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Local contributions to beta diversity in urban pond networks: Implications for biodiversity conservation and management

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Abstract

Aim: An understanding of how biotic communities are spatially organized is necessary to identify and prioritize habitats within landscape-scale biodiversity conservation. Local contribution to beta diversity (LCBD) identifies individual habitats that make a significant contribution to beta diversity and may have important practical implications, particularly for conservation of habitat networks. In this study, we develop and apply a conservation prioritization approach based on LCBD in aquatic invertebrate communities from 132 ponds.

Location: Five urban settlements in the UK: Halton, Loughborough, Stockport, Birmingham and Huddersfield.

Methods: We partition LCBD into richness difference (nestedness: ${}_{\text{RichDiff}}$LCBD) and species replacement (turnover: ${}_{\text{Repl}}$LCBD) and identify key environmental variables driving LCBD. We examine LCBD at two scales relevant to conservation planning: within urban settlements and nationally across the UK.

Results: Significant differences in LCBD values were recorded among the five settlements. In four of the five urban settlements studied, pond sites with the greatest LCBD values typically showed high replacement values. Significant LCBD sites and sites with high taxonomic diversity together supported more of the regional species pool (70%–97%) than sites with high taxonomic diversity alone (54%–94%) or what could be protected by the random selection of sites. LCBD was significantly associated with vegetation shading, surface area, altitude and macrophyte cover.

Main conclusions: Conservation prioritization that incorporates LCBD and sites with high taxonomic diversity improves the effectiveness of conservation actions within pond habitat networks, ensures sites supporting high biodiversity are protected and provides a method to define a spatial network of protected sites. Identifying new, effective conservation approaches, particularly in urban areas where resources may be scarce and conflicts regarding land use exist, is essential to ensure biodiversity is fully supported, and detrimental anthropogenic effects are reduced.

KEYWORDS
conservation, ecological uniqueness, LCBD, spatial patterns, taxonomic richness, urban ecology

1 | INTRODUCTION

One of the primary goals of ecological research is to understand spatial patterns of taxonomic richness and community composition to develop effective and ecologically relevant conservation strategies and protected area networks (Socolar et al., 2016). Ecological diversity can be divided into alpha, beta and gamma components (Whittaker, 1960), each of which offer complimentary perspectives on the spatial organization of biological communities. Interest in beta diversity (defined here as the variation in biotic communities within a defined geographical region: Whittaker, 1960) and its application in ecological conservation has increased significantly in recent years (Socolar et al., 2016). Beta diversity can be assessed by calculating taxonomic dissimilarities among ecological communities and can be separated into two distinct components: species replacement (turnover) and richness difference (nestedness; Baselga et al., 2012; Legendre, 2014). Species replacement refers to the turnover of species among sites and may reflect species gained or lost due to historical events, competition and/or environmental sorting (Baselga, 2010; Legendre, 2014). Richness difference reflects how communities differ from each other in their taxonomic richness. Taxa present at sites with low richness may comprise a subset of taxa from more species-rich sites which may reflect habitat heterogeneity or ecological processes that promote species thinning (Legendre, 2014).

Recent developments in beta diversity analyses allow an assessment of the extent to which individual sites contribute to total beta diversity within a given region (Legendre & Cáceres, 2013). The local contribution to beta diversity (LCBD) metric quantifies the ecological uniqueness of each site within the context of a wider ecosystem network, with high values for a given site indicative of high dissimilarity between the community and other sites in the region (Heino & Grönroos, 2017). Further, LCBD can be partitioned into the individual site contribution of the species replacement ($_{\mathrm{Repl}}$LCBD) and richness difference $_{\mathrm{RichDiff}}$LCBD components (Legendre, 2014). By identifying the individual sites that contribute most to beta diversity, significant ecological advances can be made in understanding spatial patterns and the processes that drive them. A limited number of studies have examined LCBD and ecological uniqueness among freshwater communities in recent years, particularly in relation to their environmental correlates (Heino et al., 2017; Heino & Grönroos, 2017; Tonkin et al., 2015). However, the environmental variables that influence the contribution of replacement and richness difference to total beta diversity remain poorly understood (but see Hill, Biggs, et al., 2017; Hill et al., 2017), and knowledge regarding local contributions to beta diversity among pond habitats is absent.

In addition to advancing ecological theory, LCBD approaches (and the replacement and richness difference components) have important practical implications, particularly for conservation planning of habitat networks (Vilmi et al., 2017). Understanding how communities are spatially organized (and what drives those patterns) can facilitate more effective biodiversity conservation strategies at a landscape (gamma) scale. For example, patterns of richness difference among communities suggest conserving individual species-rich sites should be a priority given that other sites effectively represent subsets of the most species-rich sites. However, high species replacement would suggest conserving a range of sites with contrasting biota would be more appropriate (Hill, Biggs, et al., 2017; Hill, Heino, et al., 2017; Socolar et al., 2016). Currently, pond conservation is heavily focussed on conserving individual sites of high taxonomic richness, despite recent evidence that landscape-scale pond conservation can be more effective in supporting the greatest biodiversity (Hassall et al., 2011; Hill, Biggs, et al., 2017; Hill, Heino, et al., 2017). To be considered for conservation in many regions, pond habitats need to meet specific criteria, for example, in the UK ponds are required to support several rare species, recording >50 aquatic invertebrate species and/or a Predictive System for Multimetrics score of >75% (BRIG, 2008). However, it could be that conserving ecologically unique (sites of greatest beta diversity) sites may significantly increase the proportion of the regional species pool that is protected, thereby facilitating landscape-scale conservation. In addition, LCBD approaches may identify sites of conservation importance that fall outside of the current criteria utilized for pond conservation. High LCBD values may reflect unusual species combinations and/or environmental conditions, the presence of rare taxa and therefore sites of potentially high conservation value (Heino & Grönroos, 2017). High LCBD values may also indicate sites of low taxonomic richness (high richness difference) that are suitable for restoration (Legendre, 2014). Identifying effective approaches for biodiversity conservation are required as anthropogenic activities continue to threaten global biodiversity and freshwater species loss continues (Sánchez-Bayo & Wyckhuys, 2019).

Pond networks provide ideal systems to study spatial ecological processes and nature conservation strategies as they are highly abundant and clearly delineated (local populations and communities are easily quantified) in the landscape, have a wide range of ecological and spatial (connectivity) gradients that are easy to quantify and are easy to sample in a replicable, quantitative and representative way (De Meester et al., 2005). The LCBD approach allows comparison among ponds identified as significantly contributing to LCBD with those ponds that would be considered to be of high taxonomic richness. In so doing, it is possible to explore the benefits (increased gamma diversity) of considering LCBD and richness individually, as well as in combination for the identification of pond sites for conservation. In this study, we use a large freshwater pond community dataset to explore pond conservation potential based on LCBD. We partition LCBD into richness difference and species replacement and identify, for the first time, key environmental variables that are associated with LCBD and local contributions of species replacement and richness difference among ponds. Our analysis operates at two scales that are relevant to ecological and conservation planning: within urban settlements and nationally across England.

2 | METHODS

2.1 | Data management

Macroinvertebrate and environmental data from ponds in five urban settlements across England (Halton—a local government district in Cheshire: $n = 25$, Loughborough: $n = 41$, Stockport: $n = 16$, Birmingham: $n = 30$ and Huddersfield: $n = 20$, total = 132) were compiled from previous studies (Gledhill et al., 2008; Hill et al., 2015; Pond Life Project, 2000; Thornhill, 2013; Wood et al., 2001). Ponds are defined here as lentic water bodies <2ha in area that hold water for at least 4 months of the year (Williams et al., 2010). For the location of urban pond sample sites, see Figure S1. Full details and the rationale for data management procedures are presented in Hill, Hassall, et al. (2018), Hill, Biggs, et al. (2018) and summarized here. In this study, urban settlements were defined as areas containing >10,000 people and being >20 ha in area (UKNEA, 2011). Developed land use areas (DLUA's) were used in this study to define a pond as urban (see supplementary material by Hill, Biggs, et al. (2017) for a discussion on urban pond definitions). The urban ponds studied here were located along an urban settlement gradient, from a densely populated city (Birmingham: >1 million inhabitants) to a smaller, less densely populated town (Loughborough: ~60,000 inhabitants). The ponds were located in domestic gardens, industrial sites, urban green space, adjacent to roads and in commercial districts.

Aquatic macroinvertebrate sampling methods undertaken by the five urban pond studies followed two methodologies: (1) a single 3-min sweep sample in each urban pond, divided between the microhabitats present (Loughborough, Huddersfield and Birmingham) and (2) exhaustive sampling of macroinvertebrates in all available microhabitats until no new species were recorded (Halton and Stockport). However, taxonomic richness recorded using the two sampling strategies has been demonstrated to be comparable (see Hill, Biggs, et al., 2018; Hill, Hassall, et al., 2018). Pond area, pH, altitude, pond shading (estimated percentage of the pond surface shaded by trees and scrub) and pond emergent macrophyte coverage (*EM*: estimated percentage of pond covered with emergent macrophytes) were recorded in most studies and examined here. However, pond shading was not recorded from ponds in Huddersfield and pH was not recorded from ponds in Stockport (see Hill, Hassall, et al. (2018), Hill, Biggs, et al. (2018) Table 2, for a summary of the environmental characteristics of ponds in the urban settlements). The percentage of urban land coverage within a 250 m buffer of each pond was also calculated, to account for the level of urbanity around each pond (Table S1). Land cover data around each pond were derived from the Centre for Ecology and Hydrology National River Flow Archive (https://nrfa.ceh.ac.uk/content/land-use). The invertebrate datasets collated from the contributing studies were converted into a presence–absence matrix to remove any sampling bias. Most macroinvertebrates were identified to species level, Diptera were resolved to family level, *Bithynia*, *Argulus* and *Hydroptila* to genus level, and Oligochaeta, Sphaeriidae, Collembola and Hydrachnidiae were recorded as such. It is acknowledged that the richness recorded in this study has been underestimated given that the highly diverse Diptera group were only resolved to family level.

2.2 | Data analysis

All statistical analyses were undertaken in R (R Core Team, 2019). We first calculated the pairwise total beta diversity and the contribution of species replacement and richness difference components to total beta diversity (based on Baselga family, Jaccard-based indices) using the function *beta.div.comp* from the adespatial package (Dray et al., 2019) for the entire dataset and individual urban settlements. We then calculated the local contribution to beta diversity (LCBD; using Hellinger transformed presence–absence data) for each site across the entire dataset and among sites in each urban settlement separately using the function *beta.div* in the adespatial package (Legendre & De Cáceres, 2013). The statistical significance of individual site contributions (individual LCBD values) can be calculated through random, independent permutations within the community matrix (Legendre & Cáceres, 2013). The local contributions of species replacement ($_{\text{Repl}}$LCBD) and richness difference ($_{\text{RichDiff}}$LCBD) to total beta diversity (based on Baselga family, Jaccard-based indices) were calculated using the function *beta.div.comp* (Legendre, 2014).

Differences in taxonomic richness, LCBD, $_{\text{Repl}}$LCBD and $_{\text{RichDiff}}$LCBD values among ponds from the five urban settlements were assessed using a Kruskal–Wallis test (using the *kruskal.test* function). Nemenyi post hoc tests, using the function *posthoc.kruskal.nemenyi.test* in the PMCMR package (Pohlert, 2018), were undertaken to determine where significant differences among the five urban settlements occurred. The response of LCBD, $_{\text{Repl}}$LCBD and $_{\text{RichDiff}}$LCBD values (dependent variables) was explored in relation to the taxonomic richness (independent variable) via separate sets of statistical models across the entire dataset and each of the five individual urban settlement datasets ($n = 18$; 3 responses × 6 datasets). Each statistical set modelled the influence of taxonomic richness via 4 statistical functions—linear, quadratic, exponential and logarithmic (sensu Fornaroli et al., 2019). For statistical sets performed on individual settlement datasets, traditional regression models ($y = \alpha x + \beta + \varepsilon$) were employed. A linear mixed-effect model design ($y = \alpha x + \beta + (1 \mid \text{City}) + \varepsilon$) was used on the entire dataset, whereby taxonomic richness was used as a fixed effect (as above), and each settlement was used as a random effect (to account for potential spatial autocorrelation) using the *lmer* function in the lme4 package (Bates et al., 2019). For each statistical set (each containing the same dependent variable vs. taxonomic richness modelled *via* the 4 statistical functions), statistical summaries of the model exhibiting the lowest AIC value were reported. For traditional regression models (i.e. individual settlements), the partial R^2 for each predictor variable was calculated for the final models using the function *etasq* from the heplots package (Fox et al., 2018). For linear mixed-effect models (entire dataset), partial R^2 values were derived using the *r2beta* function in the r2glmm package (Jaeger, 2017). For all traditional regression and linear mixed-effect models, residuals were plotted against fixed values to assess the homogeneity of variances and identify outliers (up to 3 data points were removed), while quantile–quantile plots were inspected to ensure that models were normally distributed. For individual urban settlements, we analysed the degree of spatial autocorrelation in the response variables based on Moran's I values using the *correlog* function in the pgirmess package (Giraudoux et al., 2018) to ensure the assumptions of independence were valid (see Supplementary Material 2). Differences in the total richness and number of unique species between significant LCBD sites and sites which recorded >50 taxa were also examined. Sites supporting >50 taxa were selected as this reflects the taxonomic diversity required for a pond to be considered for conservation in the UK.

A comparable regression-based approach was undertaken to examine the relationship between taxonomic richness, LCBD $_{\text{Repl}}$LCBD and $_{\text{RichDiff}}$LCBD values (dependent variables) and the environmental (pond area, pH, altitude, percentage pond shading and percentage emergent macrophyte coverage and spatial (% urban land cover within a 250 m buffer of each pond) variables (independent variables) across the entire dataset and each individual urban settlement. For the entire dataset, only samples where pond area, altitude, shaded area (%), pH and emergent vegetation coverage (%) were all recorded were retained, resulting in 96 samples across three urban settlements (Birmingham, Loughborough and Halton); although all settlements were individually examined using the environmental variables available in each respective dataset. Preliminary analysis using Pearsons correlation indicated that there was no collinearity among environmental variables when the entire dataset or individual urban settlements were considered. For each of these statistical sets ($n = 24$; 4 responses × 6 datasets), each dependent–independent variable paired combination was modelled using traditional regressions (and linear mixed-effect models for the entire dataset) via linear, quadratic, exponential and logarithmic statistical functions; with the optimal statistical function for each environmental variable in each statistical set then being derived from the model exhibiting the lowest AIC. For each statistical set, a final regression analysis was performed on the additive effects of all environmental variables modelled in their optimal (linear, quadratic, exponential or logarithmic) structure. The significance of individual covariates was identified through a backwards stepwise selection procedure (using the *step* function in the lmertest package; Kuznetsova et al., 2019), while the overall model significance was determined from likelihood ratio tests.

Total (gamma) richness was calculated for (1) the significant LCBD sites, (2) sites containing >50 taxa and (3) significant LCBD sites and sites containing >50 taxa combined across the entire dataset, as well as each urban settlement individually. To identify whether these three methods resulted in greater gamma diversity than would occur by chance, for each individual urban settlement and the entire dataset, we randomly selected the same number of sites as identified within each of the three methods mentioned above. These sites were randomly sampled without replacement, and this process was repeated across 1,000 simulations to produce each comparison. For each randomly selected dataset, the mean total (gamma) taxonomic richness (and standard deviation) was calculated. To examine whether the average total richness recorded from a random selection of ponds was less than the total richness recorded from significant LCBD sites and sites with >50 taxa, a one sample *t* test was performed.

3 | RESULTS

3.1 | LCBD, $_{\text{Repl}}$LCBD and $_{\text{RichDiff}}$LCBD values among ponds from the 5 urban settlements

In total, 338 macroinvertebrate taxa were recorded from ponds across the five urban settlements: Halton (108 taxa, median: 28), Loughborough (170 taxa, median: 15), Stockport (140 taxa, median: 20.5), Birmingham (193 taxa, median: 44.5) and Huddersfield (100 taxa, median: 15). The majority of variation in macroinvertebrate composition was explained by species replacement, rather than richness difference (Figure 1).

Across the entire dataset, 22 ponds recorded significant ($p < 0.05$) LCBD values (i.e. significantly contributed to total beta diversity). Significant differences (Kruskal–Wallis test $df = 4$, $\chi^2 = 67.91$, $p < 0.001$) in LCBD values were recorded among the 5 settlements (Figure 2a). Nemenyi post hoc tests indicated that ponds in Birmingham and Loughborough had significantly lower ($p < 0.01$) LCBD values than ponds in Halton, Stockport and Huddersfield. $_{\text{Repl}}$LCBD (Kruskal–Wallis test $df = 4$, $\chi^2 = 85.25$, $p < 0.001$) and $_{\text{RichDiff}}$LCBD values (Kruskal–Wallis test $df = 4$, $\chi^2 = 75.62$, $p < 0.001$) differed significantly among the 5 urban settlements (Figure 2b, c). Nemenyi post hoc test indicated that $_{\text{Repl}}$LCBD values in ponds in Birmingham and Loughborough were significantly lower ($p < 0.01$) than ponds in Halton, Stockport and Huddersfield (Figure 2b). $_{\text{RichDiff}}$LCBD values were significantly higher ($p < 0.01$) in Birmingham and Loughborough than Halton, Stockport and Huddersfield (Figure 2c). When the urban settlements were considered individually, 6 ponds in Halton, 5 in Loughborough, 2 in Stockport, 6 in Birmingham and 2 in Huddersfield significantly contributed to total beta diversity (Table 1).

3.2 | Contribution of significant LCBD sites to regional taxonomic richness

A total of 148 taxa and 21 unique taxa were recorded from the 21 significant LCBD ponds across the entire dataset (Table 1; Supplementary Material 3). Ponds that supported >50 taxa recorded a total of 240 taxa and 43 unique taxa when the entire dataset was considered. When significant LCBD ponds and those with >50 taxa were considered together, a total of 279 taxa and 71 unique taxa occurred across the entire dataset (Table 1). The total number of species and unique taxa recorded from the 5 urban settlements for significant LCBD ponds, ponds that support >50 taxa and both

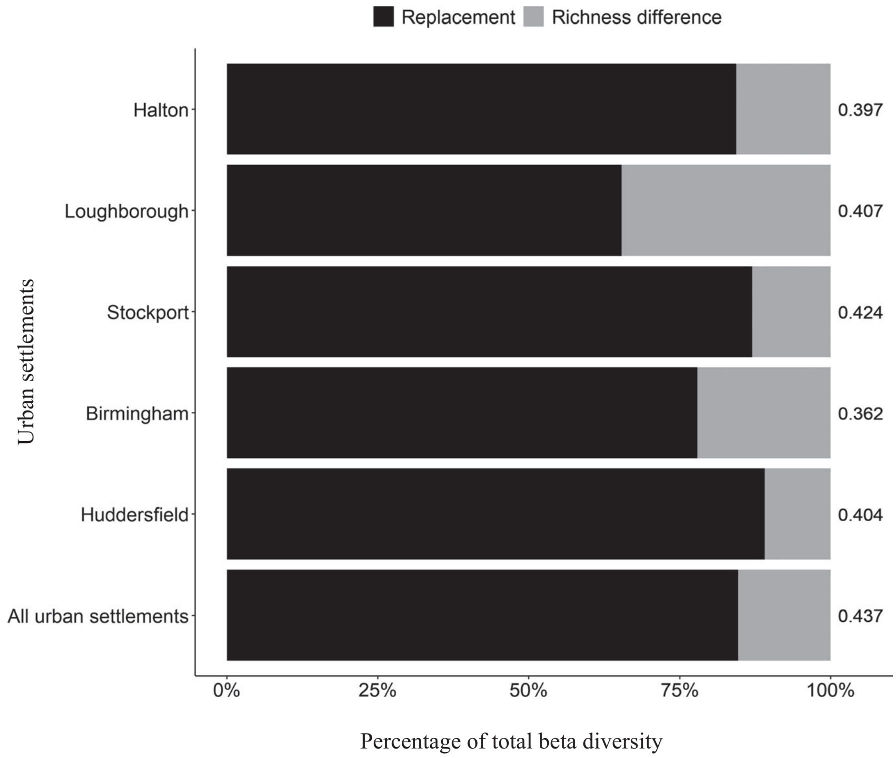

FIGURE 1 Relative contribution of species replacement and richness difference to total community variability among ponds in Halton, Loughborough, Stockport, Birmingham and Huddersfield and across the entire dataset. Values represent total Sorenson dissimilarity values

combined are reported in Table 1. A total of 31% of ponds were recorded as significant LCBD sites and/or sites with >50 taxa when all sites were considered, 66% in Birmingham, 20% in Loughborough, 10% in Huddersfield, 37% in Stockport and 24% in Halton.

The three methods to assess gamma diversity conservation potential, that is (1) significant LCBD sites, (2) sites containing >50 taxa and (3) significant LCBD sites and sites containing >50 taxa combined were applied to each of the six datasets and compared against an equal number of randomly selected samples (1,000 simulations). The total richness recorded among a random selection of sites was greater than the total richness recorded from significant LCBD sites when the entire dataset was considered (mean random richness: 197.6 ± 0.48 vs. total significant LCBD richness: 141; $t = 117.68$, $p > 0.05$) and among ponds in Loughborough (70.26 ± 0.6 vs. 67; $t = 5.45$, $p > 0.05$), Birmingham (122.79 ± 0.42 vs. 75; $t = 115$, $p > 0.05$), Stockport (45.5 ± 0.56 vs. 31; $t = 26.02$, $p > 0.05$) and Halton (71 ± 0.23 vs. 41; $t = 132.58$, $df = 999$, $p > 0.05$). However, the total richness of randomly selected sites was significantly less than the total richness recorded from significant LCBD sites in Huddersfield (26.26 ± 0.21 vs. 30; $t = -17.69$, $p < 0.05$).

Total taxonomic richness was significantly less among the randomly selected ponds compared to sites with high taxonomic diversity (sites with >50 taxa) when the entire dataset was considered (mean random richness: 190.8 ± 0.5 vs. high taxonomic diversity sites total richness: 225; $t = -67.88$, $p < 0.01$) and among ponds in Loughborough (49.48 ± 0.64 vs. 93; $t = -68.49$, $p < 0.01$), Birmingham (162.4 ± 0.24 vs. 182; $t = -81.08$, $p < 0.01$) and Stockport (73.856 ± 0.53 vs. 110; $t = -68.05$, $p < 0.01$).

The total richness of randomly sampled sites was significantly less than the total richness recorded when significant LCBD sites and sites with high taxonomic diversity were combined and considered together (mean random richness: 249.14 ± 0.36 vs. significant LCBD and high taxonomic diversity sites total richness: 271; $t = -60.97$, $p < 0.01$) and among ponds in Loughborough (89.59 ± 0.54 vs. 119; $t = -54.73$, $p < 0.01$), Birmingham (177.57 ± 0.16 vs. 187; $t = -57.21$, $p < 0.01$) and Stockport (91.66 ± 0.45 vs. 119; $t = -61.18$, $p < 0.01$). This analysis could not be undertaken for Halton and Huddersfield as no ponds were recorded with >50 taxa.

3.3 | Relationship between LCBD, $_{\text{Repl}}$LCBD, $_{\text{RichDiff}}$LCBD and taxonomic richness

LCBD yielded a significant negative association with taxonomic richness in ponds when the entire dataset was considered ($df = 2$, $\chi^2 = 86.61$, $R^2 = 0.28$, $p < 0.001$—quadratic function) and among ponds in Halton ($df = 1$, $F = 47.69$, adj. $R^2 = 0.66$, $p < 0.001$—linear function), Stockport ($df = 2$, $F = 17.81$, adj. $R^2 = 0.69$, $p < 0.001$—quadratic function) and Birmingham ($df = 1$, $F = 34.29$, adj. $R^2 = 0.53$, $p < 0.001$—linear function) (Figure 3). No significant association was recorded between LCBD and taxonomic richness among ponds in Huddersfield ($df = 1$, $F = 0.46$, adj. $R^2 = -0.02$, $p = 0.504$ – linear function) and Loughborough ($df = 2$, $F = 2.24$, adj. $R^2 = 0.05$, $p = 0.12$—quadratic function; Figure 3). $_{\text{Repl}}$LCBD and $_{\text{RichDiff}}$LCBD were also significantly associated ($p < 0.05$) with taxonomic richness when the entire dataset was considered and among ponds in Halton and Stockport (Supplementary Material 4). Among the individual urban settlements, $_{\text{Repl}}$LCBD and $_{\text{RichDiff}}$LCBD consistently demonstrated unimodal trends in response to taxonomic richness, although displayed opposing trends: $_{\text{Repl}}$LCBD values were

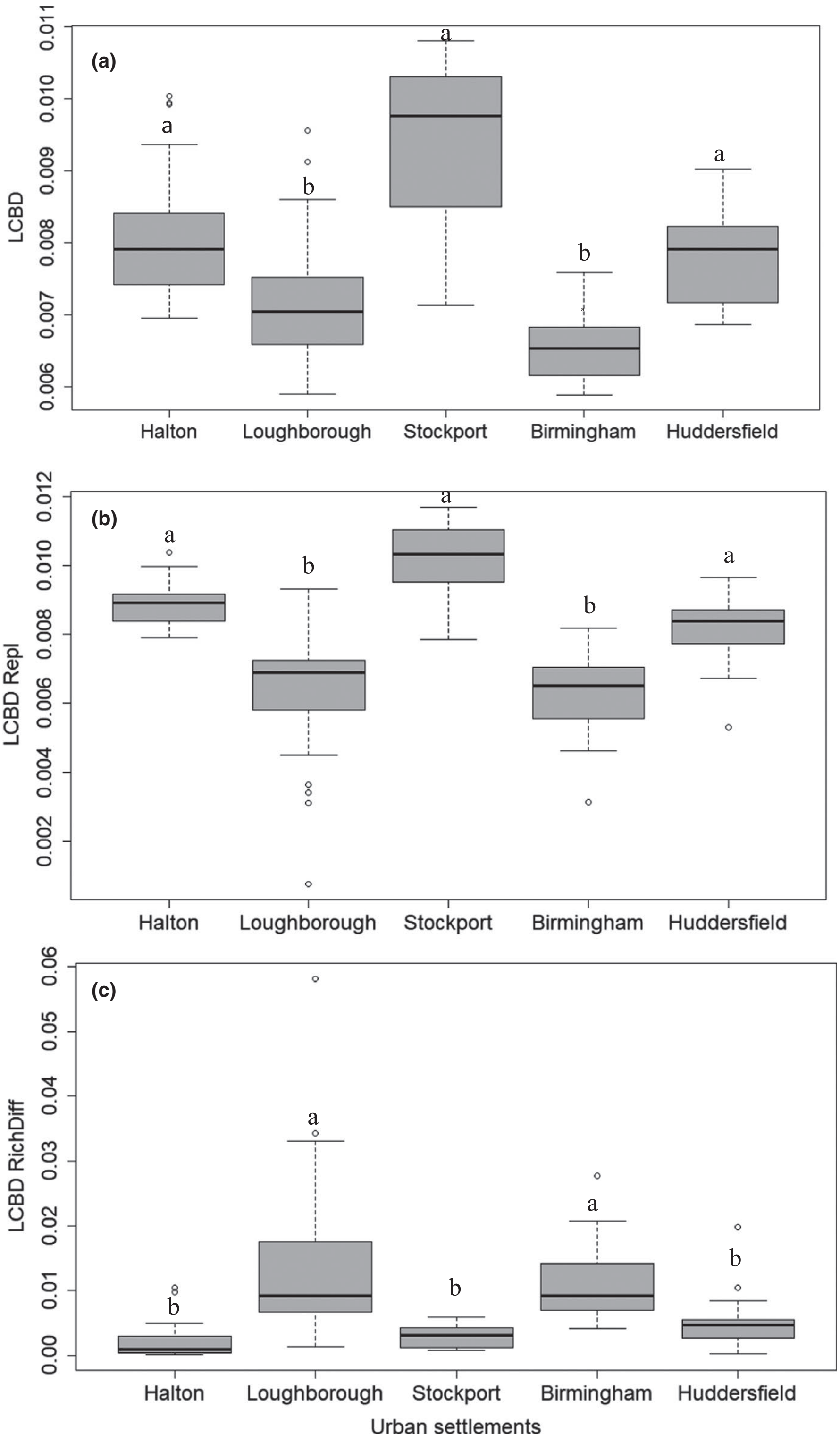

FIGURE 2 Median LCBD (a), $_{\text{Repl}}$LCBD (b) and $_{\text{RichDiff}}$LCBD (c) values recorded from ponds in Halton, Loughborough, Stockport, Birmingham and Huddersfield. Boxes show 25th, 50th and 75th percentiles and whiskers show 5th and 95th percentiles. Letters outline statistically significant differences among groups

highest at intermediate taxonomic richness values, while $_{\text{RichDiff}}$LCBD values were lowest at intermediate taxonomic richness values (Supplementary Material 4).

$_{\text{Repl}}$LCBD yielded a significant negative association with $_{\text{RichDiff}}$LCBD in ponds when the entire dataset was considered ($df = 2$, $\chi^2 = 165.65$, $R^2 = 0.61$, $p < 0.001$—quadratic function) and for ponds in Halton (quadratic, $df = 2$, $F = 8.56$, adj. $R^2 = 0.39$, $p < 0.01$), Stockport ($df = 1$, $F = 101.7$, adj. $R^2 = 0.87$, $p < 0.001$ – linear function), Huddersfield ($df = 2$, $F = 37.71$, adj. $R^2 = 0.79$, $p = 0.504$—quadratic function), Loughborough ($df = 2$, $F = 315.70$, $p = 0.001$—quadratic function) and Birmingham ($df = 1$, $F = 28.76$, adj. $R^2 = 0.49$, $p < 0.001$—linear function; Figure 4). Significant LCBD ponds recorded the highest species replacement (and lowest richness difference) values when all ponds were considered and among ponds in Loughborough, Huddersfield and

TABLE 1 Macroinvertebrate richness and unique taxa (taxa only recorded from those ponds) recorded among significant LCBD sites, sites with >50 taxa and both combined. Total number of ponds significantly contributing to LCBD or recording >50 taxa are presented in parenthesis

	Significant LCBD sites	Sites with >50 taxa	Both combined	Entire dataset (total richness)
All cities				
Macroinvertebrate richness	148 (43% of total richness: TR) (*n* = 21)	240 (71% of TR) (*n* = 20)	279 (82.5% of TR) (*n* = 41)	338
Unique taxa	21	43	71	0
Halton				
Macroinvertebrate richness	41 (38% of TR) (*n* = 6)	no pond > 50 taxa	41 (38% of TR) (*n* = 6)	108
Unique taxa	8	no pond > 50 taxa	8	0
Loughborough				
Macroinvertebrate richness	67 (39% of TR) (*n* = 5)	93 (54% of TR) (*n* = 3)	119 (70% of TR) (*n* = 8)	170
Unique taxa	7	12	20	0
Birmingham				
Macroinvertebrate richness	76 (39% of TR) (*n* = 6)	182 (94% of TR) (*n* = 14)	187 (97% of TR) (*n* = 20)	193
Unique taxa	3	73	87	0
Huddersfield				
Macroinvertebrate richness	30 (30% or TR) (*n* = 2)	no pond > 50 taxa	30 (30% or TR) (*n* = 2)	100
Unique taxa	5	no pond > 50 taxa	5	0
Stockport				
Macroinvertebrate richness	31 (22% of TR) (*n* = 2)	110 (78% of TR) (*n* = 4)	119 (85% of TR) (*n* = 6)	140
Unique taxa	5	47	56	0

Stockport (Figure 4). However, significant LCBD sites in Birmingham and Halton recorded both high species replacement and high richness difference values (Figure 4).

3.4 | Relationship between taxonomic richness, LCBD, $_{\text{Repl}}$LCBD, $_{\text{RichDiff}}$LCBD and environmental variables among the 5 urban settlements

The final model for taxonomic richness in urban ponds across the entire dataset explained 40% of the community variation (adj. $R^2 = 0.40$, $\chi^2 = 25.78$, $p < 0.01$: *urban cover, EM, altitude*) (Table 2). When taxonomic richness within ponds in individual urban settlements were examined, 22% of the variation was explained in Halton (adj. $R^2 = 0.22$, $F = 3.07$, $p < 0.05$: *EM*), 32% in Loughborough (adj. $R^2 = 0.32$, $F = 3.71$, $p < 0.05$: *urban cover, shade*), 46% in Stockport (adj. $R^2 = 0.47$, $F = 2.86$, $p < 0.05$: *surface area, EM*) and 35% in Birmingham (adj. $R^2 = 0.350$ $F = 2.95$, $p < 0.05$: *EM, pond shading*) (Table 2). No environmental variables were significant predictors of taxonomic richness in Huddersfield.

The final regression model testing how LCBD responded to different environmental variables when the entire dataset was considered explained 10% of the variation in pond LCBD ($R^2 = 0.1$) but did not exert a significant influence overall ($\chi^2 = 12.09$ $p = 0.09$). However, emergent macrophyte coverage (EM) was significantly associated with LCBD (Table 2). A total of 13% of the variation in $_{\text{Repl}}$LCBD (adj. $R^2 = 0.13$, $\chi^2 = 20.69$, $p < 0.01$) and 19% $_{\text{RichDiff}}$LCBD (adj. $R^2 = 0.19$, $\chi^2 = 25.42$, $p < 0.01$) were explained when the entire dataset was considered. Only EM was associated with $_{\text{Repl}}$LCBD, while EM and pH were associated with $_{\text{RichDiff}}$LCBD across the entire dataset (Table 2).

When the individual urban settlements were considered, the final regression model explained 38% of the variation in LCBD in Halton (adj. $R^2 = 0.38$, $F = 3.07$, $p < 0.05$; significant predictor—*EM*) and 49% in Stockport although the final model was not significant (adj. $R^2 = 0.49$, $F = 3.02$, $p = 0.07$: *EM*) (Table 2). For pond LCBD in Loughborough, the final model had poor explanatory power, explaining 3% of the statistical variation (adj. $R^2 = 0.03$, $F = 1.22$, $p = 0.32$: *EM*) (Table 2). Among ponds in Birmingham, 11% of the variation in LCBD was explained by the final regression model (adj. $R^2 = 0.11$, $F = 1.54$, $p = 0.21$: *surface area*). A total of 15% of the variation in $_{\text{Repl}}$LCBD were explained by the final regression model in Halton (adj. $R^2 = 0.15$, $F = 1.63$, $p < 0.05$: *EM*) and 50% in Stockport, although the final model was not significant (adj. $R^2 = 0.50$, $F = 3.15$, $p = 0.07$; *EM*). Surface area was a significant predictor of variation in $_{\text{RichDiff}}$LCBD in Halton, while emergent macrophytes were the only significant predictor for $_{\text{RichDiff}}$LCBD in Stockport. However, the

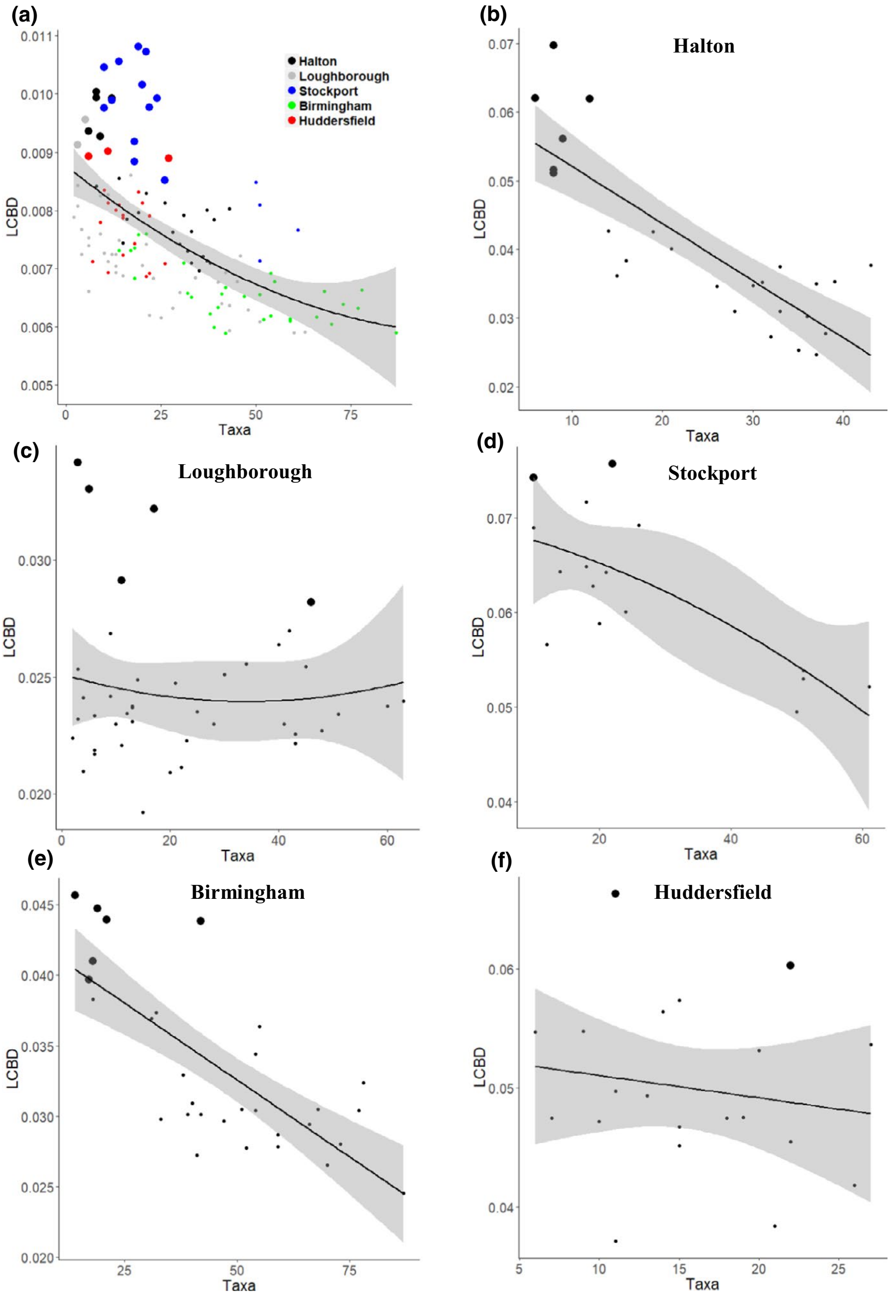

FIGURE 3 Relationship between the local contribution to beta diversity (LCBD) and taxonomic richness among ponds across the entire dataset (a) and within individual urban settlements: Halton (b), Loughborough (c), Stockport (d), Birmingham (e) and Huddersfield (f). Significant LCBD sites are presented in bold

overall significance of final regression models for ${}_{\mathrm{RichDiff}}$LCBD among Halton (adj. $R^2 = 0.258$, $F = 2.192$, $p = 0.08$; *surface area*) and Stockport (adj. $R^2 = 0.411$, $F = 2.495$, $p = 0.111$; *EM*) was not significant (Table 2). No environmental variables were significant predictors of pond, LCBD, ${}_{\mathrm{Repl}}$LCBD or ${}_{\mathrm{RichDiff}}$LCBD in Huddersfield (Table 2). In addition, no significant predictors were associated with ${}_{\mathrm{Repl}}$LCBD and ${}_{\mathrm{RichDiff}}$LCBD among ponds in Loughborough or Birmingham.

4 | DISCUSSION

This study is the first to examine the contribution of individual urban pond sites to patterns of overall beta diversity (LCBD), richness difference (${}_{\mathrm{RichDiff}}$LCBD), species replacement (${}_{\mathrm{Repl}}$LCBD), the environmental variables influencing those patterns and their relevance and potential application for biodiversity conservation at a national and city scale. Our results indicated regional variability in the association of taxonomic richness and ecological uniqueness (LCBD) between the urban settlements examined in this study. Ecological uniqueness was negatively related to macroinvertebrate taxonomic richness when all ponds were considered, and among ponds in Birmingham, Stockport and Halton, but no association was identified among ponds in Huddersfield and Loughborough. Sites with high taxonomic diversity may exhibit low LCBD values due to the increased chance of sharing species with other sites in the region (Szabó et al., 2019). A negative association between LCBD and taxonomic richness has been previously recorded among fish (Legendre & Cáceres, 2013), macroinvertebrates (Heino & Grönroos, 2017),

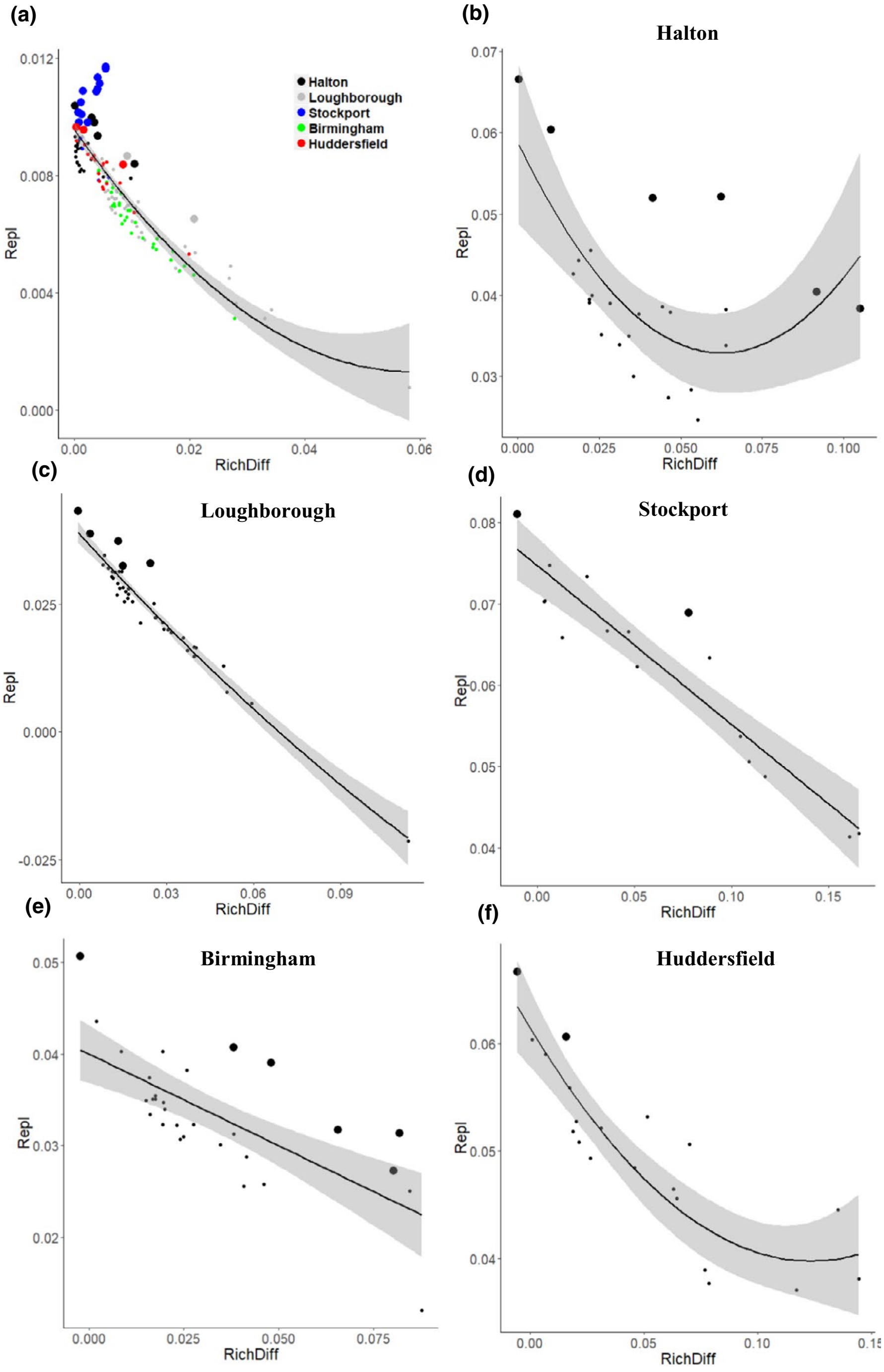

FIGURE 4 Relationship between the $_{\mathrm{Repl}}$LCBD and $_{\mathrm{RichDiff}}$LCBD among ponds across the entire dataset (a), and within individual urban settlements: Halton (b), Loughborough (c), Stockport (d), Birmingham (e) and Huddersfield (f). Significant LCBD sites are presented in bold

diatoms (Szabó et al., 2019; Vilmi et al., 2017), microbial communities (Teittinen et al., 2017), dung beetles (da Silva et al., 2018) and tree species (Qiao et al., 2015). However, some studies have recorded a positive association between LCBD values and taxonomic richness (e.g. fish assemblages—Kong et al., 2017) or no association (e.g. diatoms in lake ecosystems—Vilmi et al., 2017). A positive relationship may reflect the colonization of novel species (e.g. migratory species, rare species) in communities (da Silva et al., 2018). Qiao et al. (2015) identified a negative association when common tree species were considered but a positive association when only rare species were considered. Therefore, the occurrence of rare and common species in freshwater communities may play a significant role in determining whether the LCBD-taxonomic richness association is positive, negative or non-significant (Cucherousset et al., 2008; da Silva et al., 2018). A wide range of processes may be influencing ecological communities, resulting in different associations between LCBD and taxonomic richness including; primary productivity, environmental filtering, hydro-climatological processes, species interactions, species dispersal, disturbance regimes, stochastic processes and biotic interactions (Bennett et al., 2009; Heino & Grönroos, 2017; Tonkin et al., 2015). Furthermore, the patterns found between LCBD and taxonomic richness may be influenced by the type of data used (Szabó et al., 2019). For example, a negative association between LCBD and taxonomic richness among stream macroinvertebrates

TABLE 2 Significant predictors of taxonomic richness, local contribution to beta diversity (LCBD) and the replacement ($_{\text{Repl}}$LCBD) and richness difference ($_{\text{RichDiff}}$LCBD) components of LCBD across the entire dataset and for each urban settlement, resulting from regression analyses. The statistical function employed for each significant environmental variable is presented in parenthesis

	Variable	*F* value	*p* value	Partial R^2	Directional response
Entire Dataset					
Taxonomic richness	Urban cover (logarithmic)	9.322	<0.01	0.09	–
	Altitude	34.805	<0.01	0.21	+
	Emergent plants	5.145	<0.01	0.08	–
LCBD	Emergent macrophytes (logarithmic)	5.701	<0.05	0.01	–
$_{\text{Repl}}$LCBD	Emergent macrophytes (quadratic)	6.814	<0.01	0.02	Unimodal
$_{\text{RichDiff}}$LCBD	Emergent macrophytes (quadratic)	10.473	<0.05	0.09	Unimodal
	pH (quadratic)	3.455	<0.01	0.04	Unimodal
Halton					
Taxonomic richness	Emergent macrophytes (logarithmic)	14.616	<0.01	0.22	+
LCBD	Emergent macrophytes (logarithmic)	15.206	<0.01	0.21	–
$_{\text{Repl}}$LCBD	Emergent macrophytes (logarithmic)	6.002	<0.05	0.1	–
$_{\text{RichDiff}}$LCBD	Surface area (logarithmic)	6.409	<0.05	0.09	–
Loughborough					
Taxonomic richness	Urban coverage (quadratic)	3.99	<0.05	0.19	–
	pH (linear)	5.810	<0.05	0.11	Unimodal
LCBD	Emergent macrophytes (logarithmic)	4.625	<0.05	0.11	–
$_{\text{Repl}}$LCBD	None	–	–	–	
$_{\text{RichDiff}}$LCBD	None	–	–	–	
Stockport					
Taxonomic richness	Surface area (linear)	6.548	<0.05	0.16	+
	Emergent macrophytes (quadratic)	4.753	<0.05	0.46	Unimodal
LCBD	Emergent macrophytes (quadratic)	6.749	<0.05	0.61	Unimodal
$_{\text{Repl}}$LCBD	Emergent macrophytes (quadratic)	7.557	<0.05	0.63	Unimodal
$_{\text{RichDiff}}$LCBD	Emergent macrophytes (quadratic)	5.167	<0.05	0.44	Unimodal
Birmingham					
Taxonomic richness	Emergent macrophytes (linear)	6.794	<0.05	0.01	+
	Pond shading (logarithmic)	5.442	<0.05	0.14	–
LCBD	Pond area (logarithmic)	4.443	<0.05	0.01	–
$_{\text{Repl}}$LCBD	None	–	–	–	
$_{\text{RichDiff}}$LCBD	None	–	–	–	
Huddersfield					
Taxonomic richness	None	–	–	–	
LCBD	None	–	–	–	
$_{\text{Repl}}$LCBD	None	–	–	–	
$_{\text{RichDiff}}$LCBD	None	–	–	–	

was recorded when presence–absence data were used; however, a non-significant relationship was recorded when abundance-based data were used (Heino & Grönroos, 2017). Our results reflect and support the findings of previous research highlighting the complex relationship between taxonomic richness and LCBD across biological groups, geographical regions and different ecosystems.

Across the entire dataset and in four of the five urban settlements studied, pond sites that contributed most to total beta diversity (significant LCBD sites) were characterized by high replacement and the lowest richness difference values, indicating that there were high numbers of macroinvertebrate taxa recorded in these ponds that were not recorded in the other ponds (unique species). This finding may be due to species replacement typically being positively correlated with total beta diversity, while richness difference commonly displays a negative correlation with total beta diversity (Soininen et al., 2018). This pattern also indicates that species replacement broadly measures the same phenomenon as total beta diversity (the compositional variation between sites; Soininen et al., 2018) within pond habitats. It should be noted that while the different sampling strategies (3-min sweep sample and exhaustive sampling) employed in this study did not demonstrate any significant differences in taxonomic richness and are therefore unlikely to affect $_{\mathrm{RichDiff}}$LCBD values, they may have an effect on $_{\mathrm{Repl}}$LCBD. However, this is unlikely in this study, given that significant LCBD sites were characterized by high replacement values in urban settlements that were sampled exhaustively and using a 3-min sweep sample. Some significant LCBD sites (high ecological uniqueness) in Birmingham recorded high richness difference values, probably due to the large number of taxonomically rich ponds recorded there, increasing the number of species shared across sites and limiting the number of sites with high species replacement. In this instance, differences in taxonomic richness (richness difference) are likely to be the most important component of total beta diversity. In addition, Birmingham was the largest, most populated and developed of the urban areas studied, potentially increasing the physical barriers for dispersal and the number of disturbance events, which has been demonstrated to increase patterns of richness difference (Legendre, 2014; Picazo et al., 2012).

Ponds from the five urban settlements studied showed considerable variability in the effects of environmental variables on LCBD. Similarly, Tonkin et al. (2015) found significant variation in the relationship between LCBD and environmental variables across five different invertebrate stream datasets. When the entire dataset was considered and at a city scale, pond surface area and emergent macrophyte cover were the most important predictors of LCBD, $_{\mathrm{Repl}}$LCBD and $_{\mathrm{RichDiff}}$LCBD. This suggests they are key variables governing ecological uniqueness and have been reported in previous studies to be key predictors of compositional variation in ponds (Hassall et al., 2011; Hill et al., 2019). Interestingly, the percentage urban land coverage around a 250m buffer of each pond was not found to be an important driver of LCBD, $_{\mathrm{Repl}}$LCBD and $_{\mathrm{RichDiff}}$LCBD when the entire dataset was considered or when the individual urban settlements were considered, contrasting with the findings of Heino et al. (2017). However, increasing urban land cover was found to be a significant negative predictor of taxonomic richness when the entire dataset was considered and among ponds in Loughborough, a finding which has been documented in other aquatic and terrestrial faunal studies (e.g. Mckinney, 2008; Roy et al., 2003). Findings from this study suggest that the influence of local environmental variables on LCBD may override the effects of urban land cover; however, this explanation is speculative as there have been so few studies examining LCBD among urban freshwater habitats. LCBD, $_{\mathrm{Repl}}$LCBD and $_{\mathrm{RichDiff}}$LCBD were poorly explained by the local environmental variables in ponds from Huddersfield and Birmingham, supporting the findings in streams by Heino and Grönroos (2017). The weak relationship between local environmental variables and LCBD in this study may reflect an impacted regional species pool from anthropogenic disturbance (Tonkin et al., 2015). However, the poor prediction of LCBD may reflect other unmeasured local environmental (e.g. fish presence/density, depth, conductivity, dissolved oxygen, nutrient concentration, submerged macrophyte cover and macrophyte complexity) and spatial variables (connectivity / isolation) that may be important drivers of ecological uniqueness. Future research is required to examine the possible effects of these unmeasured variables on LCBD among ponds. This context-dependent pattern between the urban pond datasets is a key challenge in developing theoretical understanding of the environmental predictors governing the ecological uniqueness of freshwater ecosystems (Tonkin et al., 2015).

4.1 | Conservation implications

In Europe, pond conservation is currently focused on protecting individual sites with rare species or with records of very high biodiversity (Hill, Biggs, et al., 2018; Hill, Hassall, et al., 2018). However, this study and others have demonstrated that ponds contribute most to diversity at the landscape-scale (Davies et al., 2008). High beta diversity among ponds could almost entirely be attributed to species replacement indicating that pond conservation would be most effective at a landscape-scale, protecting a wide range of pond sites (Hill, Biggs, et al., 2017; Hill, Heino, et al., 2017). However, given the limited resources available for biodiversity conservation and restoration, protecting large numbers of ponds across a landscape is often impractical, particularly in urban areas. Therefore, assessing the landscape-scale conservation value of individual sites effectively is particularly important to ensure the maximum possible biodiversity is protected and sustained with the limited funding available.

Protecting sites of high ecological uniqueness (significant LCBD sites) may provide an opportunity to focus efforts on landscape-scale conservation, while not deviating from the current practice of designating individual ponds for conservation. LCBD goes beyond typical measures of beta diversity (an overall measure across the landscape) and provides a value of the contribution to beta diversity for individual sites (Heino & Grönroos, 2017). Significant LCBD sites in this study typically supported unique species (taxa only recorded in high LCBD ponds due to their high species replacement) had unique compositions of species and contributed to regional diversity within most of the urban settlements examined. However, the low taxonomic richness recorded among the significant LCBD sites may reduce their perceived importance to practitioners for conservation. If considered individually, an LCBD-based approach may not be suitable to ensure the maximum possible biodiversity is protected. However, when prioritizing significant LCBD sites and sites with high taxonomic diversity together (conserving both high taxonomic diversity and ecologically unique site) more taxa are protected than high taxonomic diversity sites alone or those sites that would be protected purely based on chance (random selection of ponds in the network). In this study, 70%–97% of the regional species pool was protected when ecologically unique and high taxonomic diversity sites (>50 taxa) were considered together compared to 54%–94% when only sites with high taxonomic diversity were considered. The LCBD metrics presented here are straightforward to incorporate into spatial planning exercises or standard conservation planning software (e.g. Zonation; Moilanen et al., 2009, Marxan; Ball et al., 2009) as an additional layer for parameterization. Indeed, complementarity of protected areas is a common principle in systematic reserve design (Margules & Pressey, 2000) but is rarely applied at smaller scales or for specific habitats (Önal & Briers, 2002). Including ecologically unique sites within current conservation practices alongside sites of high taxonomic richness: (1) effectively enables landscape-scale conservation to be undertaken, as those sites that contribute most to beta diversity are being protected; (2) continues to ensure sites of highest biodiversity are protected; (3) ensures a significant proportion of the regional richness pool is protected; and (4) expands the spatial network of protected aquatic habitats in urban areas. Further, conserving sites of high ecological uniqueness may enable conservation within areas where no ponds are currently protected (as existing pond conservation requirements may not have been met).

This study also highlighted variability between urban settlements, as significant LCBD sites in Birmingham recorded higher richness difference values, while significant LCBD sites in other urban settlements were characterized by a high species replacement. Among those urban areas (Loughborough, Halton, Stockport and Huddersfield) where pond networks are structured by species replacement, protecting ecologically unique and taxonomically rich sites will maximize the number of taxa supported. However, where there is a high contribution of richness difference to beta diversity, such as Birmingham, traditional conservation efforts could focus on sites of high taxonomic richness, rather than LCBD sites as these formed subsets of sites with high taxonomic richness and made a limited contribution to the regional species pool (>2%).

Significant LCBD sites and high diversity sites together constituted between 10% and 66% of the pond network in the urban settlements. Using LCBD as a compliment to taxonomic richness-based conservation provides significant opportunity to protect the most important ponds sites and ensure the persistence of aquatic biodiversity in urban landscapes, without needing to protect every pond in the network. Further, many of the ponds identified as significant LCBD or high diversity sites were constructed for anthropogenic purposes (e.g. stormwater collection). This pond conservation method supports a significant proportion of the regional species pool and can provide a cost-effective (minimal logistical and financial input to achieve), multifunctional approach to urban nature conservation, while also ensuring that the primary function of the ponds is maintained (Oertli & Parris, 2019). Given the variability between urban settlements, prioritizing ponds for landscape-scale conservation should be examined at an urban settlement-scale, and the use of species replacement ($_{\mathrm{Repl}}$LCBD) and richness difference ($_{\mathrm{RichDiff}}$LCBD) metrics outlined in this study can facilitate regionally effective conservation planning decisions (da Silva et al., 2018). Given the predicted increase in future urban land cover (Seto et al., 2012), identifying effective conservation approaches is essential to ensure biodiversity is sustained and where possible enhanced, and detrimental anthropogenic effects are minimized.

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AUTHOR CONTRIBUTIONS

MJH devised the study idea. MJH and JCW undertook the statistical analysis. MJH, PJW, JB, DG and IT contributed data to the study. MJH wrote the manuscript. All authors reviewed manuscript drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13239.

DATA AVAILABILITY STATEMENT

This manuscript utilizes secondary data, some of which is publicly available (e.g. Loughborough dataset: http://dx.doi.org/10.5061/dryad.1f43v). The data used in this study are publicly available from the Dryad digital repository (https://doi.org/10.5061/dryad.nk98sf7sh).

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BIOSKETCH

Matthew J. Hill is interested in all aspects of freshwater biodiversity. In particular, his research addresses the processes determining the spatial and temporal patterns of freshwater communities and the practical conservation of small water bodies.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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