statistically different across the two pond types  
284 (urban: 108.2, 95% CI: 91.4-125.0 families; non-urban: 107.5, 95% CI: 99.7-115.3 families). At  
285 an alpha scale urban ponds (median richness = 13, range = 2-44) supported significantly greater  
286 macroinvertebrate family richness compared to non-urban ponds (median richness = 12, range =  
287 2-38;  $W=20430.5$   $p<0.01$ ) although median richness values were very similar between the pond  
288 types. Species-level gamma diversity was lower in urban (observed 403 species) than non-urban  
289 sites (observed 473 species), but the Chao2 estimator showed that there was no significant  
290 difference after controlling for the number of sites (urban: 496.6, 95%CI: 445.6-547.7 species;  
291 non-urban: 572.9, 95%CI: 520.2-625.7 species). No significant difference in alpha diversity  
292 between macroinvertebrate species was recorded between urban (median: 28) and non-urban  
293 ponds (median 26;  $W=17310$   $p=0.507$ ).

294  
295 Urban ponds demonstrated a greater variability in alpha diversity among individual ponds at a  
296 family and species level (Figure 3C, 3D). A total of 25 urban ponds (11% of total urban pond  
297 number) supported >25 macroinvertebrate families, whilst only 9 non-urban ponds (1.5% of total  
298 non-urban pond number) supported macroinvertebrate communities with >25 families. In  
299 addition, the greatest number of invertebrate families recorded was from an urban pond (46 taxa)  
300 and 5 of the 6 ponds with the greatest macroinvertebrate family richness were located in urban  
301 environments. Only two families of macroinvertebrates were statistically associated with non-urban  
302 ponds (one family of Plecoptera, one family of Ephemeroptera), while 20 families were identified as  
303 indicator taxa for urban ponds, including seven families of Diptera. Strongest associations for families are



304 presented in Table 2 (see Supplementary Material Table S10 for the full list of statistically significant  
305 family indicator values, and Supplementary Table S11 for significant indicator values of  
306 macroinvertebrate species).

307

308 When non-urban ponds designated as degraded were removed and the macroinvertebrate  
309 diversity in the remaining ponds was compared to urban ponds, alpha diversity was significantly  
310 greater in urban ponds (median: 13;  $W=18057$   $p<0.01$ ) than the higher quality non-urban ponds  
311 (median: 12) at a family level, although mean and median richness values were similar between  
312 the pond types (see Supplementary Information Part 2). There was no significant difference in  
313 alpha diversity ( $W=14653.5$   $p=0.358$ ) at the species level between urban ponds (median: 28) and  
314 higher quality non-urban ponds (median: 25). Estimated gamma diversity for higher quality non-  
315 urban ponds at a family (98.7) and species scale (575.1) was marginally higher compared to  
316 gamma diversity when all non-urban ponds were considered.

317

318 Chironomidae, Tipulidae, Crangonyctidae and Oligochaeta had a greater frequency of  
319 occurrence in urban ponds, whilst Gyrinidae, Hydrophilidae and Notonectidae displayed a  
320 greater occurrence in non-urban ponds (Figure 4; for complete data see Tables S8 and S9 for  
321 family and species level prevalence, respectively). Macroinvertebrate families that score highly  
322 within biological monitoring surveys of ponds and other waterbodies (e.g., PSYM and BMWP)  
323 such as Phryganeidae, Leptoceridae, Libellulidae and Aeshnidae occurred at similar frequencies  
324 in the urban and non-urban ponds (Figure 4). Crangonyctidae were present in 49.0% of urban  
325 ponds and only 29.0% of non-urban ponds. All specimens of this family from the species-level  
326 dataset were the North American invasive *Crangonyx pseudogracilis*. A similar pattern is also

327 seen in the species-level dataset with the invasive New Zealand mud snail, *Potamopyrgus*  
328 *antipodarum*, being found in 21.3% of urban ponds and 9.5% of non-urban ponds.

### 329 *Community Heterogeneity*

330 Multivariate dispersion for environmental characteristics were significantly lower in non-urban  
331 ponds (median distance: 1116) than urban ponds (median distance: 1978;  $F=5.774$   $p<0.05$ ,  
332 Figure 5A). PERMANOVA showed that there was a small but significant difference between  
333 environmental characteristics ( $R^2=0.03$   $p<0.001$ ) and faunal communities at a family ( $R^2=0.09$   
334  $p<0.001$ ) and species level ( $R^2=0.03$   $p<0.001$ ). A relatively clear distinction between aquatic  
335 macroinvertebrate community composition in urban and non-urban ponds was observed at the  
336 family and species level within the NMDS ordination (Figure 5B, C). Among faunal  
337 communities, multivariate dispersion was significantly higher at the family (median distance -  
338 urban: 0.451, non-urban: 0.406;  $F=27.584$   $p<0.01$ ) and species scale (median distance - urban:  
339 0.579, non-urban: 0.550;  $F=17.626$   $p<0.01$ ) for urban ponds compared to non-urban ponds.

340

341 There was significant positive spatial autocorrelation for urban ( $r=0.31$   $p<0.01$ ) and non-urban  
342 ponds ( $r=0.17$   $p<0.01$ ) at the family level for the smallest distance class (0-50 km), indicating  
343 that those ponds in close geographical proximity have similar macroinvertebrate community  
344 compositions (Figure 6A). At middle distance classes (distance class three: 100-150 km) urban  
345 and non-urban ponds demonstrated a significant negative Mantel spatial autocorrelation,  
346 although this effect was weak for non-urban ponds (urban:  $r=-0.18$   $p<0.01$ , non-urban:  $r=-0.05$   
347  $p<0.01$ ) (Figure 6A). At larger distances spatial autocorrelation declined in strength for urban  
348 and non-urban ponds. The same analyses carried out on species-level data showed similar spatial

349 patterns, but with stronger positive correlation at shorter distances (0-50km, urban:  $r=0.45$ ,  
350  $p<0.01$ ; non-urban:  $r=0.27$ ,  $p<0.01$ ) and stronger negative correlation at middle distances (100-  
351 150km, urban:  $r=-0.29$ ,  $p<0.01$ ; non-urban:  $r=-0.08$ ,  $p<0.01$ ; Figure 6B).

352

### 353 *Macroinvertebrate - environment relationships*

354 Redundancy Analysis (RDA) of the pond macroinvertebrate family community data and  
355 environmental parameters highlighted clear differences between urban and non-urban ponds  
356 (Figure 7A). The RDA axes were highly significant ( $F=3.06$   $p<0.001$ , Adjusted  $R^2=0.02$ ),  
357 explaining 3.8% of the variation in family assemblage on all constrained axes (see  
358 Supplementary Information Table S4). Stepwise selection of environmental parameters identified  
359 four significant physicochemical variables correlated with the first two RDA axes: altitude,  
360 emergent macrophytes (all  $p<0.05$ ), surface area and location within urban area (both  $p<0.01$ )  
361 (Figure 7A). RDA indicated that urban and non-urban pond invertebrate communities were  
362 separated on the first and second axes along gradients associated with pond surface area and  
363 emergent macrophyte cover/their location within the urban landscape (Figure 7A). Non-urban  
364 ponds were characterized by a greater pond area and emergent macrophyte cover, whilst urban  
365 ponds were associated with smaller surface areas and less emergent macrophytes (Figure 7).  
366 RDA of pond macroinvertebrate species community data showed similar patterns: urban and  
367 non-urban ponds were strongly separated along the first RDA axis, with significant effects of  
368 urbanisation, pond area, altitude, and shading on community structure (Figure 7B). However, in  
369 both RDA analyses the explanatory power of the models was very low (see Supplementary  
370 Information Table S4).

371

372 **Discussion**

373 *Urban freshwater diversity*

374 This is the first study to provide a large scale, inter-city approach to test the biological response  
375 of entire pond macroinvertebrate communities to urbanization. The results provide a contrast  
376 with previous work on terrestrial and lotic habitats which has shown greater fragmentation,  
377 reduction in habitat quality (e.g., pollution/contaminant build up), alterations to biogeochemical  
378 cycles, higher air surface temperatures, increased disturbance frequencies, proliferation of non-  
379 native taxa, biotic homogenization and an overall decline in biological richness in urban areas  
380 (e.g., McKinney, 2002; McKinney, 2006; Grimm *et al.*, 2008). The ecological consequences of  
381 urbanization for ponds do not appear to follow the same patterns identified elsewhere for  
382 terrestrial habitats.

383

384 Urban ponds and non-urban ponds support similar alpha diversity of aquatic macroinvertebrates  
385 at a family and species level (reject hypothesis 1) and estimated gamma diversity was similar at a  
386 family level, although non-urban ponds recorded higher estimated gamma diversity at a species  
387 scale. These findings are consistent with a recent study of terrestrial invertebrates that showed  
388 comparable levels of diversity of particular indicator groups inhabiting birch trees (*Betula*  
389 *pendula*) between urban and agricultural areas (Turrini and Knop, 2015). However, an analysis  
390 of the same dataset showed a homogenization of arboreal invertebrates within urban areas (Knop,  
391 2016), consistent with other terrestrial ecosystem studies (McKinney, 2008) but not with our data  
392 for freshwater macroinvertebrates. The lack of agreement in ecological patterns between ponds  
393 (which, in this study, show similar patterns of diversity across urban boundaries) and  
394 lotic/terrestrial habitats (which tend to show reduced faunal richness with increasing urbanisation)

395 in cities may reflect the ability of pond communities to recover relatively quickly from  
396 temporary anthropogenic disturbance (Thornhill, 2013). This resilience is supported by the high  
397 dispersal abilities of many semi-aquatic invertebrates (Goertzen & Suhling, 2015). Despite  
398 commonly occurring in clusters, ponds are discrete habitats with small catchment areas (Davies  
399 *et al.*, 2008) and disturbance in one pond or its catchment has little impact on others in the  
400 network cluster, whilst a single disturbance event in, for example, a river system would impact  
401 an entire reach (Thornhill, 2013). Aside from rare taxa, there were few families that showed a  
402 different prevalence between urban and non-urban ponds, including indicator taxa with high  
403 BMWP scores (indicative of high water quality). However, there was also a higher prevalence of  
404 Oligochaeta and Chironomidae in urban ponds which is consistent with historical disturbance  
405 and subsequent recolonization by disturbance tolerant taxa, and higher prevalence of the invasive  
406 *C. pseudogracilis* and *P. antipodarum* in urban ponds supports previous findings that urban  
407 ecosystems favour the establishment of invasive species (Shochat *et al.*, 2010).

408

409 We propose two potential explanations, which are not mutually exclusive, for the similarity  
410 between urban and non-urban pond biodiversity. First, it has been estimated that 80% of ponds in  
411 the wider UK landscape are in a degraded state (Williams *et al.*, 2010). Hence non-urban ponds  
412 and urban ponds may be suffering from external pressures and mismanagement leading to the  
413 similar alpha diversities recorded. With both pond types in degraded states the biodiversity value  
414 of urban ponds must be treated with caution, as their richness is compared to similar degraded  
415 non-urban ponds. However, our secondary analysis demonstrated that urban ponds still show  
416 comparable biodiversity to higher quality, non-degraded non-urban ponds. Research examining  
417 the diversity of high-quality urban and non-urban ponds is required to fully quantify the

418 biodiversity value of urban ponds. Second, intensive management in cities may actually promote  
419 biodiversity. Whilst many ponds in non-urban areas (e.g., agricultural land) are left unmanaged,  
420 neglected, and at late successional stages (Hassall *et al.*, 2012; Sayer *et al.*, 2012), ponds in urban  
421 areas are often managed (primarily for purposes other than biodiversity) and a wide-range of  
422 successional stages are maintained. Furthermore, in many cases local residents (e.g., pond  
423 warden schemes) monitor and manage large numbers of urban ponds for the benefit of ecological  
424 communities, improving their habitat/water quality and promoting high biological richness  
425 (Boothby, 1995; Hill *et al.*, 2015). Results from the present study show that urban areas have the  
426 potential to become reservoirs of freshwater biodiversity rather than “ecological deserts”, which  
427 incorporate a wide range of aquatic habitats including ponds, canals, urban reservoirs and  
428 wetlands (Hassall & Anderson, 2015). However, it should be noted that diversity was highly  
429 variable in this study at both the family and species level of taxonomic resolution and previous  
430 research has demonstrated that some urban ponds can be of low ecological quality if  
431 anthropogenic stressors such as eutrophication are allowed to persist (Noble & Hassall, 2014).

432

433 Urban ponds were also characterized by contrasting values of some environmental parameters to  
434 non-urban ponds. As expected, urban ponds were smaller than non-urban ponds reflecting the  
435 high level of competition and the economic value of urban land. Lower emergent macrophyte  
436 coverage was recorded in urban ponds compared to non-urban ponds which reflects their primary  
437 function for flood water storage/water treatment and the management practices undertaken to  
438 achieve this (Le Viol *et al.*, 2009). Reduced emergent macrophyte cover in urban areas may also  
439 be the result of public perceptions of pond attractiveness (clean, open water and surrounding  
440 vegetation mown; Nassauer, 2004) which pond amenity managers aim to replicate, or other

441 management practices for amenity purposes such as angling or boating (Wood *et al.*, 2001).  
442 Urban ponds were significantly more shaded than non-urban ponds, which is most likely the  
443 result of urban ponds location within high density, built environments providing significant  
444 additional artificial shading to that provided by trees. In addition, reduced shading of non-urban  
445 ponds may be because many non-urban ponds were located in landscapes typically free of  
446 shading (trees) including wetland meadows and the low numbers of trees in British agricultural  
447 landscapes where many non-urban ponds are situated (however high levels of pond shading from  
448 trees has been recorded in some UK agricultural areas: Sayer *et al.*, 2012).

449

#### 450 *Community heterogeneity*

451 Small but significant differences in faunal communities (family and species) were observed  
452 between urban and non-urban ponds in this study (reject hypothesis 2). Differences (albeit subtle)  
453 in community composition found in the present study contrast with the findings of Hassall and  
454 Anderson (2015) and Le Viol *et al.* (2009) and suggest that at greater spatial scales urban ponds  
455 contribute as much to the regional biodiversity pool as non-urban ponds. The higher community  
456 dissimilarity among urban ponds may reflect the different levels of disturbance and diverse  
457 management practices (reflecting their primary function e.g., flood alleviation, biodiversity,  
458 amenity), as well as general pond characteristics such as small catchments which result in highly  
459 heterogeneous environmental conditions (greater environmental multivariate distances than non-  
460 urban ponds) even in ponds that are in close proximity (Davies *et al.*, 2008).

461

462 Significant positive spatial autocorrelation at the smallest distance class and significant negative  
463 spatial autocorrelation at medium distances suggest that: 1) ponds within individual cities have  
464 similar communities which reflect similar city-region environmental characteristics; and 2)  
465 ponds at greater spatial distances from one another in different cities have increasingly dissimilar  
466 communities reflecting the high variability in environmental (Heino & Alahuhta, 2015) and  
467 historical factors (Baselga, 2008; Heino & Alahuhta, 2015) among cities. Spatial patterns of  
468 management may influence geographical variation in community structure to a greater extent  
469 than landscape connectivity, making it difficult to evaluate our third hypothesis. However, we  
470 demonstrate stronger spatial structuring of urban communities at finer spatial scales, which  
471 would be expected under lower connectivity. Greater connectivity in non-urban landscapes  
472 enhances species movement leading to weaker spatial structuring at finer spatial scales in non-  
473 urban ponds. Hence our observations support our third hypothesis, but further work is needed to  
474 evaluate the consequences of spatial patterns for management. Historically, urban environments  
475 were highly degraded (physically, chemically and biologically) but significant improvements to  
476 urban freshwater quality have been achieved in recent decades despite urban sprawl and  
477 intensification (Vaughan & Ormerod, 2012). Therefore, it is possible that cities are still being  
478 recolonized by aquatic taxa from different regional species pools using different dispersal routes,  
479 creating a dynamic pattern of communities.

480

#### 481 *Conservation implications*

482 Urban ponds support relatively high alpha and gamma diversity comparable to non-urban ponds.  
483 A lack of monitoring of urban freshwaters (particularly ponds that are excluded from the EU  
484 Water Framework Directive) may be hiding considerably more diversity such that urban planners



485 fail to identify high biodiversity sites (Hassall, 2014). There is a need for a concerted,  
486 comparative, empirical approach to freshwater management that incorporates biodiversity as  
487 well as other ecosystem services alongside social and political considerations. Fundamental to  
488 the conservation of ponds is an integrated landscape approach that recognizes the need for  
489 networks of ponds (Boothby, 1997). Hence the prioritization of ponds for conservation will need  
490 to take into account their location relative to other sites, requiring a complementary approach  
491 that creates new habitats, improves degraded habitats, and conserves those habitats that have  
492 already achieved good quality. Changes in the management of ponds more generally has led to  
493 change in the environmental conditions within and around these habitats, such as the reduction in  
494 riparian tree management around agricultural ponds which has consequences for light, oxygen,  
495 and temperature (Sayer et al., 2013). Urban ponds are well suited to biodiversity enhancement as  
496 many are sites of high diversity (Hassall, 2014) and even small changes to current management  
497 strategies in urban freshwaters (e.g., the planting of native macrophytes in amenity ponds; Hill *et*  
498 *al.*, 2015) are likely to significantly augment biodiversity in urban landscapes. Cities are highly  
499 complex, multifunctional landscapes designed primarily for anthropogenic use yet they still  
500 support considerable aquatic diversity and represent scientifically and ecologically important  
501 habitats.

502

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644

Table 1 – Summary table of the geographic scale, sampling methodology and taxonomic resolution of contributing studies.

Reference Number	Geographic Scale	Aquatic macroinvertebrate Sampling Methodology	Taxonomic Resolution	Taxa Included	Reference
1	UK wide n= 152	Individual ponds sampled for 3 minutes in spring, summer and autumn using a sweep sample technique. Sampling time was divided between the mesohabitats recorded in each pond.	Species, except for Oligochaeta, Diptera and small bivalves	Aquatic macroinvertebrates (water mites, zooplankton and other micro-arthropods were not included)	Biggs <i>et al.</i> , 1998
2	Dunfermline, Fife, Scotland n= 14	Individual ponds were sampled annually between 2007-2011 in the summer following the methods of the National Pond Survey.	Species, except for Oligochaeta, Ostracoda and Diptera	Aquatic macroinvertebrates	Briers, 2014
3	Leicestershire, UK n = 41	Individual ponds were sampled over spring, summer and autumn seasons. Sampling time was proportional to surface area, up to a maximum of three minutes. Sampling time designated to each pond was divided between the mesohabitats recorded.	Species, except for Diptera, Oligochaeta, Hydrachnidiae and Collembola	Aquatic macroinvertebrates (zooplankton and other micro arthropods were not included)	Hill <i>et al.</i> , 2015
4	West Yorkshire, UK n = 36	Individual ponds were sampled during the summer and autumn, following the guidelines of the National Pond Survey. In addition, soft benthic samples were taken using an Eckman Grab.	Species, except Ostracoda, Copepoda and Diptera	Aquatic macroinvertebrates	Wood <i>et al.</i> , 2001
5	Bradford, UK n = 21	Individual ponds were sampled for 3 minutes in the summer. Sampling time was divided between the mesohabitats present.	Family level	Aquatic macroinvertebrates (presence of fish and amphibians noted)	Noble & Hassall, 2014
6	Birmingham, UK n = 30	Individual ponds were sampled for 3 minutes in the spring and summer, following the guidelines of the National Pond Survey.	Species, except Diptera, Sphaeriidae and Oligochaeta	Aquatic macroinvertebrates	Thornhill, 2013

7	Halton, UK n = 37	Individual ponds were sampled twice per year (summer and autumn) for 2 years. Samples were taken from all available mesohabitats using a standard pond net until no new species were recorded.	Species	Aquatic macroinvertebrates, Aquatic macrophytes, Amphibians	Gledhill <i>et al.</i> , 2008
8	North West England n = 425	Samples were taken from all available mesohabitats using a standard pond net until no new species were recorded. Logs and debris was lifted to look for macroinvertebrates located beneath.	Species except Diptera, and Oligochaeta which were not examined.	Aquatic macroinvertebrates, Aquatic macrophytes, Amphibians	Pond life Project, 2000
9	Leeds, UK n = 11	Individual ponds were sampled for 3 minutes in the summer. Sampling time was divided between the mesohabitats present.	Family level	Aquatic macroinvertebrates	Moyers & Hassall unpub.
10	UK wide n = 169	Individual ponds were sampled for 3 minutes in spring, summer and autumn using a sweep sample technique. Sampling time was divided between the mesohabitats recorded in each pond.	Species, except for Oligochaeta, Diptera and small bivalves	Aquatic macroinvertebrates (water mites, zooplankton and other micro-arthropods were not included)	FHT Realising Our Potential Award dataset unpub.
11	UK wide n = 76	Individual ponds sampled for 3 minutes in spring, summer and autumn using a sweep sample technique. Sampling time was divided between the mesohabitats recorded in each pond.	Species, except for Oligochaeta, Diptera and small bivalves	Aquatic macroinvertebrates (water mites, zooplankton and other micro-arthropods were not included)	FHT Temporary Ponds dataset unpub.
12	Leeds, UK n = 10	Individual ponds were sampled for 3 minutes in the summer. Sampling time was divided between the mesohabitats present.	Family level	Aquatic macroinvertebrates	Barber & Hassall unpub.

646 Table 2 - Aquatic macroinvertebrate families identified as indicator taxa for urban (top 6 out of 20) and  
 647 non-urban ponds (the only two significant values) based on indicator value analysis (see text for details).  
 648 \* =  $p < 0.05$ , \*\* =  $P < 0.01$ .

<b>Non-Urban ponds</b>	Stat	<b>Urban ponds</b>	Stat
Nemouridae**	0.34	Chironomidae**	0.72
Heptageniidae*	0.20	Oligochaeta**	0.69
		Crangonyctidae**	0.63
		Sphaeriidae**	0.51
		Certaopogonidae**	0.48
		Dixidae**	0.46

649

650

651 **Figure legends**

652 Figure 1 - Map of Great Britain showing the locations of the surveyed urban (light grey circles)  
653 and non-urban (dark grey circles) ponds.

654 Figure 2: Comparison of environmental values between non-urban and urban ponds for (a)  
655 altitude, (b) shading, (c) pH, (d) pond area, and (e) emergent plant cover. Each dot represents a  
656 site, and dots are offset to illustrate multiple sites at the same value.

657 Figure 3: Species accumulation curves of family richness (a) and species richness (b): grey area  
658 with black line = urban ponds, black area with white line = non-urban ponds, and median  
659 macroinvertebrate family richness (c) and species richness (d) for urban and non-urban ponds.  
660 Boxes show 25<sup>th</sup>, 50<sup>th</sup>, and 75<sup>th</sup> percentiles and whiskers show 5<sup>th</sup> and 95<sup>th</sup> percentiles.

661 Figure 4: Prevalence of aquatic macroinvertebrate families (a) and species (b) in urban and non-  
662 urban ponds. Macroinvertebrate families listed in text are presented as grey circles and have been  
663 named (see Table S8 and Table S9 for raw data).

664 Figure 5: Non-metric multidimensional scaling plots of variation in (a) environmental variables,  
665 (b) aquatic macroinvertebrate families and (c) aquatic macroinvertebrate species from urban and  
666 non-urban ponds (light grey symbols = urban ponds and dark grey symbols = non-urban ponds).

667 Figure 6 - Mantel correlogram for presence-absence macroinvertebrate data at (a) family and (b)  
668 species level along 50 km distance intervals (distances between pond study sites). Triangles =  
669 non-urban sites, circles = urban sites. Filled symbols indicate statistically significant Mantel  
670 correlations.

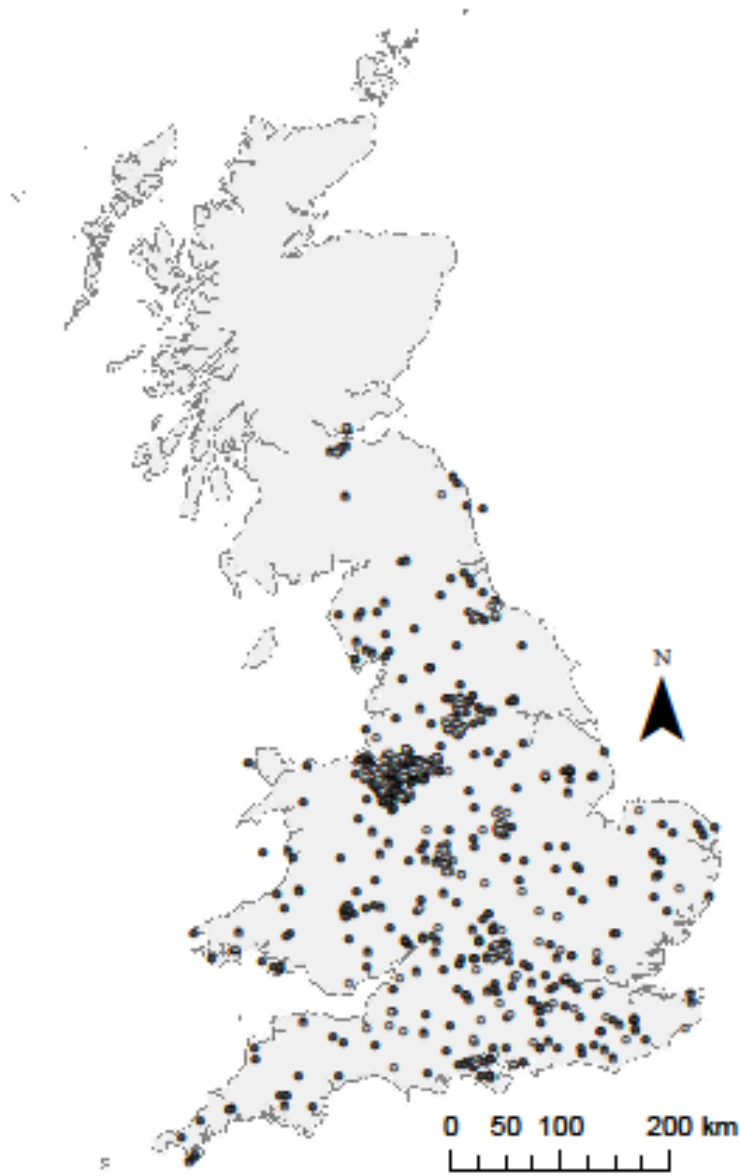
671 Figure 7 - RDA site plots of (a) family-level and (b) species-level macroinvertebrate  
672 communities recorded from the urban and non-urban pond types studied across the UK. Only

673 significant environmental parameters are presented. Dark grey circles = urban ponds, light grey  
674 circles = non-urban ponds.

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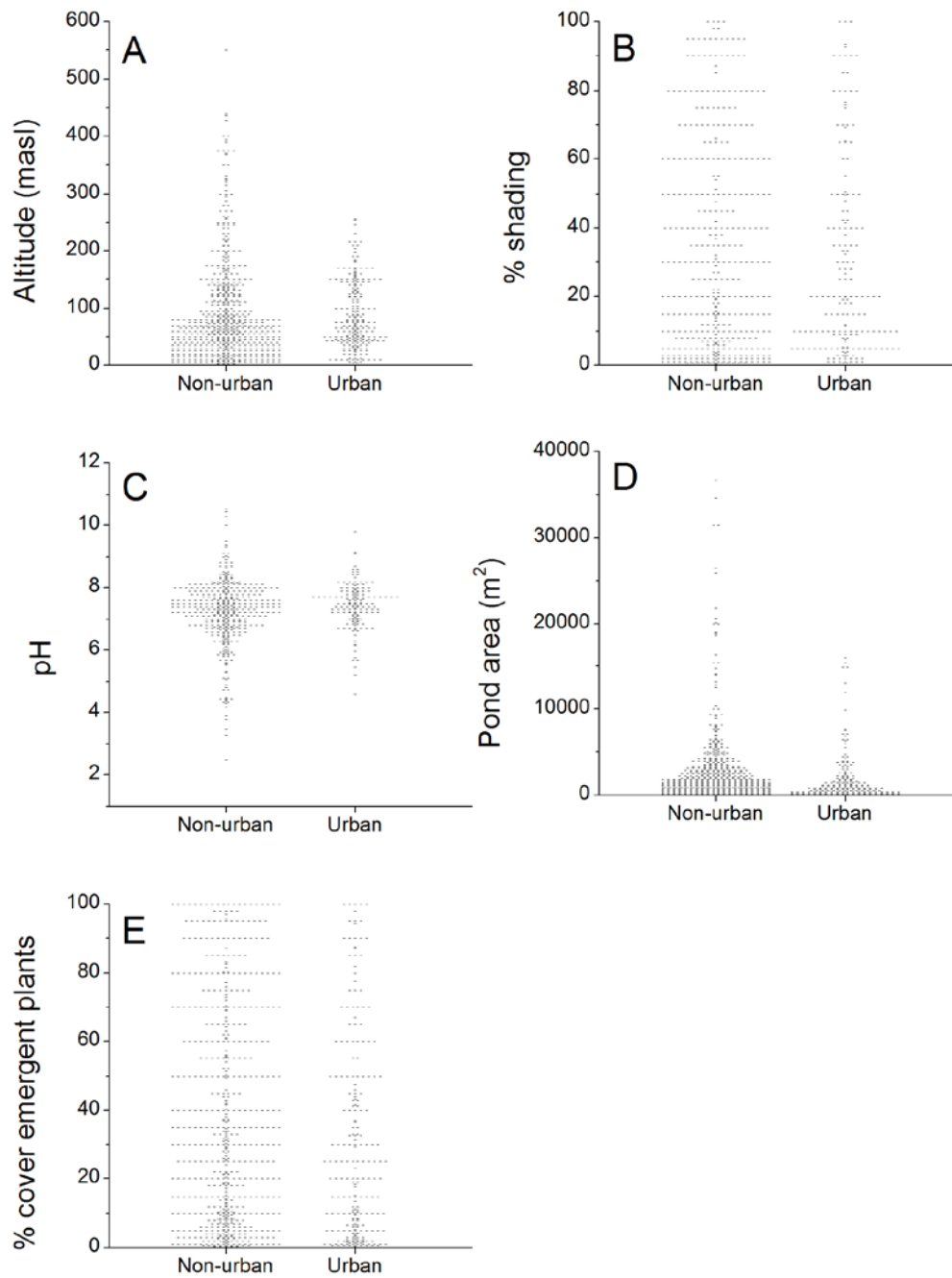
676 **Figures**

677 Figure 1



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679 Figure 2

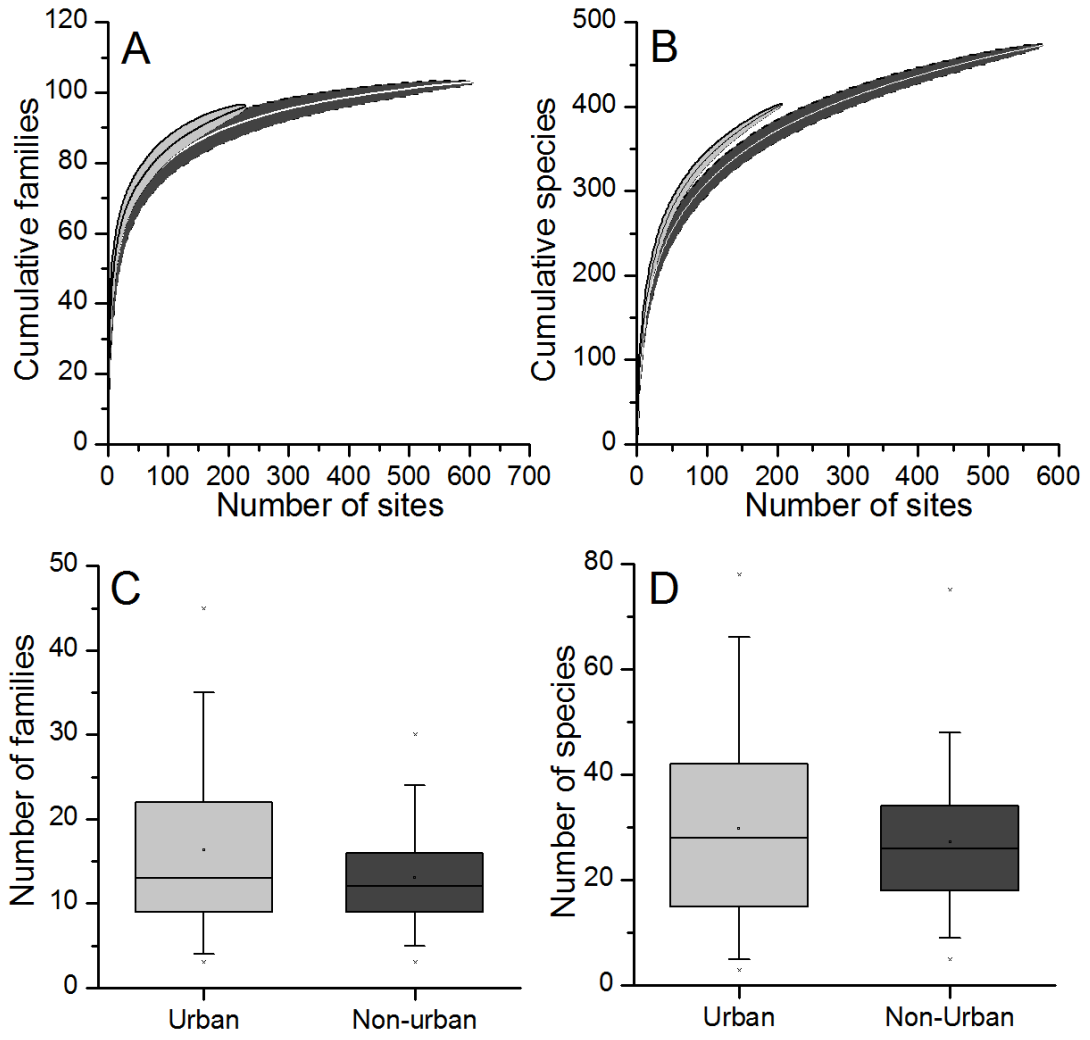


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683 Figure 3



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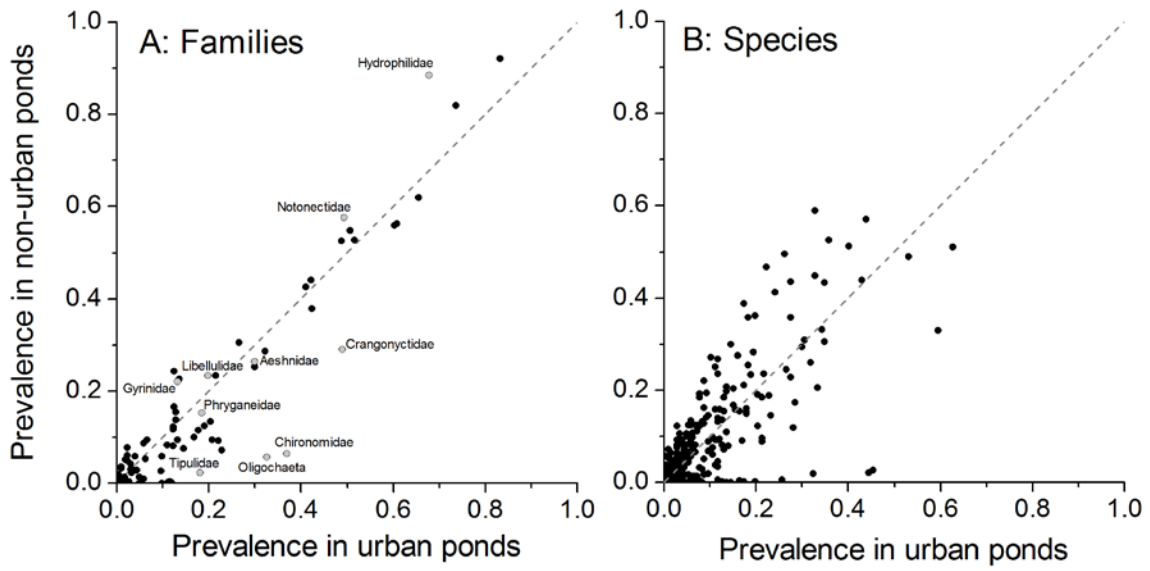
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689 Figure 4



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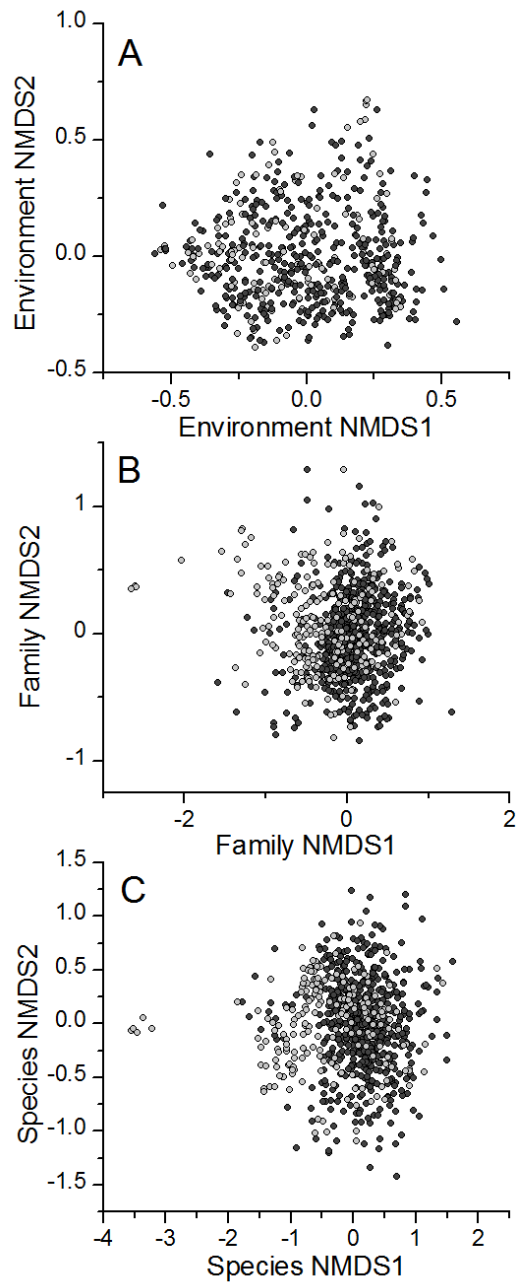
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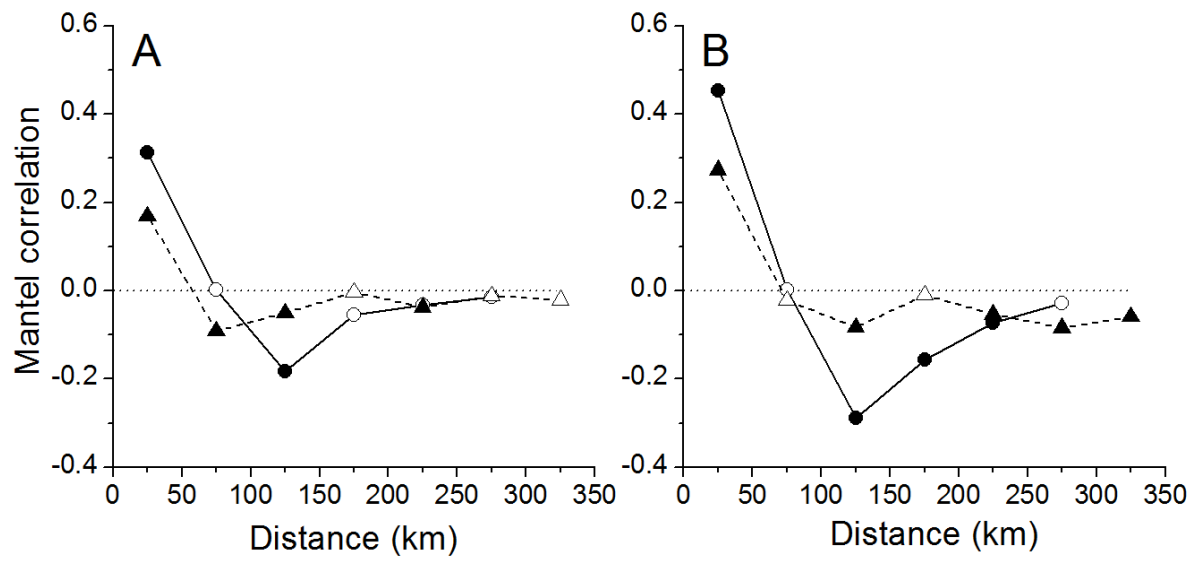
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707 Figure 6



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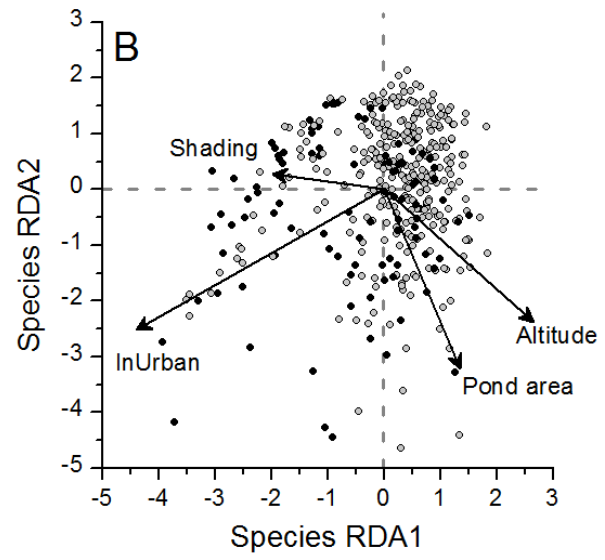
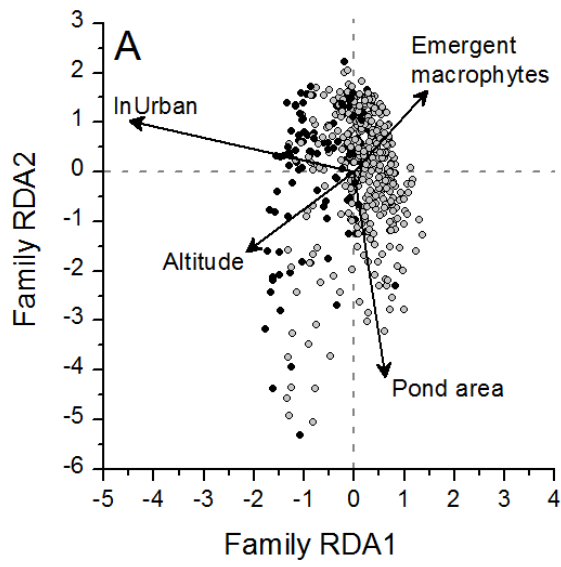
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720 Figure 7



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