



The importance of blue and green landscape connectivity for biodiversity in urban ponds

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Abstract

The negative impact of urbanization on biodiversity can be buffered by blue (e.g., rivers, ponds) and green (e.g., parks, forests) spaces. However, to prevent biodiversity loss and reduce the risk of local extinctions, blue and green spaces need to be connected by corridors, so that organisms may disperse between sites. Landscape connectivity affects local community composition and metacommunity dynamics by facilitating dispersal. The goal of this study was to test the relative roles of pond environmental properties, spatial structure, and functional landscape connectivity on differentiation of invertebrate metacommunities in urban ponds in the city of Stockholm, Sweden. We characterized functional connectivity as blue connectivity (distance to water bodies), green connectivity (land use), and combined blue-green connectivity. We estimated functional connectivity by using electrical circuit theory to identify dispersal corridors. Interestingly, while circuit theory is often used in single-taxon studies, this method has rarely been applied to multiple taxa forming a metacommunity, as we have done in this study. Indeed, our study contributes toward an increased focus on the role of dispersal at the metacommunity level. We determined that functional connectivity was the most important factor in explaining community differentiation, with the local environment contributing comparatively little, and spatial structure the least. Combined blue-green functional connectivity had a major influence on structuring urban pond communities, explaining 7.8% of the variance in community composition across ponds. Furthermore, we found that increased functional connectivity was associated with an increase in the number of species. In summary, our results suggest that to preserve biodiversity in urban ponds, it is important to enhance functional connectivity, and that open green spaces could augment blue corridors in maintaining functional connectivity in urban pond metacommunities. To generalize these findings, future urban biodiversity studies should compare how functional connectivity affects metacommunities across multiple major cities.

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Introduction

Landscape connectivity can be defined as the effect that the landscape has on “movement along resource patches” (Taylor, Fahrig, Henein & Merriam, 1999). In fragmented landscapes, organisms survive in habitat patches that are linked by dispersal (Leibold et al., 2004). Therefore, the deterioration of landscape connectivity has negative consequences for biodiversity conservation (Hanski, 2005). Habitat loss and fragmentation are a major threat to biodiversity (Tilman et al., 2017). Thus, optimizing habitat patch connectivity, or landscape connectivity, is one way to reduce the negative impact of habitat loss and fragmentation. However, to estimate landscape connectivity, we need to understand how landscape features are configured. This leads to two basic estimates of connectivity: structural and functional. Structural connectivity is the physical (Euclidean) distance between patches, irrespective of how organisms move across the landscape (Dunning, Danielson & Pulliam, 1999; Tischendorf & Fahrig, 2000). Functional connectivity, instead, takes movement behavior into account by estimating the route between patches which are suitable for dispersal (Tischendorf & Fahrig, 2000). Studies investigating landscape connectivity provide useful information for landscape managers on how to optimize patch connectivity and thus decrease the negative effects of habitat loss on biodiversity (e.g., Mitchell, Bennett & Gonzalez, 2013).

One factor that causes habitat loss is urbanization. It has been estimated that 55% of the world's population currently lives in urban areas and, by 2030, this percentage is predicted to increase to 68% (United Nations, 2018). The negative impact of urbanization on biodiversity can be buffered by green spaces, which can harbor high levels of biodiversity (e.g., Pautasso et al., 2011), and may benefit threatened species (Ives et al., 2016). Additionally, green spaces are beneficial to human health (Garrett et al., 2019; Gascon et al., 2016). However, to optimize biodiversity in urban green spaces, we need information on both local environmental variables and landscape connectivity.

In the last few decades, there has been an increased interest in blue spaces in urban areas (Oertli & Parris, 2019). Blue spaces include lakes, rivers, ponds, and other water bodies. Ponds are defined as water bodies with a surface area less than 5 ha (Oertli et al., 2005). Many artificial water bodies, including ponds, have been constructed in the last few decades (reviewed in Knapp, Schmauck & Zehndorf, 2019). Artificial ponds have served different purposes, such as water purification, esthetic value, as well as leisure activities (e.g., fishing). Studies have shown that pond biodiversity is determined by various environmental variables, including artificial surfaces in a pond's vicinity, pond area and depth, aquatic and terrestrial vegetation (Briers, 2014; Céréghino, Boix, Cauchie, Martens & Oertli, 2014; Goertzen & Suhling, 2013; Hassall, 2014; Heino et al., 2017b; Hill et al., 2018; Johansson et al., 2019). However, urban ponds remain less studied than urban streams, urging increased interest in

understanding the effects of urbanization on aquatic biodiversity (Gál, Szivák, Heino & Schmera, 2019).

Apart from local environmental variables, landscape connectivity affects variation in local community composition and metacommunity dynamics, via the role it plays in facilitating dispersal of organisms (Fahrig & Merriam, 1985; Hanski, 1999). Several proxies for dispersal have been proposed (J. Heino et al., 2017). Among these, Euclidean distance has been a classic measure of structural connectivity, which assumes that shorter distances allow for more exchange of individuals among patches (Fahrig & Merriam, 1985). Such studies have found spatially structured plant and bird distributions in urban areas (Schleicher, Biedermann & Kleyer, 2011; Shanahan, Miller, Possingham & Fuller, 2011). In contrast, Heino et al., 2017b found that species richness of aquatic invertebrates in city ponds was spatially independent. However, in heterogeneous landscapes, where suitable habitats are embedded in an unsuitable matrix, the shortest distance between two patches might not be the main dispersal route (CañedoArgüelles et al., 2015; Kärnä et al., 2015). In this case, dispersal routes through suitable habitat (i.e., functional connectivity) might better describe community similarities among ponds. Functional connectivity modeling techniques include least-cost path analysis, circuit theory and other graph models (reviewed by LaPoint, Balkenhol, Hale, Sadler & vanderRee, 2015). Though functional connectivity has been used to study connectivity of single species in urban areas (Balbi et al., 2018; Horta et al., 2018), few studies have used information on functional connectivity among city ponds at the metacommunity level.

Electrical circuit theory can be used to model functional connectivity by identifying habitat pathways or corridors facilitating the dispersal of organisms (McRae, Dickson, Keitt & Shah, 2008). Circuit theory treats landscapes as resistance surfaces, with individuals (or genes) moving across a landscape as electrons flow through a circuit (McRae et al., 2008). Areas with higher resistance to movement are assigned higher resistance values. For instance, roads are typically assigned high resistance values, as they represent a barrier to movement for most organisms. A resistance surface is a spatial layer that assigns a value to each landscape or environmental feature, with values representing the extent to which that feature impedes or facilitates connectivity for an organism (Spear, Balkenhol, Fortin, McRae & Scribner, 2010). To date, circuit theory has been used in many fields of study, including conservation science, ecology, epidemiology, and evolutionary biology (reviewed by Dickson et al., 2019). While there is an increasing number of efforts to describe functional connectivity for multiple taxa (Walpole et al. 2012; Koen et al. 2014; Pelletier et al. 2014; Leonard et al. 2016) including entire communities of animals (MoránOrdóñez et al., 2015) and plants (Thiele, Buchholz & Schirmel, 2018), circuit theory has rarely been applied to multiple taxa comprising a metacommunity.

Many terrestrial and aquatic taxa use riparian zones as dispersal routes (J. Heino et al., 2017). However, the

connectivity provided by these landscape features may be disrupted by urbanization and associated increases in artificial surfaces. Thus, in this study, we collected data from invertebrate metacommunities in urban ponds in Stockholm (Sweden), with the goal of assessing the effects of aquatic and terrestrial connectivity on metacommunity structure and species diversity. To do so, we aimed to disentangle the relative contributions to metacommunity structure (if present) of local environmental variables, landscape configuration, and connectivity facilitated by blue and green spaces. Furthermore, we aimed to understand how connectivity influences species diversity, independent of the effect of local pond environments. To quantify the role of connectivity, the intervening landscape was represented both in terms of structural and functional (blue and green) connectivity, with the latter modeled using the circuit theory approach. Knowledge of the importance of blue and green functional connectivity for biodiversity is important for landscape planners, because it will help them determine the necessary arrangement of blue and green spaces to maximize the conservation of urban biodiversity.

Materials and methods

Analytical framework

Our analytical framework included three steps: 1a) calculating dissimilarity among pond communities to use as the

multivariate response, 1b) identifying multivariate predictors summarizing local pond environments, 1c) identifying structural connectivity predictors, 1d) optimizing resistance surfaces and using them to set up functional connectivity predictors; 2) calculating the variance in community composition (i.e., community differentiation) attributable purely to the local environment versus structural or functional connectivity; 3a) classifying ponds based on local environmental characteristics and quantifying community composition and functional connectivity differences among pond classes; and 3b) assessing the relationship between functional connectivity and species diversity, and how this relationship may vary across pond classes.

To represent the local environment, we used: i) within-pond measurements such as water chemistry and macrophyte cover, and ii) land use variables (e.g., artificial surfaces, forests, etc.) for a 250-m radius around each pond. The estimates of landscape connectivity included: i) structural connectivity, and ii) blue and green functional connectivity. These estimates were determined by the spatial arrangement of ponds as well as landscape features facilitating between-pond dispersal.

Sampling

We sampled aquatic invertebrates in 80 ponds in Stockholm, Sweden. The extent of the study area covered the entire city. The city itself has ca. 900,000 inhabitants, with another 600,000 living in the suburbs of the Stockholm

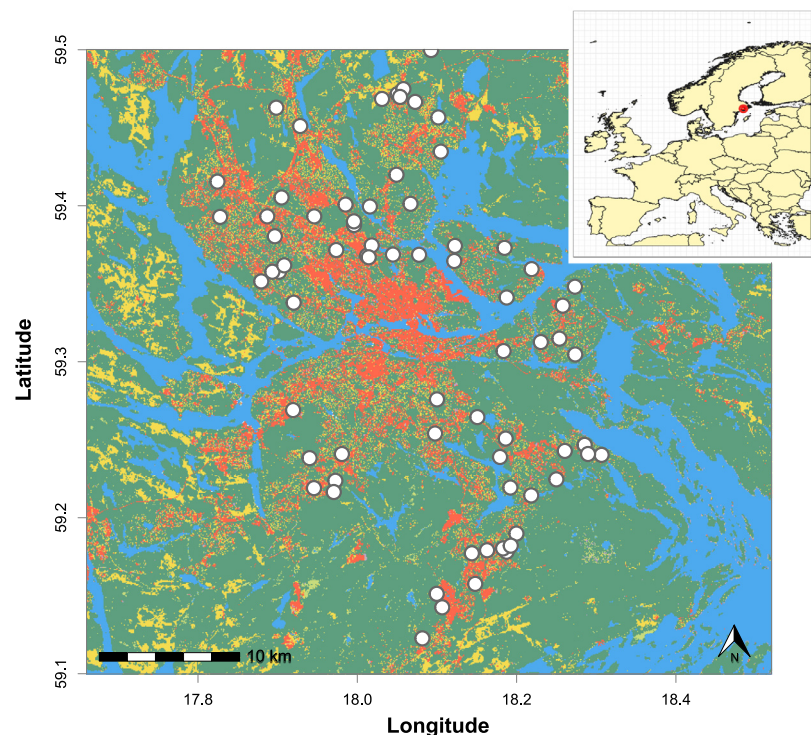


Fig. 1. Sampling of urban ponds in Stockholm. The red, green, and yellow colors represent artificial surfaces, forests, and grassland, respectively. The inset shows a map of Europe, with the red area representing the study area in the city of Stockholm and its suburbs.

metropolitan area. We defined ponds as natural or artificial water bodies with an area between 2 m² and 5 ha, with a hydroperiod of at least 4 consecutive months (Biggs, Williams, Whitfield, Nicolet & Weatherby, 2005). Our focus was on densely populated areas in the city. Therefore, ponds were selected based on maps as well as information provided by municipalities. All ponds were sampled in May–June 2019. While sampling was performed at 80 sites in the Stockholm metropolitan area, we removed sites for which we did not have a complete set of environmental measurements. The remaining 72 sites (Fig. 1) were included in all analyses.

The ponds were surveyed for aquatic life stages of the orders Odonata, Trichoptera (larvae), Coleoptera and Hemiptera (larvae and adults), as well as adult-stage freshwater snails (class Gastropoda). These invertebrates represent several assemblages (i.e., taxonomically related groups of species) as well as functional feeding groups, and may thus represent the overall biodiversity of aquatic fauna in the sampled pond habitats (but see Westgate, Tulloch, Barton, Pierson & Lindenmayer, 2017). The invertebrates were sampled using a bottom scoop net with a diameter of 20 cm and a mesh size of 1.5 mm. Six samples were taken in each pond at a depth of 20–30 cm. We did eight 1 m sweeps along the bottom alternating direction each time. These six samples covered all types of representative microhabitats along the shoreline (e.g., soft versus hard bottom, with and without vegetation). Samples were preserved in 70% ethanol and taken to the laboratory for taxonomic identification. Individuals that could not be identified at the species level were still included in the final analysis at the genus or family level.

Step 1a – dissimilarity among pond communities

The total number of taxa identified across all sampling sites was 152. After removing taxa that were only detected at a single site, we obtained a dataset with 96 taxa. The abundance matrix was Wisconsin double standardized (Bray & Curtis, 1957). A comparison of analysis results showed no substantial differences between the 152-taxon and 96-taxon datasets, and we therefore report the results of the 96-taxon dataset. The response variable was a matrix of pairwise Bray–Curtis dissimilarities (Bray & Curtis, 1957) between sampling sites. While the arcsine square root transformation has been applied in the past to improve the non-linearity of the Bray–Curtis dissimilarity matrix (Loucks, 1962), we used min-max normalization, as this method achieved better improvement.

Step 1b – local environment

The following within-pond measurements were taken for each pond: area (m²), maximum depth (m), pH, total phosphorus (TP; $\mu\text{g/L}$), total nitrogen (TN; mg/L), total organic carbon

(TOC; mg/L), and macrophyte cover. These variables have been shown to affect biodiversity in many ponds (e.g., Hassall, Hollinshead & Hull, 2011) and were therefore selected here. We used QGIS (QGIS Development Team, 2021) to estimate pond area in an automated way from terrain maps available through Lantmäteriet (The Swedish mapping, cadastral and land registration authority). Water depth was measured with a ruler in the deepest part of the pond. Water chemistry variables were sampled in May–June 2019 and analyzed in the laboratory at Uppsala University using standard methods. Macrophyte cover was estimated visually in August 2019 and scored on a scale of 0 to 10 (equivalent to 0–100%). Macrophyte cover was categorized into floating and emergent vegetation, as well as bushes and bare ground (i.e., surfaces with no vegetation) along the shore.

We used land use variables as an additional characterization of the local environment. The following land use variables were calculated for a 250-m radius around each pond: percentage of water, wetlands, “grassland” (i.e., grass, herbs, and bushy sclerophyllous vegetation), “forests” (i.e., deciduous and coniferous tree cover), “cultivated areas” (i.e., areas with arable land), “natural surfaces” (i.e., natural bare areas, including rocks, boulders, stones, and bare soils), and “artificial surfaces” (i.e., buildings, roads, sidewalks, parking lots, and other impervious surfaces). The land cover data were retrieved from <http://s2glc.cbk.waw.pl/>. The data were produced by applying automatic classification methodology to Sentinel-2 remote-sensed satellite images collected during the year 2017. The classification methodology was developed in the framework of the Sentinel-2 Global Land Cover (S2GLC) project (Malinowski et al., 2020). The S2GLC 2017 dataset was available at 10-meter resolution.

Within-pond measurements and land use variables together represented the “local environment” of each pond. To deal with multicollinearity (i.e., correlation among variables), we used principal component analysis (PCA) to transform the original variables into orthogonal (non-correlated) principal components. Additionally, as the original data were on different scales, we performed z-score standardization ($\mu = 0$, $\sigma = 1$) prior to PCA.

Step 1c – structural connectivity

To characterize structural connectivity (herein also referred to as spatial structure, or geography), we investigated whether neighboring local communities are more similar than more distant ones. We examined the spatial structure of local communities by applying Principal Coordinates analysis of Neighbor Matrices (PCNM) to Euclidean geographic distances. To obtain PCNM axes summarizing spatial structure, we used the *pcnm* function in the package ‘vegan’ (Oksanen et al., 2012) written for the R programming environment (R Core Team, 2021). We used a backward selection procedure to select a subset of PCNM axes (see the “Community differentiation” section for further details).

Step 1d – functional connectivity

To characterize functional connectivity, we first identified landscape features relevant to dispersal of organisms among urban ponds. Blue connectivity was estimated based on distance of urban ponds from other water bodies, while green connectivity was characterized as the amount of forests, grassland, and cultivated areas interspersed in an urban matrix. We then parameterized these features to represent strength of resistance to dispersal. Since parameterization of resistance surfaces is a key step, and to avoid the subjective nature of manually assigning resistance values to landscape features (reviewed by Zeller, McGarigal & Whiteley, 2012), we opted for an automated solution. We used the R package ‘ResistanceGA’ (Peterman, 2018), which takes advantage of the genetic algorithm approach to optimization, as implemented in the ‘GA’ package (Scrucca, 2013, 2017).

An ideal solution to resistance surface optimization is to simultaneously optimize multiple resistance surfaces and create a composite resistance surface. We parameterized both blue and green resistance surfaces, as well as a composite blue-green resistance surface. For blue resistance to movement, we used distance from water bodies computed using the ‘raster’ package (van Etten, 2013) in R. To calculate these distances, we first constructed a map of water bodies in the study area by combining lake and river subsets of terrain maps available through Lantmäteriet. The green resistance surface was estimated using the S2GLC land cover map, which included all land cover classes. To calculate current density maps and “resistance distance” matrices from these resistance surfaces, we used the Circuitscape algorithm implemented in the Julia programming language (Anantharaman, Hall, Shah & Edelman, 2019). R scripts used to parameterize resistance surfaces and Julia commands to obtain current density maps and resistance distances are available online at https://github.com/chazhyseni/pond_conn.

To represent functional connectivity in continuous space (i.e., dispersal corridors through which metacommunities are connected), we mapped electrical current densities, which reflect the number of times current flows through each point on the map. To model the effect of functional connectivity on community differentiation, we used resistance distances, which capture pairwise distances between ponds, thus reflecting resistance to movement across the intervening landscape. We performed a principal coordinates analysis (PCoA) to transform the resistance distance matrices to continuous orthogonal vectors, which were then used as predictors of community differentiation.

Step 2 – community differentiation

We used a multivariate approach to model the effect on community differentiation of between-pond differences in local environment and landscape connectivity. We performed distance-based redundancy analysis (db-RDA;

Legendre & Andersson, 1999) using the *capscale* function of the ‘vegan’ package. Then, to estimate the contributions of these predictors to community differentiation, we used the *varpart* function in ‘vegan’. We used the F-statistic with 9999 permutations for significance testing.

The predictors we used were ordination scores: PCA axes summarizing the local environment of each pond, PCNM axes for structural connectivity, and PCoA axes for blue, green, and composite blue-green functional connectivity. To avoid overfitting, we selected a subset of ordination scores. We modeled community differentiation separately for each set of predictors (environmental, spatial, blue connectivity, green connectivity, and blue-green connectivity). For each of these sets, we used a backward selection process, involving iterative removal of non-significant ordination scores ($\alpha = 0.05$) until all the remaining ordination scores were significant (R scripts available at https://github.com/chazhyseni/pond_conn). For each set of predictors, significance was determined using ANOVA, after adjusting for the main effects of the other predictors. Provided any PCNM axes contributed significantly to community differentiation, we performed db-RDA conditioned on geography (i.e., significant PCNM axes), with local environment (PCA axes) and connectivity (PCoA axes) as predictors.

Step 3a – pond classification

To determine how communities respond to interactions between functional connectivity and the local environment, we first used environmental variables to determine whether ponds included in this study could be clustered into different classes, and then we examined differences in connectivity within each pond class (if more than one). To classify ponds based on the local environment, we used the Louvain method (Blondel, Guillaume, Lambiotte & Lefebvre, 2008), as implemented in the Orange machine learning and data mining suite of Python scripts and visual programming (Demšar et al., 2013). The Louvain clustering algorithm was applied to the first 10 axes derived from the PCA of local environmental data (see above), which accounted for 87.5% of the total variation in the original data. We used 10 k-nearest neighbors (kNN). Next, we identified clusters by applying the Louvain algorithm to the kNN solution with the resolution parameter set to 3.

To visualize connectivity among ponds, we used the inverse of resistance distances to represent connectivity. To create a force-directed layout from these connectivity values, we applied the Fruchterman-Reingold algorithm (Fruchterman & Reingold, 1991), as implemented in the ‘qgraph’ package (Epskamp, Cramer, Waldorp, Schmittmann & Borsboom, 2012). The thickness of the edges in the resulting graph is proportional to the degree of connectivity. Ponds with lower connectivity values are located peripherally in the network. We used 500 iterations, after which the maximum displacement of each node becomes smaller, and a

layout is achieved in which the distance between nodes reflects the absolute edge weight between nodes.

We then examined differences in connectivity among pond classes. We used the *dist_groups* function of the ‘usedist’ package (Bittinger, 2020) in R to group connectivity values by pond and calculated the mean of connectivity of each pond with the other 71 ponds. To test for mean connectivity differences among pond classes (as defined by the local environment), we performed an ANOVA with a post-hoc comparison of group means using Tukey’s test. We also performed two-tailed pairwise t-tests, with p-values adjusted for multiple comparisons using the Benjamini and Hochberg (1995) method.

To characterize community composition patterns, for each class of ponds we calculated metrics (R scripts available at https://github.com/chazhyseni/pond_conn) measuring species richness (α and γ), diversity (H' : Shannon & Weaver, 1963; and J' : Pielou, 1966), and differentiation (β , dispersion, and FST). While γ denotes the total number of species in a pond class, we used the mean number of species across ponds in each class to represent α . We also used the mean for H' and J' . We calculated the β metric as $(\gamma/\alpha) - 1$. In addition to the β metric, we also measured differentiation by using multivariate dispersion (Anderson, Ellingsen & McArdle, 2006). Using the *betadisper* function of the ‘vegan’ package, we calculated dispersion in multivariate space as the mean of the difference of each pond from the centroid of its corresponding pond class. The F_{ST} metric—typically a measure of population differentiation due to genetic structure—was calculated based on Gilbert and Levine (2017). Here, the F_{ST} metric is a measure of the variance of relative species abundances among ponds within a class, expressed as a proportion of the total within-class variance. Classes that include ponds with more divergent relative abundances will have higher F_{ST} values.

Step 3b — association between connectivity and diversity

To understand how biodiversity in urban ponds responds to interactions between functional connectivity and the local environment, we investigated how the relationship between connectivity and species diversity varies by pond environment. For each pond class, we regressed both species richness (number of species in each pond) and evenness (Pielou’s J' , calculated for each pond) on blue-green connectivity. As a measure of connectivity, we used the mean of connectivity of each pond with all the other ponds (irrespective of pond class).

To visualize associations of any taxa with communities differentiated by connectivity and environment, we first ran db-RDA models constrained by combined sets of significant connectivity and environmental variables (see the “Community differentiation” section). Next, to visualize associations of taxa with specific communities differentiated by

connectivity, we performed db-RDA constrained by connectivity after conditioning on environment. Because significance of the sets of connectivity and environmental variables was determined in separate analyses, we performed backward selection again to determine if any of the combined variables were non-significant and needed to be removed. In both sets of db-RDA ordinations, we also examined whether any taxa were more likely to be found in a particular pond class. Finally, we used the *hotelling.test* function of the ‘Hotelling’ package (Curran, 2018) to perform pairwise comparisons of differences in multivariate means among pond classes.

Results

The local environment

Estimated pond size ranged from 20 m² to 6.7 ha. Only one pond was 6.7 ha, while the remaining ponds were smaller than 1.7 ha, with the median being 1000 m². Since the environmental data were normalized and PCA scores were used instead of the original variables, the outlier pond (6.7 ha) did not affect results and was therefore retained for downstream analyses. The median pH was 7.3. The median for TOC was 15.3 mg/L, while the median for TN and TP was 1.0 mg/L and 40.5 μ g/L, respectively. The environment surrounding the ponds (250-m radius) was characterized by forests (median = 38.0%), grassland (median = 21.7%), and artificial surfaces (median = 12.2%).

The first two PCA axes explained 32% of the variance in the original environmental variables (see Table 1). These two were the only PCs with significant contribution to community dissimilarity (see below). PC1 was most strongly correlated with pond nutrients (TOC, TN, and TP), showing negative correlation ranging from -0.43 (TP) to -0.49 (TN). PC2 was most strongly correlated with amount of forested area ($r = 0.46$). Additionally, it was negatively correlated with cultivated areas ($r = -0.37$) and artificial surfaces ($r = -0.36$).

Connectivity

The geographic distance between ponds ranged from 161 m to 42 km (mean of 16 km). Following resistance surface parameterization, blue resistance to movement (unitless) ranged from 1 to 1205, green resistance from 1 to 66,899, and the composite blue-green resistance from 1 to 463. Low resistance to movement was observed in or near water bodies in the blue resistance surface, while in the green resistance surface low resistance to movement was recorded for areas where vegetation was present, and high resistance in areas with artificial surfaces (Fig. 2). In the blue-green composite, locations near water, that were not dominated by artificial surfaces, generally had lower resistance values.

Table 1. Principal component analysis of local environmental variables. The table shows correlation of the original variables (rows) with principal components (PC). Only absolute values greater than 0.25 are shown. The bottom row shows the cumulative variance (in percent) that PCs explain in the original variables. Floating and emergent vegetation is abbreviated as “float. veg.” and “emerg. veg.,” natural and artificial surfaces as “nat. surf.” and “artif. surf.,” and cultivated areas as “cultiv. area.” TOC, TN, and TP are used for total organic carbon, total nitrogen, and total phosphorus.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17
Pond Area		0.28		0.38	0.28	0.27					0.45	0.29	0.43				
Pond Depth	0.27	0.28			0.35	0.26							−0.58	−0.42			
pH			0.49		−0.26					−0.37	0.33	−0.40		−0.33			
Float. Veg.			−0.27	−0.54								−0.43	0.42	−0.34			
Emerg. Veg.	−0.26		−0.25	0.35			−0.36	0.27		0.29				−0.59			
Bushes			−0.40			−0.30		0.27	0.26	−0.57		0.32					
Bare Ground		−0.30	0.27			0.39			0.44		−0.42	0.30		−0.34			
TOC	−0.47														0.28	−0.72	
TN	−0.49												−0.25		0.54	0.55	
TP	−0.43							0.30							−0.69		
Artif. Surf.		−0.36	−0.38			0.50			−0.27								0.55
Cultiv. Area		−0.37			0.30				0.66		0.39						
Forest		0.46			−0.27			0.26		0.27							0.63
Grassland	−0.27		0.36		0.38	−0.32			−0.28			0.28					0.48
Wetland		0.27			−0.33			−0.73			0.33						
Nat. Surf.							0.78			0.47							
Water				0.51	0.35						−0.38	−0.43					
Cumulative																	
Variance (%):	17.4	32.3	42.4	51.8	60.1	67.7	73.9	79.3	83.8	87.6	91.2	94.0	96.5	98.1	99.2	100.0	100.0

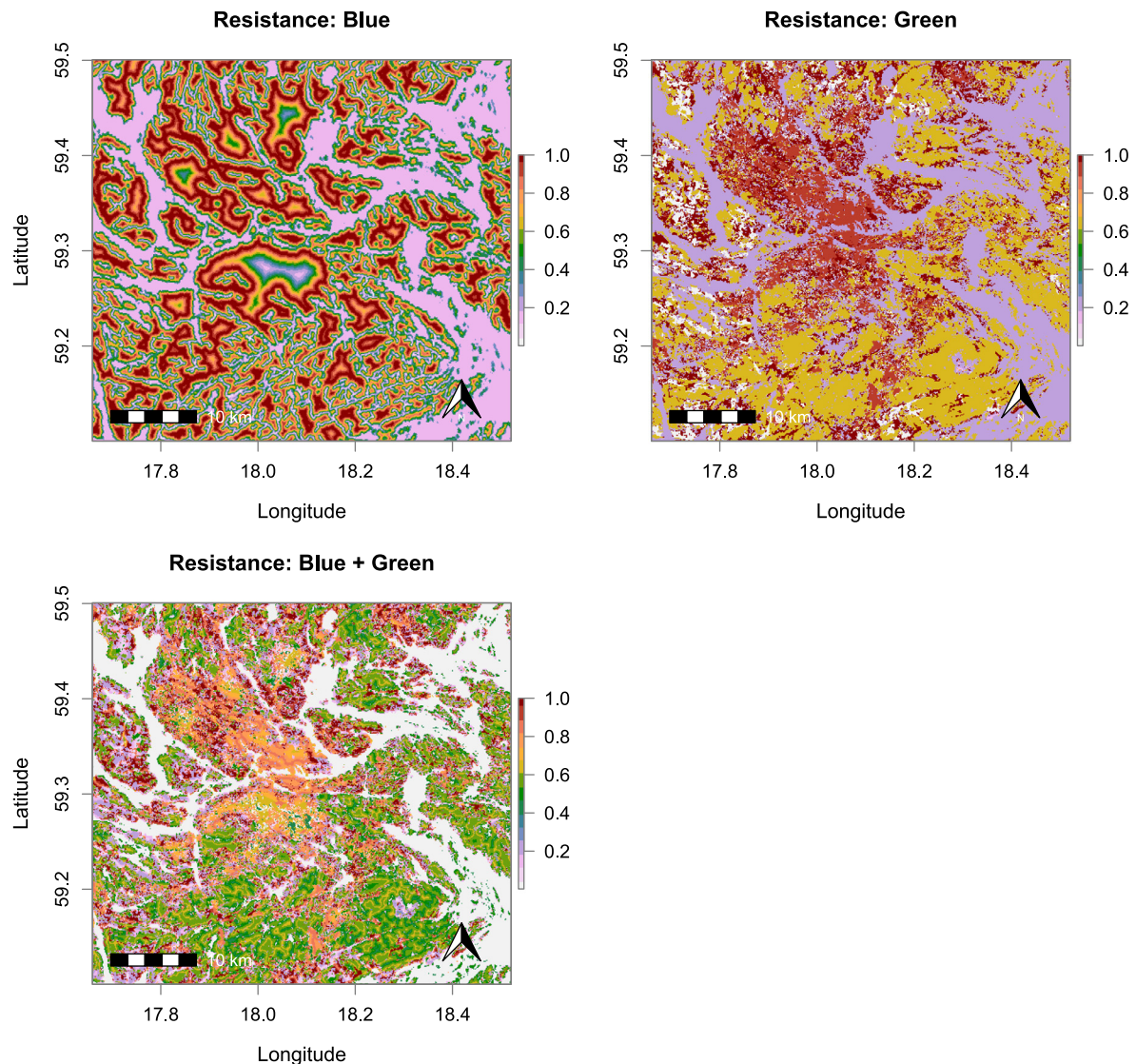


Fig. 2. Parameterization of landscape resistance surfaces. The original resistance values have been put on the same scale as a visual aid, with 0 representing low resistance, and 1 high resistance. The blue resistance surface shows low resistance to movement in or near water bodies. The green resistance surface depicts high resistance in areas with artificial surfaces, and low resistance where vegetation is present. The third panel represents a composite blue-and-green resistance surface.

Density maps, obtained from blue, green, and blue-green resistance surfaces, showed that the central and western parts of the study area had fewer dispersal corridors (Fig. 3 and Appendix A: Fig. A1). The number of blue dispersal corridors was higher in the north and southeast, but low centrally and to the southwest (Appendix A: Fig. A1). Green corridors were generally more numerous in the east than the west, with fewer centrally as well. Similarly, blue-green corridors were less abundant to the west and centrally (Fig. 3 and Appendix A: Fig. A1).

Community differentiation

After the backward selection process of removal of non-significant PCNM axes, one PCNM axis was retained. Two

local PCA axes (PC1 and PC2; Table 1) contributed significantly to community differentiation. Two blue and four green PCoA axes were significant, with the composite blue-green connectivity comprising seven significant PCoA axes.

Using db-RDA variance partitioning, we determined that functional connectivity explained a larger proportion of the variance in community composition than either spatial structure or the local environment. Spatial structure alone contributed 1.4% to the variance, while the local environment contributed 1.3%. In separate analyses, we determined that blue, green, and the composite blue-green connectivity accounted for 2.8%, 2.8%, and 7.8% of community differentiation, independently of spatial structure and the local environment. The shared fraction of connectivity and local environment explained an additional 0.2% (blue), 1.4% (green), and 1.6% (blue-green) of community

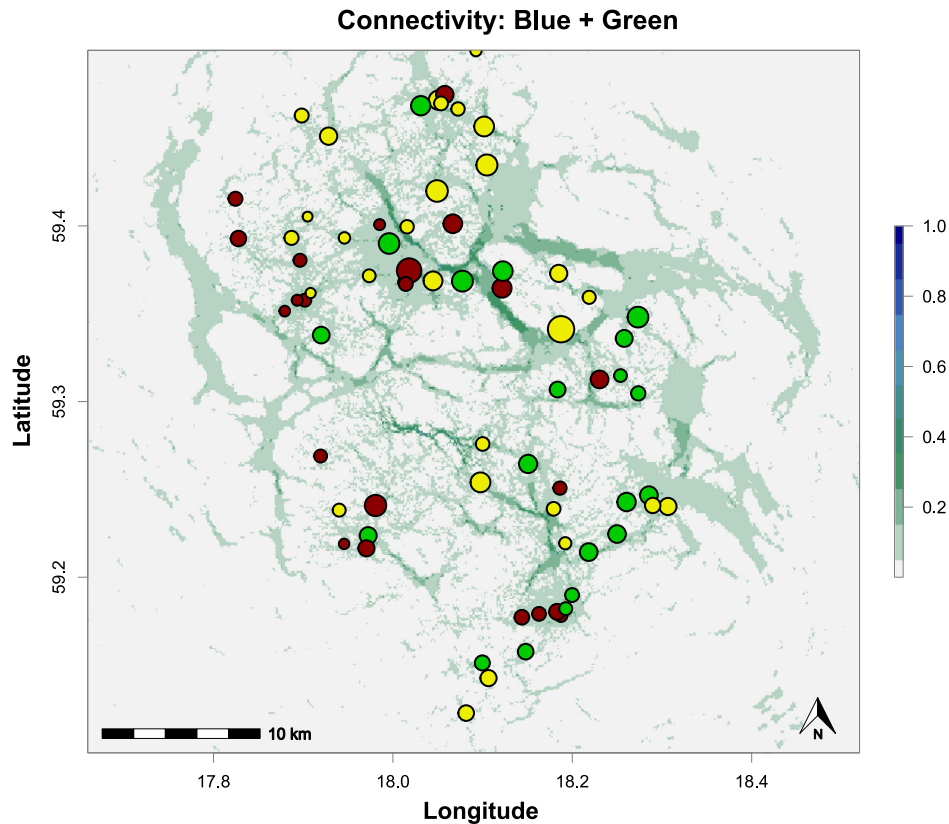


Fig. 3. Blue-green functional connectivity among ponds. Blue-green functional connectivity is represented by electrical current densities obtained using Circuitscape. These densities reflect the number of times current flows through each point on the map, thus representing dispersal pathways through which urban pond communities are connected. Current density (i.e., connectivity) is shown on a scale of 0 (white) to 1 (blue), with medium values represented in green. Additionally, mean connectivity (inverse of resistance distance) for each pond is superimposed on the map. These values represent the mean of connectivity of each pond with the other 71 ponds. Dots are color-coded by pond class, and the size is proportional to the value of mean connectivity.

differentiation. The shared fractions of spatial structure and the other predictors were nearly zero.

Pond classes and the association between diversity and connectivity

Louvain clustering identified three pond clusters (i.e., classes). Cluster 1 ponds were characterized by a high percentage of grassland in the surrounding area, with the median being 41.5%. Cluster 2 ponds were characterized by artificial surfaces (median: 39.3%), while cluster 3 ponds had more forests (median: 65.6%; Table 2). The grassland-dominated ponds had higher TN (median: 1.3 mg/L) and TP (median: 72 $\mu\text{g/L}$). The artificial-surface-dominated ponds were generally smaller (median pond area: 503 m^2 ; Table 2), while the forest-dominated ponds were larger (median pond area: 2008 m^2 ; Table 2).

Green connectivity was not significantly different among the three pond classes. In contrast, blue connectivity was significantly lower among ponds within cluster 2

(dominated by artificial surfaces), compared to the grassland and forest clusters (Appendix A: Fig. A2). This pattern was visualized using a force-directed graph, where isolated ponds with lower connectivity values (cluster 2) were located peripherally in the network (Appendix A: Fig. A2). Blue-green connectivity was significantly higher in cluster 3 (dominated by forests), compared to the other two clusters (Appendix A: Fig. A2). This was also captured by a force-directed graph, where ponds in cluster 3 were located centrally with thicker edges (representing higher connectivity values).

Artificial-surface-dominated ponds, which had the lowest blue connectivity, also had the lowest species richness ($\alpha = 9.913$ and $\gamma = 67$) as well as the highest differentiation among communities ($\beta = 5.759$, dispersion = 0.555, and $F_{\text{ST}} = 0.256$; Table 3). These ponds also had the lowest diversity (Shannon-Weaver's $H' = 1.780$) and evenness (Pielou's $J' = 0.859$). The grassland-dominated ponds had the highest richness ($\alpha = 14.103$ and $\gamma = 84$) and lowest differentiation ($\beta = 4.956$, dispersion = 0.525, and $F_{\text{ST}} = 0.184$), but intermediate diversity ($H' = 2.250$) and evenness ($J' = 0.890$). Forest-dominated ponds had

Table 2. Clustering of ponds based on local environmental variables. The median and interquartile range (25%–75%) are shown for each environmental variable in each of the three clusters that sampling sites have been classified into using Louvain clustering (see Step 3a). Cluster 1 is characterized by a high percentage of grassland (median = 41.5%), cluster 2 by artificial surfaces (39.3%), and cluster 3 by forests (65.6%). The same abbreviations for local environmental variables are used as in Table 1. Units are given in parentheses.

		Cluster 1: Grassland		Cluster 2: Artif. Surf.		Cluster 3: Forest	
		Median	25%–75%	Median	25%–75%	Median	25%–75%
Within Pond	Pond Area (m ²)	1105.0	[738.5–1973.5]	503.0	[206–1089.5]	2008.0	[640.5–4019]
	Pond Depth (m)	0.6	[0.4–0.8]	0.7	[0.4–0.9]	1.1	[0.6–1.5]
	pH (0–14)	7.4	[7.1–7.6]	7.3	[7–7.5]	7.2	[6.9–8]
	Float. Veg. (0–10)	2.0	[0–3]	2.8	[0–4.5]	2.0	[0.3–4.5]
	Emerg. Veg. (0–10)	3.2	[2–5.5]	3.0	[1.5–4.5]	2.0	[1–3]
	Bushes (0–10)	2.0	[1–3]	3.0	[1–4]	2.5	[1–4]
	Bare Ground (0–10)	0.0	[0–1.3]	0.0	[0–5.5]	0.0	[0–0.8]
	TOC (mg/L)	15.6	[12.2–20.7]	16.1	[10.2–18.6]	16.9	[13.1–20.7]
	TN (mg/L)	1.3	[0.9–1.7]	0.9	[0.7–1.4]	1.0	[0.9–1.4]
	TP (μg/L)	72.0	[30–148]	57.0	[21.9–148]	39.0	[25.8–76.5]
250-m Radius	Artif. Surf. (%)	10.4	[5.8–16]	39.3	[24–52.4]	4.6	[1.4–8.4]
	Cultiv. Area (%)	9.8	[7–16.1]	11.4	[6.5–14.9]	3.5	[1.9–7.2]
	Forest (%)	28.2	[18.8–43.1]	26.1	[17.7–40.5]	65.6	[59–75.9]
	Grassland (%)	41.5	[29.2–50.1]	13.7	[10.2–23.1]	13.0	[7.2–16.6]
	Wetland (%)	1.5	[1–3.4]	1.1	[0.6–1.8]	3.3	[1.2–7.5]
	Nat. Surf. (%)	0.3	[0–0.8]	1.3	[0.8–2]	0.2	[0.1–0.6]
	Water (%)	0.0	[0–0.7]	0.0	[0–0]	0.0	[0–0.6]

Table 3. Metacommunity metrics by pond class. The table shows species richness (α and γ), diversity (Shannon-Weaver's diversity = H' ; and Pielou's evenness = J'), and differentiation metrics (β , dispersion, and F_{ST}) for metacommunities in each of the three pond classes: grassland-dominated, artificial-surface-dominated (artif. surf.), and forest-dominated.

		Grassland	Artif. Surf.	Forest
Richness:	γ	84	67	80
	α	14.103	9.913	13.000
Diversity:	H'	2.250	1.780	2.302
	J'	0.890	0.859	0.939
Differentiation:	β	4.956	5.759	5.154
	dispersion	0.525	0.555	0.547
	F_{ST}	0.184	0.256	0.205

intermediate richness and differentiation values (Table 3), but also the highest diversity ($H' = 2.302$) and evenness ($J' = 0.939$).

There was no significant relationship of either richness or evenness with blue-green connectivity in the forest class of ponds. Blue-green connectivity was also not significantly correlated with species evenness in either the artificial-surface or the grassland class of ponds (Fig. 4). However, the positive correlation between blue-green connectivity and species richness was significant both in artificial-surface-dominated ponds (Fig. 4; $F_{1,19} = 6.01$, $R^2 = 0.24$, $p = 0.02$) and in grassland ponds (Fig. 4; $F_{1,26} = 5.00$, $R^2 = 0.16$, $p = 0.03$).

We detected a strong correlation ($r = -0.66$) of the caddisfly genus *Limnephilus* with axis 1 of the ordination of a

db-RDA model conditioned on geography (one PCNM axis) and constrained by blue-green connectivity and environment (Fig. 5). This axis separated the three pond classes, as was evident from the negative-to-positive position of the centroids along the axis (Fig. 5), ordered from the artificial-surface to the forest class, with the grassland class being intermediate. The forest versus artificial-surface class of ponds was the only comparison that resulted in significantly different multivariate means ($p = 0.03$). *Limnephilus* was found more frequently in pond communities dominated by artificial surfaces and grassland. This was also the case for hemipterans, such as the water boatmen (Corixidae). Conversely, the dragonfly *Cordulia aenea* was more associated with ponds surrounded by forested habitat (positively correlated with axis 1; $r = 0.26$), while predaceous diving beetles in the Dytiscidae family, such as *Hygrotus inaequalis*, were associated with ponds in the grassland class.

PC2 was strongly correlated ($r = 0.56$) with axis 1. This reflects the fact that community differentiation in the forest class is influenced by forested habitat around ponds (see Table 1; PC2 is positively correlated with amount of forested habitat). Backward selection of explanatory variables resulted in PC2 being retained, while PC1 became non-significant when combined with the seven PCoA axes, all of which were still significant and thus retained. Using db-RDA models conditioned on geography (Appendix A: Fig. A3), as well as models conditioned on both geography and local environment (Appendix A: Fig. A4), we detected associations of taxa with local communities influenced by blue and green connectivity separately, as well as the combined blue-green effect. For instance, a species of water beetle,

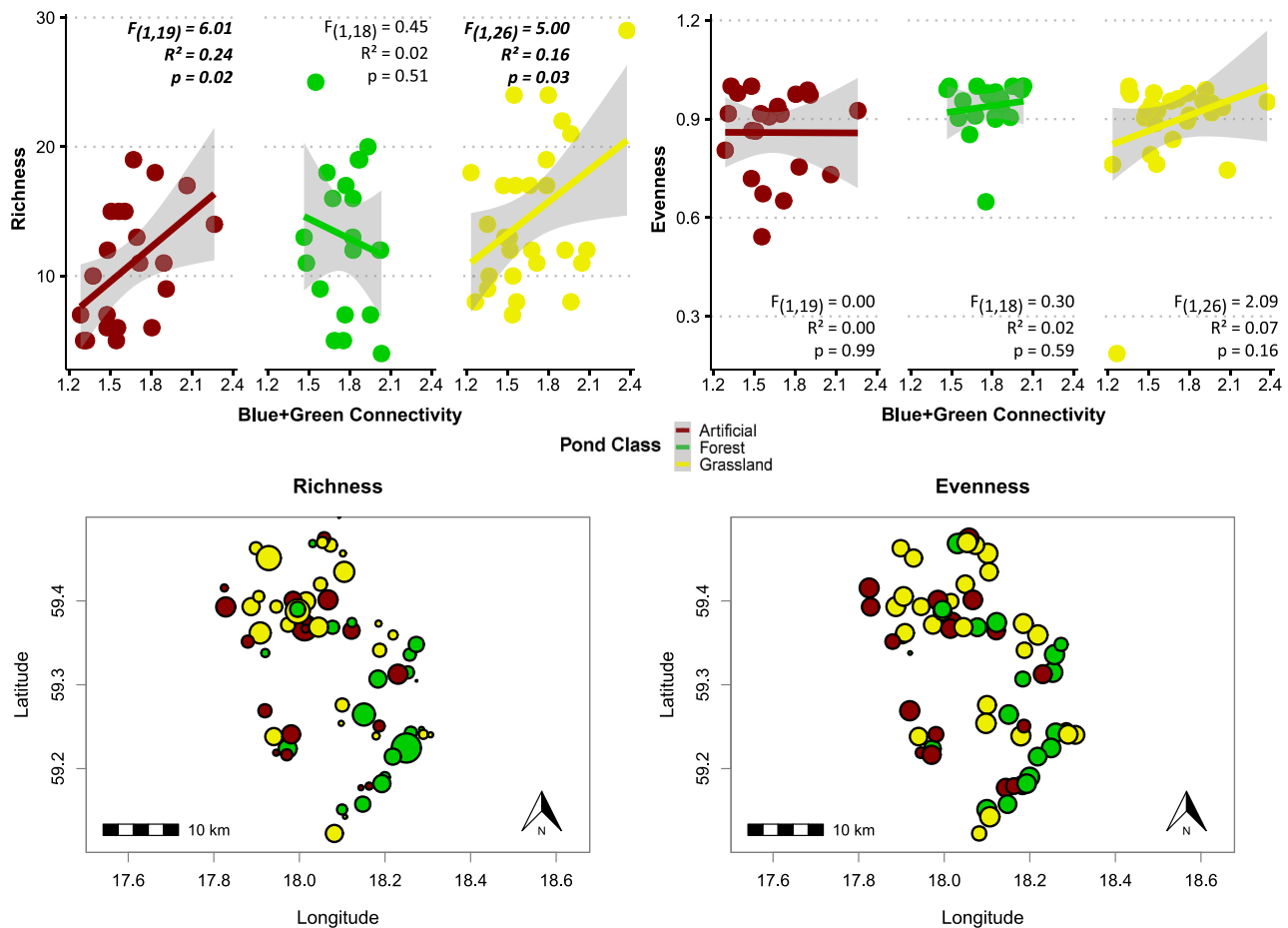


Fig. 4. Connectivity among ponds and the relationship with species richness/evenness. The top left graph shows regressions of species richness on blue-green connectivity (i.e., the mean of connectivity for each pond with all other ponds). The top right graph shows regressions of species evenness on blue-green connectivity. F , R^2 , and p -values are shown for models run separately for each class of pond (red = ponds surrounded by a large proportion of artificial surfaces; green = forested areas; and yellow = grassland). The two graphs in the bottom show spatial distribution of species richness (left) and evenness (right). Ponds are color-coded based on classification. The size of each circle is proportional to species richness and evenness values.

Clemnius decoratus, was more likely to be found in pond communities belonging to the grassland and forest class of ponds, which was largely due to green connectivity alone (Appendix A: Fig. A3 and Fig. A4).

Discussion

Metacommunity structure is jointly shaped by local environmental variables, landscape configuration, and connectivity among communities (Aggemyr, Auffret, Jädergård & Cousins, 2018; Brown & Swan, 2010; Chisholm, Lindo & Gonzalez, 2011; Heino et al., 2021; Ryberg & Fitzgerald, 2016). Here, we found that blue-green connectivity was the principal predictor of invertebrate community structure in urban ponds. In contrast, local environmental variables, including land use in the immediate vicinity of ponds, had

lower explanatory power for the observed variance in community composition.

Our study is one of the first to show this quantitatively in urban areas, and thus represents an important step toward a better understanding of how landscape connectivity influences biodiversity relative to other factors. This is also an issue highlighted by Fletcher, Burrell, Reichert, Vasudev and Austin (2016). The importance of blue connectivity, confirmed by our study, mirrors results found in other studies of urban aquatic communities. For instance, Gledhill, James and Davies (2008) found that species richness was higher in clusters of connected ponds. However, while connectivity was an important factor in our study, explaining 7.8% of the variance in community composition, other factors, such as the degree of pond intermittency (e.g., some ponds are temporary, while others are permanent), and presence of aquatic vertebrate predators could be two of several other factors contributing to the remaining unexplained

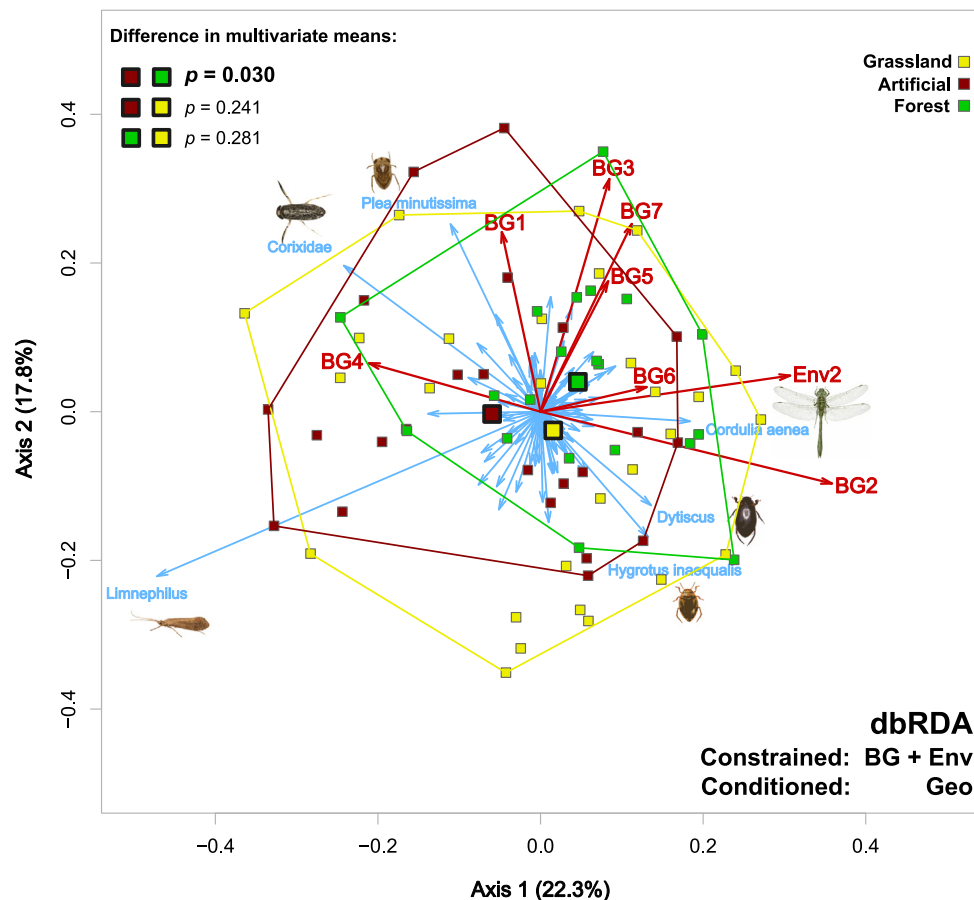


Fig. 5. Distance-based Redundancy Analysis (db-RDA) constrained by local environment and connectivity. The results shown here represent community variation explained by local environment and connectivity, after the effect of spatial structure (Geo) has been removed. Significant PCoA axes are shown for blue-green connectivity (BG) and the local environment (Env2 = PC2 from Table 1). The small squares represent individual ponds, color-coded by pond class (yellow = grassland-dominated ponds; red = artificial-surface-dominated; green = forest-dominated). Pond class centroids are depicted as large squares with thick outlines. All ponds belonging to the same class are shown within each of the three convex hulls. Red arrows show strength of correlation of connectivity/environment with db-RDA axes 1 and 2, while blue arrows represent taxa. Percentage of variation captured by each of these two axes is shown in the axis labels. Illustrations are included for the taxa most correlated with the two axes. The position of these taxa near particular communities is indicative of their presence in those communities and thus association with a particular pond class (e.g., the caddisfly genus *Limnephilus* is found more frequently in artificial-surface- and grassland-dominated ponds).

proportion of the variance. Furthermore, permanent ponds are typically larger and deeper, and may thus show less stochasticity and have higher habitat heterogeneity than temporary ponds. This may also affect biodiversity in ponds (Hill, Heino, White, Ryves & Wood, 2019).

Classification of ponds into three types—those with surrounding areas dominated by artificial surfaces, grassland, or forests—provided additional insight into the structuring of aquatic invertebrate communities in urban ponds in our study area. Species richness was highest in the grassland-dominated ponds, since both local and regional (i.e., meta-community) measures of diversity were high. Additionally, differentiation among local communities was highest for artificial-surface-dominated ponds, and lowest for grassland-dominated ponds. This may be a result of high blue connectivity in grassland-dominated ponds, where aquatic

corridors—especially those in the northeastern parts of the study area—may facilitate dispersal of aquatic invertebrates. Variability in blue-green connectivity was high in both the artificial-surface and grassland class of ponds. Furthermore, an increase in blue-green connectivity among these ponds was associated with increased species richness. High species richness could result from occasional dispersal of transient taxa. This would, however, increase differentiation within communities and decrease evenness, as is the case with artificial-surface-dominated ponds. The high evenness and low differentiation, observed together with high species richness, in many of the grassland-dominated ponds, are indicative of frequent long-distance dispersal events facilitated by a great degree of connectivity maintained over time. Similarly, forest-dominated ponds harbored communities with some of the highest evenness and lowest differentiation values.

Notably, species richness did not show any relationship with blue-green connectivity in this class of ponds. Also, these forest-dominated ponds generally had high levels of blue-green connectivity. It is possible that a network of well-connected forest ponds maintains stable communities with high species richness and evenness, thus dampening the relationship between connectivity and richness.

Our results suggest that to preserve and improve biodiversity in urban ponds, it is important to enhance functional connectivity in artificial-surface-dominated areas. Additionally, the high connectivity observed among some of the grassland-dominated ponds suggests that open green spaces could augment the potential of riparian corridors to maintain functional connectivity in urban pond metacommunities. Streams and their riparian zones serve as dispersal routes and corridors for many terrestrial and aquatic taxa (J. Heino et al., 2017). For instance, albeit undisturbed corridors are preferred, several mammal species have been shown to use even anthropogenically disturbed riparian corridors in agricultural landscapes (Hilty & Merenlender, 2004). By providing dispersal corridors, riparian zones are also extremely important in mitigating effects of climate change (Beier, 2012; Fremier et al., 2015; Seavy et al., 2009). Here, we show that blue connectivity is maintained among many urban ponds. However, an extensive cover of artificial surfaces disrupts blue connectivity, and we suggest that these areas should be targeted for riparian corridor restoration and management.

Urban ponds support highly heterogeneous communities, which is likely a consequence of the range of environmental conditions present across urban landscapes. Focusing on the local environment of ponds, we found that the PCs that contributed significantly to variation in community structure were most correlated with pond size (i.e., area and depth), nutrients (TOC, TN, TP) in ponds, shoreline vegetation, as well as presence of grassland and forests in a 250-m radius around ponds. These PCs reflected the pond classification results, with grassland-dominated ponds having higher levels of nutrients and emergent vegetation, and forest-dominated ponds being larger and having more vegetation along shores (i.e., less bare ground). Similar results were reported in previous studies on pond biodiversity in Stockholm, which found that pond size and vegetation contributed significantly to biodiversity in these ecosystems (Heino et al., 2017b; Johansson et al., 2019). We note that the study by Heino et al., 2017b also found that nutrients had a large effect on biodiversity patterns. Interestingly, biodiversity of aquatic invertebrates does not necessarily correlate positively with pond size (Hassall et al., 2011; Oertli et al., 2002; but see Biggs et al., 2005).

Despite the ubiquity of urban areas, we know little about what urban features promote dispersal of organisms. In a review of studies of ecological connectivity in urban areas, LaPoint et al. (2015) found that connectivity was rarely explicitly measured, and the level of urban development of study sites was infrequently characterized. Furthermore,

they found that most of these studies focused on large mammals, but rarely on invertebrates and other animals, or plants. Nevertheless, previous studies have suggested that dispersal in urban areas is affected by population size (Penteado, 2020), availability of habitats (Hostetler & Holling, 2000), human disturbance (Dickman & Doncaster, 1989), and human infrastructure (Zipperer, 2015). In addition, for the majority of the taxa found in this study we lack information on habitat preference in urban areas. For example, the caddisfly genus *Limnephilus* was found frequently in pond communities dominated by artificial surfaces and grassland. However, species in this genus have varying habitat preferences (Müller-Peddinghaus & Herling, 2013), and a comparison of these preferences is beyond the scope of this study. In contrast, the water beetle *Clemnius decoratus* was more likely to be found in the grassland and forest class of ponds, which is consistent with previous studies suggesting that the species prefers small water bodies overgrown with emergent plants (Cuppen, 1983). Hence, more studies on connectivity in urban areas, such as the one presented here, are needed for a better understanding of how dispersal and habitat choice of aquatic invertebrate taxa determine biodiversity patterns in urban ponds. Furthermore, connectivity among habitat patches should be considered not only as part of direct efforts to conserve biodiversity, but also in the management of invasive species with the goal of reducing their negative impact on native biodiversity (Glen, Pech & Byrom, 2013).

An interesting question is whether the pattern found here is unique to the city of Stockholm, or universal for cities in general. Indeed, Stockholm is one of the greener cities in Europe, with artificial surfaces covering 14% of the metropolitan area (cf. Berlin 39%, London 48%, Paris 66%; Kourdouli & Jönsson, 2020). Ample green spaces in Stockholm probably help maintain connectivity among ponds. Even ponds surrounded by a larger proportion of artificial surfaces have relatively high green connectivity. However, blue connectivity is much lower for these ponds. Indeed, we found that levels of blue-green connectivity were lower in the western parts of the Stockholm metropolitan area, where the surroundings of many ponds have a high density of artificial surfaces. Restoration, management, and construction of additional dispersal corridors would probably benefit the biodiversity in these areas of the city. Corridors are fundamental to strengthening the effectiveness and resilience of landscape ecological networks (e.g., Dondina, Saura, Bani & Mateo Sánchez, 2018), and the level of connectivity we identified here is a reason for optimism for sustainable urban environments. In agreement with the importance of connectivity highlighted by our study, a meta-analysis found that patch area and corridors had the strongest positive effects on urban biodiversity (Beninde, Veith & Hochkirch, 2015).

In summary, many cities around the world are expanding, and urbanization is expected to drastically increase in the future. At the same time, the integration of green and blue

spaces is widely promoted in urban development, potentially offering numerous benefits for biodiversity. This may be particularly relevant for blue spaces such as urban ponds, which often support threatened species (Oertli & Paris, 2019). Encouragingly, even artificial ponds can positively affect biodiversity of aquatic insects, such as odonates (Simaika, Samways & Frenzel, 2016). Importantly, there is growing awareness of the contribution of ponds to aquatic biodiversity (e.g., Biggs, vonFumetti & KellyQuinn, 2017; Stewart et al., 2017), and since connectivity is an important feature that allows maintaining biodiversity at many spatial scales and organizational levels, from alleles to communities (Fletcher et al., 2016), it needs to be considered in urban areas if we are to diminish and mitigate the negative effects of urbanization on biodiversity. Finally, our study highlights the utility of using landscape resistance surfaces to model functional connectivity at the level of entire communities and metacommunities. Electrical circuit theory has been used extensively to model resistance of landscape features to dispersal at the level of populations or species. This approach has been applied less frequently to multiple taxa, however. To the best of our knowledge, this study is the first to do so for urban pond metacommunities, paving the way for further investigations on how to conserve and manage urban biodiversity.

Author contributions

CH and FJ conceived the study, FJ collected field data, CH performed statistical analyses and wrote the first draft, and CH, FJ, JH, LMB and UB edited subsequent drafts of the manuscript.

Data accessibility

The data used in this study and the R scripts written to perform the analyses are all available online at https://github.com/chazhyseni/pond_conn.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baaec.2021.10.004](https://doi.org/10.1016/j.baaec.2021.10.004).

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