

1 Effects of dispersal mode on the environmental and spatial correlates of nestedness and species
2 turnover in pond communities

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24 **Abstract**

25 Advances in metacommunity theory have made a significant contribution to understanding the drivers
26 of variation in biological communities. However, there has been limited empirical research exploring
27 the expression of metacommunity theory for two fundamental components of beta diversity:
28 nestedness and species turnover. In this paper, we examine the influence of local environmental and a
29 range of spatial variables (hydrological connectivity, proximity and overall spatial structure) on total
30 beta diversity and the nestedness and turnover components of beta diversity for the entire
31 macroinvertebrate community and active and passively dispersing taxa within pond habitats. High
32 beta diversity almost entirely reflects patterns of species turnover (replacement) rather than nestedness
33 (differences in species richness) in our dataset. Local environmental variables were the main drivers
34 of total beta diversity, nestedness and turnover when the entire community was considered and for
35 both active and passively dispersing taxa. The influence of spatial processes on passively dispersing
36 composition, total beta diversity and nestedness was significantly greater than for actively dispersing
37 taxa. Our results suggest that species sorting (local environmental variables) operating through niche
38 processes was the primary mechanism driving total beta diversity, nestedness and turnover for the
39 entire community and active and passively dispersing taxa. In contrast, spatial factors (hydrological
40 connectivity, proximity and spatial eigenvectors) only exerted a secondary influence on the nestedness
41 and turnover components of beta diversity.

42 Key words: biodiversity, community ecology, connectivity, mass effects, proximity, spatial variables,
43 species sorting

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50 **Introduction**

51 Beta diversity can be defined as the spatial or temporal variation in community composition among
52 sites within a defined geographical area of interest (Whittaker 1960). Quantifying and examining beta
53 diversity provides ecologists with a greater understanding of the processes that drive compositional
54 variation of biological communities in ecosystems (Legendre and De Caceres 2013; Anderson et al.
55 2011). Community dissimilarity has often been used to measure beta diversity, and can be separated
56 into two distinct components: species turnover and nestedness (Legendre 2014). Species turnover
57 reflects the replacement of species from one site to the next and may be the result of either species
58 gain or loss due to environmental sorting, historical constraints and competition (Baselga 2010).
59 Where species turnover dominates, local species richness (alpha diversity) in sites may be relatively
60 low compared to regional diversity (gamma diversity; Corti and Datry 2015). Communities are
61 considered to be nested when sites with fewer taxa comprise a subset of communities with a greater
62 number of taxa (Almeida-Neto et al. 2008), which may reflect species loss as a result of any
63 ecological process that promotes species thinning and the disaggregation of biological communities
64 (Baselga 2010; Legendre 2014). However, the two beta diversity components often demonstrate
65 complementarity, i.e., communities are rarely organised by nestedness or turnover related processes
66 alone but are often structured by varying contributions of both to total beta diversity. However, it is
67 still not fully understood how local environmental and spatial processes interact and influence the
68 relative contribution of each component to total beta-diversity (but see Brendonck et al. 2014 and
69 Gianuca et al. 2016).

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71 A metacommunity can thus be defined as ‘a set of local communities that are linked by dispersal of
72 multiple potentially interacting species’ (Leibold et al. 2004). Metacommunity theory provides a
73 framework to describe the underlying local and spatial environmental processes influencing
74 community composition and beta diversity. ‘Local’ processes refer to interspecific interactions
75 (competition and predation) and ‘local’ abiotic environmental variables, while ‘spatial’ processes
76 refer to the dispersal of individuals between habitats and the landscape features

77 (connectivity/proximity) of the study area (Cottenie et al. 2005, Grönroos et al. 2013). Ponds are ideal
78 systems to test the relative contribution of local and spatial variables to compositional variation and
79 the components of beta diversity (i.e. nestedness and turnover) since they are typically discrete in
80 space, small and often demonstrate gradients across a wide range of environmental conditions
81 (Vanschoenwinkel et al. 2007; Gianuca et al. 2016). Recent empirical studies examining lentic
82 invertebrate metacommunities have concluded that local environmental variables (species sorting) are
83 generally more important than spatial variables in driving ecological community structure (species
84 track preferred environmental conditions; Cottenie 2005, Thornhill et al. 2017), although there is
85 considerable variability amongst regions and macroinvertebrate groups (Van de Meutter et al. 2007,
86 Vanschoenwinkel et al. 2007, Heino et al. 2012, Tonkin et al. 2016).

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88 It has been proposed that environmental gradients, species dispersal and spatial connectivity between
89 sites shape the nestedness and turnover components of beta diversity (Tonkin 2015). Within
90 heterogeneous landscapes, species can track suitable environmental gradients where dispersal is
91 sufficient, increasing the importance of species turnover but, in homogenous landscapes, increased
92 dispersal has been shown to decrease species turnover resulting in assemblages that are nested subsets
93 of those sites with higher species richness (Gianuca et al. 2016). Spatial patterns of nestedness may be
94 driven by habitat isolation, limiting dispersal, and by the availability of habitable area at a regional
95 scale (McAbendroth et al. 2005). At larger biogeographical scales, habitat isolation may result in
96 species turnover through processes of speciation and extinction; however, historical extinction may
97 also generate patterns of nestedness where speciation is low (Florencio et al. 2011; Gianuca et al.
98 2016). Given the different dispersal strategies of active (readily disperse and select sites for
99 colonisation) and passively (rely on vectors for dispersal) dispersing species, the mechanisms driving
100 the two components of beta diversity may differ between taxa using these two strategies. Among pond
101 habitats, passive macroinvertebrate groups may demonstrate much stronger spatial structuring and
102 reduced control by local environmental factors, while actively-dispersing macroinvertebrates may
103 display stronger community structuring caused by variation in environmental conditions and weak

104 spatial structuring (Van de Meutter et al. 2007; Vanschoenwinkel et al. 2007; De Bie et al. 2012;
105 Heino 2013a). However, the interaction and influence of local environmental and spatial processes on
106 the nestedness and turnover components of beta-diversity among actively and passively dispersing
107 taxa has received little research attention to date.

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109 While metacommunities have received considerable theoretical consideration in recent years (Logue
110 et al. 2011; Heino 2013b, Meynard et al. 2013; Soininen 2016), there has been an empirical focus on
111 community assembly and overall beta diversity, with few attempts to examine the local and spatial
112 drivers of the two components of beta diversity: nestedness and turnover (see Si et al. 2016; Gianuca
113 et al. 2016). In addition, most pond studies examining nestedness and turnover have focussed on non-
114 urban ponds with little consideration given to ponds within urban landscapes. Urbanisation may affect
115 the processes driving the two components of beta diversity among urban ponds given the very
116 different spatial organisation, structural architecture and the high levels of anthropogenic disturbance
117 typically associated with urban landscapes compared to non-urban landscapes. Examination of the
118 environmental and spatial processes influencing these two components of beta diversity will add
119 significant detail to our understanding of biodiversity patterns spatially and may contribute to regional
120 conservation planning (Socolar et al. 2016). For example, strong patterns of nestedness among
121 communities would suggest conserving species-rich sites as a priority given that other sites are nested
122 subsets of the most species-rich sites. In contrast, high species turnover would suggest conserving a
123 range of sites with different species composition as a priority given the high species replacement
124 between sites.

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130 In this study, we examined the relative influence of local environmental and spatial variables on
131 patterns of nestedness, turnover and overall beta diversity among the entire pond macroinvertebrate
132 community. In addition, we examined whether the influence of local environmental and spatial
133 variables differed for patterns of nestedness, turnover and overall beta diversity among actively and
134 passively dispersing macroinvertebrate assemblages.

135 **Materials and Methods**

136 *Study area*

137 A total of 95 ponds were selected for study in Leicestershire, UK (Fig. 1). This region has a temperate
138 climate with an average annual minimum temperature of 6.1 °C, an average annual maximum
139 temperature of 13.9 °C and mean annual precipitation of 620 mm (1981-2010, data provided by the
140 UK Met Office; Met Office 2016). The study region comprised an area of ca. 280 km² encompassing
141 a range of landuse types typical of lowland regions within the UK, including (1) non-urban
142 landscapes: floodplain meadows protected for nature conservation; intensively cultivated arable land
143 dominated by one or two row crops (typically rapeseed or wheat) and; oak or mixed woodland (oak,
144 silver birch, alder and European ash) and (2) urban environments (Loughborough, population ~
145 60,000) including residential gardens, public spaces, school grounds and high density commercial
146 developments (urban drainage ponds; industrial, roadside and city centre locations; see Hill et al.
147 2015). The ponds examined displayed considerable variability in environmental characteristics (Table
148 1).

149

150 *Macroinvertebrate data collection*

151 Sampling was conducted during March, June and September 2012 corresponding to the spring,
152 summer and autumn seasons using a method based on that of the National Pond Survey (Biggs et al.,
153 1998). Samples were taken using a sweep technique from the mesohabitats (e.g., emergent
154 macrophytes, submerged macrophytes, floating macrophytes, open water) present in each pond.
155 Sampling time at each pond was proportional to its surface area. A total of 30 seconds of sampling

156 time was allocated for every 10 m² surface area up to 50 m²; for ponds greater than 50 m² a total of
157 three minutes sampling time was assigned (Hill et al. 2015). The length of time allocated to sample
158 each pond was divided equally between the mesohabitats although, if one mesohabitat dominated the
159 pond, sampling time was divided further to reflect this. Larger substrates (e.g., rocks) that could not
160 be sampled using the pond net were examined visually for attached individuals. Immediately after
161 sampling macroinvertebrates were preserved in 10% formaldehyde and taken to the laboratory to be
162 sorted and identified. Mesohabitat samples from each pond were pooled for the final analyses. Full
163 details of field sampling are outlined in Hill et al. (2015) and summarised here. Most
164 macroinvertebrate taxa were identified to species level where possible, although Diptera larvae,
165 Planariidae and Physidae were identified to family level and Collembola, Hydrachnidae and
166 Oligochaeta were identified as such. In this study, macroinvertebrate taxa were determined as active
167 or passive dispersers based on the classification outlined by Tachet et al. (2010) and Van de Meutter
168 et al. (2007). When macroinvertebrate communities (entire community and actively and passively
169 dispersing taxa) recorded from the three sampling seasons were examined separately in preliminary
170 analyses, similar results were recorded for the three seasons (see Supplementary Material part 1 for
171 analysis of the individual sampling seasons). As a result, we present here the pooled
172 macroinvertebrate data (seasonal data from individual ponds were combined) and the mean values of
173 environmental parameters.

174

175 *Environmental and spatial data*

176 At each sample site a range of local (physicochemical and biological) and spatial variables were
177 measured for each pond (Table 1). Local environmental variables included: mean water depth (cm),
178 surface area (m²), the percentage of the pond margin that was shaded, dry phase length (duration
179 during the 12-month study period that the pond was dry - a total of 27 ponds dried for between 3 and
180 7 months of the year), conductivity ($\mu\text{S cm}^{-1}$), pH, percentage dissolved oxygen concentration (DO)
181 and the percentage of the pond covered by submerged macrophytes, emergent macrophytes and
182 floating macrophytes. Spatial variables included: pond connectivity (the number of waterbodies

183 hydrologically connected to the sample site through surface connections) and pond proximity (the
184 number of other waterbodies within 500 m: Waterkeyn et al. 2008), defined here as ‘hydrological
185 proximity effects’, which were recorded using maps/aerial imagery (Google Earth 2015) and through
186 field observations (extensively walking around each sample site during each season to identify any
187 nearby waterbodies). Every attempt was made to record all waterbodies within 500 m of each pond
188 site; however, ephemeral ponds and garden ponds were particularly difficult to identify as they are not
189 typically recorded on national maps (e.g., OS MasterMap) and are not always observable from
190 satellite imagery (Google Earth 2015), particularly when overgrown or covered by riparian
191 vegetation. It is therefore acknowledged that a small number of ephemeral and garden ponds may
192 have been overlooked in this investigation. In addition, eigenfunction spatial analysis (Principal
193 Coordinates of Neighbour Matrices (PCNM); Borcard and Legendre 2002, Griffith and Peres-Neto et
194 al. 2006) was undertaken using the PCNM package in R (Legendre et al. 2012), to create a series of
195 spatial variables and to determine the overall spatial structure in ecological communities. The
196 truncation threshold was calculated using the default setting in the PCNM package in R (the longest
197 distance in the minimum spanning tree; Oksanen et al. 2016). Only the eigenvectors that model
198 positive spatial correlation were used in the statistical analyses. It has been proposed that eigenvectors
199 better capture the community spatial patterns than latitude and longitude alone as the eigenvectors
200 represent the spatial structuring of study sites across multiple scales (Borcard and Legendre 2002,
201 Dray et al. 2012). All ponds in the study region were incorporated into the eigenfunction spatial
202 analysis.

203

204 *Statistical analysis*

205 All statistical analyses were performed in the R environment (R Development Core Team 2013).
206 Total beta diversity of the pooled macroinvertebrate community dataset (calculated using triangular
207 matrices of Jaccard distances on presence-absence macroinvertebrate data) was partitioned into
208 species turnover and nestedness components using the function *beta.multi* from the package *betapart*
209 (Baselga et al. 2015). Redundancy Analysis (RDA), which analyses variation in biotic assemblages in

210 relation to explanatory variables (Legendre and Legendre 2012), was chosen as the constrained
211 ordination method. Distance matrices accounting for the spatial nestedness and turnover components
212 of beta diversity, and the sum of both values (total beta diversity) were calculated using the function
213 *beta.pair* in the *betapart* package. Principle Coordinate analysis (PCoA) was undertaken on the
214 derived distance matrices (nestedness, turnover and total beta diversity) employing the Lingoes
215 correction to account for negative eigenvalues (Legendre 2014), using the function *pcoa* in the
216 package *ape* (Paradis et al. 2016). The PCoA eigenvectors (principle coordinates) for nestedness,
217 turnover and total beta diversity were used as input response variables in separate variance
218 partitioning analyses (see below). Environmental variables were \log_{10} transformed to eliminate their
219 physical units (Legendre and Birks 2012). Separate RDA analyses employing a forward selection
220 procedure were undertaken using the function *ordiR2step* in *vegan* to identify the significant local
221 environmental variables, hydrological proximity effects and spatial variables (eigenvectors)
222 influencing the nestedness component of beta diversity, species turnover and total beta diversity. This
223 forward selection method employs three stopping rules: (1) when the adjusted R^2 begins to decrease;
224 (2) when the preselected permutational significance level is exceeded ($p < 0.05$); and (3) when the
225 adjusted R^2 of the full model is exceeded (Oksanen et al. 2016). To examine the relative contribution
226 of local environmental conditions, landscape type (urban/non-urban) and spatial structuring
227 (hydrological proximity effects and PCNM eigenvectors) on spatial patterns of nestedness, turnover
228 and total beta diversity for the entire community and among actively and passively dispersing taxa
229 from study sites, variance partitioning (Borcard et al. 1992) was performed using the *varpart* function
230 in the *vegan* package (Oksanen et al. 2016). RDA was undertaken including all significant
231 environmental variables identified and the total percentage of variation explained divided into a
232 unique and shared contribution for four sets of predictors using variance partitioning: (1) local
233 environmental variables; (2) hydrological proximity effects; (3) landscape type (urban/non-urban);
234 and (4) PCNM spatial variables. Statistical significance of the full model and the unique contributions
235 of the four sets of predictors were undertaken using the *anova* function in *vegan*. The adjusted R^2
236 fractions are reported in this study as they have been widely recommended previously and are
237 unbiased (Peres-Neto et al. 2006). Variance partitioning analysis was undertaken separately on the

238 nestedness component to beta diversity, species turnover and total beta diversity of the entire
239 macroinvertebrate community across the study sites. To examine whether the relative importance of
240 local and spatial variables differed for total beta diversity, the nestedness component of beta diversity
241 and species turnover of taxa with active and passive dispersal mechanisms, variance partitioning
242 analyses were performed separately on taxa employing both dispersal strategies.

243

244 **Results**

245 *Relative contribution of local and spatial factors on total beta diversity, nestedness and turnover for*
246 *the entire macroinvertebrate metacommunity*

247 A total of 228 macroinvertebrate taxa from 21 orders and 68 families were recorded from the 95
248 ponds examined (Table 2; see Supplementary Material Table S2 for the full list of species recorded in
249 this study). Aquatic macroinvertebrate communities displayed high levels of beta diversity when the
250 entire community was considered (Jaccard's 0.986; Table 3). Compositional variation in
251 macroinvertebrate communities could be explained almost entirely by species turnover (98.2%) rather
252 than the nestedness component of beta diversity (1.8%). When the total beta diversity of the entire
253 macroinvertebrate community was examined, forward selection identified four significant PCNM
254 spatial variables, nine local environmental variables (pond surface area, pH, percentage of the pond
255 margin shaded, dry phase length, conductivity, dissolved oxygen concentration, percentage coverage
256 of emergent macrophytes, submerged macrophytes and floating macrophytes) and two hydrological
257 proximity effects (connectivity and pond isolation). These variables were subsequently used in
258 variance partitioning analysis. A total of 24.9% of the variation in overall beta diversity could be
259 explained by the local and spatial variables, based on the adjusted R^2 values. Local environmental
260 variables alone explained more of the variance in community structure (12.5%) compared to the
261 spatial parameters (hydrological proximity effects: 1.8%, eigenvectors: 1.1%; Fig. 2a). Landscape
262 type (urban / non-urban) did not significantly influence overall beta diversity (Fig. 2a).

263

264 Five environmental variables (pond surface area, percentage of the pond margin shaded, dry phase
265 length, conductivity and percentage coverage of submerged macrophytes) and two hydrological
266 proximity effects (connectivity and pond isolation) were found to significantly influence spatial
267 patterns of nestedness when the entire community was considered. These variables were subsequently
268 used in the variance partitioning analyses. No PCNM spatial variables were found to significantly
269 influence the nestedness component of beta diversity and as a result were excluded from variance
270 partitioning analysis. Based on the adjusted R^2 value, a total of 17.4% of variation in nestedness could
271 be explained by the local environmental variables ($p < 0.05$), hydrological proximity effects and
272 landscape type (Fig. 2b). The nestedness component of beta-diversity was more effectively explained
273 by local environmental variables (10.3%) when compared to hydrological proximity effects (1.5%)
274 and landscape type (0.9%; Fig. 2b). Forward selection identified a total of 16 parameters that
275 significantly influenced species turnover; comprising nine local environmental variables (percentage
276 coverage of submerged macrophytes, emergent macrophytes and floating macrophytes, pH, dry phase
277 length, percentage of the pond margin shaded, depth, dissolved oxygen concentration and
278 conductivity), six spatial eigenvectors and one hydrological proximity effect (connectivity). Based on
279 the adjusted R^2 values, local and spatial parameters explained 19.3% of the variation in species
280 turnover when the entire community was considered. Local environmental parameters (9.9%) and
281 spatial eigenvectors (2.7%) explained more of the variation in species turnover than hydrological
282 proximity effects: 0.8% and landscape type: 0.6%; Fig. 2c). All four local and spatial variable groups
283 significantly influenced species turnover (Fig. 2c).

284 *Relative contribution of local and spatial factors on actively dispersing macroinvertebrate taxa*

285 Actively dispersing taxa demonstrated high levels of beta diversity across study sites (0.986) although
286 species turnover (98.2%) contributed considerably more to dissimilarity among actively dispersing
287 taxa than nestedness (1.8%: Table 3). Local environmental variables and hydrological proximity
288 effects significantly influenced ($p < 0.05$) overall beta diversity. Local environmental conditions
289 accounted for a greater proportion of the variance in beta diversity (12%) among actively dispersing

290 taxa compared to spatial variables (all spatial variables combined: 3.7%) and landscape type (0.3%:
291 Fig. 3a).

292

293 Local environmental variables were the only predictor group recorded to significantly influence
294 patterns of nestedness among actively dispersing taxa and accounted for 10.1% of the variance
295 recorded (Fig. 3b). Hydrological proximity effects explained 0.6% of the variation in nestedness
296 among active dispersing taxa, while landscape type explained 0.3% (Fig. 3b). All four sets of
297 predictor variables were found to significantly ($p < 0.05$) influence macroinvertebrate turnover among
298 actively dispersing taxa. Local environmental variables explained more variance in species turnover
299 for actively dispersing taxa (8.6%) compared to other predictor variables (Fig. 3c). Spatial
300 eigenvectors (2%) had a greater influence on species turnover among actively dispersing taxa than
301 hydrological proximity variables (1.6%) and landscape type (0.7%: Fig.3c).

302

303 *Relative contribution of local and spatial factors on passively dispersing macroinvertebrate taxa*

304 High levels of beta diversity were recorded among passively dispersing taxa (Jaccard's 0.986).
305 Variation in macroinvertebrate composition could almost entirely be explained by species turnover
306 (97.5%) rather than nestedness (2.5%: Table 3). Variation in total beta diversity among passively
307 dispersing taxa was more effectively explained by local environmental factors (12.3%) when
308 compared to hydrological proximity effects (2.6%), spatial eigenvectors (0.5%) or landscape type
309 (0.2%); although the latter two were not statistically significant (Fig. 4a). Results of variance
310 partitioning for total beta diversity among passively dispersing taxa (Fig. 4a) were similar to those
311 recorded for actively dispersing taxa (Fig. 3a), although landscape type accounted for more of the
312 variation in total beta diversity among passively dispersing taxa than actively dispersing taxa.

313

314 Overall spatial structuring (spatial eigenvectors) was not identified by the forward selection procedure
315 to significantly influence nestedness among passively dispersing taxa and was not used in subsequent

316 variance partitioning analysis. Only local environmental variables and hydrological proximity effects
317 were identified to significantly influence patterns of nestedness among passively dispersing taxa.
318 Local environmental variables (9.6%) were able to account for more of the variance in nestedness for
319 passively dispersing taxa compared to the other predictor variables (hydrological proximity effects:
320 2.5% and landscape type: 0.4%; Fig. 4b). A greater proportion of the variance in species turnover
321 among passively dispersing taxa could be explained by local environmental variables (7.5%) when
322 compared to the other sets of predictors, although hydrological proximity effects (1.5%) and the
323 spatial eigenvectors (1.2%) accounted for a similar proportion of variation in species turnover (Fig.
324 4c). Local environmental variables, hydrological proximity effects and the spatial eigenvectors
325 significantly ($p < 0.05$) influenced species turnover for passively dispersing taxa.

326

327 **Discussion**

328 Both local environmental and spatial processes were important in structuring patterns of total beta
329 diversity, nestedness and species turnover in ponds when the entire community was considered. This
330 result is in agreement with the local environmental-spatial continuum of metacommunity theory
331 (Gravel et al. 2006; Heino et al. 2012). The high beta diversity of macroinvertebrate communities
332 among the ponds could almost entirely be attributed to species turnover (species replacement from
333 one pond to another; Baselga 2010), indicating that dissimilarity among ponds was largely driven by
334 variation in community composition, rather than differences in taxonomic richness (nestedness; Viana
335 et al. 2016). Local environmental variables were the dominant drivers of total beta diversity and the
336 nestedness and species turnover components of beta diversity when the entire community was
337 considered, and they accounted for significantly more of the variance in comparison to spatial
338 variables (supporting hypothesis 1). Soininen (2014) found species sorting to be the dominant driver
339 of composition at a metacommunity scale where biogeographic processes (such as speciation) were
340 isolated. However, our results also clearly indicate that spatial factors should not be overlooked and
341 can, individually or in combination with local environmental variables, have a significant effect on the
342 two components of beta diversity (nestedness and turnover). Hydrological proximity effects

343 (connectivity and proximity) were the most important spatial factors affecting total beta diversity,
344 nestedness and turnover when all ponds across the study region were considered, suggesting that
345 localized spatial processes are of greater importance than overall spatial structures (spatial
346 eigenvectors) within a metacommunity. Direct hydrological connectivity between waterbodies
347 (including ditches and ephemeral channels) has previously been shown to provide direct migration
348 pathways for taxa to utilise (Medley and Havel 2007).

349

350 The dominance of local environmental variables and the high species turnover among ponds suggests
351 that species sorting operating through niche mechanisms are the key processes driving variation
352 among aquatic pond macroinvertebrate communities (Cottenie et al. 2003; Cottenie and de Meester
353 2004; Viana et al. 2016). However, it should be acknowledged that a combination of mass effects,
354 dispersal limitation and species sorting has been reported to most effectively explain variation among
355 pond macroinvertebrate assemblages (Cottenie et al. 2005, Vanschoenwinkel et al. 2007, Ng et al.
356 2009) and beta diversity components (Tonkin et al. 2015). Spatial variables (hydrological proximity
357 effects and overall spatial structuring) are proxies for the dispersal and colonization of invertebrates
358 within a metacommunity, but it is the heterogeneity of local environmental factors (species sorting
359 and associated niche processes) that largely regulates and drives variation in beta diversity and the
360 nestedness and turnover components of beta diversity (Cottenie et al. 2003, Cottenie and De Meester,
361 2004, Viana et al. 2016). The dominance of local environmental variables on patterns of nestedness
362 may reflect high spatial connectivity via dispersal in the metacommunity (enough to override niche
363 processes that enable species to colonise non-suitable habitats), increasing spatial nestedness (Tonkin
364 et al. 2015). However, local environmental conditions may increase spatial nestedness where pond
365 isolation persists as the environmental conditions may be unsuitable in a nested fashion, causing
366 species losses and increases in nestedness (Gianuca et al. 2016). It may be very difficult for any
367 predictor variables to effectively explain the differences in nestedness, given the very small
368 contribution of nestedness (<3%) to the organisation of the entire macroinvertebrate community and
369 active and passively dispersing taxa. In other studies, the nestedness component of beta diversity has

370 been demonstrated to be at least as important as turnover among lentic habitats where environmental
371 conditions are harsh and spatial connectivity is reduced (Henriques-Silva et al. 2013; Gianuca et al.
372 2016); for example, amongst temporary ponds (Florencio et al. 2011; Fernandes et al. 2013;
373 Brendonck et al. 2014).

374

375 Landscape type (urban /non-urban) had consistently less influence (often displaying no significant
376 effect) than other predictors of variation in beta diversity, species turnover and nestedness for the
377 entire community or among active and passively dispersing taxa. This suggests that the physical
378 architecture of urban landscapes (e.g., industrial buildings, dense residential estates and fences/walls)
379 may not significantly affect the macroinvertebrate metacommunities within the study area.

380 Loughborough is a medium sized UK town, with a moderate density of urban development and a
381 relatively high number of ponds. It may be that hydrological connectivity and proximity (hydrological
382 proximity effects) between urban ponds in Loughborough are offsetting the influence that the urban
383 built environment may have. Local-scale spatial signals among urban pond communities may be the
384 result of mass effects, where dispersal from a source pond enables the persistence at a sink site
385 resulting in a significant spatial effect in variance partitioning analysis (Grönroos et al. 2013). The
386 construction of new habitat corridors has the potential to increase direct connectivity between aquatic
387 habitats in urban areas (Hamer and McDonnell 2008, Ribeiro et al. 2011), facilitate dispersal and
388 colonisation of macroinvertebrate taxa between ponds and reduce the influence of urbanisation.

389 Private gardens typically constitute a significant proportion of urban environments (e.g., vegetated
390 land cover in gardens constitutes 14% of London, the UK's largest city area; Smith et al. 2011), and
391 utilising this abundant green space for the creation of new ponds provides a significant opportunity to
392 increase aquatic habitat connectivity in urban areas (Hill and Wood 2014). The relatively minor effect
393 that landscape type had on variation in beta diversity in the study area may also simply reflect the
394 relative unimportance of the surrounding terrestrial matrix for the majority of pond macroinvertebrate
395 taxa. As long as suitable terrestrial habitat for macroinvertebrates to complete their life histories is
396 available (e.g., local fragmented natural habitat within urban park/gardens or green buffers

397 surrounding ponds), species will continue to colonise urban ponds providing that local environmental
398 conditions are also suitable. However, the minor effect of landscape type may also reflect
399 anthropogenic disturbance among non-urban ponds. In this study, a number of ponds were located on
400 intensively cultivated agricultural land and, across the wider UK landscape, it has been estimated that
401 80% of UK ponds are in a degraded state (Williams et al. 2010). Both urban and non-urban ponds in
402 this study may be subject to anthropogenic disturbance and the resulting pressures may reduce the
403 importance of landscape type among the urban and non-urban metacommunities (Hill et al. 2016). In
404 addition, the clustered spatial structure of urban ponds may affect the low influence of the landscape
405 type dummy variable in the variance partitioning, as it may share a high proportion of variance with
406 the spatial structure.

407

408 In this study, spatial factors had a greater influence on total beta diversity and nestedness for passively
409 dispersing taxa than actively dispersing taxa (partially supporting hypothesis 2). In addition, spatial
410 variables had a greater influence on the patterns of nestedness than species turnover for passively
411 dispersing species (partially supporting hypothesis 3). However, local environmental variables
412 nevertheless explained significantly more variation in total beta diversity and nestedness than spatial
413 parameters for passively and actively dispersing taxa. Passive dispersal may occur through vectors
414 including animals, wind or water (Vanschoenwinkel et al. 2008), limiting the ability of taxa to select
415 suitable habitat (dispersal limitation) and increasing the influence of spatial processes. The greater
416 influence of spatial effects on patterns of nestedness than turnover among passively dispersing taxa
417 may be the result of (1) mass effects from increasing connectivity, facilitating the dispersal of taxa
418 from a highly populated source to less suitable sink habitat (Cottenie et al. 2003) and/or (2) dispersal
419 limitation reflecting the spatial isolation between ponds (Leibold et al. 2004), which may limit the
420 opportunity of species to find their optimum conditions and increasing the importance of nestedness at
421 the metacommunity scale. Further, total beta diversity and the nestedness component of beta diversity
422 among actively dispersing taxa indicated stronger environmental relationships compared to passively
423 dispersing taxa among the studied ponds. This also suggests that actively dispersing taxa can more

424 effectively track environmental gradients in the landscape and select more favourable habitats
425 compared to passively dispersing taxa, although empirical evidence for this is remains limited (De Bie
426 et al. 2012; Grönroos et al. 2013).

427

428 Examining beta diversity among aquatic and terrestrial landscapes could help inform the location of
429 protected sites, the design of biodiversity sites, the management of non-native flora and fauna within
430 aquatic and terrestrial habitats, and could help quantify the suitability of reserve networks to protect
431 regional biodiversity (Angeler 2013; Socolar et al. 2016). In addition, quantifying the components of
432 beta diversity (nestedness and species turnover) can provide evidence to facilitate the identification of
433 important biodiversity hot-spots that may subsequently be incorporated into landscape-scale
434 biological conservation efforts. In this study, the high beta diversity among ponds could almost
435 entirely be attributed to species turnover (species replacement between ponds) rather than nestedness,
436 which suggests that pond conservation would be most efficient at a network scale (Hill et al. 2016).

437

438 Caution should be used when comparing the results between local environmental and spatial drivers
439 of community structure, total beta diversity, turnover and nestedness in studies of differing spatial
440 scales. The results from one study cannot be easily compared to other studies undertaken at different
441 spatial scales (Heino et al. 2012). This is because environmental controls (species sorting) on
442 communities are likely to be dominant at smaller spatial scales compared to larger regions, while
443 spatial structuring will have a greater influence on community structure at larger spatial scales (Heino
444 et al. 2015a). For example, Declerck et al. (2011) examined zooplankton communities at a range of
445 spatial scales and found environmental variables to be the key driver of community structure within
446 individual wetlands but at a valley scale, incorporating a number of wetlands, variation in community
447 structure was more effectively explained by dispersal limitation. Further, the explanatory variables
448 measured in this study explained $\leq 26\%$ of the variance in total beta diversity, nestedness or turnover
449 among actively dispersing taxa, passively dispersing taxa or when the entire community was
450 considered. The relatively low total proportion of variance explained in this study is typical of that

451 recorded across recent freshwater metacommunity studies and suggests that the structure of
452 freshwater metacommunities is inherently difficult to model or predict (Heino et al. 2015b). Ponds are
453 often characterised by stochastic processes both in terms of flora or fauna and environmental
454 conditions (Jeffries, 1988, Chase, 2007), which may provide some justification for the relatively large
455 proportion of unexplained variation recorded and lead to a less definitive explanation of community
456 variance by environmental variables (Heino et al. 2015a). Other unquantified variables are likely to
457 have an important role in determining the nestedness and turnover components of beta diversity and
458 would have strengthened the findings. Water chemistry was not extensively recorded in this study and
459 has been reported in other studies to be influential for lentic macroinvertebrate community structure
460 (Biggs et al. 2005, Heino 2013a). Further, historical community assembly could not be examined in
461 this study, but it has been demonstrated to influence contemporary community structure in pond
462 habitats in other studies (e.g. Chase 2003).

463

464 We found that high beta diversity recorded across the pond sites almost entirely reflects patterns of
465 species turnover rather than nestedness. Species sorting operating through niche processes was the
466 dominant driver of total beta diversity, nestedness and species turnover when the entire
467 macroinvertebrate community was considered, and among actively and passively dispersing taxa.
468 Evidence for this is provided by the dominance of local environmental variables over spatial
469 mechanisms in explaining the variation in spatial patterns of nestedness and turnover among ponds in
470 the study. The lack of nested patterns across the ponds examined most likely reflects the reduced
471 influence of spatial factors on pond macroinvertebrate metacommunities. However, it should also be
472 acknowledged that a combination of spatial processes and environmental controls provided the best
473 explanation for the variance in the two components of beta diversity in this study. Spatial parameters
474 were more important for total beta diversity and nestedness among passively dispersing taxa
475 compared to actively dispersing taxa reflecting the inability of passively dispersing taxa to select
476 suitable habitats / sites. Spatial factors were of similar importance for species turnover in actively and
477 passively dispersing taxa. Addressing the relative influence of local and spatial drivers of nestedness

478 and turnover will add greater detail our understanding of the ecological structure and functioning of
479 aquatic communities and provide more accurate information for biodiversity conservation and
480 restoration.

481

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491

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635 **Tables**

636 Table 1 - Summary table of measured environmental variables from all ponds across the study region. PMS = Surface water shaded, EM = emergent
 637 macrophytes, SM = submerged macrophytes, FM = floating macrophytes, COND = conductivity, DO = Dissolved Oxygen, Connect = Connectivity,
 638 PondProx = pond proximity. N = 95 ponds.

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	Area (m²)	Depth (cm)	PMS (%)	EM (%)	SM (%)	FM (%)	pH	COND ($\mu\text{S cm}^{-1}$)	DO (%)	Connect	PondProx
Mean	552.4	60.7	23.4	23.6	23.1	9.2	7.8	567.2	75.3	3	9
Standard Error	149.5	5.6	3.4	2.8	2.4	2	0.1	31.1	2.5	0.5	0.7
Min	0.8	4	0	0	0	0	6.2	63.7	13.1	0	0
Max	9309	>100	100	100	100	7	9.8	1494	131.6	14	30

640 Table 2 - Summary table of macroinvertebrate diversity recorded from all ponds across the study
641 region. N = 95 ponds.

	Pond sites
Total number of species	228
Mean (Standard Error)	29 (2)
Range	2-73
Number of actively dispersing taxa*	187
Number of passively dispersing taxa*	41

642 * Dispersal traits derived from Tachet et al (2003)

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657 Table 3 - Relative contribution of species turnover and nestedness to multiple site dissimilarity
658 (Jaccards dissimilarity) among actively dispersing taxa, passively dispersing taxa and the entire
659 community for the pond sites. Percentage contribution is presented in parentheses.

	Species turnover	Nestedness	Overall beta diversity
Actively dispersing taxa	0.968 (98.2)	0.018 (1.8)	0.986 (100)
Passively dispersing taxa	0.958 (97.5)	0.025 (2.5)	0.983 (100)
Entire community	0.968 (98.2)	0.018 (1.8)	0.986 (100)

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677 **Figure Captions**

678 **Figure 1** - Location of the surveyed ponds in Leicestershire, UK and its location in relation to England
679 and Wales (inset).

680 **Figure 2** - The relative contribution of local environmental variables, hydrological proximity effects,
681 landscape type (urban/non-urban) and PCNM eigenvectors to total beta diversity (a), the nestedness
682 component of beta diversity (b) and species turnover (c) when the entire macroinvertebrate communities
683 with pond study sites was considered. Values represent the adjusted R^2 values. Negative fraction values
684 are not presented.

685 **Figure 3** - The relative influence of local environmental variables, hydrological proximity effects,
686 landscape type (urban/non-urban) and PCNM eigenvectors on total beta diversity (a), the nestedness
687 component of beta diversity (b) and species turnover (c). Values represent the adjusted R^2 values.
688 Negative fraction values are not presented.

689 **Figure 4** - The relative contribution of local environmental variables, hydrological proximity effects,
690 landscape type (urban/non-urban) and PCNM eigenvectors on passively dispersing macroinvertebrate
691 composition (a), the nestedness component of beta diversity (b) and species turnover (c). Values
692 represent the adjusted R^2 values. Negative fraction values are not presented.

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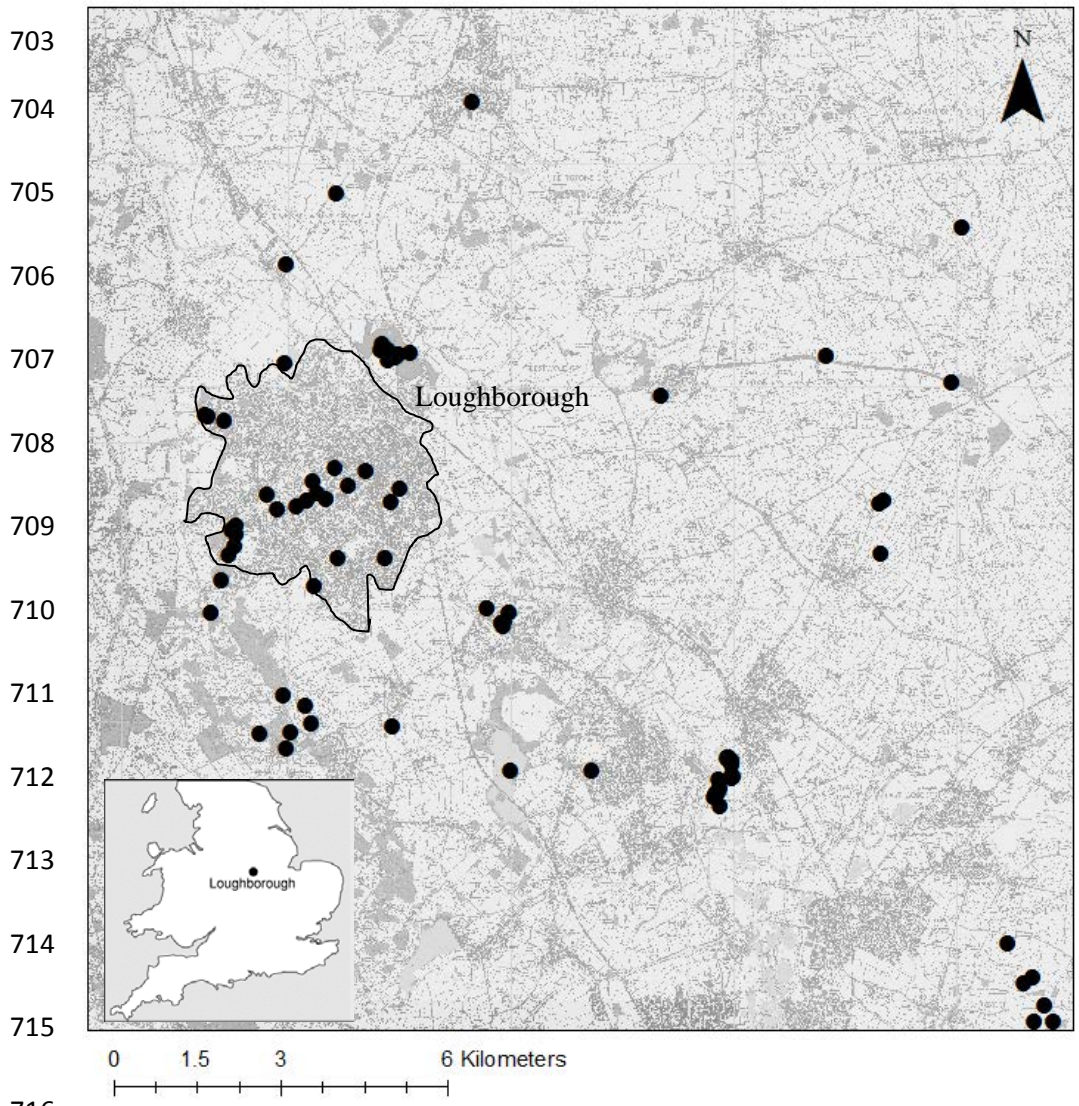
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702 **Figure 1**



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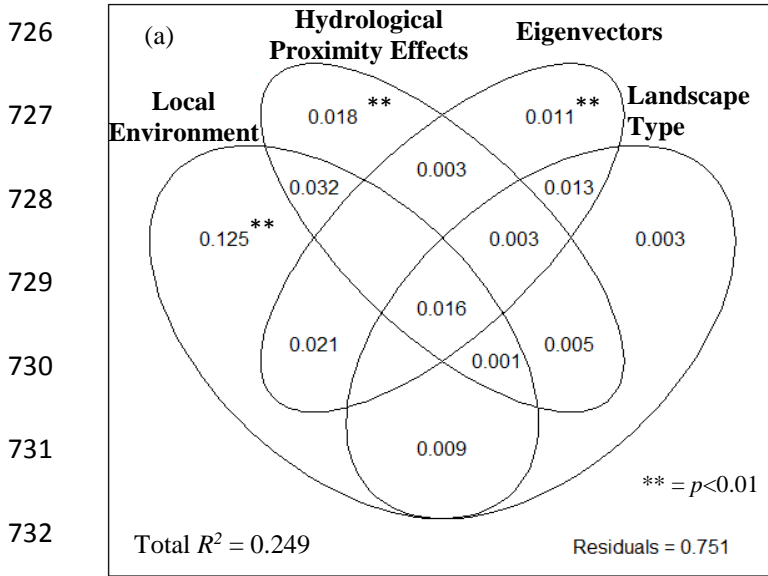
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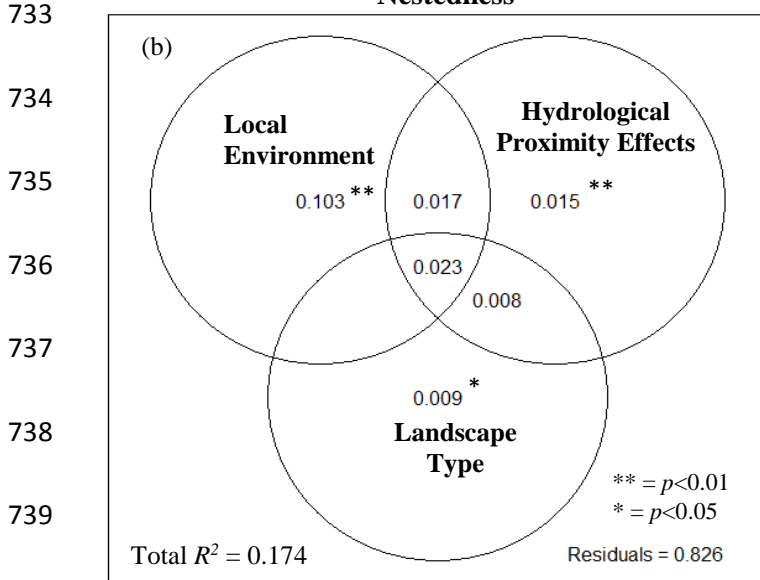
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725 **Figure 2**

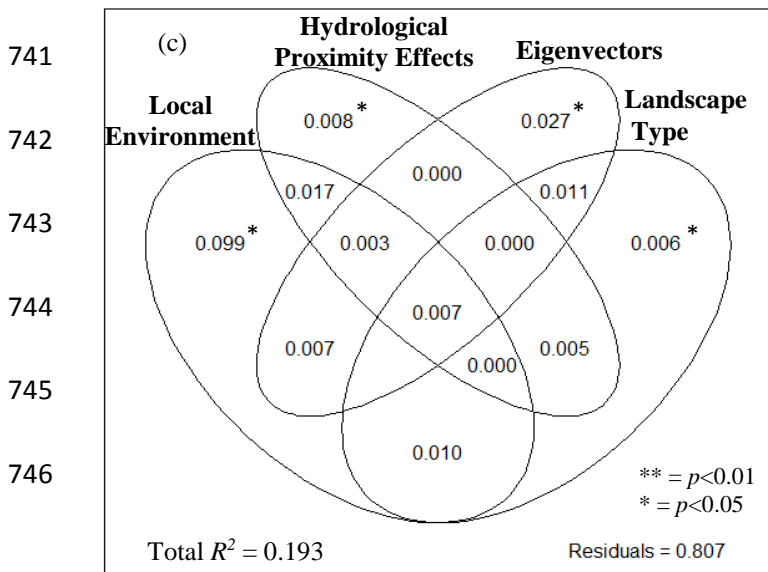
Total Beta Diversity



Nestedness

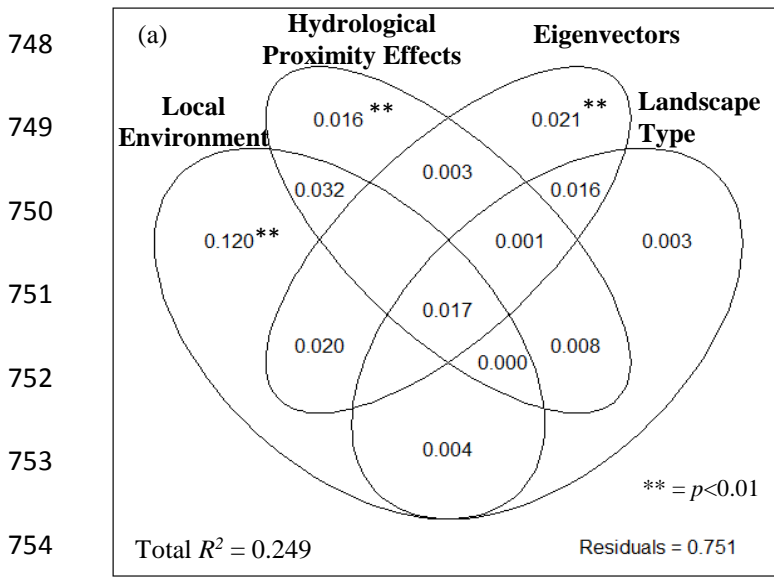


Turnover

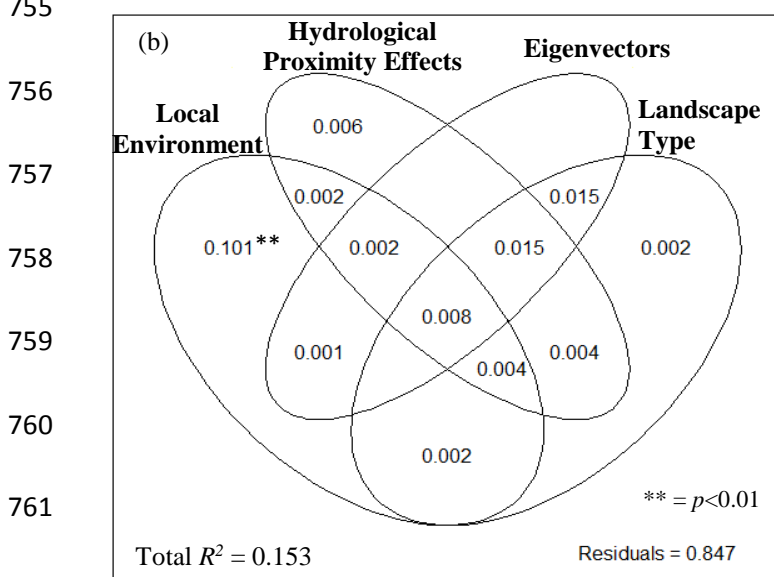


747 **Figure 3**

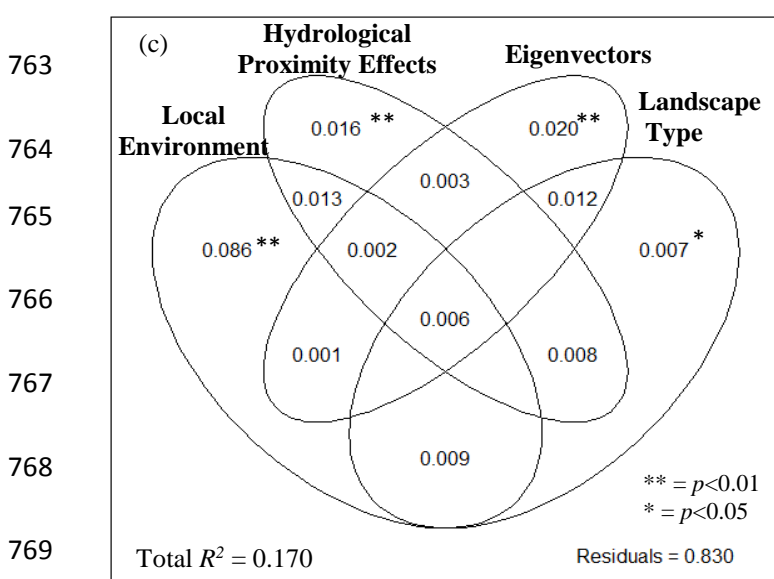
Total Beta Diversity



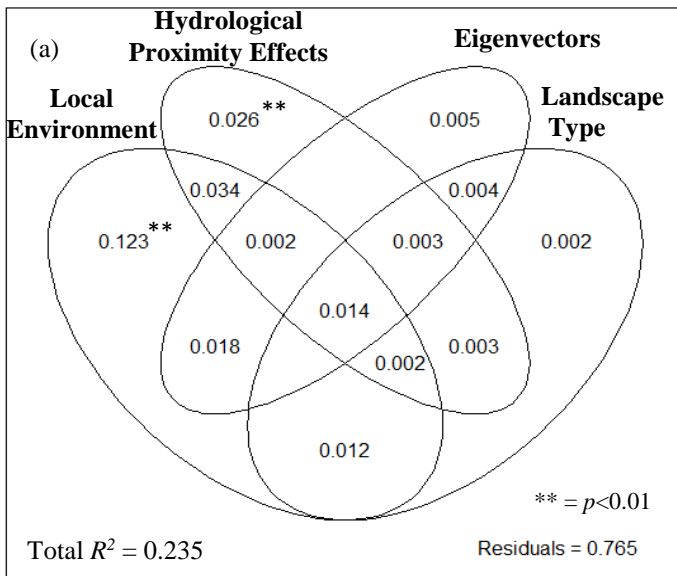
Nestedness



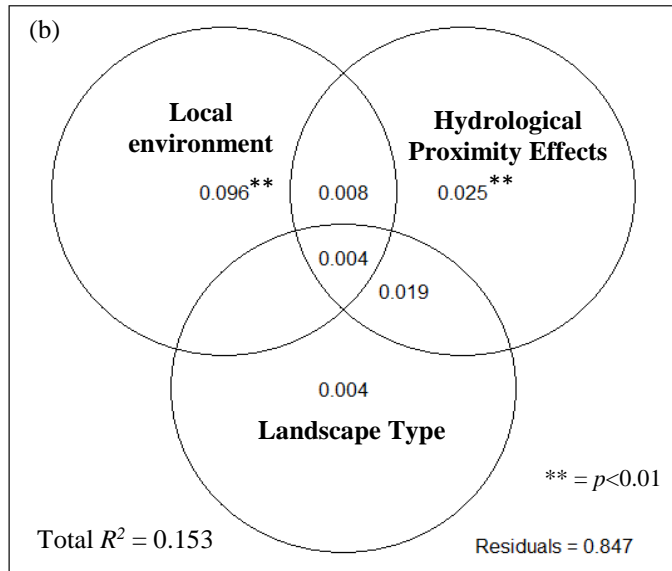
Turnover



Total Beta Diversity



Nestedness



Turnover

