

1 **Environmental factors are primary determinants of different facets of pond macroinvertebrate**
2 **alpha and beta diversity in a human-modified landscape**

3 **Running title:** Pond biodiversity in a human-modified landscape

4
5 **Abstract**

6 Understanding the spatial patterns and environmental drivers of freshwater diversity and community
7 structure is a key challenge in biogeography and conservation biology. However, previous studies
8 have focussed primarily on taxonomic diversity and have largely ignored the phylogenetic and
9 functional facets resulting in an incomplete understanding of the community assembly. Here, we
10 examine the influence of local environmental, hydrological proximity effects, land-use type and
11 spatial structuring on taxonomic, functional and phylogenetic (using taxonomic relatedness as a
12 proxy) alpha and beta diversity (including the turnover and nestedness-resultant components) of pond
13 macroinvertebrate communities. Ninety-five ponds across urban and non-urban land-uses in
14 Leicestershire, UK were examined. Functional and phylogenetic alpha diversity were negatively
15 correlated with species richness. At the alpha scale, functional diversity and taxonomic richness were
16 primarily determined by local environmental factors while phylogenetic alpha diversity was driven by
17 spatial factors. Compositional variation (beta diversity) of the different facets and components of
18 functional and phylogenetic diversity were largely determined by local environmental variables. Pond
19 surface area, dry phase length and macrophyte cover were consistently important predictors of the
20 different facets and components of alpha and beta diversity. Our results suggest that pond
21 management activities aimed at improving biodiversity should focus on improving and/or restoring
22 local environmental conditions. Quantifying alpha and beta diversity of the different biodiversity
23 facets facilitates a more accurate assessment of patterns in diversity and community structure.
24 Integrating taxonomic, phylogenetic and functional diversity into conservation strategies will increase
25 their efficiency and effectiveness, and maximise biodiversity protection in human-modified
26 landscapes.

27 **Key Words:** connectivity, functional traits, environmental filtering, macroinvertebrates, pond
28 network, taxonomic distinctness

29

30 **Highlights**

- 31 • Functional and taxonomic alpha diversity were determined by local environmental factors
- 32 • Functional and phylogenetic beta diversity were determined by local environmental factors.
- 33 • Pond management activities should focus on improving local environmental conditions
- 34 • Taxonomic, functional and phylogenetic diversity should be integrated into conservation
35 strategies.

36

37 **1. Introduction**

38 Understanding the spatial patterns and environmental drivers of diversity and community assembly
39 are central to the fields of community ecology, biogeography and conservation biology (Richardson
40 Whittaker, 2010; Socolar et al., 2016; Soininen, 2016). Examining spatial biodiversity patterns has
41 typically been based on taxonomic richness (Ricklefs, 2004; Hill et al., 2018). However, focussing
42 primarily on the taxonomic facet fails to acknowledge that biotic assemblages are composed of taxa
43 with different evolutionary histories and functional roles within ecosystems (Cardoso et al., 2014),
44 which may not provide a complete or comprehensive understanding of the community assembly
45 (Heino and Tolonen, 2017a). Current diversity measures largely ignore the fact that a change in
46 species numbers or environmental conditions can have a significant effect on evolutionary legacy or
47 ecosystem functioning, as taxonomic diversity treats species as evolutionarily equivalent and
48 functionally similar entities (Arnan et al., 2017). Recently, research has begun to recognise that
49 multiple aspects of biodiversity, such as phylogenetic and functional diversity, need to be specifically
50 considered and that in doing so it may provide complementary information to increase our
51 understanding of the mechanisms shaping patterns of biodiversity (Meynard et al., 2011; Cisneros et
52 al., 2015; Heino and Tolonen, 2017b;). Phylogenetic diversity reflects the evolutionary history of an

53 ecological community (Webb et al., 2002) and as a result, communities with identical taxonomic
54 diversity may demonstrate significant phylogenetic diversity depending on the evolutionary history of
55 the organisms at specific sites (Cardoso et al., 2014). Functional diversity refers to the aspects of
56 biodiversity that influence ecosystem functioning and incorporates the diversity of phenotypic
57 (morphological and physiological) and ecological traits within a biotic community (Petchey and
58 Gaston, 2006). Both mismatches and congruencies between functional, phylogenetic and taxonomic
59 diversity have been recorded among biotic communities (Devictor et al., 2010). For example, sites
60 with high taxonomic richness may be characterized by low functional diversity, as different taxa
61 among sites may possess similar functional roles (Villegger et al., 2012); while other studies have
62 shown taxonomic richness to be correlated to phylogenetic and functional diversity (Heino and
63 Tolonen 2017a). Incorporating functional and phylogenetic approaches into biodiversity research may
64 provide a greater understanding of ecosystem functioning-environment associations (Dray et al.,
65 2014), variation in community productivity (Cadotte et al., 2009), the resilience of ecosystem
66 functioning (Thornhill et al., 2018), and the evolutionary constraints on patterns in community
67 composition (Webb et al., 2002).

68

69 Biodiversity can be divided into alpha, gamma, and beta diversity (Whittaker, 1960). Gamma diversity
70 represents the total species diversity in the landscape (Whittaker, 1960). Alpha diversity represents the
71 taxonomic richness within an individual (local) site; while beta diversity refers to the compositional
72 variation in communities among sites within a pre-determined area (Whittaker, 1960). Total beta
73 diversity can be further partitioned into nestedness and turnover components (Baselga, 2010). Species
74 turnover refers to the replacement of species from one site to another; while the nestedness component
75 of beta diversity refers to taxa in species poor sites representing a subset of species within high
76 diversity sites (Baselga et al., 2012; Legendre, 2014). In this study, we focussed on alpha and beta
77 diversity, as this enables an understanding of the processes that drive phylogenetic, functional and
78 taxonomic diversity, and compositional variation at the gamma scale (Heino and Tolonen, 2017a, b).
79 At a local (alpha) scale, phylogenetic, functional, and taxonomic diversities have been shown to vary

80 slightly and to be significantly influenced by different environmental variables in lentic
81 macroinvertebrate metacommunities (Heino and Tolonen 2017a). Recent pond and lake studies have
82 also found that phylogenetic, functional and taxonomic beta diversity (and their turnover and
83 nestedness components) are typically explained by local environmental factors at the landscape-scale
84 (Gianuca et al., 2017; Heino and Tolonen 2017b). However, at larger scales, spatial variables, such as
85 those associated with dispersal limitation, may explain more of the variation in macroinvertebrate
86 assemblages compared to environmental gradients (Cai et al., 2018). Despite this, to our knowledge
87 no studies have examined the influence of environmental and spatial variables on the turnover and
88 nestedness components of macroinvertebrate phylogenetic and functional beta diversity within pond
89 habitats (defined here as lentic waterbodies <2 ha in area). This approach may further increase our
90 understanding of community assembly processes in small lentic ecosystems (Myers et al. 2013;
91 Gianuca et al., 2018).

92

93 Biodiversity conservation almost exclusively focusses on taxonomic diversity (EC, 1992; Strayer
94 Dudgeon, 2010), despite global environmental changes influencing ecosystem functioning (often
95 independently from changes in taxonomic diversity) and phylogenetic diversity through a loss of
96 evolutionary history and opportunities for future diversification (Devictor et al., 2010). Further,
97 protected areas delineated primarily on taxonomic diversity may be incongruent with sites of high
98 functional or phylogenetic diversity, suggesting that focussing solely on taxonomic diversity for
99 conservation decisions may be based on an incomplete representation of biodiversity (Devictor et al.,
100 2010; Strecker et al., 2011; Arnan et al., 2017). Functional and phylogenetic diversity can be better
101 predictors of ecosystem productivity, vulnerability and stability than taxonomic diversity, and may
102 therefore provide critical information, and contribute to the identification of sites that provide more
103 effective, resilient and comprehensive biodiversity conservation (Strecker et al., 2011). Conservation
104 of pond habitats has been demonstrated to be most effective at the landscape-scale, reflecting the high
105 beta diversity (species turnover) and environmental heterogeneity (Williams et al., 2003; Hill et al.,
106 2017). Examining beta diversity (and the nested and turnover components) of all three facets of pond

107 diversity could provide additional information required to increase the effectiveness of landscape-
108 scale pond conservation. However, the contribution of functional and phylogenetic alpha and beta
109 diversity to biodiversity conservation remains poorly quantified across freshwater habitats.

110

111 In this study, we examined the relative influence of local environmental and spatial variables on
112 taxonomic, functional and phylogenetic facets of alpha and beta diversity (and their turnover and
113 nestedness-resultant components). We hypothesised: (1) that local environmental factors would
114 overcome the effects of spatial and landscape-type factors for taxonomic, functional and phylogenetic
115 (taxonomic relatedness) alpha diversity, and (2) that local environmental factors would be the most
116 important factor driving phylogenetic (taxonomic relatedness) and functional total beta diversity, and
117 the nestedness-resultant and turnover components of beta diversity, based on the results of previous
118 studies (Heino and Tolonen 2017a; Hill et al., 2017; Gianuca et al 2018; Rocha et al., 2018). Finally,
119 we discuss the implications of the biodiversity-environment and biodiversity-space relationships for
120 ecological conservation and management in human-modified landscapes.

121

122 **2. Materials and Methods**

123 *2.1 Study area*

124 A total of 95 ponds were studied across a c. 280km² area in Leicestershire, UK (for a detailed outline
125 of the study area, see Hill et al., 2017). Ponds selected for study were located in: (1) urban landscapes
126 (Loughborough: ~35 km², approx. population of 60,000) including urban parks, school grounds,
127 roadsides, high density commercial developments (such as sustainable urban drainage ponds in city
128 centres and industrial areas) and domestic gardens, and (2) non-urban landscapes including floodplain
129 meadows (located in nature reserves protected for nature conservation), woodland (oak or mixed
130 woodland - oak, silver birch, alder and European ash) and agricultural land (dominated by one or two
131 crops such as rapeseed or wheat). Considerable variability in environmental characteristics was
132 recorded among the ponds selected for study (Table 1).

133

134 *2.2 Environmental data collection and spatial variables*

135 A total of 10 local environmental variables measured within each pond comprised: surface water area
136 (m²), mean water depth (cm), percentage of pond covered by submerged, emergent and/or floating
137 macrophytes, dissolved oxygen (percentage saturation), pH, percentage of pond margin shaded, dry
138 phase length (duration that the pond was dry over the 12-month period - 27 ponds dried for between 3
139 and 7 months) and conductivity (μ S cm⁻¹). A total of four spatial variables were included in this
140 study; pond isolation, pond connectivity, PCNM eigenvectors and landscape type. Pond isolation (the
141 number of aquatic habitats within 500m of the sampled pond) and pond connectivity (the number of
142 other aquatic habitats hydrologically connected through surface links to the focal pond site), defined
143 as ‘hydrological proximity effects’ (Hill et al., 2017) were measured at each site. The hydrological
144 proximity effects were recorded using aerial imagery (Google Earth, 2017), ordnance survey maps
145 and field observations. While every attempt was taken to record all aquatic habitat within 500 m of
146 each study site, we acknowledge that a small number of ephemeral and garden ponds may have been
147 overlooked in this study, as they are often not recorded on national maps (e.g., OS MasterMap) and
148 difficult to identify from satellite imagery. Principal coordinates of neighbour matrices (PCNM; a
149 total of 14 eigenvectors were derived in this study) were created using the PCNM package in R
150 (Borcard and Legendre 2002; Legendre et al., 2012). PCNM creates a series of spatial variables to
151 quantify the overall spatial structure in biological communities. The truncation threshold was
152 calculated as the longest distance in the minimum spanning tree (Legendre et al., 2012), and only the
153 eigenvectors that model positive spatial autocorrelation were used in the statistical analyses. Spatial
154 eigenvectors have been suggested to better capture spatial patterns in ecological communities than
155 latitude and longitude as the eigenvectors can represent the spatial structuring of study sites at a range
156 of scales (Borcard and Legendre 2002, Dray et al. 2012). Each pond’s location within the urban or
157 non-urban landscape was recorded.

158

159 *2.3 Macroinvertebrate field surveys*

160 Aquatic macroinvertebrate samples were taken during the spring (March), summer (June) and autumn
161 (September) seasons in 2012, following the National Pond Survey sampling methods (Biggs et al.,
162 1998). Full details of field sampling are outlined in Hill et al., (2015) and summarised here. Sampling
163 time allocated at each pond site was proportional to its surface area; for every 10 m² surface area 30
164 seconds of sampling time was allocated up to 50 m², with ponds greater than 50 m² sampled for 3
165 minutes. The sweep technique was used to collect samples from the available mesohabitats (e.g., open
166 water, emergent macrophytes, submerged macrophytes and floating macrophytes) in each pond.
167 Sampling time at each pond was divided equally among the mesohabitats present. However, if one
168 mesohabitat dominated, sampling time was proportionally divided to reflect this (Biggs et al., 1998).
169 Mesohabitat samples from each pond were pooled for the final analyses. A visual examination of
170 larger substrates that could not be sampled with a pond net (e.g., wood debris and rocks) was
171 undertaken at each pond for a maximum of 60 seconds. The majority of macroinvertebrate taxa were
172 identified to species level, however Physidae, Planariidae and Diptera larvae were resolved to family
173 level and Oligochaeta, Collembola and Hydrachnidia were recorded as such. Seasonal
174 macroinvertebrate data from individual ponds were pooled (see Hill et al., (2017) Appendix part 1 for
175 preliminary analyses of individual season macroinvertebrate data) and the mean values of
176 environmental parameters were derived.

177

178 *2.4 Macroinvertebrate trait and phylogenetic data*

179 Macroinvertebrate functional traits were derived from a trait database developed by Tachet et al.,
180 (2010) and applies to fauna residing within European freshwater habitats (Usseligo-Polatera et al.,
181 2000) Functional traits are reported here by their ‘grouping feature’ (represents a functional trait
182 category) and ‘traits’ (represents the modalities residing within individual grouping features) (see
183 Schmera et al., 2015; White et al., 2017 for terminology). A total of 11 grouping features were used in
184 this study representing the phenotypic properties of fauna: body size, life cycle duration, potential
185 number of cycles per year, aquatic stages, reproduction, dispersal, resistance forms, respiration,
186 locomotion-substrate relation, food and feeding habit. A total of 63 traits from the 11 grouping

187 features were used in this study (see Table S1 for species traits for each grouping feature). These
188 biological grouping features and traits were selected as they provide the fundamental biological
189 characteristics of freshwater macroinvertebrates (Tachet et al., 2010; Merrit and Cummins, 1996), as
190 opposed to their ecological preferences. Trait information within the database is typically available at
191 species- or genus-level and only taxa resolved to an equal or lower taxonomic resolution within this
192 study were included within the functional analyses. As such, a total of 11 taxa out of 228 were
193 excluded as they were deemed to possess high functional variability (or were identified at a too coarse
194 level); Ceratopogonidae, Chaoboridae, Chironomidae, Chrysomelidae, Dixidae, Empididae,
195 Simuliidae, Diptera Other, Hydrachnidae, Planariidae, Collembola, Hydrophilidae larvae, Dytiscidae
196 larvae, Scirtidae larvae and Sphaeriidae. In addition, trait information was lacking for some taxa:
197 *Dicranota* sp., *Cercyon marinus*, *Callicorixa wollastoni*, *Succinea putris*, and Zonitidae. Where trait
198 information was only available for macroinvertebrates at the genus level, species were aggregated to
199 the genus level.

200

201 As the true phylogenetic tree was unavailable for the macroinvertebrate taxa recorded in this study,
202 taxonomic distance based on the path lengths in the taxonomic trees was used as a proxy for the true
203 phylogenetic tree. The derived taxonomic tree used equal branch lengths and seven taxonomic levels
204 (species, genus, family, suborder, order and phylum), which were based on numerous aquatic
205 macroinvertebrate identification keys (Macan 1977; Elliot and Mann 1979; Hynes, 1984; Fres, 1985;
206 Elliot et al., 1988; Friday, 1988a; Savage, 1989; Smith, 1989; Gledhill et al., 1993; Edington and
207 Hildrew 1995; Wallace et al., 2003; Cham, 2009 and; Foster and Friday 2011).

208

209 *2.5 Statistical analyses*

210 *2.5.1 Alpha diversity*

211 All statistical analyses were performed in the R environment (R Core Team, 2016). The taxa-
212 abundance macroinvertebrate dataset was converted into a presence-absence dataset prior to alpha and

213 beta diversity statistical analyses (see Fig. S1, S2 and S3 for the taxonomic, functional and
214 phylogenetic alpha and beta diversity statistical procedures).

215

216 Using the derived taxonomic tree outlined above (as a surrogate for a phylogenetic tree), taxonomic
217 distances between species were calculated using the function *taxa2dist* in the *vegan* package (Oksanen
218 et al., 2017). To determine trait distances between species, the Gower dissimilarity was calculated
219 using the original trait data, using the function *gowdis* from the *FD* package (Laliberte et al., 2014),
220 Mean pairwise distance (MPD) indices were used to calculate observed taxonomic relatedness (proxy
221 for phylogenetic diversity) among sites (using the taxonomic distances between species), and
222 functional alpha diversity (using the Gower dissimilarity of the trait dataset and species presence-
223 abundance data). MPD for taxonomic relatedness and functional data was calculated using the
224 function *ses.mpd* from the *picante* package (Kembel et al., 2016). MPD was chosen as the alpha
225 diversity index in this study as the *ses.mpd* function can use any species-by-species distance matrix
226 (e.g., Gower dissimilarity) as input in addition to a site-by-species matrix. Taxonomic relatedness has
227 been used in other studies examining phylogenetic diversity and demonstrated to be a suitable proxy
228 for true phylogeny when it is unavailable (Ruhi et al., 2013; Heino and Tolonen 2017a; Cai et al.
229 2018; Heino and Tolonen 2018). Taxonomic alpha diversity was calculated as the taxonomic richness
230 (number of taxa) in each sampled site.

231

232 To examine the environmental variables significantly explaining the variation in taxonomic,
233 functional and phylogenetic alpha diversity, partial linear regression was undertaken. Initially,
234 separate partial linear regression analyses (for taxonomic, functional and phylogenetic alpha diversity)
235 employing a forward selection process (using the function *ordiR2step* in the *vegan* package) was
236 undertaken to identify the significant local environmental variables, hydrological proximity effects,
237 and spatial eigenvectors influencing taxonomic, phylogenetic and functional alpha diversity. Three
238 stopping rules were employed when applying this forward selection method: (1) once the adjusted R^2
239 begins to decrease, (2) once the permutational significance level was exceeded ($\alpha = 0.05$) and (3) once

240 the full model adjusted R^2 was exceeded (Hill et al., 2017; Oksanen et al., 2017). Environmental
241 parameters were \log_{10} transformed to downweight extreme values consistently across all abiotic
242 parameters (Legendre and Birks 2012). Variance partitioning analysis (Borcard et al., 1992), based on
243 partial linear regression, was undertaken to identify the pure and shared contribution of 4 sets of
244 predictors; (1) local environmental conditions, (2) hydrological proximity effects, (3) landscape type
245 and (4) spatial structuring (PCNM eigenvectors) on phylogenetic and functional alpha diversity
246 (observed MPD). Variance partitioning analysis was performed using the *varpart* function in the
247 vegan package. Statistical significance of the four sets of predictors and the full model were
248 calculated using the *anova* function. The adjusted R^2 fractions are presented in this study as they
249 provide unbiased estimations of explained variation which corrects for the number of explanatory
250 variables (Peres-Neto et al., 2006).

251

252 Pearson correlation (r) was calculated (using the function *cor.test* in the stats package) to examine the
253 correlation between the taxonomic, functional and phylogenetic alpha diversity among pond sites.
254 Moran's I correlograms were constructed to examine the degree of spatial autocorrelation of
255 phylogenetic alpha diversity, functional alpha diversity of the MPD for phylogenetic and functional
256 communities, using the function *correlog* in the pgirmess package (Giraudoux, 2017).

257

258 2.5.2 Beta diversity

259 We examined variation in macroinvertebrate phylogenetic and functional total beta diversity, and the
260 turnover and nestedness-resultant components. RDA was chosen as the constrained ordination method
261 to analyse the variation in phylogenetic and functional beta diversity in relation to local and spatial
262 explanatory variables (Legendre and Legendre 2012). Taxonomic beta diversity was not analysed here
263 as it has previously been examined (Hill et al. 2017). For phylogenetic beta diversity analyses,
264 taxonomic distance (as a proxy for true phylogeny) between macroinvertebrate taxa was calculated
265 using the *taxa2dist* function (Heino and Tolonen 2017b). A taxonomic tree was constructed by

266 building a clustering tree using the function *hclust* (using the ‘complete’ agglomeration method), and
267 converting the clustering tree into a taxonomic tree using *as.phylo* function in the *ape* package
268 (Paradis et al., 2017). Pair-wise distance matrices based on the Sørensen dissimilarity (using a site-by-
269 species matrix and the taxonomic tree), accounting for the phylogenetic nestedness-resultant and
270 turnover components of beta diversity, and total beta diversity, were calculated using the
271 *phylo.beta.pair* function in the *betapart* package (Baselga et al., 2017). Principal coordinate analyses
272 (PCoA, with Lingoes correction accounting for negative eigenvalues) was undertaken on the three
273 taxonomic distance matrices (turnover, nestedness-resultant and total beta diversity) using the
274 function *pcoa* in the *ape* package (as performed by Hill et al., 2017) to derive ‘taxonomic vectors’
275 describing species taxonomic relatedness. The principal coordinates (eigenvectors) for the three
276 taxonomic dissimilarity matrices were used as response variables in separate variance partitioning
277 analyses. For functional beta diversity analyses, the dimensionality of the original trait data was
278 reduced, and trait distances between species were calculated using the Gower distance (Gower, 1971)
279 using the function *gowdis*. PCoA was undertaken on the trait Gower dissimilarity matrix using the
280 function *pcoa*. Only the first two PCoA vectors were used in calculating convex hull volumes shaping
281 any two communities in functional space, as further dimensions caused overly long computational
282 times. Three functional pair-wise distance matrices (using a site-by-species matrix and quantitative
283 traits data, in this case two PCoA trait vectors) accounting for the functional turnover and nestedness-
284 resultant components of beta diversity, and total beta diversity were calculated using the
285 *functional.beta.pair* function in the *betapart* package (based on Sørensen dissimilarity; Heino and
286 Tolonen 2017b). On each of the functional dissimilarity matrices (nestedness-resultant, turnover and
287 total beta diversity), PCoA analyses were undertaken using the function *pcoa*. The principal
288 coordinates (eigenvectors) for the three functional dissimilarity matrices were used as response
289 variables in separate variance partitioning analyses.

290

291 Prior to variance partitioning analysis, environmental variables were transformed (\log_{10}). RDA
292 analyses using a forward selection process (using the function *ordiR2step*) were performed on

293 functional and phylogenetic total beta diversity, and the functional and phylogenetic nestedness-
294 resultant and turnover matrices (as represented by the corresponding principal coordinates, see
295 above), to identify the significant local environmental and spatial parameters (hydrological proximity
296 effects, PCNM eigenvectors). To examine the individual and shared contribution of local
297 environmental variables, hydrological proximity effects, land-use type and spatial structuring (PCNM
298 eigenvectors) on the functional and phylogenetic total beta diversity, turnover and nestedness-
299 resultant dissimilarity matrices (based on the PCoA eigenvectors), variance partitioning analysis were
300 undertaken as above. Separate variance partitioning analysis was undertaken on: (1) total phylogenetic
301 beta diversity, (2) total functional beta diversity, (3) the functional nestedness-resultant component,
302 (4) the phylogenetic nestedness-resultant component, (5) phylogenetic turnover, and (6) functional
303 turnover. Significance of the full model and the contributions of the predictor groups (local
304 environmental variable, land-use type, hydrological proximity effects and PCNM eigenvectors) was
305 undertaken for each of the variance partitioning analyses using the *anova* function.

306

307 **3. Results**

308 In total, 228 macroinvertebrate taxa were recorded from 68 families and 21 orders from the studied
309 pond sites. In terms of taxonomic richness, communities were dominated by insects, particularly
310 Coleoptera (75 taxa), Hemiptera (32 taxa), Trichoptera (35 taxa), Odonata (19 taxa) and Diptera (14
311 taxa). Preliminary analyses indicated that dissimilarity (based on Sørensen dissimilarity) in functional
312 and phylogenetic communities were significantly correlated (Mantel test: $r=0.87$, $p<0.001$).
313 Taxonomic alpha diversity was significantly negatively correlated with functional (Pearson
314 correlation: $r = -0.64$, $p<0.001$; Fig. 1a) and phylogenetic alpha diversity (Pearson correlation: $r = -$
315 0.39 , $p<0.001$; Fig. 1b).

316

317 *3.1 Alpha diversity*

318 One hydrological proximity effect (connectivity) and three local environmental variables (percentage
319 coverage of submerged macrophytes, conductivity, percentage dissolved oxygen) were identified to
320 significantly influence functional alpha diversity. No PCNM spatial filters significantly influenced
321 functional alpha diversity and were subsequently removed from the variance partitioning analysis
322 (Fig. 2a). A total of 37.6% of variation in functional alpha diversity was explained by local and spatial
323 parameters, based on the adjusted R^2 . Local environmental variables (22.5%) was the only predictor
324 group that significantly influenced functional alpha diversity and explained more of the statistical
325 variation than hydrological proximity effects (0%), and landscape type (1.1%)

326

327 Two PCNM spatial eigenvectors and one hydrological proximity effect (connectivity) were significant
328 influences on phylogenetic alpha diversity. No local environmental variables significantly influenced
329 phylogenetic alpha diversity and were excluded from the analyses. In total, 19.4% of variation in
330 phylogenetic alpha diversity was explained by the variance partitioning model (Fig. 2b). PCNM
331 Spatial filters (5.5%) was the only predictor group that significantly influence phylogenetic alpha
332 diversity and accounted for more of the statistical variation than landscape type (1.4%) and
333 hydrological proximity effects (0.8%; Fig. 2b).

334

335 When taxonomic alpha diversity (richness) was examined, six local environmental variables (pond
336 surface area, dry phase length, percentage coverage of submerged macrophytes and floating
337 macrophytes, conductivity, and percentage of the pond margin shaded), two hydrological proximity
338 effects (connectivity and pond isolation) and one PCNM spatial filter influenced taxonomic alpha
339 diversity. A total of 74.4% of variation in taxonomic alpha diversity was explained by the local and
340 spatial variables (Fig. 2c). Local environmental parameters alone significantly explained taxonomic
341 alpha diversity more effectively (46%) than the hydrological proximity effects (0.3%) and the PCNM
342 spatial filters (5.6%; Fig. 2c).

343

344 *3.2 Beta diversity*

345 Two significant PCNM spatial eigenvectors, two hydrological proximity effects (connectivity and
346 pond isolation) and nine local environmental variables (pond surface area, dry phase length, dissolved
347 oxygen concentration, percentage coverage of submerged macrophytes, emergent macrophytes and
348 floating macrophytes, pH, conductivity, and percentage of the pond margin shaded) were identified to
349 influence total phylogenetic beta diversity. A total of 32.6% of the variation in total phylogenetic beta
350 diversity was accounted for by local and spatial variables. Local environmental variables alone
351 explained phylogenetic beta diversity more effectively (19.5%) than the PCNM spatial eigenvectors
352 (0.9%) and hydrological proximity effects (1.4%; Fig. 3a).

353

354 When the total functional beta diversity was examined, landscape type, one PCNM spatial eigenvector
355 and five local environmental variables (pond surface area, dry phase length, dissolved oxygen
356 concentration, percentage coverage of submerged macrophytes, and percentage of the pond margin
357 shaded) were significant in influencing functional beta diversity and used in the variance partitioning
358 analysis. A total of 31.5% of the variation in total functional beta diversity was explained by local and
359 spatial variables. Local environmental variables accounted for a greater proportion of the variance in
360 functional beta diversity (20.2%) than the landscape type (2.3%) or spatial eigenvectors (1.9%; Fig.
361 3b).

362

363 Three significant spatial eigenvectors, one hydrological proximity effect (connectivity) and nine local
364 environmental variables (pond surface area, dry phase length, pond depth, percentage coverage of
365 submerged macrophytes, emergent macrophytes and floating macrophytes, pH, conductivity, and
366 percentage of the pond margin shaded) influenced pond phylogenetic turnover. A total of 18.7% of
367 the variation in phylogenetic turnover could be explained by the local and spatial variables (Fig. 3c).
368 Local environmental variables (9.9%) and hydrological proximity effects (0.7%) were the only
369 predictor groups recorded to significantly influence phylogenetic turnover among ponds (Fig. 3c).

370

371 A total of three local environmental variables (pond surface area, pond depth and the percentage
372 coverage of submerged macrophytes) were identified to significantly influence the variance in
373 functional turnover. No PCNM spatial eigenvectors or hydrological proximity effects influenced the
374 variability in functional turnover and were excluded from the variance partitioning analysis. A total of
375 10.9% of the variation in functional turnover was explained by local environmental variables and
376 landscape type (Fig. 3d). Local environmental variables (7.7%) and landscape type (1.1%) both
377 significantly influenced spatial patterns in functional turnover (Fig. 3d).

378

379 Spatial patterns of phylogenetic nestedness were significantly influenced by five local environmental
380 variables (pond surface area, dry phase length, conductivity, percentage of the pond margin shaded
381 and the percentage coverage of submerged macrophytes), and one hydrological proximity effect (pond
382 isolation). No PCNM spatial filters significantly influenced spatial patterns of phylogenetic
383 nestedness and were excluded from the variance partitioning analysis (Fig. 3e). A total of 31.4% of
384 the variation in phylogenetic nestedness could be explained by the local and spatial variables
385 examined. Local environmental variables explained more of the variation in phylogenetic nestedness
386 (22%) than hydrological proximity effects: (1.6%) and landscape type (1%; Fig. 3e).

387

388 A total of five local environmental variables (pond surface area, dry phase length, dissolved oxygen
389 concentration, percentage coverage of submerged macrophytes, and percentage of the pond margin
390 shaded) one hydrological proximity effect (connectivity) and one PCNM spatial eigenvector
391 influenced spatial patterns of functional nestedness. A total of 35.5% of the variation in functional
392 nestedness was explained by the local and spatial variables (Fig. 3f). Local environmental variables
393 (23.3%) explained more of the variation in spatial patterns of functional nestedness than landscape
394 type (2.3%), hydrological proximity effects (0.7%), or the spatial eigenvectors (0.7%).

395

396 **4. Discussion**

397 The results of this research have highlighted several ecologically important and interesting patterns
398 that advance fundamental understanding on the phylogenetic, functional and taxonomic diversity
399 patterns of lentic macroinvertebrate metacommunities. Taxonomic richness was most strongly
400 explained by environmental variables, including pond surface area, dry phase length, macrophyte
401 cover, conductivity and shading, which corresponds to the findings from multiple previous studies of
402 small lentic waterbodies (including Oertli et al., 2002; Hassall et al., 2011; Heino, 2013; Heino et al.,
403 2017c). Many of these variables are directly or indirectly related to ‘area effects’ (MacArthur Wilson,
404 1967), ‘disturbance effects’ (Vanshoenwinkel et al., 2013), and ‘environmental heterogeneity effects’
405 (Stein et al., 2014) on biodiversity, with increasing surface area, short dry periods and high
406 macrophyte cover providing more habitat space (and structural complexity) for pond
407 macroinvertebrates spatially and temporally. Taxonomic richness was also affected by hydrological
408 proximity effects and spatial variables, but their unique effects were low. Similarly, functional alpha
409 diversity was primarily driven by local environmental factors, and was minimally affected by spatial
410 factors. Given the importance of dissolved oxygen and macrophyte cover in determining functional
411 alpha diversity, this suggests that functional alpha diversity is locally determined by variables
412 affecting macroinvertebrate traits responsible for respiration or traits that reflect adaptations to living
413 in macrophyte beds (see Tachet et al., 2010). In contrast, phylogenetic alpha diversity was not
414 significantly affected by local environmental factors but was most strongly correlated with spatial
415 variables and secondarily with landscape type. This suggests that phylogenetic alpha diversity shows
416 spatially-structured variation at the landscape-scale similar to that observed in previous studies
417 conducted across broad spatial scales (Strecker et al., 2011; Cai et al., 2018). However, in our
418 landscape-scale study, such spatial variation may be difficult to interpret as a signal of evolutionarily
419 distinct lineages living in different parts of the study area, but rather as a sign that some spatially-
420 structured local environmental variables that influence phylogenetic alpha diversity were not
421 accounted for in this study.

422

423 Patterns in total beta diversity were not as strong as those for alpha diversity, which is typical of
424 studies centred on community structure. In this study the percentage of variation explained by local
425 and regional variables was <35%, but this figure has been frequently reported to be much lower in
426 other comparable studies on freshwater ecosystems (Heino et al., 2015; Hill et al., 2017). However,
427 previous studies examining community assembly in freshwaters have almost exclusively focussed on
428 taxonomic community structure (e.g., Vanschoenwinkel et al., 2007; Viana et al., 2016), whereas we
429 utilised information on phylogenetic and functional features of pond macroinvertebrate communities.
430 Rarely have these two facets been tested concurrently to examine community structural variation, so
431 reference points are difficult to find in the literature. Gianuca et al. (2018) found that all three facets
432 and components of biodiversity of pond zooplankton communities varied along an urbanization
433 gradient, with land use close to a pond and local environmental variables being responsible for
434 generating variation in functional traits and phylogenetic relatedness. Rocha et al. (2018) reported that
435 of the spatial, climatic, catchment and local environmental variables they examined, only local
436 environmental and spatial variables were important in determining variation in taxonomically-,
437 functionally- and phylogenetically-defined stream macroinvertebrate communities, broadly
438 corresponding to the findings of this study. We found that total functional and phylogenetic beta
439 diversities were mostly affected by local environmental variables, suggesting that trait selection and
440 taxonomic relatedness (used in our study as a surrogate for phylogenetic biodiversity) were
441 determined at the local pond scale. This finding is plausible, given the relatively small geographical
442 scale of this research (c. 280 km²) and the fact that at small spatial-scales, these facets should be
443 predominantly shaped by environmental controls (Heino and Tolonen 2017b).

444

445 Variation in the turnover and nestedness-resultant components of taxonomic, functional and
446 phylogenetic beta diversity were primarily determined by local environmental variables. Given that
447 very few studies that have focussed on the turnover and nestedness components of beta diversity in
448 freshwater ecosystems, broad comparisons are not possible. However, Gianuca et al. (2017) reported
449 that local environmental factors, in terms of nutrient enrichment, negatively affected local taxonomic

450 zooplankton diversity. This produced a pattern of beta diversity derived from nestedness in
451 unconnected and environmentally heterogeneous landscapes. Increasing dispersal resulted in a weak
452 pattern of nestedness, with the replacement component of beta diversity increasing in importance. Our
453 findings did not provide as clear indications as Gianuca et al.'s (2017) study regarding the separation
454 of the effects of dispersal and local environmental factors on the turnover and nestedness components
455 of beta diversity. However, we found that the nestedness-resultant components of both functional and
456 phylogenetic beta diversity were better explained by the predictor variables compared to the turnover
457 components. For both components, pond surface area, dry phase length and macrophyte cover
458 remained the most important predictors of beta diversity. This finding suggests that these are 'master'
459 variables governing variation in pond macroinvertebrate communities, corroborating the findings of
460 numerous previous studies (Rundle et al., 2002; Biggs et al., 2005; Hassall et al., 2011; Florencio et
461 al., 2014; Hill et al., 2015; Heino and Tolonen, 2017b; Hill et al., 2017).

462

463 *4.1 Implications for biodiversity conservation*

464 Our study has direct implications for the conservation of pond biodiversity in human-modified
465 landscapes characterised by multiple land-use types. First, it would be advisable for management
466 activities to focus on improving or restoring local environmental conditions to support locally diverse
467 pond faunas at a landscape-scale through increased environmental heterogeneity. For example, major
468 foci should be pond surface area, depth, macrophyte cover and variation in hydroperiod length (Biggs
469 et al., 2005; Hassall et al., 2011; Florencio et al., 2014; Thornhill et al., 2018). This is important
470 because taxonomic and functional alpha diversity were primarily determined by local environmental
471 conditions. In particular, increasing pond surface area and the coverage of submerged macrophytes
472 will promote functional and taxonomic alpha diversity. However, given that no single site can support
473 all species in a regional pool, promoting environmental heterogeneity among ponds should result in
474 high levels of taxonomic, functional and phylogenetic beta diversity (Sayer et al., 2012). In addition,
475 spatial effects were highlighted to be important for phylogenetic alpha diversity, but not for functional
476 or taxonomic diversity. This low amount of variation in community data explained may be because

477 measuring between-site connectivity (and consequent dispersal) is particularly difficult (Heino et al.,
478 2017d). Consequently, more accurate measurements of the spatial structure of pond networks, may
479 highlight a stronger influence of spatial structuring on biodiversity. Hence, increasing knowledge of
480 connectivity effects on pond biodiversity (Oertli et al., 2008; Ribeiro et al., 2011) should also be a
481 priority for conservation at a landscape-scale.

482

483 Recently, Cai et al., (2018) analysed broad-scale congruence among species richness, functional
484 diversity and phylogenetic diversity using an approach similar to that reported here. They proposed
485 that, as conservation planning is typically limited by available resources, defining priorities that
486 simultaneously protect all biodiversity facets would be a desirable goal. Findings from some studies
487 highlight that different facets of alpha diversity may be strongly correlated across broad spatial scales
488 (e.g. Heino et al., 2008; Strecker et al., 2011), which suggests that protecting all facets and
489 components of biodiversity simultaneously could be achieved by focussing on the protection of
490 species richness. However, contradictory results have also emerged in studies at both national (Cai et
491 al., 2018) and regional scales (Heino et al., 2005), where different facets of alpha diversity were
492 weakly correlated. Our results demonstrate that for pond macroinvertebrates both functional and
493 phylogenetic alpha diversity were negatively correlated with species richness. This pattern may be
494 driven by the properties of each facet of diversity whereby increases in species richness and functional
495 diversity may only generate a small change in phylogenetic diversity (Cai et al. 2018). Furthermore,
496 the negative association between taxonomic richness and functional diversity may be driven by high
497 redundancy or high niche differentiation within the regional metacommunity (Siqueira et al. 2012;
498 Wellnitz and Poff 2001). Implementing conservation strategies using a single facet of diversity
499 (typically taxonomic richness) as a cure-for-all should be avoided (Devictor et al., 2010). Instead, our
500 results suggested that the three distinct facets of alpha diversity cannot be used as good surrogates of
501 one another, but rather that conservation of pond macroinvertebrate biodiversity in human-modified
502 landscapes requires a multi-faceted approach incorporating different biodiversity facets. However,
503 focussing conservation efforts exclusively on different facets of alpha diversity is also unlikely to be

504 effective. Quantifying the beta diversity (total, turnover and nestedness-resultant components) of the
505 different biodiversity facets facilitates a more accurate and complete assessment of compositional
506 variation, and the identification of the most suitable locations for biodiversity conservation that
507 incorporate all diversity facets (Socolar et al., 2016). Indeed, high beta diversity is typically associated
508 with high gamma diversity and, therefore, focussing conservation actions on maintaining both beta
509 and gamma diversity should be a priority (Bush et al., 2016). This can likely be achieved by
510 guaranteeing environmental heterogeneity among ponds at the landscape-scale. An integrative
511 approach that combines taxonomic, phylogenetic and functional facets of alpha and beta diversity will
512 provide more efficient and effective biodiversity conservation strategies that maximise the amount of
513 biodiversity protected and ecological resilience.

514

515 Our approach will help the understanding of biodiversity–environment relationships that are
516 fundamental for linking theory to management and the development of sound management actions for
517 ponds in the face of environmental change. As global change threatens biodiversity and ultimately
518 ecosystem services humans are relying on (IPBES 2019), we suggest that future studies should
519 incorporate functional and phylogenetic diversity to characterise ecosystem functions and services.
520 Doing so, would also help predict how global change will alter the functioning and evolutionary
521 capability of pond biota in the future.

522

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750 **Tables**

751 Table 1. Descriptive statistics of measured environmental variables and biodiversity indices across the
 752 95 ponds selected for study. MPD = mean pairwise distance, SES = standard effects size.

	Mean	Standard Deviation	Coefficient of Variation	Minimum	Maximum
Area (m ²)	552.4	1457	263.7	0.8	9309
Depth (cm)	60.7	54.9	90.4	4	>100
Pond Margin Shaded (%)	23.4	32.6	139.1	0	100
Emergent Macrophytes (%)	23.6	27.6	116.9	0	100
Submerged Macrophytes (%)	23.1	23.6	102.2	0	100
Floating Macrophytes (%)	9.2	19.3	210.4	0	96.7
pH	7.8	0.6	8	6.2	9.8
Conductivity	567.2	302.9	53.4	63.7	1494
Dissolved Oxygen (%)	75.3	24.7	32.8	13.1	131.6
Pond Isolation	9	7	77.4	0	30
Pond Connectivity	3	4.7	178.1	0	14
Phylogenetic MPD	80.8	5.8	7.1	66.7	100
Phylogenetic MPD SES	1.3	1.2	96.4	-2.3	3.9
Functional MPD	0.27	0.02	8.6	0.24	0.35
Functional MPD SES	1.15	0.99	87.2	-1.81	2.85
Taxonomic Richness	29.5	19.5	66.3	2	73

753

754 **Figure legends**

755 **Figure 1.** Scatter plots of species richness and (a) functional alpha diversity and (b) phylogenetic
756 alpha diversity.

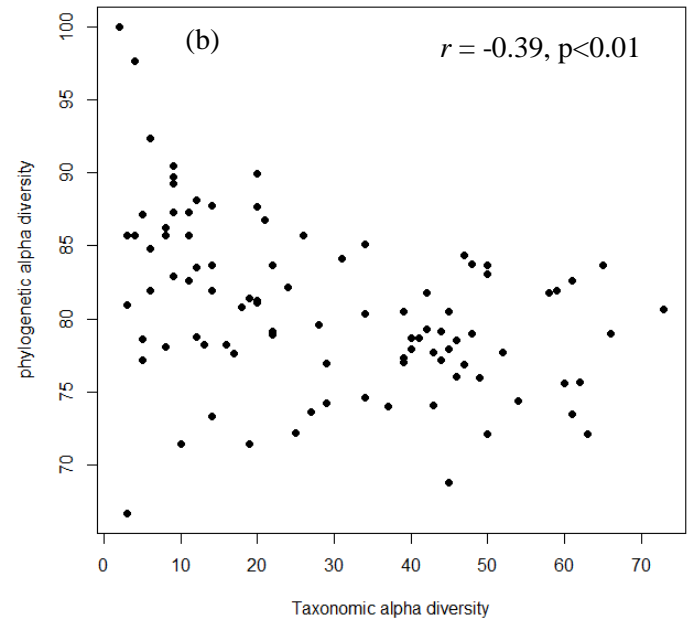
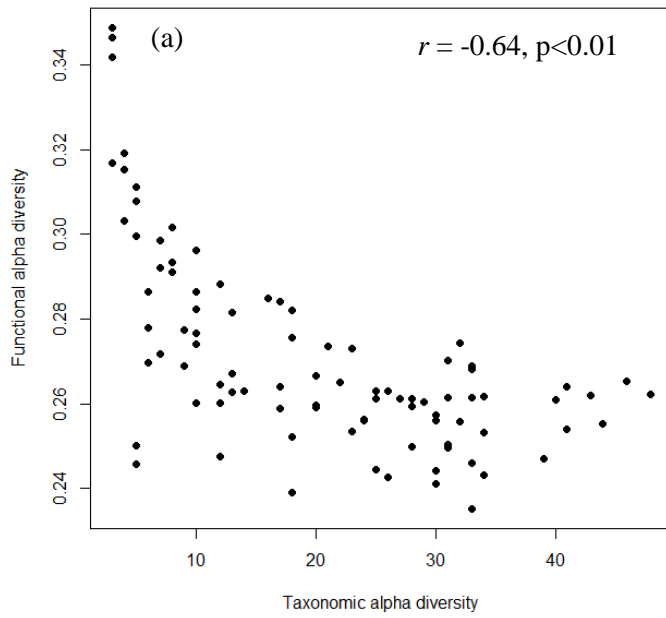
757 **Figure 2.** The relative contribution of PCNM eigenvectors, hydrological proximity effects, landscape
758 type (urban/non-urban) and local environmental variables to: (a) functional alpha diversity (mean
759 pairwise distance), (b) phylogenetic alpha diversity (mean pairwise distances), and (c) taxonomic
760 alpha diversity. Negative fractions are not presented in the figure. Values represent the adjusted R^2
761 values.

762 **Figure 3.** The relative contribution of PCNM eigenvectors, hydrological proximity effects, landscape
763 type (urban/non-urban) and local environmental variables to: (a) total phylogenetic beta diversity, (b)
764 total functional beta diversity, (c) phylogenetic turnover, (d) functional turnover, (e) the nestedness
765 component of phylogenetic beta diversity, and (f) the nestedness component of functional beta
766 diversity. Negative fractions are not presented in the figure. Values represent the adjusted R^2 values.

767 **Figures**

768 Figure 1

769



770 Figure 2

