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ORIGINAL ARTICLE

The Ecology and Conservation of Urban Insects

Environmental correlates of aquatic macroinvertebrate diversity in garden ponds: Implications for pond management

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Abstract

1. Garden ponds are a ubiquitous feature of urban landscapes and have the potential to be an important resource for biodiversity. However, the environmental and spatial factors influencing ecological communities within garden ponds have been poorly quantified to date, despite such evidence being critical to the development of effective management strategies that support biodiversity.
2. This study aims to identify the environmental and spatial factors influencing macroinvertebrate richness, abundance and compositional variation among garden ponds and provide management recommendations at the local and landscape scale. In total, 99 macroinvertebrate taxa were recorded from 30 garden ponds.
3. A negative association was recorded between ecological uniqueness (measured as the Local Contribution to Beta-Diversity) and taxonomic richness among the garden ponds, and those ponds with high ecological uniqueness typically displayed high replacement (turnover) values. Surface area, total plant richness and non-native plant richness were positively associated with macroinvertebrate richness. Taxonomic richness and abundance predominantly displayed a negative association with conductivity levels.
4. Current management practices for garden ponds are highly variable, often focussed on individual ponds. Based on the findings of this study, we recommend that management should focus on making garden pond surface areas as large as possible, ensure that there is a wide variety of native aquatic plant species present and manage conductivity levels. Garden ponds likely comprise a significant component of the urban freshwater network, and considering their management at both local and landscape scales will ensure that biotic communities inhabiting urban landscapes can be more effectively supported.

KEYWORDS

freshwater conservation, landscape-scale, LCBD, macroinvertebrate, taxonomic richness, urban ponds

INTRODUCTION

Urbanisation has been widely documented to be one of the main drivers of terrestrial and aquatic biodiversity loss globally, through

increased disturbance, changes in physical and chemical conditions, anthropogenic pollution, the presence of invasive species, and habitat homogenisation, fragmentation and destruction (Fenoglio et al., 2021; Gál et al., 2019). Given that global urban land cover is predicted to be

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2–6 times higher in 2100 compared with 2000 (Gao & O'Neill, 2020) and that 68% of the global population will reside in urban landscapes by 2050 (United Nations, 2019), there has been increasing concern regarding conservation of urban ecosystems (Tilman et al., 2017). Urbanisation has been widely associated with reductions in biodiversity and increased biotic homogenisation among terrestrial and lotic systems (Fenoglio et al., 2021; Liu, et al., 2020) and some pond networks (Noble & Hassall, 2015). However, larger scale studies have demonstrated that urban ponds can support similar macroinvertebrate richness to non-urban ponds and have high biotic heterogeneity among sites (Hill et al., 2017; Hill et al., 2018). Ponds may, therefore, provide suitable habitat to support freshwater biodiversity in urban areas and facilitate dispersal through the wider urban matrix (Hassall, 2014; Thornhill et al., 2018).

An important component of the urban freshwater network is garden ponds. For example, in the UK, there are estimated 2.5–3.5 million garden ponds that collectively cover 349 ha (Davies et al., 2009). Garden ponds are popular among the public and have been built for multiple purposes including to support biodiversity, ornamental fish, aesthetic value and education (Holden & Abbott, 2023). Despite their high abundance and popularity, garden ponds remain poorly studied. However, limited research has highlighted that garden ponds can support high numbers of non-native plants and animals (Patoka et al., 2017) and a lower macroinvertebrate diversity compared with non-urban ponds (Gaston et al., 2005; Hill & Wood, 2014). However, Hill et al. (2021b) reported that while alpha diversity (taxonomic richness within individual ponds) was significantly lower in garden ponds compared with non-urban ponds, the maximum taxonomic richness recorded from an individual site observed among the garden ponds was comparable with the average diversity in non-urban ponds. Such evidence suggests that garden ponds could support comparable biodiversity with ponds in the wider landscape. Furthermore, private garden ponds can increase connectivity in the most urbanised areas where public ponds are absent (Thornhill, 2013), act as stepping stones between waterbodies and provide important habitat for species of specific conservation interest (e.g., Amphibians: Villasenor et al., 2017; Cayuela et al., 2020).

Previous research has highlighted the importance of considering ecological uniqueness in landscape-scale biodiversity and conservation research, demonstrating that ponds with high ecological uniqueness often make a large contribution to the regional species pool (despite themselves typically supporting low taxonomic richness) and may warrant management or conservation (Hill et al., 2021a). The local contribution to beta-diversity (LCBD) metric allows for the ecological uniqueness (or dissimilarity for other sites) of each sample site to be quantified (Legendre & De Cáceres, 2013). However, the ecological uniqueness of individual sites within garden pond networks is yet to be tested. Given their high abundance and capacity to support freshwater biodiversity, garden ponds have considerable potential to offset wider urban biodiversity decline. This is being increasingly recognised by the media and environmental charities and trusts in the United Kingdom, who have widely encouraged the construction of garden ponds to support urban wildlife (RSPB, 2022; The Wildlife Trusts, 2022).

While the potential of garden ponds to significantly improve urban freshwater biodiversity is evident, their current limited biodiversity may reflect the original purpose of the garden pond (e.g., aesthetics or ornamental fish) or a lack of biodiversity-focused management. There is a large volume of information available to the public on how to create and manage a garden pond for wildlife (Bradbury, 2021; Steel, 2016; The Wildlife Trusts, 2019). However, there are few scientific studies examining garden pond management or the key information that underpins management, such as environmental factors influencing pond communities. Among ponds more widely, physicochemical and habitat properties (e.g., surface area, aquatic plant coverage, electrical conductivity and dissolved oxygen) have been shown to dominate over regional factors (pond connectivity and land use) in shaping the patterns of macroinvertebrate taxonomic richness and composition (Heino et al., 2017; Hill et al., 2019; Johansson et al., 2019). Noticeably, ponds with larger surface areas and high aquatic macrophyte richness/coverage are consistently associated with higher macroinvertebrate diversity, whereas surface water shading and high nutrient concentrations are correlated with low diversities (Kadoya et al., 2004; Oertli et al., 2002; Sayer et al., 2012; Thornhill et al., 2017). However, this has not been studied among garden pond networks. Consequently, there remains a pressing need to understand the environmental factors influencing freshwater taxonomic richness and composition within garden ponds, to help inform effective and ecologically meaningful management strategies that support biodiversity.

The majority of management recommendations available to garden pond owners are focussed on the individual pond scale (e.g., managing water levels and aquatic plants in ponds: RHS, 2022). However, many ecological processes occur at larger spatial and temporal scales (Hansson et al., 2012), and many species possess life cycle requirements that operate at broader scales than the individual garden (Goddard et al., 2010). Furthermore, the greatest contribution to freshwater biodiversity by ponds occurs at the landscape scale, reflecting high compositional heterogeneity among ponds that is driven by a wide range of local environmental gradients (Hill et al., 2019; Williams et al., 2004). As a result, garden pond management at local and network scales is needed to support aquatic biodiversity, although there has been minimal research examining landscape-scale garden pond management (but studies have examined landscape-scale management of terrestrial garden habitats: Egerer et al., 2019; Goddard et al., 2010; Shwartz et al., 2013).

Given the lack of quantitative assessments of the major factors influencing garden pond biodiversity, this study aims to identify the environmental factors influencing macroinvertebrate taxonomic richness and compositional variation (beta-diversity) among garden ponds. Based on species-environment associations reported among urban ponds and wetlands more widely (Goertzen & Suhling, 2013; Hassall et al., 2011; Heino et al., 2017; Oertli & Parris, 2019), it is hypothesised that (i) pond area and total plant richness will be positively associated with macroinvertebrate richness and abundance, (ii) non-native plant richness, percentage urban coverage, percentage surface water shaded and total phosphorus will be negatively associated with

macroinvertebrate richness and abundance and (iii) percentage surface water shaded and percentage urban land coverage will be positively associated with ecological uniqueness (high LCBD values). Management recommendations will be outlined to support freshwater biodiversity in garden ponds at both the local and landscape scales.

MATERIALS AND METHODS

Site selection

A total of 30 garden ponds were selected for study in autumn 2009. Garden pond sites were located over an area of approximately 8 km², the majority of which were located in suburban areas of the town of Abingdon, Oxfordshire, UK (Figure 1). One garden pond site was located in a garden approximately 3 km outside of Abingdon and another pond was located in school grounds (the surroundings of this pond—lawns, buildings and scattered trees—were similar to the domestic garden ponds used in this study and retained here for analysis; Figure 1). Abingdon has an average annual precipitation of 681 mm, and an average annual minimum temperature and an average annual maximum temperature of 7.12 and 15.02°C, respectively (1991–2020, UK Meteorological Office, 2022). The study sites comprise a broad spectrum of garden ponds including those managed for (1) predominantly biodiversity purposes by wildlife enthusiasts and (2) ornamental fish and amenity purposes. The garden ponds studied were typically small (0.6–20 m²), often

artificially lined and surrounded by lawns, and ornamental shrubbery and plants.

Environmental data collection

At each garden pond site, water depth (m), silt depth (m), altitude (m.a.s.l) and surface area (m²) were recorded. A visual estimation of the percentage of pond water shaded by overhanging trees and vegetation (shading) was recorded. The total number of aquatic submerged, floating and emergent plant species, and the total number of non-native aquatic plant species in each garden pond were quantified in situ using UK identification keys. Electrical conductivity and pH were recorded from each garden pond site using standard portable meters. Nitrogen and phosphorus, measured as NO₃-N, and Total Phosphorus were determined using standard laboratory procedures (determined by digesting and spectrophotometry using JENWAY 7315; Bibby Scientific Limited, UK); the accuracy was ± 5 ug/L for TP; ± 20 ug/L for NO₃-N). Fish intensity was recorded based on a visual estimation of the abundance of fish in each garden pond (based on a semi-quantitative scale spanning 0–5: 0 = no fish present, 5 = very high fish abundance). Pond connectivity (the number of other waterbodies within 500 m of each focal garden pond) was recorded using aerial imagery from the year macroinvertebrates were sampled (2009: Google Earth, 2021). The percentage of urban land (impervious surfaces) coverage within a 250 m buffer of each pond site was calculated. Urban land use information was derived from the

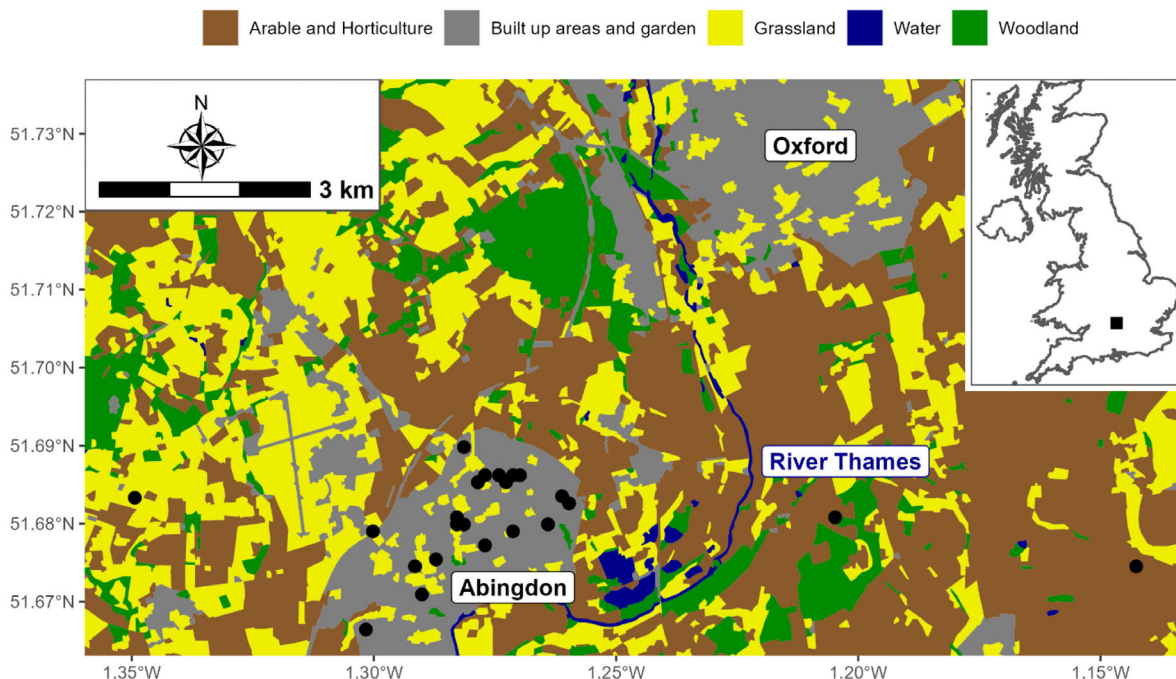


FIGURE 1 Location of the 30 surveyed garden ponds in Oxfordshire, and their location in relation to the UK (inset). Land cover from the Centre for Ecology and Hydrology 2007 land cover map (Morton et al., 2014), with classifications being grouped into one of five categories presented regionally based on classes outlined in <https://nrfa.ceh.ac.uk/content/land-use>.

Centre for Ecology and Hydrology 2007 land cover map (Morton et al., 2014).

Macroinvertebrate data collection

Aquatic macroinvertebrates were sampled from the garden ponds following the UK National Pond Survey procedure (Biggs et al., 1998). Garden ponds were sampled for a total of 3 min using a sweep technique with a 30 cm × 30 cm pond hand net (1 mm mesh). Discrete mesohabitats (e.g., submerged vegetation, woody debris and open water) were identified within each garden pond, and the 3-min sampling time was divided equally between individual mesohabitats (Hill et al., 2021b). Macroinvertebrate taxa that could confidently be identified to species level live were identified during sample sorting in situ (e.g., Hemiptera, aquatic Coleoptera and distinctive molluscs), with all other macroinvertebrate taxa preserved in 70% industrial methylated spirits and returned to the laboratory for identification. Wherever possible, macroinvertebrate identification was undertaken to the lowest taxonomic resolution (species or genus); however, Diptera were identified to family level, and Oligochaeta was recorded as such.

Statistical analysis

Taxa richness and abundance were defined as the number of macroinvertebrate taxa and individuals recorded from each pond site, respectively. Total beta-diversity of the garden pond macroinvertebrate community dataset and the contribution of richness difference (nestedness) and species replacement (turnover) to total beta-diversity were calculated (based on the Baselga family, Jaccard-based indices) using the *beta.div.comp* in the *adespatial* package (Dray et al., 2021). Species replacement reflects the turnover of taxa from one site to another, whereas richness difference reflects how communities differ from each other in their taxonomic richness (Legendre, 2014). For example, communities in taxa poor sites represent subsets of the communities in taxa rich sites (nestedness: Hill et al., 2017). The local contribution to beta-diversity (LCBD) for each garden pond site was derived using the *beta.div* function in the *adespatial* package (Dray et al., 2021). LCBD partitions the total beta-diversity of a study site into individual site contributions, demonstrating the ecological uniqueness of each garden pond site (Hill et al., 2021a). Random, independent permutations within the macroinvertebrate community matrix were used to assess the statistical significance of individual LCBD values (Legendre & De Cáceres, 2013). LCBD can be partitioned into the individual site contribution of the species replacement (turnover— $_{\text{Repl}}\text{LCBD}$) and richness difference (nestedness— $_{\text{RichDiff}}\text{LCBD}$) components (Legendre, 2014), to identify which was contributing most to the LCBD in each site.

Prior to regression-based analysis, environmental variables were examined for multicollinearity using variance inflation factor (VIF) analysis via the *vif* function in the *car* package (Fox et al., 2021). For this, the environmental variable with the highest VIF value was iteratively

removed until all values were <3. Furthermore, to examine the spatial autocorrelation of the macroinvertebrate community structure, LCBD, $_{\text{Repl}}\text{LCBD}$ and $_{\text{RichDiff}}\text{LCBD}$, correlograms (based on Moran I statistics) were constructed, using the *correlog* function in the *pgirmess* package.

After multicollinearity checks, four variables (connectivity, silt depth, depth and nitrate) were removed from subsequent analyses (see Table S2 for the final VIF scores). Subsequently, the response of taxonomic richness, abundance and LCBD (dependent variables) to the effect of each remaining environmental variable (independent variables: surface area, total plant richness, non-native plant richness, percentage surface water shaded, conductivity, total phosphorus, turbidity, pH, fish intensity and percentage urban coverage within a 250 m buffer) was initially examined via separate sets of statistical models, each testing a unique dependent–independent pairwise relationship ($n = 20$: 2 dependent variables × 10 independent variables). Each statistical set comprised four regression models, whereby the effects of each environmental variable were modelled via linear, quadratic, exponential and logarithmic statistical functions (Fornarioli et al., 2019). The optimal statistical function for each environmental variable affecting each dependent variable was identified using the model possessing the lowest AIC. This statistical procedure was performed to identify the optimal relationship between each dependent–independent variable paired combination, which was necessary given that previous research has indicated that taxonomic richness, abundance and LCBD values respond linearly and non-linearly to different environmental parameters (Hill et al., 2021a). Final regression models were then constructed for taxonomic richness and LCBD values by testing the additive effects of all 10 independent variables, each modelled using its optimal statistical function (linear, quadratic, exponential or logarithmic). The significance (p value) of each final regression model and the amount of statistical variation explained (adjusted R^2) were calculated.

A comparable regression-based approach was undertaken to examine the association between LCBD (dependent variable) and $_{\text{Repl}}\text{LCBD}$, $_{\text{RichDiff}}\text{LCBD}$ and taxonomic richness (independent variables). For this, three statistical sets corresponding to each individual independent variable ($_{\text{Repl}}\text{LCBD}$, $_{\text{RichDiff}}\text{LCBD}$ and taxonomic richness) were explored in relation to LCBD. Each of these sets modelled the independent variable effects on LCBD via four functions (linear, exponential, logarithmic and exponential). The optimal structure was identified as the regression model possessing the lowest AIC value, and the significance (p value) and amount of statistical variation (adjusted R^2) explained by these models were quantified. All analyses were undertaken in the R environment (R Core Team, 2021).

RESULTS

Taxonomic richness, abundance, LCBD, $_{\text{Repl}}\text{LCBD}$ and $_{\text{RichDiff}}\text{LCBD}$ values among garden ponds

In total, 99 macroinvertebrate taxa and 20,364 individuals from 45 families and 15 orders were recorded from the 30 garden ponds. Coleoptera (30 taxa), Diptera (12), Hemiptera (12) and Gastropoda (10) comprised the

greatest number of taxa from the sites surveyed (Figure 2). The most abundant taxa were *Cloeon dipterum* (4904), *Asellus aquaticus* (4616 individuals), *Crangonyx pseudogracilis* (2279 individuals) and the family Chironomidae (1384 individuals). The macroinvertebrate taxa most widely distributed across the garden pond sites were *A. aquaticus* (Isopoda: Asellidae, 23 ponds), Chironomidae (20 ponds), Oligochaeta (17 ponds), *C. dipterum* (Ephemeroptera: Baetidae, 16 ponds), *Pyrrhosoma nymphula* (Odonata: Coenagrionidae, 14 ponds) and *C. pseudogracilis* (Amphipoda: Gammaridae, 14 ponds). Of the 99 taxa recorded, 56 (57%) were only recorded in one or two garden ponds. At an alpha scale, garden ponds supported a mean of 12 (min: 1 and max: 35) macroinvertebrate taxa.

Most of the variation (Jaccards index: 0.43) in macroinvertebrate community composition was explained by species replacement (0.34: 78.9%), rather than richness difference (0.090: 21.1%). When total

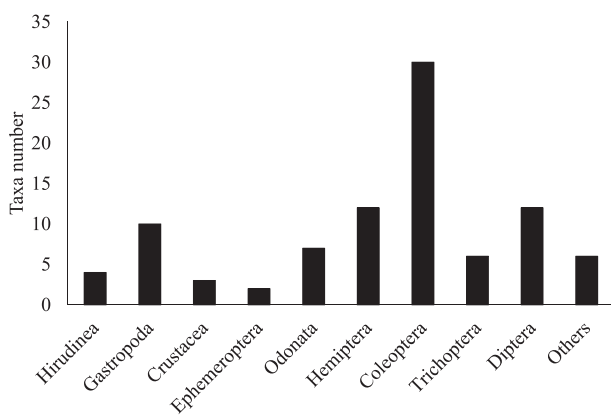


FIGURE 2 Total number of macroinvertebrate taxa recorded within the surveyed garden ponds for selected macroinvertebrate groups.

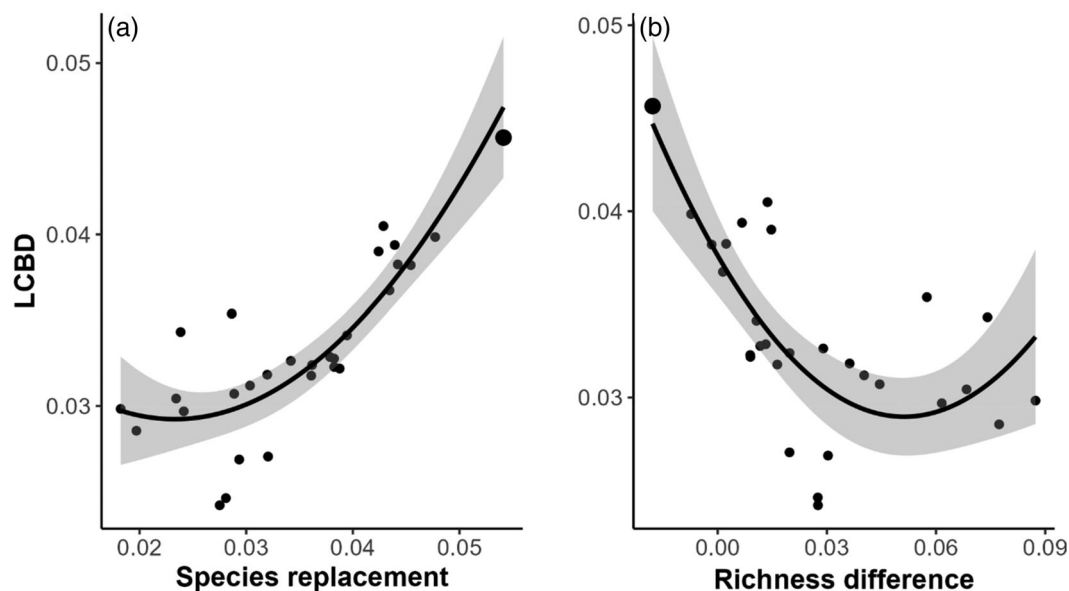


FIGURE 3 Relationship between local contribution to beta diversity (LCBD) and (a) the species replacement component of LCBD (b) the richness difference component of LCBD among the 30 surveyed garden ponds. Significant LCBD site is presented in bold. Grey shading represents the 95% confidence interval.

beta-diversity among the studied garden ponds was partitioned into individual site contributions, only one pond (LCBD: 0.05) was recorded to significantly ($p < 0.001$) contribute to total beta-diversity. A significant positive association was demonstrated between the LCBD and $_{\text{Repl}}\text{LCBD}$ values (adj. $R^2 = 0.73$, $F = 37.9$, $p < 0.010$ —quadratic function), whereas a significant negative association was recorded between the LCBD and $_{\text{RichDiff}}\text{LCBD}$ values (adj. $R^2 = 0.50$, $F = 15.0$, $p < 0.010$ —quadratic function: Figure 3). The high or significant LCBD values recorded the high species replacement and low richness difference values (Figure 3). The five ponds with the highest LCBD values supported eight taxa (*Gyraulus laevis*, *Hydroporus discretus*, Corixidae nymph, *Hesperocorixa moesta*, *Velia caprai*, *Limnephilus extricatus*, *Mystacides azurea* and Ceratopogonidae) that were not recorded from any other ponds. A negative association was recorded between LCBD and taxonomic richness among the garden ponds studied (Figure 4), although this was not statistically significant (adj. $R^2 = 0.05$, $F = 2.48$, $p = 0.126$ —logarithmic function). However, $_{\text{Repl}}\text{LCBD}$ demonstrated a significant negative association (adj. $R^2 = 0.19$, $F = 7.76$, $p < 0.010$ —quadratic function) with taxonomic richness, whereas $_{\text{RichDiff}}\text{LCBD}$ recorded a significant overall positive association with taxonomic richness (adj. $R^2 = 0.43$, $F = 11.64$, $p < 0.001$ —quadratic function: Figure S1).

Relationship among taxonomic richness, LCBD and environmental variables among the surveyed garden ponds

Preliminary analyses indicated that (1) there was no spatial autocorrelation (Moran's statistic) among macroinvertebrate communities, LCBD, $_{\text{Repl}}\text{LCBD}$ and $_{\text{Richdiff}}\text{LCBD}$ (Figure S2 and Table S1); (2) four variables (silt depth, water depth, nitrate and connectivity) needed to

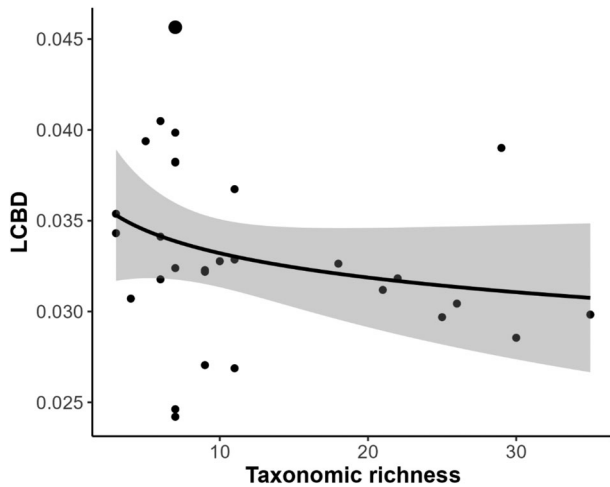


FIGURE 4 Relationship between the local contribution to beta diversity (LCBD) and macroinvertebrate taxonomic richness among the surveyed garden ponds. Significant LCBD sites are presented in bold. Grey shading represents the 95% confidence interval.

be removed to satisfy multicollinearity, resulting in 10 variables used in the final analysis (Table S2); and (3) values of the environmental variables retained were highly heterogeneous among garden ponds (Table 1). The final regression model for taxonomic richness explained 76% of the statistical variation (adj. $R^2 = 0.76$, $F = 7.76$, $p < 0.001$). Surface area, total plant richness and non-native plant richness were positively associated with taxonomic richness (Table 2; Figure 5). Conductivity displayed a negative association with taxonomic richness (Figure 5), although a single garden pond with a high conductivity value ($581 \mu\text{S cm}^{-1}$) recorded the second highest taxonomic richness (30 taxa). The final regression model of the association between macroinvertebrate abundance and environmental variables among the garden ponds explained 19% of the statistical variation (adj. $R^2 = 0.19$, $F = 1.51$, $p = 0.200$). Conductivity was significantly negatively associated with macroinvertebrate abundance (Table 2 and Figure 6). No environmental variables displayed a significant association with LCBD.

DISCUSSION

Environmental correlates of macroinvertebrate richness and abundance

In recent years, there has been increasing interest in garden pond ecosystems, with research indicating the biodiversity potential of garden ponds for wider urban ecology (Gaston et al., 2005; Hill et al., 2021b). However, evidence-based management strategies that support or enhance freshwater biodiversity in garden ponds are largely missing. This study demonstrated a positive association between taxonomic richness versus surface area and total plant richness (accept Hypothesis i). These variables have been recorded as key predictors of taxonomic richness in several previous pond studies

TABLE 1 Summary table of environmental characteristics for the surveyed garden ponds.

	Surface area (m^2)	Depth (cm)	Total plant richness	Non-native plant rich	SWS (%)	Conductivity ($\mu\text{S cm}^{-1}$)	TP	Nitrate ($\text{NO}_3\text{-N}$)	Turbidity	pH	Fish intensity	Urban cover (%)	Connectivity	Taxonomic richness
Mean	5	27.36	6.83	0.9	18.3	337.53	1.36	0.38	6.88	8.04	1.11	83.91	4.17	11.97
Median	3	24.1	6	1	0	319.5	0.38	0.29	4.15	7.9	0	97.36	5	8
Std. error	1	3.30	0.77	0.16	5.63	28.67	0.73	0.059	1.61	0.11	0.32	5.28	0.38	1.67
Min	0.6	5.2	1	0	0	57	0.02	0.21	1	6.84	0	0	0	1
Max	20	78	18	3	100	699	21.9	1.85	46	9.58	5	100	7	35

Abbreviations: SWS, pond surface area shaded; TP, total phosphorus.

TABLE 2 Significant environmental predictors of taxonomic richness for the studied garden ponds.

	Variable	F value	p value	Directional response
Taxa richness	Area (log)	43.04	<0.001	+
	Plant richness (linear)	4.25	0.05	+
	Non-native plant richness (log)	5.39	<0.05	+
	Conductivity (quadratic)	15.41	<0.01	-
Abundance	Conductivity (log)	5.41	<0.05	-

Note: For each significant environmental variable, the statistical function is presented in parenthesis.

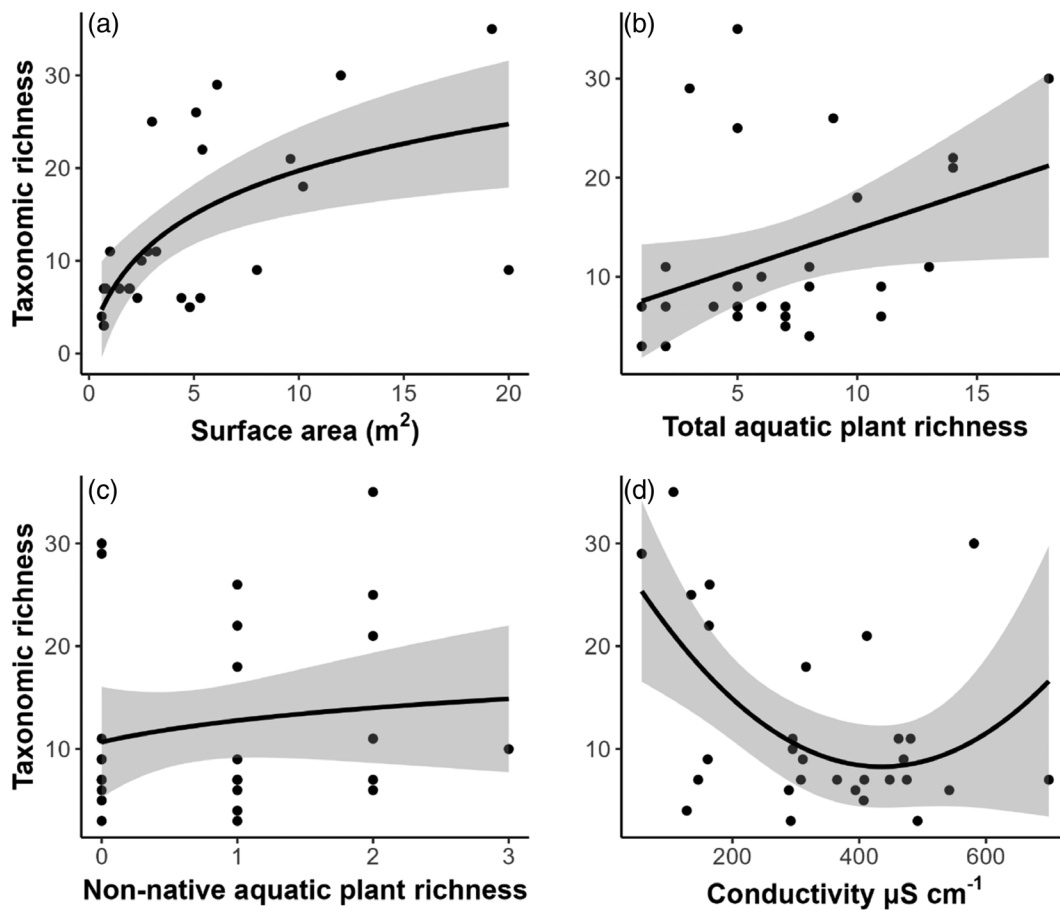


FIGURE 5 Relationship between taxonomic richness and significant environmental predictors: surface area (a), total plant richness (b), non-native plant richness (c) and conductivity (d). Grey shading represents the 95% confidence interval.

(Hassall et al., 2011; Hill et al., 2019), suggesting that they may be key variables governing macroinvertebrate biodiversity patterns in pond networks. ‘Area effects’ have been widely recorded across a range of freshwater and terrestrial habitats (Liu, et al., 2019; MacArthur & Wilson, 1967), and the positive association between garden pond size and taxonomic richness recorded among garden ponds in this study supports the majority of other studies that have considered pond size and taxonomic richness in the wider landscape (Hassall et al., 2011; Kadoya et al., 2004; Oertli et al., 2002). Increasing the surface area of small garden ponds in this study (median: 3 m²) would provide more habitat space for macroinvertebrates to inhabit and would likely yield

a strong positive effect on macroinvertebrate richness. However, Oertli et al. (2002) noted that at the landscape scale, a network of smaller ponds may support a greater taxonomic richness than a single large pond of equivalent area. We, therefore, acknowledge the ecological importance of having a range of different pond sizes/areas in the landscape and that the creation of a limited number of large ponds should not be at the expense of other smaller ponds in the landscape.

The positive association between total plant richness and macroinvertebrate taxonomic richness (supporting Hypothesis i) among the garden ponds in this study has been widely reported within pond habitats (e.g., Fontanarrosa et al., 2013; Hassall et al., 2011); this likely

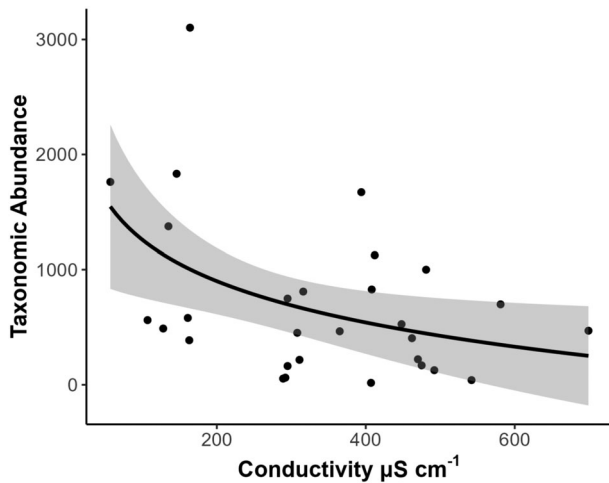


FIGURE 6 Relationship between macroinvertebrate abundance and conductivity. Grey shading represents the 95% confidence interval.

reflects the increased habitat complexity, food resources and oviposition sites required by different taxonomic groups (Heino et al., 2017). Furthermore, increased aquatic plant species richness may also provide sites of shelter and refuge from predation by fish, which can inhabit garden ponds in high densities (Hill & Wood, 2014). There was also a positive association between non-native plant richness and macroinvertebrate taxonomic richness (partially reject Hypothesis ii), most likely reflecting the fact that non-native plants likely provide similar ecological benefits to native plant species. Many non-native plants are widely sold in horticultural shops and may be chosen by garden pond owners ahead of native plants for their aesthetic value (Novák et al., 2022; Patoka et al., 2017). While the results indicate that aquatic macroinvertebrates will utilise non-native aquatic plants in garden ponds, there is an increased risk of biological invasion from the sale/purchase of problematic non-native aquatic plants (Maki & Galatowitsch, 2004; van Kleunen et al., 2018) and the unintentional transportation of other species such as bivalves and insect larvae, which may be attached to the plants (Patoka & Patoková, 2021). As a result, the use of native plants in garden ponds should be encouraged to support overall freshwater biodiversity.

Taxonomic richness and abundance broadly displayed a negative association with conductivity. Such trends are in keeping with previous studies (Johnson et al., 2013; Reyne et al., 2021) and suggest that high conductivities may selectively remove sensitive taxa from the garden ponds. For example, elevated conductivity has been demonstrated to inhibit the growth and development of larval mayflies (Johnson et al., 2013; Johnson et al., 2015). In addition, conductivity can be a good proxy for pollution levels (Meland et al., 2020), and the low taxonomic richness and abundance recorded may reflect increased nutrient loading in garden ponds, potentially from fish food, or soils/potting compost from ornamental aquatic plants. It should be noted that our findings showed an increase in taxonomic richness at the highest conductivity values, which appeared to be driven by a small number of data points (residual plots indicated these were not

outliers or influential points). It is unlikely that notably high conductivity levels can facilitate ecological improvements, but these findings suggest that the negative impacts of high conductivity levels can be context-specific. For instance, this association may be determined by the species pools present that are governed by a wider array of biological controls (e.g., biotic interactions) and environmental conditions. For instance, Meland et al. (2020) reported a positive association between taxonomic richness and conductivity in stormwater ponds in south-east Norway, which was attributed to the dominance of generalist taxa, whereas other studies have recorded no significant association between macroinvertebrate richness and conductivity (Hassall et al., 2011; Nicolet et al., 2004; Oertli et al., 2008) in ponds.

Interestingly, there was no effect of urban land cover on taxonomic richness among garden ponds (partially reject Hypothesis ii), which supports the findings of previous studies reporting no association between freshwater macroinvertebrates in ponds and urban land cover (Noble and Hassall, 2015; Hill et al., 2017). However, the association between urban land-use and pond biodiversity is often highly variable, with several previous studies reporting these variables being negatively associated (Heino et al., 2017), whereas others have reported higher richness in urban ponds compared with agricultural ponds (Goertzen & Suhling, 2019). The low statistical detectable influence of urban land cover on garden ponds may be due to such waterbodies being surrounded by green spaces (e.g., trees and hedgerows), which allows many species to complete the terrestrial phase of their life cycles (e.g., feeding and mating). The presence of green spaces within and around gardens may facilitate dispersal among freshwater habitats and attract more ovipositing taxa to garden ponds (Heino et al., 2017). Given the green buffer around garden ponds, they may be more resilient to anthropogenic disturbance and provide suitable stepping stones for macroinvertebrates through the urban matrix (Thornhill et al., 2018). Results from this study indicate that the effects of physicochemical variables on macroinvertebrate communities in garden ponds may override the effects of urban land cover. However, further research is needed as there have been few studies examining the environmental predictors of garden pond diversity. In particular, the lack of association between taxonomic richness and urban land cover in a 250 m buffer indicates a need to examine finer resolution land-use information, which may be of relevance to taxa inhabiting small garden ponds (Novikmec et al., 2016).

No effect of fish intensity on macroinvertebrate richness was also recorded among the 30 ponds studied, despite previous research demonstrating that high densities of fish can reduce macroinvertebrate diversity (Angélibert et al., 2004; Diehl, 1992; Fairchild et al., 2000), or in some cases benefitting particular macroinvertebrate groups (e.g., water mites and water bugs: Nieoczym et al., 2023). The lack of association in this study may be due to low fish intensities across the studied garden ponds (only one garden pond recorded the highest fish intensity score) or the presence of aquatic plants reducing fish predation (Wood et al., 2001). The limited fish intensity gradient makes it challenging to ascertain the overall effect of fish in garden ponds. At the low-moderate levels of fish intensity recorded in this study, it is clear that fish did not reduce macroinvertebrate richness

(Harper et al., 2021; Stefanoudis et al., 2017). However, it should also be noted that the visual, semi-quantitative methods used here to calculate fish intensity may not provide an accurate enough measure of the effect of fish and have contributed to the absence of association recorded in this study.

It is likely that other environmental variables not studied here will be important in driving taxonomic richness, abundance and, particularly, ecological uniqueness given that none of the environmental variables were associated with LCBD (reject Hypothesis iii). For example, several previous studies have found the coverage of aquatic plants to be the main predictor of taxonomic richness, ecological uniqueness and composition across urban ponds (Hassall et al., 2011; Heino et al., 2017; Hill et al., 2019; Hill et al., 2021; Solimini et al., 2010). Aquatic plants oxygenate pond habitats, stabilise benthic sediments, and provide habitat heterogeneity, oviposition sites and food for aquatic macroinvertebrates, and a site of refuge from predation (Diehl & Kornijów, 1998; Heino, 2009; Walker et al., 2013). In addition, pond connectivity was not included in the final analysis but has been reported to be an important factor in structuring macroinvertebrate communities among urban ponds (Hyseni et al., 2021). Additional research is needed that quantifies aquatic macroinvertebrate richness, composition and uniqueness, and considers a more comprehensive set of environmental and spatial variables, over multiple garden pond networks.

Implications for garden pond management

Gardens have been demonstrated to be a critically important component of the urban ecological landscape (Goddard et al., 2010) and comprise a considerable portion of urban blue space (Davies et al., 2009). Current management practices for garden ponds are highly variable, which reflects the wide range of primary functions of garden ponds, including aesthetic purposes, fish keeping, or wildlife conservation more generally. Where guidance is provided for the establishment and management of garden ponds for wildlife, scientific studies assessing the effectiveness of these strategies are currently largely missing. Based on the findings of this study, several management recommendations can be made to support macroinvertebrates within individual garden ponds:

- Wherever possible, ensure the garden pond is as large as possible, ideally $>5\text{ m}^2$. It is fully recognised that there are likely to be size constraints on pond size in domestic garden, but maximising the size of the ponds will help ensure that there is space for a range of habitat types and environmental conditions. However, prior to the creation of a garden pond or management to increase its size, health and safety considerations are required.
- Ensure that there is a variety of native aquatic plant species present in the pond, to provide habitat complexity, food resources, oviposition sites and refuge sites for a wide range of aquatic macroinvertebrates.
- Maintain low, or reduce, conductivity levels ($<350\ \mu\text{S}$). Topping up garden ponds with rainwater will help manage conductivity levels.

Lower conductivity levels will enable environmentally sensitive species to persist in the garden ponds. Given that conductivity may also act as a proxy for pollution, maintaining vegetation buffer strips around each pond may help reduce pollutant inputs (e.g., salts, pesticides and nutrients) to the pond (Vought et al., 1995).

Garden ponds are often managed on an individual basis (reflecting their private ownership), despite previous research demonstrating that ponds contribute most to biodiversity at a landscape scale, driven by their wide environmental gradients (Davies et al., 2008). The local management practices suggested here should be considered within a landscape context, to ensure that a wide gradient of environmental conditions exist across the pond network, and not all ponds are managed in an identical manner. In this study, the high ecological uniqueness (high LCBD values) of ponds was almost entirely explained by species replacement, indicating that ponds with high ecological uniqueness supported macroinvertebrate taxa that were not recorded in other ponds, thus contributing to the regional species pool. Therefore, to maximise the macroinvertebrate regional species pool, ponds with high ecological uniqueness need to be managed and conserved alongside sites of high taxonomic richness (Hill et al. 2021a). The establishment of community groups of garden pond owners to co-ordinate management of their ponds at a landscape scale would enable garden pond owners to improve their condition and ensure there is environmental heterogeneity to support garden ponds across the landscape with high taxonomic richness and ecological uniqueness.

CONCLUSION

With increasing urban development and the loss of larger urban green and blue spaces, the potential importance of garden ponds to support biodiversity has received increasing attention from researchers and the wider public. However, the establishment of evidence-based management strategies to maximise biodiversity in ponds is still largely missing. This study demonstrates that both local and landscape-scale measures are required to ensure that macroinvertebrate biodiversity among garden ponds can be maintained (Goddard et al., 2010). Furthermore, there is a need to co-ordinate garden pond management within the wider urban freshwater network, as they may make up the dominant freshwater habitat in urban landscapes and could improve connectivity among freshwater patches through an urban matrix. It is evident that garden ponds have considerable potential to support biodiversity, and by including garden ponds in wider freshwater management strategies, freshwater biodiversity may be better supported in urban landscapes.

AUTHOR CONTRIBUTIONS

Matthew J. Hill: Conceptualization; methodology; formal analysis; visualization; writing – review and editing; writing – original draft.
Paul J. Wood: Writing – review and editing; writing – original draft; conceptualization.
James C. White: Formal analysis; methodology;

writing – original draft; writing – review and editing. **Ian Thornhill:** Writing – review and editing. **Win Fairchild:** Investigation. **Penny Williams:** Investigation; writing – review and editing. **Pascale Nicolet:** Investigation; writing – review and editing. **Jeremy Biggs:** Investigation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

Figure S1. Relationship between taxonomic richness and $_{\text{Repl}}\text{LCBD}$ (a) and $_{\text{RichDiff}}\text{LCBD}$ (b).

Figure S2. Moran's I statistics for garden pond taxonomic diversity (a), LCBD values (b), $_{\text{Repl}}\text{LCBD}$ values (c), and $_{\text{RichDiff}}\text{LCBD}$ values (d), distance class are in kilometers.

Table S1. Moran I statistics (and significance values) for garden pond taxonomic diversity (a), LCBD values (b), $_{\text{Repl}}\text{LCBD}$ values (c), and $_{\text{RichDiff}}\text{LCBD}$ values (d), distance class are in kilometers.

Table S2. Variance Inflation Factor (VIF) Values for environmental parameters, once correlated variables (conductivity, connectivity, silt depth, depth and nitrate) were removed. SWS = surface water shaded, Cond = conductivity, TP = total phosphorus.

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