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

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

Beta diversity can be defined as the spatial or temporal variation in community composition among sites within a defined geographical area of interest (Whittaker 1960). Quantifying and examining beta diversity provides ecologists with a greater understanding of the processes that drive compositional variation of biological communities in ecosystems (Anderson et al. 2011, Legendre and De Caceres 2013). Community dissimilarity has often been used to measure beta diversity, and can be separated into two distinct components: species turnover and nestedness (Legendre 2014). Species turnover reflects the replacement of species from one site to the next and may be the result of either species gain or loss due to environmental sorting, historical constraints and competition (Baselga 2010). Where species turnover dominates, local species richness (alpha diversity) in sites may be relatively low compared to regional diversity (gamma diversity; Corti and Datry 2015). Communities are considered to be nested when sites with fewer taxa comprise a subset of communities with a greater number of taxa (Almeida-Neto et al. 2008), which may reflect species loss as a result of any ecological process that promotes species thinning and the disaggregation of biological communities (Baselga 2010, Legendre 2014). The two beta diversity components often demonstrate complementarity, i.e. communities are rarely organised by nestedness or turnover related processes alone but are often structured by varying contributions of both to total beta diversity. However, it is still not fully understood how local environmental and spatial processes interact and influence the relative contribution of each component to total beta-diversity (but see Brendonck et al. 2015, Gianuca et al. 2017).

A metacommunity can thus be defined as 'a set of local communities that are linked by dispersal of multiple potentially interacting species' (Leibold et al. 2004). Metacommunity theory provides a framework to describe the underlying local and spatial environmental processes influencing community composition and beta diversity. 'Local' processes refer to interspecific interactions (competition and predation) and 'local' abiotic environmental variables, while 'spatial' processes refer to the dispersal of individuals between habitats and the landscape features (connectivity/proximity) of the study area (Cottenie 2005, Grönroos et al. 2013). Ponds are

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

It has been proposed that environmental gradients, species dispersal and spatial connectivity between sites shape the nestedness and turnover components of beta diversity (Tonkin et al. 2015). Within heterogeneous landscapes, species can track suitable environmental gradients where dispersal is sufficient, increasing the importance of species turnover but, in homogenous landscapes, increased dispersal has been shown to decrease species turnover resulting in assemblages that are nested subsets of those sites with higher species richness (Gianuca et al. 2017). Spatial patterns of nestedness may be driven by habitat isolation, limiting dispersal, and by the availability of habitable area at a regional scale (McAbendroth et al. 2005). At larger biogeographical scales, habitat isolation may result in species turnover through processes of speciation and extinction; however, historical extinction may also generate patterns of nestedness where speciation is low (Florencio et al. 2011, Gianuca et al. 2017). Given the different dispersal strategies of active (readily disperse and select sites for colonisation) and passively (rely on vectors for dispersal) dispersing species, the mechanisms driving the two components of beta diversity may differ between taxa using these two strategies. Among pond habitats, passive macroinvertebrate groups may demonstrate much stronger spatial structuring and reduced control by local environmental factors, while actively-dispersing macroinvertebrates may display stronger community structuring caused by variation in environmental conditions and weak spatial structuring (Van De Meutter et al. 2007, Vanschoenwinkel et al. 2007, De Bie et al. 2012, Heino 2013a). However, the interaction and influence of local environmental and spatial processes on the nestedness and turnover components of beta-diversity among actively and passively dispersing taxa has received little research attention to date.

While metacommunities have received considerable theoretical consideration in recent years (Logue et al. 2011, Heino 2013b, Meynard et al. 2013, Soininen 2016), there has been an empirical focus on community assembly and overall beta diversity, with few attempts to examine the local and spatial drivers of the two components of beta diversity: nestedness and turnover (Si et al. 2016, Gianuca et al. 2017). In addition, most pond studies examining nestedness and turnover have focussed on non-urban ponds with little consideration given to ponds within urban landscapes. Urbanisation may affect the processes driving the two components of beta diversity among urban ponds given the very different spatial organisation, structural architecture and the

high levels of anthropogenic disturbance typically associated with urban landscapes compared to non-urban landscapes. Examination of the environmental and spatial processes influencing these two components of beta diversity will add significant detail to our understanding of biodiversity patterns spatially and may contribute to regional conservation planning (Socolar et al. 2016). For example, strong patterns of nestedness among communities would suggest conserving species-rich sites as a priority given that other sites are nested subsets of the most species-rich sites. In contrast, high species turnover would suggest conserving a range of sites with different species composition as a priority given the high species replacement between sites.

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

Material and methods

Study area

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

Macroinvertebrate data collection

Sampling was conducted during March, June and September 2012 corresponding to the spring, summer and autumn seasons using a method based on that of the National Pond Survey (Biggs et al. 1998). Samples were taken using a sweep technique from the mesohabitats (e.g. emergent macrophytes, submerged macrophytes, floating macrophytes, open water) present in each pond. Sampling time at each pond was proportional to its surface area. A total of 30 s of sampling time was allocated for every 10 m² surface area up to 50 m²; for ponds greater than 50 m² a total of three minutes sampling time was assigned (Hill et al. 2015). The length of time allocated to sample each pond
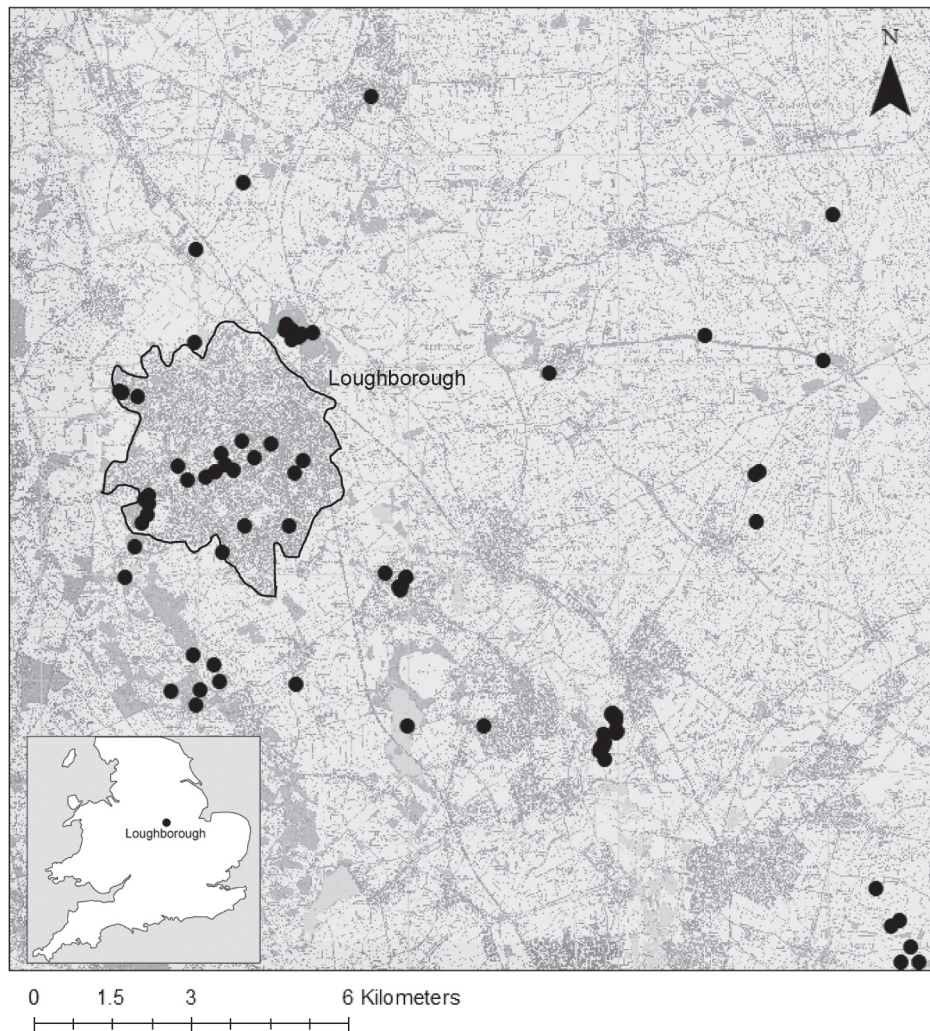
Figure 1. Location of the surveyed ponds in Leicestershire, UK and its location in relation to England and Wales (inset).

was divided equally between the mesohabitats although, if one mesohabitat dominated the pond, sampling time was divided further to reflect this. Larger substrates (e.g. rocks) that could not be sampled using the pond net were examined visually for attached individuals. Immediately after sampling macroinvertebrates were preserved in 10% formaldehyde and taken to the laboratory to be sorted and identified. Mesohabitat samples from each pond were pooled for the final analyses. Full details of field sampling are outlined in Hill et al. (2015) and summarised here. Most macroinvertebrate taxa were identified to species level where possible, although Diptera larvae, Planariidae and Physidae were identified to family level and Collembola,

Hydrachnidiae and Oligochaeta were identified as such. In this study, macroinvertebrate taxa were determined as active or passive dispersers based on the classification outlined by Tachet et al. (2010) and Van De Meutter et al. (2007). When macroinvertebrate communities (entire community and actively and passively dispersing taxa) recorded from the three sampling seasons were examined separately in preliminary analyses, similar results were recorded for the three seasons (see Supplementary material Appendix 1 part 1 for analysis of the individual sampling seasons). As a result, we present here the pooled macroinvertebrate data (seasonal data from individual ponds were combined) and the mean values of environmental parameters.

Table 1. Summary table of measured environmental variables from all ponds across the study region. PMS = pond margin shaded, EM = emergent macrophytes, SM = submerged macrophytes, FM = floating macrophytes, COND = conductivity, DO = dissolved oxygen, Connect = connectivity, PondProx = pond proximity. n = 95 ponds.

	Area (m²)	Depth (cm)	PMS (%)	EM (%)	SM (%)	FM (%)	pH	COND (µS 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
SE	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	96.7	9.8	1494	131.6	14	30

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Environmental and spatial data

At each sample site a range of local (physicochemical and biological) and spatial variables were measured for each pond (Table 1). Local environmental variables included: mean water depth (cm), surface area (m^2), the percentage of the pond margin that was shaded, dry phase length (duration during the 12-month study period that the pond was dry – a total of 27 ponds dried for between three and seven months of the year), conductivity ($\mu S \, cm^{-1}$), pH, percentage dissolved oxygen concentration (DO) and the percentage of the pond covered by submerged macrophytes, emergent macrophytes and floating macrophytes. Spatial variables included: pond connectivity (the number of waterbodies hydrologically connected to the sample site through surface connections) and pond proximity (the number of other waterbodies within 500 m: Waterkeyn et al. 2008), defined here as 'hydrological proximity effects', which were recorded using maps/aerial imagery (Google Earth 2015) and through field observations (extensively walking around each sample site during each season to identify any nearby waterbodies). Every attempt was made to record all waterbodies within 500 m of each pond site; however, ephemeral ponds and garden ponds were particularly difficult to identify as they are not typically recorded on national maps (e.g. OS MasterMap) and are not always observable from satellite imagery (Google Earth 2015), particularly when overgrown or covered by riparian vegetation. It is therefore acknowledged that a small number of ephemeral and garden ponds may have been overlooked in this investigation. In addition, eigenfunction spatial analysis (principal coordinates of neighbour matrices (PCNM); Borcard and Legendre 2002, Griffith and Peres-Neto 2006) was undertaken using the PCNM package in R (Legendre et al. 2012), to create a series of spatial variables and to determine the overall spatial structure in ecological communities. The truncation threshold was calculated using the default setting in the PCNM package in R (the longest distance in the minimum spanning tree; Oksanen et al. 2016). Only the eigenvectors that model positive spatial correlation were used in the statistical analyses. It has been proposed that eigenvectors better capture the community spatial patterns than latitude and longitude alone as the eigenvectors represent the spatial structuring of study sites across multiple scales (Borcard and Legendre 2002, Dray et al. 2012). All ponds in the study region were incorporated into the eigenfunction spatial analysis.

Statistical analysis

All statistical analyses were performed in the R environment (<www.r-project.org>). Total beta diversity of the pooled macroinvertebrate community dataset (calculated using triangular matrices of Jaccard distances on presence–absence macroinvertebrate data) was partitioned into species turnover and nestedness components using the function 'beta.multi' from the package betapart (Baselga et al. 2015). Redundancy analysis (RDA), which analyses variation in biotic assemblages in relation to explanatory variables (Legendre and Legendre 2012), was chosen as the constrained ordination method. Distance matrices accounting for the spatial nestedness and turnover components of beta diversity, and the sum of both values (total beta diversity) were calculated using the function 'beta.pair' in the betapart package. Principle coordinate analysis (PCoA) was undertaken on the derived distance matrices (nestedness, turnover and total beta diversity) employing the Lingoes correction to account for negative eigenvalues (Legendre 2014), using the function 'pcoa' in the package ape (Paradis et al. 2016). The PCoA eigenvectors (principle coordinates) for nestedness, turnover and total beta diversity were used as input response variables in separate variance partitioning analyses. Environmental variables were $\log_{10}$ transformed to eliminate their physical units (Legendre and Birks 2012). Separate RDA analyses employing a forward selection procedure were undertaken using the function 'ordiR2step' in vegan to identify the significant local environmental variables, hydrological proximity effects and spatial variables (eigenvectors) influencing the nestedness component of beta diversity, species turnover and total beta diversity. This forward selection method employs three stopping rules: 1) when the adjusted R^2 begins to decrease; 2) when the preselected permutational significance level is exceeded ($p < 0.05$); and 3) when the adjusted R^2 of the full model is exceeded (Oksanen et al. 2016). To examine the relative contribution of local environmental conditions, landscape type (urban/non-urban) and spatial structuring (hydrological proximity effects and PCNM eigenvectors) on spatial patterns of nestedness, turnover and total beta diversity for the entire community and among actively and passively dispersing taxa from study sites, variance partitioning (Borcard et al. 1992) was performed using the 'varpart' function in the vegan package (Oksanen et al. 2016). RDA was undertaken including all significant environmental variables identified and the total percentage of variation explained divided into a unique and shared contribution for four sets of predictors using variance partitioning: 1) local environmental variables; 2) hydrological proximity effects; 3) landscape type (urban/non-urban); and 4) PCNM spatial variables. Statistical significance of the full model and the unique contributions of the four sets of predictors were undertaken using the 'anova' function in vegan. The adjusted R^2-fractions are reported in this study as they have been widely recommended previously and are unbiased (Peres-Neto et al. 2006). Variance partitioning analysis was undertaken separately on the nestedness component of beta diversity, species turnover and total beta diversity of the entire macroinvertebrate community across the study sites. To examine whether the relative importance of local and spatial variables differed for total beta diversity, the nestedness component of beta diversity and species turnover of taxa with active and passive dispersal mechanisms, variance partitioning analyses were performed separately on taxa employing both dispersal strategies.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1f43v> (Hill et al. 2017b).

Table 2. Summary table of macroinvertebrate diversity recorded from all ponds across the study region. n = 95 ponds.

	Pond sites
Total number of species	228
Mean (SE)	29 (2)
Range	2–73
No. of actively dispersing taxa*	187
No. of passively dispersing taxa*	41

*Dispersal traits derived from Tachet et al. (2010).

Results

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

A total of 228 macroinvertebrate taxa from 21 orders and 68 families were recorded from the 95 ponds examined (Table 2; see Supplementary material Appendix 1 Table A2 for the full list of species recorded in this study). Aquatic macroinvertebrate communities displayed high levels of beta diversity when the entire community was considered (Jaccard's 0.986; Table 3). Compositional variation in macroinvertebrate communities could be explained almost entirely by species turnover (98.2%) rather than the nestedness component of beta diversity (1.8%). When the total beta diversity of the entire macroinvertebrate community was examined, forward selection identified four significant PCNM spatial variables, nine local environmental variables (pond surface area, pH, percentage of the pond margin shaded, dry phase length, conductivity, dissolved oxygen concentration, percentage coverage of emergent macrophytes, submerged macrophytes and floating macrophytes) and two hydrological proximity effects (connectivity and pond isolation). These variables were subsequently used in variance partitioning analysis. A total of 24.9% of the variation in overall beta diversity could be explained by the local and spatial variables, based on the adjusted R^2-values. Local environmental variables alone explained more of the variance in community structure (12.5%) compared to the spatial parameters (hydrological proximity effects: 1.8%, eigenvectors: 1.1%; Fig. 2a). Landscape type (urban/non-urban) did not significantly influence overall beta diversity (Fig. 2a).

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

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

Actively dispersing taxa demonstrated high levels of beta diversity across study sites (0.986) although species turnover (98.2%) contributed considerably more to dissimilarity among actively dispersing taxa than nestedness (1.8%: Table 3). Local environmental variables and hydrological proximity effects significantly influenced ($p < 0.05$) overall beta diversity. Local environmental conditions accounted for a greater proportion of the variance in beta diversity (12%) among actively dispersing taxa compared to spatial variables (all spatial variables combined: 3.7%) and landscape type (0.3%: Fig. 3a).

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

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

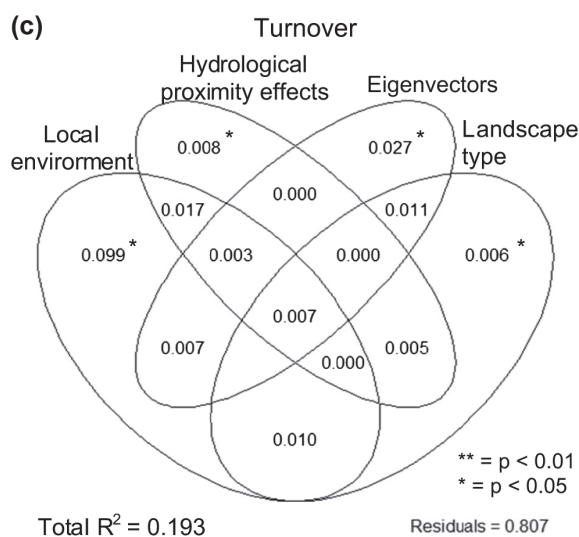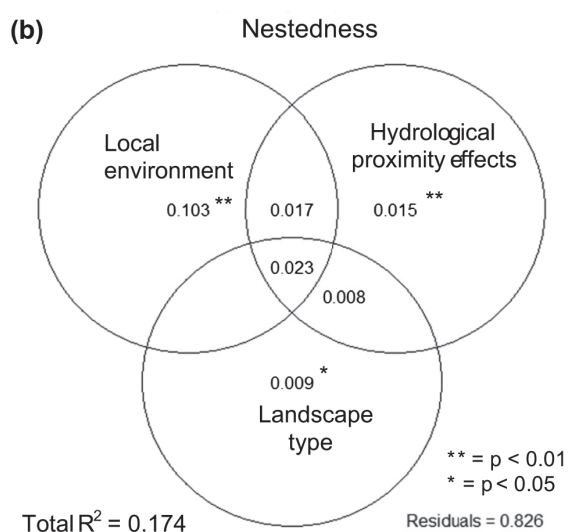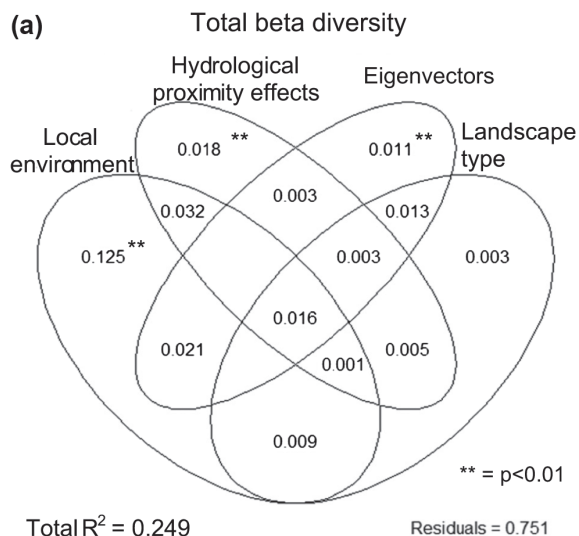|	Species turnover	Nestedness	Overall beta diversity
Actively dispersing taxa	0.968 (98.2)	0.018 (1.8)	0.986 (100)
Passively dispersing taxa	0.958 (97.5)	0.025 (2.5)	0.983 (100)
Entire community	0.968 (98.2)	0.018 (1.8)	0.986 (100)

Figure 2. The relative contribution of local environmental variables, hydrological proximity effects, landscape type (urban/non-urban) and PCNM eigenvectors to total beta diversity (a), the nestedness component of beta diversity (b) and species turnover (c) when the entire macroinvertebrate communities with pond study sites was considered. Values represent the adjusted R^2-values. Negative fraction values are not presented.
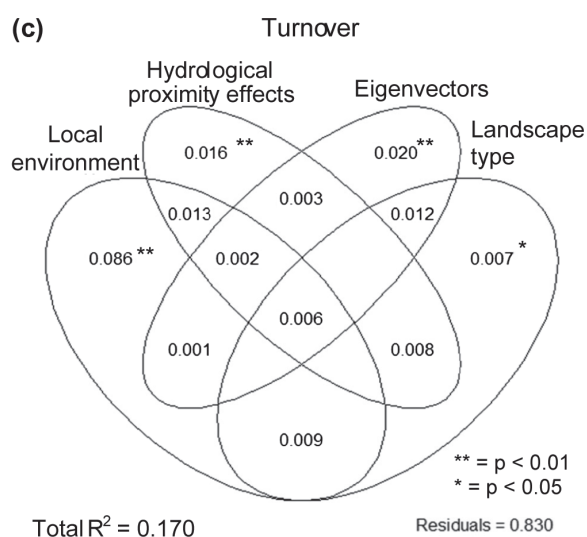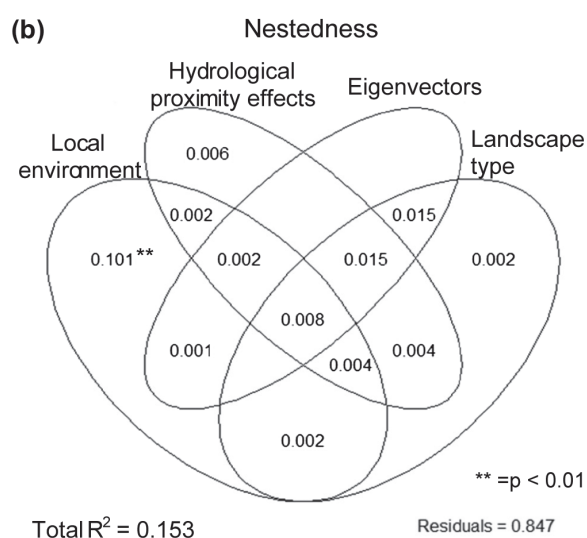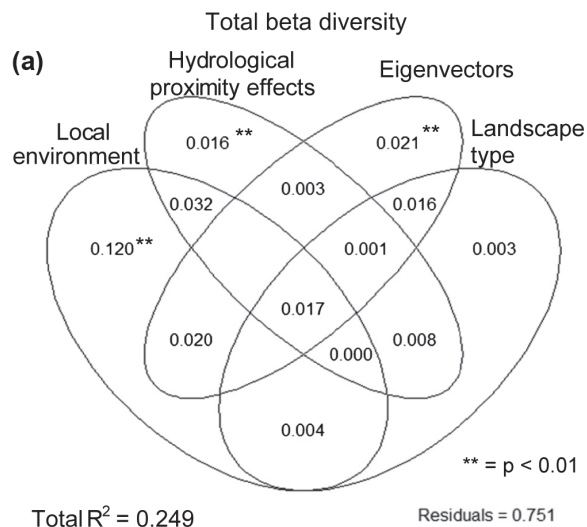
Figure 3. The relative influence of local environmental variables, hydrological proximity effects, landscape type (urban/non-urban) and PCNM eigenvectors on total beta diversity (a), the nestedness component of beta diversity (b) and species turnover (c). Values represent the adjusted R^2-values. Negative fraction values are not presented.

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

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

Overall spatial structuring (spatial eigenvectors) was not identified by the forward selection procedure to significantly influence nestedness among passively dispersing taxa and was not used in subsequent variance partitioning analysis. Only local environmental variables and hydrological proximity effects were identified to significantly influence patterns of nestedness among passively dispersing taxa. Local environmental variables (9.6%) were able to account for more of the variance in nestedness for passively dispersing taxa compared to the other predictor variables (hydrological proximity effects: 2.5% and landscape type: 0.4%; Fig. 4b). A greater proportion of the variance in species turnover among passively dispersing taxa could be explained by local environmental variables (7.5%) when compared to the other sets of predictors, although hydrological proximity effects (1.5%) and the spatial eigenvectors (1.2%) accounted for a similar proportion of variation in species turnover (Fig. 4c). Local environmental variables, hydrological proximity effects and the spatial eigenvectors significantly ($p < 0.05$) influenced species turnover for passively dispersing taxa.

Discussion

Both local environmental and spatial processes were important in structuring patterns of total beta diversity, nestedness and species turnover in ponds when the entire community was considered. This result is in agreement with the local environmental–spatial continuum of metacommunity theory (Gravel et al. 2006, Heino et al. 2012). The high beta diversity of macroinvertebrate communities among the ponds could almost entirely be attributed to species turnover (species replacement from one pond to another; Baselga 2010), indicating that dissimilarity among ponds was largely driven by variation in community composition, rather than differences in taxonomic richness (nestedness; Viana et al. 2016). Local environmental variables were the dominant drivers of total beta diversity and the nestedness and species turnover components of beta diversity when the entire community was considered, and they accounted for significantly more of the variance in comparison to spatial variables (supporting hypothesis 1). Soininen (2014) found species sorting to be
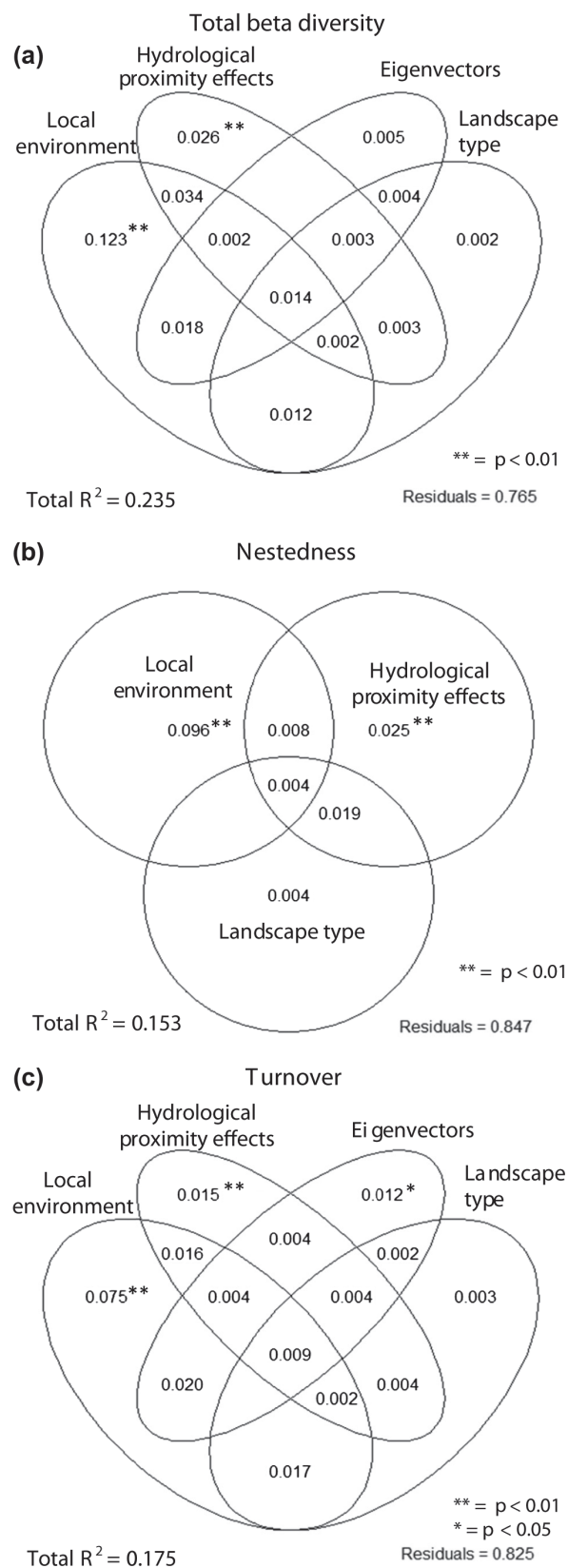

Figure 4. The relative contribution of local environmental variables, hydrological proximity effects, landscape type (urban/non-urban) and PCNM eigenvectors on passively dispersing macroinvertebrate composition (a), the nestedness component of beta diversity (b) and species turnover (c). Values represent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

the dominant driver of composition at a metacommunity scale where biogeographic processes (such as speciation) were isolated. However, our results also clearly indicate that spatial factors should not be overlooked and can, individually or in combination with local environmental variables, have a significant effect on the two components of beta diversity (nestedness and turnover). Hydrological proximity effects (connectivity and proximity) were the most important spatial factors affecting total beta diversity, nestedness and turnover when all ponds across the study region were considered, suggesting that localized spatial processes were of greater importance than overall spatial structures (spatial eigenvectors) within a metacommunity. Direct hydrological connectivity between waterbodies (including ditches and ephemeral channels) has previously been shown to provide direct migration pathways for taxa to utilise (Medley and Havel 2007).

The dominance of local environmental variables and the high species turnover among ponds suggests that species sorting operating through niche mechanisms were the key processes driving variation among aquatic pond macroinvertebrate communities (Cottenie et al. 2003, Cottenie and De Meester 2004, Viana et al. 2016). However, it should be acknowledged that a combination of mass effects, dispersal limitation and species sorting has been reported to most effectively explain variation among pond macroinvertebrate assemblages (Cottenie 2005, Vanschoenwinkel et al. 2007, Ng et al. 2009) and beta diversity components (Tonkin et al. 2015). Spatial variables (hydrological proximity effects and overall spatial structuring) are proxies for the dispersal and colonization of invertebrates within a metacommunity, but it is the heterogeneity of local environmental factors (species sorting and associated niche processes) that largely regulates and drives variation in beta diversity and the nestedness and turnover components of beta diversity (Cottenie et al. 2003, Cottenie and De Meester, 2004, Viana et al. 2016). The dominance of local environmental variables on patterns of nestedness may reflect high spatial connectivity via dispersal in the metacommunity (enough to override niche processes that enable species to colonise non-suitable habitats), increasing spatial nestedness (Tonkin et al. 2015). However, local environmental conditions may increase spatial nestedness where pond isolation persists as the environmental conditions may be unsuitable in a nested fashion, causing species losses and increases in nestedness (Gianuca et al. 2017). It may be very difficult for any predictor variables to effectively explain the differences in nestedness, given the very small contribution of nestedness ($<$ 3%) to the organisation of the entire macroinvertebrate community and active and passively dispersing taxa. In other studies, the nestedness component of beta diversity has been demonstrated to be at least as important as turnover among lentic habitats where environmental conditions are harsh and spatial connectivity is reduced (Henriques-Silva et al. 2013, Gianuca et al. 2017); for example, amongst temporary ponds (Florencio et al. 2011, Fernandes et al. 2013, Brendonck et al. 2015).

Landscape type (urban /non-urban) had consistently less influence (often displaying no significant effect) than other predictors of variation in beta diversity, species turnover and nestedness for the entire community or among active and passively dispersing taxa. This suggests that the physical architecture of urban landscapes (e.g. industrial buildings, dense residential estates and fences/walls) may not significantly affect the macroinvertebrate metacommunities within the study area. Loughborough is a medium sized UK town, with a moderate density of urban development and a relatively high number of ponds. It may be that hydrological connectivity and proximity (hydrological proximity effects) between urban ponds in Loughborough are offsetting the influence that the urban built environment may have. Local-scale spatial signals among urban pond communities may be the result of mass effects, where dispersal from a source pond enables the persistence at a sink site resulting in a significant spatial effect in variance partitioning analysis (Grönroos et al. 2013). The construction of new habitat corridors has the potential to increase direct connectivity between aquatic habitats in urban areas (Hamer and McDonnell 2008, Ribeiro et al. 2011), facilitate dispersal and colonisation of macroinvertebrate taxa between ponds and reduce the influence of urbanisation. Private gardens typically constitute a significant proportion of urban environments (e.g. vegetated land cover in gardens constitutes 14% of London, the UK's largest city area; Smith et al. 2011), and utilising this abundant green space for the creation of new ponds provides a significant opportunity to increase aquatic habitat connectivity in urban areas (Hill and Wood 2014). The relatively minor effect that landscape type had on variation in beta diversity in the study area may also simply reflect the relative unimportance of the surrounding terrestrial matrix for the majority of pond macroinvertebrate taxa. As long as suitable terrestrial habitat for macroinvertebrates to complete their life histories is available (e.g. local fragmented natural habitat within urban park/gardens or green buffers surrounding ponds), species will continue to colonise urban ponds providing that local environmental conditions are also suitable. However, the minor effect of landscape type may also reflect anthropogenic disturbance among non-urban ponds. In this study, a number of ponds were located on intensively cultivated agricultural land and, across the wider UK landscape, it has been estimated that 80% of UK ponds are in a degraded state (Williams et al. 2010). Both urban and non-urban ponds in this study may be subject to anthropogenic disturbance and the resulting pressures may reduce the importance of landscape type among the urban and non-urban metacommunities (Hill et al. 2017a). In addition, the clustered spatial structure of urban ponds may affect the low influence of the landscape type dummy variable in the variance partitioning, as it may share a high proportion of variance with the spatial structure.

In this study, spatial factors had a greater influence on total beta diversity and nestedness for passively dispersing taxa than actively dispersing taxa (partially supporting hypothesis 2). In addition, spatial variables had a greater influence on the patterns of nestedness than species turnover for passively dispersing species (partially supporting hypothesis 3). However, local environmental variables nevertheless explained significantly more variation in total beta diversity and nestedness than spatial parameters for passively and actively dispersing taxa. Passive dispersal may occur through vectors including animals, wind or water (Vanschoenwinkel

et al. 2008), limiting the ability of taxa to select suitable habitat (dispersal limitation) and increasing the influence of spatial processes. The greater influence of spatial effects on patterns of nestedness than turnover among passively dispersing taxa may be the result of 1) mass effects from increasing connectivity, facilitating the dispersal of taxa from a highly populated source to less suitable sink habitat (Cottenie et al. 2003) and/or 2) dispersal limitation reflecting the spatial isolation between ponds (Leibold et al. 2004), which may limit the opportunity of species to find their optimum conditions and increasing the importance of nestedness at the metacommunity scale. Further, total beta diversity and the nestedness component of beta diversity among actively dispersing taxa indicated stronger environmental relationships compared to passively dispersing taxa among the studied ponds. This also suggests that actively dispersing taxa can more effectively track environmental gradients in the landscape and select more favourable habitats compared to passively dispersing taxa, although empirical evidence for this is remains limited (De Bie et al. 2012, Grönroos et al. 2013).

Examining beta diversity among aquatic and terrestrial landscapes could help inform the location of protected sites, the design of biodiversity sites, the management of non-native flora and fauna within aquatic and terrestrial habitats, and could help quantify the suitability of reserve networks to protect regional biodiversity (Angeler 2013, Socolar et al. 2016). In addition, quantifying the components of beta diversity (nestedness and species turnover) can provide evidence to facilitate the identification of important biodiversity hot-spots that may subsequently be incorporated into landscape-scale biological conservation efforts. In this study, the high beta diversity among ponds could almost entirely be attributed to species turnover (species replacement between ponds) rather than nestedness, which suggests that pond conservation would be most efficient at a network scale (Hill et al. 2017a).

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

et al. 2015b). Ponds are often characterised by stochastic processes both in terms of flora or fauna and environmental conditions (Jeffries 1988, Chase 2007), which may provide some justification for the relatively large proportion of unexplained variation recorded and lead to a less definitive explanation of community variance by environmental variables (Heino et al. 2015a). Other unquantified variables are likely to have an important role in determining the nestedness and turnover components of beta diversity and would have strengthened the findings. Water chemistry was not extensively recorded in this study and has been reported in other studies to be influential for lentic macroinvertebrate community structure (Biggs et al. 2005, Heino 2013a). Further, historical community assembly could not be examined in this study, but it has been demonstrated to influence contemporary community structure in pond habitats in other studies (Chase 2003).

We found that high beta diversity recorded across the pond sites almost entirely reflects patterns of species turnover rather than nestedness. Species sorting operating through niche processes was the dominant driver of total beta diversity, nestedness and species turnover when the entire macroinvertebrate community was considered, and among actively and passively dispersing taxa. Evidence for this is provided by the dominance of local environmental variables over spatial mechanisms in explaining the variation in spatial patterns of nestedness and turnover among ponds in the study. The lack of nested patterns across the ponds examined most likely reflects the reduced influence of spatial factors on pond macroinvertebrate metacommunities. However, it should also be acknowledged that a combination of spatial processes and environmental controls provided the best explanation for the variance in the two components of beta diversity in this study. Spatial parameters were more important for total beta diversity and nestedness among passively dispersing taxa compared to actively dispersing taxa reflecting the inability of passively dispersing taxa to select suitable habitats/sites. Spatial factors were of similar importance for species turnover in actively and passively dispersing taxa. Addressing the relative influence of local and spatial drivers of nestedness and turnover will add greater detail our understanding of the ecological structure and functioning of aquatic communities and provide more accurate information for biodiversity conservation and restoration.

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Supplementary material (available online as Appendix oik-04266 at <www.oikosjournal.org/appendix/oik-04266>). Appendix 1.