

# Unravelling the correlates of species richness and ecological uniqueness in a metacommunity of urban pond insects



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## ABSTRACT

City ponds have the potential to harbour a rich biodiversity of aquatic insects despite being located in an urban landscape. However, our current knowledge on the correlates of pond biodiversity is limited and even less is known about the factors that influence the ecological uniqueness of urban ponds. The multiple environmental gradients, at different spatial scales, that may affect biodiversity and ecological uniqueness of urban ponds can thus be seen both as an opportunity and as a challenge for a study. In this study, we aimed to fill this gap by focusing on aquatic insect assemblages in 51 ponds in the Swedish city of Stockholm, using a metacommunity perspective. We found that species richness was primarily determined by the density of aquatic insects, water depth and proportion of buildings around the pond. The uniqueness of ponds was estimated as local contributions to beta diversity (LCBD), and it was primarily related to the proportion of arable land and industry around the ponds. With regard to the metacommunity we found two interesting patterns. First, there was a negative relationship between richness and LCBD. Second, biodiversity was spatially independent, suggesting that spatially-patterned dispersal did not structure species richness or LCBD. These last two patterns are important when considering conservation efforts of biodiversity in city ponds. We hence suggest that the conservation of insect biodiversity in urban pond should consider the surroundings of the ponds, and that high-richness ponds are not necessarily those that require most attention because they are not ecologically the most unique.

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## 1. Introduction

Metacommunity ecology, a recently-emerged branch of ecology, aims to find underlying causes for variation in biodiversity across a landscape. Current ideas in metacommunity ecology emphasize that not only local environmental conditions (e.g. productivity, ecosystem size and predation pressure) but also dispersal between localities affect biodiversity (Leibold et al., 2004). Disentangling the roles of environmental conditions and dispersal for biodiversity may be difficult (Cottenie, 2005), since it requires dispersal proxies (Jacobson and Peres-Neto, 2010) and because there might be spatial autocorrelation in local environmental conditions and biological data (Pinel-Alloul et al., 1995). However, provided

that there is low spatial autocorrelation in environmental conditions, two scenarios can be expected with regard to the roles of local environmental conditions and dispersal in affecting biodiversity. First, if species are able to track environmental heterogeneity, then we should see hot-spots and cold-spots in biodiversity scattered across the landscape. Second, if dispersal limitation is important, then we should see spatial structure in biodiversity, such that localities situated far from each other harbour different levels of biodiversity partly irrespective of local environmental conditions (Heino et al., 2015). Here, we focus on two aspects of biodiversity (i.e. species richness and ecological uniqueness of a biological community) and examine spatial patterns in an insect metacommunity of urban ponds.

Freshwaters harbour very high levels of biodiversity in relation to the areal extent they cover (Dudgeon et al., 2006). Biodiversity in freshwater ecosystems is affected by factors operating at both local and landscape scales (Allan, 2004). Natural local factors

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of importance to biodiversity include the classical effects of area (i.e. increasing species richness with increasing ecosystem size; MacArthur and Wilson, 1967; Sepkoski and Rex, 1979), habitat heterogeneity (i.e. higher species richness with increasing habitat heterogeneity; e.g. Stein et al., 2014) and passive sampling (i.e. a higher number of individuals sampled results in higher species richness; e.g. Kuusela (1979). A positive relationship between species richness and number of individuals may also arise due to relevant ecological processes because high population sizes are associated, for instance, with high resource availability and low rates of local extinction (Gotelli and Colwell, 2001).

Other typical factors affecting biodiversity in freshwater ecosystems include nutrients (i.e. species richness either increasing or decreasing with nutrients levels; e.g. Heino, 2009) and acidity (i.e. species richness is typically lower in acidic freshwater ecosystems; e.g. Brönmark and Hansson, 2005). Also, landscape degradation, including conversion of riparian forest to agricultural and urban land-uses, may affect biodiversity in freshwater systems (Allan, 2004; Smith et al., 2009). While such effects of local and land-use factors have been extensively studied in stream systems (Sandin and Johnson, 2004; Heino et al., 2007), few studies have focused on their relative roles in urban freshwater systems (Goertzen and Suhling, 2013; Teittinen et al., 2015).

Urban landscapes are typically complex mixtures of built-up areas, roads, parks and green corridors (Goertzen and Suhling, 2013), contributing to environmental heterogeneity and dispersal routes for species (Smith et al., 2009). Urbanization may either decrease or increase environmental heterogeneity of urban ecosystems, such as freshwaters, which may have important consequences for biodiversity (McKinney, 2006; Hassall, 2014). Freshwater ecosystems in urban landscapes are also to some degree isolated from each other by not only spatial distances but also by degraded riparian zones, roads and built-up areas unsuitable for dispersal between localities. However, these issues have been little studied so far (Smith et al., 2009). Taken together, it is still premature to suggest generalities as to the roles of environmental conditions and dispersal for freshwater biodiversity in urban landscapes.

Urban ponds are a special type of freshwater ecosystems (Chester and Robson, 2013). Biodiversity of urban ponds varies much but is often surprisingly high (Hassall, 2014), and it may sometimes be comparable to that found in natural freshwater ecosystems (Hassall and Anderson, 2015). For example, studying stormwater management ponds in the Canadian city of Ottawa, Hassall and Anderson (2015) found that macroinvertebrate diversity was roughly similar to that in more natural ponds. Goertzen and Suhling (2013) found that dragonfly species richness varied from zero to 17 in urban ponds in the German city of Dortmund, and that species richness was mainly related to aquatic vegetation in and terrestrial vegetation surrounding a pond. These studies also underscore the importance of urban ponds in maintaining biodiversity (Goertzen and Suhling, 2013) and providing ecosystem services, as well as aesthetic and educational value (Hassall, 2014).

Biodiversity in urban ponds has rarely been studied from a meta-community perspective. We aimed to fill this gap by focusing on aquatic insect assemblages of ponds in an area of the Swedish city of Stockholm. Stockholm harbours ca. 100 ponds, which are typically located in parks or less populated areas of the city. Specifically, we focused on the spatial patterning and determinants of species richness (i.e. number of insect species in a pond) and ecological uniqueness (i.e. the contribution of a locality to total beta diversity; see Legendre and De Cáceres, 2013). Our aim was to disentangle the roles of environmental conditions measured at different scales (in-pond and land use variables) underlying biodiversity variation in an urban landscape. We hypothesised that insect biodiversity would be primarily determined by local environmental variables, as has

been found in more natural lentic (e.g. Heino, 2013) and lotic freshwaters (e.g. Landeiro et al., 2012), and suggested by findings from urban ponds (e.g. Goertzen and Suhling, 2013). However, we also expected that land use and geographic position affect biodiversity.

## 2. Methods

### 2.1. Study area

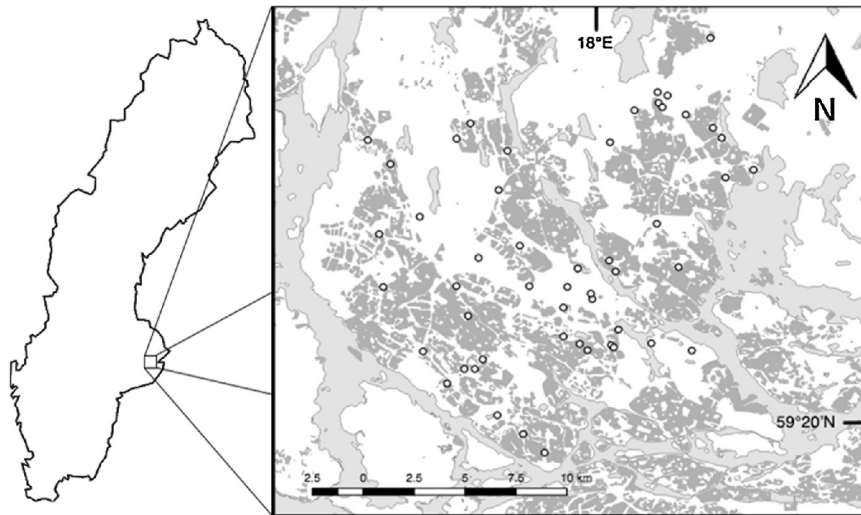
Our study was conducted in the core area of the city of Stockholm, capital of Sweden, and includes 51 ponds (i.e. covering all ponds) in the northern half of the city (Fig. 1). The sampled area covers 50% of the city area and should thus be representative for the whole city. The city has ca. 900 000 residents, but the metropolitan area is home to approximately 1.5 million inhabitants. We defined city ponds as natural or man-made water bodies with an area between 2 m<sup>2</sup> and 2 ha and holding water for at least 4 months of the year (Biggs et al., 2005). Ponds were selected from maps and by using information from municipalities' officials. Since our focus was on the densely-populated areas in the city, we divided Stockholm into 1 × 1 km squares and only considered squares where >75% of the area is covered by developed area as defined in a terrain map (Terrängkartan<sup>TM</sup>) of the Swedish mapping, cadastral and land registration authority (Lantmäteriet). Hence, ponds located in golf courses or large forested areas, most often situated outside the populated areas, were not included, even though these golf courses have shown a great potential for fostering biodiversity in urban areas (Colding et al., 2009). All ponds were sampled in May or June 2013 and 2014, and the resulting database was originally used to study the effects of socio-economic factors and management on biodiversity (Malgorzata et al., 2016a, 2016b). However, those two studies did not study metacommunity aspects and beta-diversity patterns as we do here.

### 2.2. Local variables

The following local environmental variables were measured for each pond: area, maximum depth, pH, total phosphorus (total P), total nitrogen (total N), total organic carbon (TOC), and macrophyte cover, and presence/absence of fish and newts. These variables have been shown to affect biodiversity in many rural ponds and were therefore selected in this study on urban ponds (e.g. Hassall et al., 2011). Pond area was estimated from the Terrängkartan<sup>TM</sup> map from Lantmäteriet (The Swedish mapping, cadastral and land registration authority) using the software ArcGIS 9 (Environmental Systems Research Institute, 2009), and water depth with a ruler in the deepest part of the pond. Water chemistry variables were sampled in May–June 2013/2014 and analysed at the Limnology laboratory at Uppsala University. Macrophyte cover was estimated visually in August in units of 10, ranging from 0 to 100% of cover and included submerged, floating and emergent vegetation. Initially the presence/absence of fish and newts were also included, but they were removed from the dataset since they did not affect species richness or LCBD.

### 2.3. Land use variables

The following land use or landscape variables were estimated: distance to the nearest pond, and the land cover variables percentage of water, forest (deciduous + coniferous), area with buildings (low rise + high rise buildings), area with industry and arable land. Past studies have shown that many of these variables affect terrestrial biodiversity (e.g. McKinney, 2008), but few studies have used them for urban pond biodiversity. They were retrieved from the



**Fig. 1.** Maps showing Sweden and the northern part of the city of Stockholm where the dots represent the 51 ponds included in the study. The grey area shows developed land.

Terrängkartan™ map. The percentages were estimated within a 200-m radius of each pond.

#### 2.4. Measuring species richness

Species richness in the ponds was estimated as richness of aquatic life stages of the orders Odonata, Trichoptera (larvae), Coleoptera (larvae and adults) and Hemiptera (larvae and adults). These invertebrates represent various functional groups, and may thus represent the overall biodiversity of aquatic insects in pond habitats (Sánchez-Fernández et al., 2006; Hassall et al., 2011; but see Heino (2010) and Westgate et al., 2014). The insects 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. The net was swept along the bottom in opposite directions (left to right) eight times on a 1 m stretch, which constituted one sample. These six samples covered all types of representative microhabitats along the shoreline, e.g. soft bottom and hard bottom, as well as with and without vegetation. The sampling strategy was derived from the guidelines by the Swedish Environmental Protection Agency (2006). All insects were determined to taxonomic order at the pond site and were preserved in 70% ethanol. Thereafter, samples were taken to the laboratory for species determination. Specimens that could not be determined to species level were still included in the final analysis and set to family or genus-level and hence regarded as separate taxa. The majority of these cases considered larval specimens of the order Odonata belonging to either *Coenagrion pulchella* (Vander Linden, 1825) or *C. pulchellum* (Linnaeus, 1758), which are not distinguishable and were, therefore, regarded as the same species in the analysis. In addition, three pairs of species belonging to the order Trichoptera could not be distinguished. These were: (i) *Limnephilus affinis* Curtis, 1834 and *L. incisus*, Curtis, 1834 (ii) *Limnephilus luridus* Curtis, 1834 and *L. ignavus* McLachlan, 1865 and (iii) *Oligotricha striata* Linnaeus 1759 and *O. lapponica* (Hagen 1864). Finally, nymphs of the genus *Notonecta* and the family Corixidae were regarded as one taxon, respectively.

#### 2.5. Statistical analysis

Our analytical strategy included four main steps. First, we defined our response variables (i.e., species richness and ecological uniqueness). Second, we analysed the spatial patterns in these response variables to verify the need for using spatial regression

methods. Third, we used two approaches for dealing with multicollinearity. Fourth, we modelled the relationship between our response variables and explanatory variables (local and land use variables). These steps are described in more detail in the next subsections.

#### 2.6. Response variables

Species richness was calculated as the number of insect taxa found in a pond. We calculated the ecological uniqueness of each pond (i.e., local contributions to beta diversity; hereafter LCBD) according to the method recently developed by Legendre and De Cáceres (2013). In this method, the elements of an abundance data matrix (with  $n$  sites and  $p$  species) are, first, Hellinger-transformed. According to Legendre and De Cáceres (2013), the Hellinger coefficient of dissimilarity, based on data previously Hellinger-transformed, has all essential properties for beta diversity assessment (e.g., minimum of zero and positiveness, symmetry, monotonicity to changes in abundance, double-zero asymmetry, etc.). Second, the squared difference between each Hellinger-transformed value and the mean abundance of the corresponding species is calculated. Third, the elements of this matrix containing the squared differences are summed up to obtain the total sum of squares (SS) of the abundance data matrix. Then, the total beta diversity is obtained by dividing the total sum of squares by the number of sites minus 1.0 (see equation 1, 2 and 3 in Legendre and De Cáceres, 2013; respectively). Finally, the local contribution to beta diversity of a given site is calculated by dividing the sum of squares corresponding to this site by the total sum of squares (see equation 5b in Legendre and De Cáceres, 2013). The R function used to estimate LCBD can be found in the Supplementary material (ele12141-sup-0005-AppendixS4.R) of the article published by Legendre and De Cáceres (2013).

#### 2.7. Spatial autocorrelation analysis

A variable is said to be spatially autocorrelated when pairs of values, measured at given distances in space, are not independent (i.e., values are more or less similar than expected by chance alone, for positive and negative autocorrelation, respectively; Legendre and Legendre, 2012). Thus, one of the main assumptions of classical statistical methods, that observations are independent, does not hold and, consequently, type I errors are inflated (Peres-Neto and Legendre, 2010).

We used Moran's *I* based correlograms to test for spatial autocorrelation in our response variables (species richness and LCBD) and in the residuals of the models. A spatial correlogram is a graph that relates the levels of spatial autocorrelation (in ordinate) with the geographic distances between pairs of sites (in abscissa; Legendre and Fortin, 1989). We conducted this analysis using the function *correlog* of the R package *pgirmess* (Giraudoux, 2015). By using this analysis, we first tested whether nearby ponds are similar with regard to our response variables, which would allow us to formulate hypotheses on the importance of spatial processes (e.g., dispersion or spatially structured environmental variation) in driving pond biodiversity. Second, this analysis, when applied to the residuals of our models, was useful to test for the independence assumption and to verify the need for using spatial regression methods (Zuur et al., 2010).

### 2.8. Multicollinearity analysis

When we attempt to model ecological phenomena, in addition to the problems caused by spatial autocorrelation, we are faced with the problems caused by multicollinearity (i.e. when the explanatory variables of interest are correlated). Indeed, despite being frequently overlooked, multicollinearity is an issue that occurs in most ecological datasets (Graham, 2003). The basic problem is that multicollinearity causes the so-called instability in parameter estimation. Coarsely, this instability means that the magnitudes and signs of estimated regression coefficients change depending of which (collinear) explanatory variables are included in the model. Multicollinearity is highly expected in our study because, for instance, eutrophication causes simultaneous changes in different environmental variables (e.g. total P, total N and pH).

From onset, we concur with Dormann et al. (2013) that the problem of multicollinearity cannot be solved. However, different approaches can be used to minimize it and as a way to check for the stability of the results. The use of the variance inflation factor (VIF), for instance, is advantageous because it provides a detailed view of the explanatory variables that are causing multicollinearity (Dormann et al., 2013). Thus, considering the local explanatory variables, we firstly used VIF following the procedure described in Zuur et al. (2010). This procedure consists in sequentially removing explanatory variable with the highest VIF, recalculating the VIFs and repeating this process until "all VIFs are smaller than a pre-selected threshold" (Zuur et al., 2010). For this task, we used the function *vif* from the R package *CAR* (Fox et al., 2015) and adopted a threshold of  $VIF \geq 1.9$ . Secondly, for local variables we used a correlation-based principal component analysis (PCA) and used the Kaiser-Guttman criterion to select components (axes), which were posteriorly used as explanatory variables (see below). This criterion consists in selecting only those components associated with eigenvalues larger than 1.0 (Legendre and Legendre, 2012). Local variables (including total density), except pH and aquatic macrophyte cover, were log-transformed before analysis. We did not use a PCA for the land use variables because these variables did not show strong correlation among each other. Thus, the PCA included only local variables.

### 2.9. Models

Both local species richness and LCBD were regressed against local and land use variables. The following variables represented the list of local variables: pH, aquatic macrophyte cover, total phosphorous, total nitrogen, total organic carbon concentrations, maximum depth and pond area. In the list of local variables for the species richness model, we also included the total density of macroinvertebrates as a covariate (Bailey et al., 2014). The land use variables were represented by distance to the nearest pond,

area covered by water bodies (other than the sampled ponds), proportional area covered by forests, buildings, industries and arable lands. Local variables were analysed as original variables or as PCA axes extracted as above (associated with eigenvalues higher than 1.0).

Species richness, given its discrete nature, was modelled as a function of our explanatory variables using generalized linear models (GLMs) with Poisson error terms. As proposed by O'Hara and Kotze (2010), the use of GLM is advisable as this statistical procedure provides lower bias and root mean-squared error compared to log-transforming count data. GLMs were fitted using the function *glm* from the R package *stats*. The use of more complex models to take spatial autocorrelation into account (e.g. Generalized Linear Mixed Model, GLMM; see Dormann et al., 2007) was not necessary because species richness was not spatially autocorrelated (see Results).

LCBD was modelled using ordinary least squares multiple regression analysis. Again, the use of spatial models was not necessary due to the absence of spatial patterns in the response variable (i.e. LCBD; see Results).

To produce a minimum adequate model (MAM) for each response variable, we sequentially removed explanatory variables from the full models until all explanatory variables remaining were significant. We tested the stability of the MAMs using the function *stepAIC* from the R package *MASS* (Ripley et al., 2015).

## 3. Results

We found large variation in the land use and local variables (Table 1). For instance, among land use variables, the proportions of area occupied by arable lands and industries ranged from 0% to 76.3% and from 0% to 29%, respectively. Among local variables, total phosphorus and total nitrogen concentrations ranged from  $19.9 \mu\text{gL}^{-1}$  to  $1111.3 \mu\text{gL}^{-1}$  and from  $438.2 \mu\text{gL}^{-1}$  to  $5430.0 \mu\text{gL}^{-1}$ , respectively.

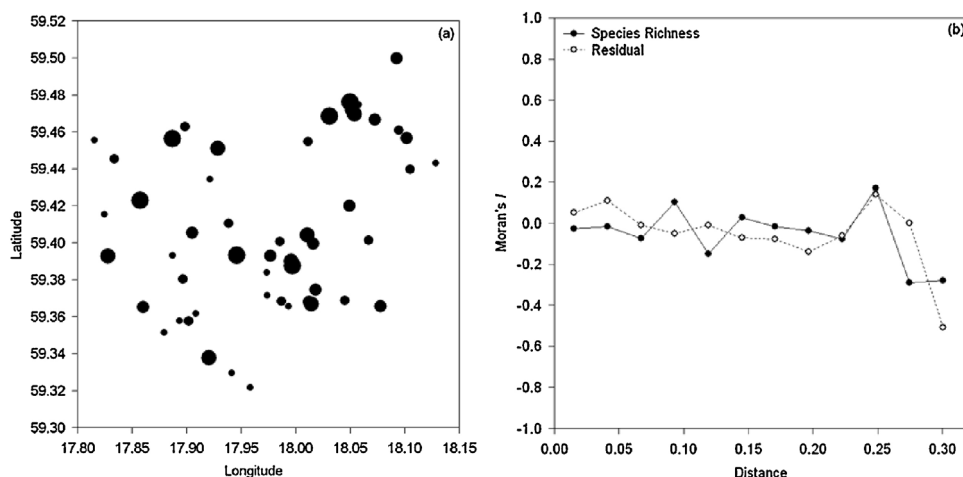
### 3.1. Species richness

Insect species richness ranged from 1 to 22 (median=9.0 species). Lowest and highest values were found in different areas of Stockholm (Fig. 2a), and spatial autocorrelation analysis indicated that species richness was spatially independent (Fig. 2b). The list of candidate explanatory variables to predict insect species richness, after controlling for multicollinearity (using the VIF approach), included: depth, total phosphorous, TOC, density of insects, aquatic macrophyte cover, distance to the nearest pond and proportions of area covered by water, forest, building, industry and arable land (Table S1). Our minimal adequate model (MAM) indicated that species richness was strongly and positively related to the density of insects and, to a lesser extent, to depth, total P concentration and aquatic macrophytes cover (Table 2). The proportion of area occupied by buildings was negatively related to species richness (Table 2; Fig. 3). Residuals from this model were spatially independent (Fig. 2b) and normally distributed ( $W=0.9837$ ,  $P=0.7038$ ; Shapiro-Wilk test). Results obtained with the use of the Akaike Information Criterion (AIC) were similar, except for the inclusion of percentage of water cover in the best-supported model (Table 2).

Following the Kaiser-Guttman criterion (i.e., selection of axes with eigenvalues  $> 1.0$ ), we retained the first three principal component axes for further analyses. These axes accounted for 67.3% of the total variation in local data. The first principal component (PC1) was positively correlated with area and pH. PC1 was also negatively correlated with total phosphorus, total nitrogen and TOC. The second principal component (PC2) was mainly correlated with aquatic macrophyte cover and insect density, whereas the third

**Table 1**  
Basic statistics of the explanatory variables.

Variables	Unit	Mean	SD	CV	Min	Max
Area	m <sup>2</sup>	1794.7	2861.9	159.5	13.0	17219.0
Depth	cm	95.0	48.1	50.6	16.0	200.0
pH		7.3	0.6	8.6	5.8	8.6
Total Phosphorus	μg.L <sup>-1</sup>	168.4	209.6	124.5	19.9	1111.3
Total Nitrogen	μg.L <sup>-1</sup>	1675.6	1032.4	61.6	438.2	5430.0
Total Organic Carbon	μg.L <sup>-1</sup>	23.8	33.8	141.8	5.9	163.0
Macrophyte Cover	%	58.2	34.0	58.4	0.0	100.0
Distance to the nearest pond	m	1186.5	715.7	60.3	161.5	3416.2
Water	%	0.02	0.1	246.6	0.0	0.27
Forest	%	0.27	0.2	78.8	0.0	0.76
Building	%	0.22	0.2	106.0	0.0	0.79
Industry	%	0.03	0.1	287.4	0.0	0.29
Arable land	%	0.05	0.1	297.3	0.0	0.76



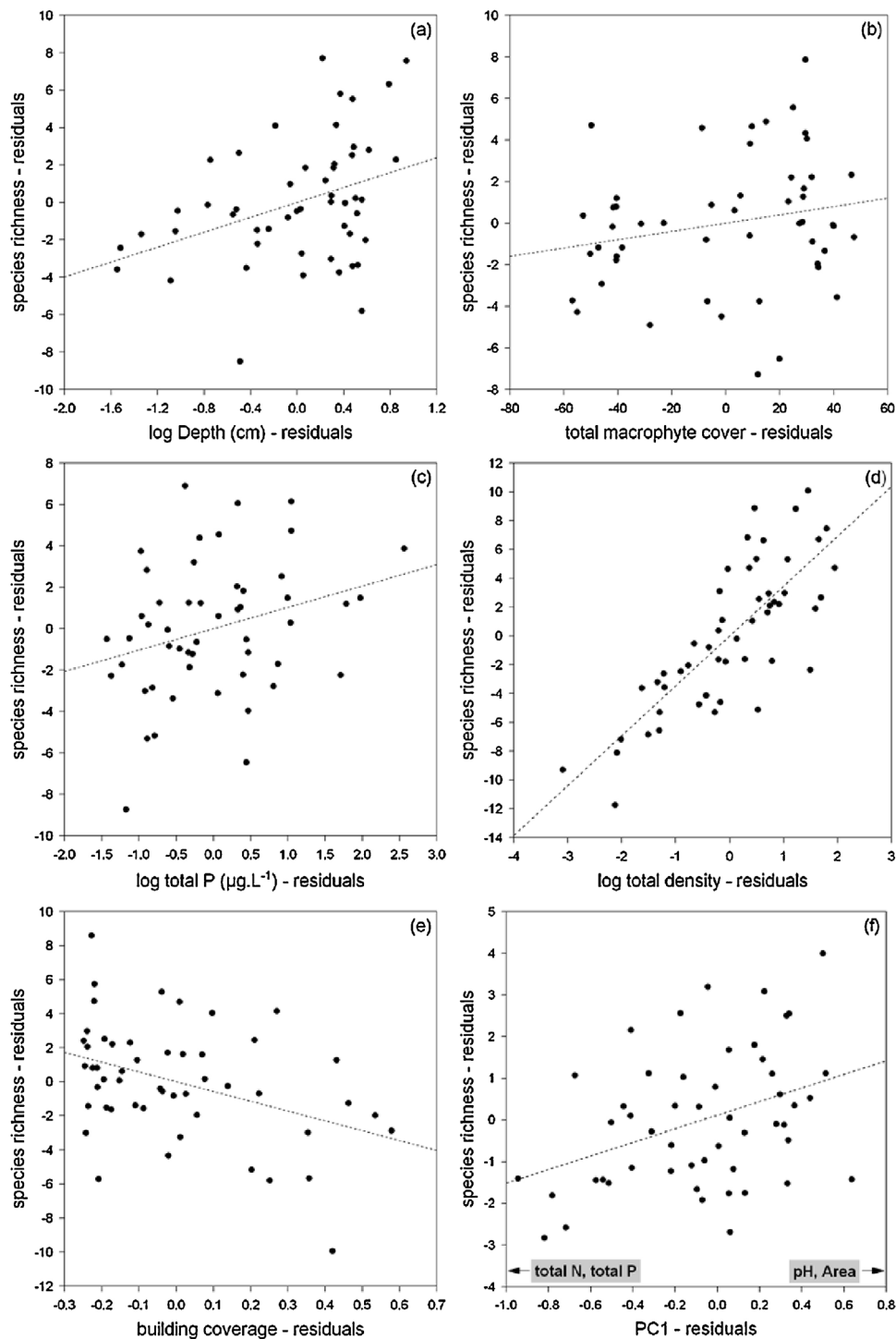
**Fig. 2.** Spatial variation in insect species richness (a) and spatial autocorrelation analysis (b) of the original variable and of the residuals of the minimum adequate model.

**Table 2**  
GLM results considering insect species richness as the response variable. The column “Data Reduction” indicates whether the local variables entered the models as original variables or as axes from a principal component analysis (PCA).

Approach	Data Reduction	Variables	Estimate	SE	Z	P
MAM	Original	(Intercept)	-1.014	0.503	-2.02	0.0436
		Depth	0.628	0.180	3.49	0.0005
		Macrophyte	0.003	0.001	2.02	0.0440
		total P	0.225	0.105	2.14	0.0324
		Density	0.994	0.110	9.04	0.0000
		Building	-0.559	0.209	-2.68	0.0073
StepAIC	Original	(Intercept)	-1.139	0.506	-2.25	
		Depth	0.649	0.181	3.59	
		Macrophyte	0.003	0.001	2.00	
		total P	0.258	0.105	2.46	
		Density	1.026	0.111	9.21	
		Building	-0.543	0.209	-2.60	
MAM	PCA	(Intercept)	2.370	0.061	39.147	0.0000
		PC1	0.536	0.124	4.322	0.0000
		PC2	0.704	0.176	4.001	0.0001
		Building	-0.596	0.204	-2.918	0.0035
		(Intercept)	3.115	0.423	7.359	
StepAIC	PCA	PC1	0.569	0.125	4.547	
		PC2	0.638	0.181	3.524	
		Distance	-0.251	0.142	-1.772	
		Building	-0.603	0.207	-2.919	

principal component (PC3) was so with TOC (Table 3). GLM results, using these axes and land use variables as explanatory variables, indicated that species richness was positively correlated with the first two components, and negatively correlated with the proportion of area occupied by buildings (Table 2, Fig. 3). Taken together,

these results indicate an increase in species richness with increasing pH, pond area, insect density, depth and aquatic macrophyte cover. Also, they indicate a decrease in species richness in nutrient-rich ponds, which are located in areas more extensively occupied by buildings. Results obtained using the Akaike Information Crite-



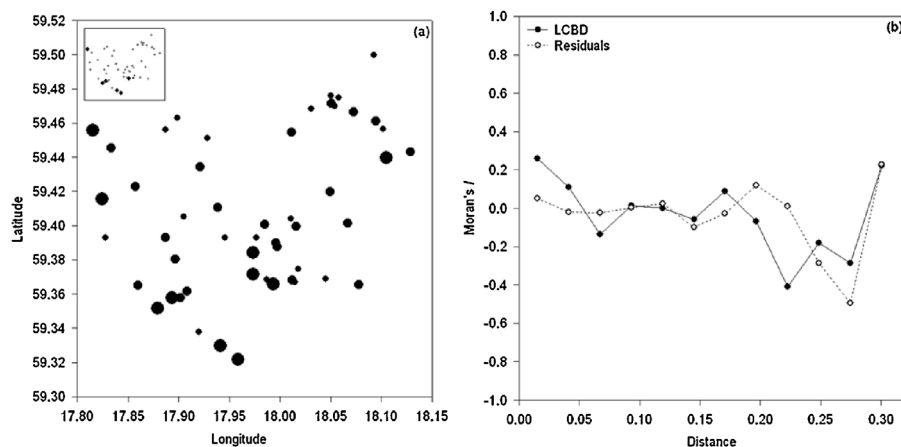
**Fig. 3.** Partial residual plots from the minimum adequate model for species richness. Shown are the relationships between the residuals of species richness from a model allowing for all variables (except the one shown in the abscissa of each plot) and the residuals of a specific explanatory variable from a model allowing for all other explanatory variables. PC1: first principal component axis (more influential variables in this axis are shown in insets – see Table 3).

tion (AIC) were similar, except by the inclusion of the distance to the nearest pond in the best-supported model (Table 2). Our results are hence somewhat conflicting because of the way by which we dealt with multicollinearity changes the interpretations, i.e. the VIF or PCA approach. For instance, after using VIF to minimize multicollinearity effects, we found a positive relationship between species richness and total P concentration. However, when the PCA axes were used as explanatory variables, we found a negative

relationship between species richness and nutrient concentrations (total N and total P).

### 3.2. Local contributions to beta diversity

The largest local contributions to beta diversity (LCBD) were found mainly in ponds located in the south-western and south-eastern edges of the study area, whereas significant values of LCBD were concentrated in the south-western part (Fig. 4a). However,



**Fig. 4.** Spatial variation in local contribution to beta diversity (LCBD) (a) and spatial autocorrelation analysis (b) of the original variable and of the residuals of the minimum adequate model. The inset in (a) indicates the  $P$ -values associated with LCBD (black large symbols:  $P \leq 0.05$ ; grey small symbols:  $P > 0.05$ ).

**Table 3**

Principal component (PC) loadings from a principal component analysis applied to the local data.

Variables	PC1	PC2	PC3
Area	0.71	-0.43	0.14
Depth	0.44	-0.45	-0.46
pH	0.74	0.00	0.32
total P	-0.75	-0.22	0.02
total N	-0.86	-0.22	0.13
TOC	-0.45	0.11	0.56
Density	0.50	0.54	0.38
Macrophyte	-0.09	0.71	-0.53
Eigenvalues	<b>3.00</b>	<b>1.29</b>	<b>1.09</b>
% of Explanation	37.53	16.19	13.63

spatial autocorrelation analysis did not detect significant spatial patterns (Fig. 4b).

The list of candidate explanatory variables to predict LCBD, after removing collinear variables, was similar to the one for species richness and included depth, macrophyte cover, total N, TOC, species richness, distance to the nearest pond, and land use variables (Table S1). The minimal adequate model (MAM) indicated that LCBD was negatively correlated with species richness and the proportion of area occupied by arable lands (adjusted  $R^2 = 0.48$ ; Table 4). Residuals from this model were spatially independent (Fig. 4b) and normally distributed ( $W = 0.97$ ,  $P = 0.1638$ ; Shapiro-Wilk test). The final model using AIC also included the proportion of areas occupied by industries and by other aquatic systems. The same results were obtained when local variables entered the models as principal component axes (Table 4).

According to Legendre and De Cáceres (2013), a negative relationship between species richness and LCBD is not obligatory. Therefore, we repeated the model selection excluding species richness from the list of explanatory variables. By doing so, we still found a significant relationship between LCBD and the proportion of arable land, despite the substantial decrease in the coefficient of determination (adjusted  $R^2 = 0.12$ ; Table 4). The final model using AIC, with the previous exclusion of species richness as a candidate variable, also indicated that LCBD was mainly (and negatively) related with the proportion of arable land and, to a lesser extent, with total aquatic macrophyte cover (Table 4). When local variables were entered in the models as principal component axes and sequentially removing non-significant explanatory variables, the final model also revealed a sole significant effect of the proportion of arable land. The final model using AIC, despite indicating that the proportion of arable land was the main predictor of LCBD, also suggested that the first two principal components and the propor-

tion of areas occupied by industries and by other aquatic systems should be used for inference.

## 4. Discussion

We found that both local and land use variables accounted for variation in aquatic insect biodiversity in a metacommunity of urban ponds. Importantly, our findings indicate that species richness and ecological uniqueness (LCBD; local contribution to beta diversity) were negatively associated with the proportional areas around ponds covered by buildings and arable lands, respectively. Also, these results were robust to methodological choices (i.e., model selection strategy and summarizing or not local variables by a PCA). We found no significant spatial patterns with regard to species richness or LCBD, suggesting that spatial arrangement of ponds does not have a detectable effect on insect diversity in these urban ponds. The latter finding suggests, therefore, that variations in these biodiversity variables are not strongly determined by spatially-structured dispersal processes in the metacommunity (see also Heino et al., 2015). Interestingly, we found that LCBD and richness were negatively correlated with each other, and if this pattern is common in city areas, it has implications for pond conservation and management.

### 4.1. Predictors of species richness

Species richness in ponds was related to both biotic and abiotic factors. One primary predictor that affected species richness was insect density. This cannot be interpreted as a simple effect of variation in sampling effort because our sampling effort was strictly standardized across the ponds. Variation in abundance may instead be related to variation in resources and environmental conditions (Gotelli and Colwell, 2001), which, in turn, affect demographic parameters, local extinction rates and result in spatial variation of species richness. Another primary predictor of species richness was pond depth, which was positively associated with species richness. A deeper pond probably has more heterogeneous habitat conditions and is also less likely to dry out during warm summers (i.e. a factor related to water permanence; Collinson et al., 1995). Both these factors have been found to be positively related to species richness in ponds (Ripley and Simovich, 2009; Hassall et al., 2011). Finally, we found that the percentage of land covered by built up areas around a pond had a negative effect on species richness. This finding may be related to the fact many aquatic insects need green areas around a pond for mating and feeding as adults (Buchwald, 1992). Similarly, it is possible that green areas around

**Table 4**

Minimum adequate model (MAM) for local contribution to beta diversity (LCBD). MAM-1 and StepAIC-1 are estimated models without species richness as a candidate variable. Note that using original (local variables) or PCA gave the same results for three of the models.

Approach	Data reduction	Variables	Estimate	SE	t	P
MAM	Original & PCA	(Intercept)	0.0237	0.0007	32.74	0.0000
		Richness	−0.0004	0.0001	−5.93	0.0000
		Arable land	−0.0079	0.0025	−3.20	0.0024
StepAIC	Original & PCA	(Intercept)	0.0245	0.0007	32.94	
		Richness	−0.0004	0.0001	−6.45	
		Arable land	−0.0089	0.0024	−3.76	
		Industry	−0.0097	0.0045	−2.16	
		Water	−0.0105	0.0057	−1.85	
MAM-1	Original & PCA	(Intercept)	0.0201	0.0005	41.28	0.0000
		Arable land	−0.0090	0.0032	−2.84	0.0066
StepAIC-1	Original	(Intercept)	0.0212	0.0009	22.40	
		Arable land	−0.0097	0.0032	−3.04	
		Macrophyte	−0.00002	0.000014	−1.44	
	PCA	(Intercept)	0.0206	0.0005	38.37	0.0000
		PC1	−0.0024	0.0012	−2.08	0.0429
		PC2	−0.0036	0.0018	−2.07	0.0446
		Arable land	−0.0087	0.0031	−2.77	0.1605
		Industry	−0.0107	0.0060	−1.79	0.0795
		Water	−0.0104	0.0073	−1.43	0.0081

a pond attract more ovipositing insects as compared to heavily-built areas since insects might have a search image for such green areas (Buchwald, 1992). Buildings may also be seen as impervious surfaces hindering dispersal and colonisation, which is the incentive behind urban green corridors (Dramstad et al., 1996). In the study of socio-economic effects on pond biodiversity by Malgorzata et al. (2016b), the urbanisation factors included buildings of various types and showed a negative effect on species richness also at a 500 m or 800 m radius from the pond. They stressed connectivity of green areas in the urban landscape as a limiting factor for pond biodiversity, but without actually analysing beta diversity patterns and spatial autocorrelation as we do here. Similar negative impact of urbanization has been found for other animal groups in cities (McKinney, 2008). Goertzen and Suhling (2013), on the other hand, did not detect a negative relationship between the amount of sealed ground around city ponds and odonate diversity. Their and our results suggest that the effect of urbanization on pond biodiversity is far from fully understood.

Secondary predictors of insect richness were macrophyte cover and total P. These variables also had positive relationships with species richness, but their explanatory power was not particularly strong. Macrophyte density has been shown to be positively correlated with species richness in other studies (Hassall et al., 2011; Goertzen and Suhling, 2013; Heino, 2013), and a high plant species cover probably results in a more heterogeneous habitat as well as provides resources for different species groups (Heino, 2009). An active pond management towards intermediate vegetation cover was recommended by Malgorzata et al. (2016b), although optimal management strategies may vary for different taxonomic groups. The positive relationship between species richness and total P is probably caused by higher productivity, although species richness might decrease at very high levels of productivity (Waide et al., 1999; but see below). Interestingly, insect species richness and macrophyte cover might both decrease as total P values increase over and above a threshold. However, we did not find such a hump-shaped relationship.

The local correlates of species richness we found in our study are, to some extent, contingent on the method used to address multicollinearity (Dormann et al., 2013). For example, species richness was significantly correlated with the first two axes from a PCA applied to the local variables. Chiefly, the first principal component (PC1), which was positively associated with species richness, was

negatively correlated with total N and total P concentrations and positively correlated with pH and pond area. The second principal component (PC2), which was positively correlated with species richness, was mainly associated with aquatic macrophyte cover. Taken together, these relationships indicate a positive association between species richness, pond area, pH and aquatic macrophyte cover and also a negative association between species richness and nutrient concentrations. Some of these relationships between local pond variables and species richness have been found in other studies, including pond area and pH. For example, Biggs et al. (2005) found that pond area was positively associated with species richness, and such a positive species-area relationship (MacArthur and Wilson, 1967) is also a general pattern that holds for many freshwater systems (Heino, 2009). Despite these results, at least in aquatic systems, area is not always everything (e.g. Oertli et al., 2002). Goertzen and Suhling (2013), for example, found a negative relationship between pond size and Odonata diversity in urban ponds. They explained this pattern by the fact that larger city ponds often were severely disturbed by such phenomena as high numbers of ducks. The situation is different in our study region because nutrient concentrations were negatively correlated with pond area. Water pH has also been found to have a positive relationship with aquatic insect species richness (Heino, 2009), which is in accordance with our results when a PCA is used to summarize the local data. The generality of a negative relationship between eutrophication and pond biodiversity has recently been questioned (Rosset et al., 2014). However, our results suggest that the role of eutrophication (as summarized in part by the first principal component axis – PC1), with an adverse effect on insect species richness, especially in small ponds, cannot be discarded.

#### 4.2. Predictors of 'local contribution to beta diversity'

Ecological uniqueness, which was estimated as 'local contribution to beta diversity' (LCBD), did not show the same pattern as species richness with regard to local and land use variables. LCBD was not strongly associated with any of the local abiotic variables. One reason for this finding could be that LCBD is immune to variation in local conditions, but is more affected by environmental variables at larger scales. Indeed, LCBD was negatively affected by three land use variables: percent of water, industry and arable land. The negative relationships could be explained by isolation

effects. One reason could be that more ecologically unique communities form at isolated sites because dispersal is limited and because chance extinctions might lead to species composition that deviates most from 'typical' local communities in a metacommunity. In this regard, industry and arable land may directly prevent dispersal among sites, whereas the more ponds there are nearby, the higher among-site dispersal can be expected. However, this explanation remains largely speculative owing to the scarcity of studies that have used LCBD as a measure of biodiversity (but see [Da Silva and Hernández, 2014](#); [Tonkin et al., 2016](#)).

It was notable that we found a negative relationship between richness and LCBD. This implies that ponds with a high uniqueness of species have low species richness, a finding also shown by [Legendre and De Cáceres \(2013\)](#) and [da Silva and Hernández \(2014\)](#). From a conservation biology point this is a very important finding because it suggests that it is not enough to preserve ponds with high species richness if we want to preserve biodiversity in urban ponds. It is probable, or even likely, that some species poor sites harbour rare species, and those sites thus contribute strongly to overall beta diversity in a metacommunity.

#### 4.3. Biodiversity was not spatially patterned

We found that biodiversity was spatially independent, suggesting that spatially-patterned dispersal did not structure species richness or LCBD. This was somewhat surprising, as dispersal should be constrained by suitable routes in urban landscapes. It is thus possible that these features of biodiversity are largely silent to variation in spatially-patterned dispersal effects, which is similar to findings of variation in community structure in many aquatic metacommunities (see review by [Heino et al., 2015](#)). This finding is important with regard to urban ponds because it suggests either that dispersal has no clear structuring effects on adjacent communities (cf. mass effects; see [Leibold et al., 2004](#)) or that dispersal is so limited (cf. dispersal limitation; see [Heino et al., 2015](#)) that aquatic insect communities are mostly separated from any species pool effects on local communities. The complexity of dispersal routes for insects in urban landscapes ([Smith et al., 2009](#)) and intervening hostile land use may exacerbate the effects of dispersal limitation on local insect communities in ponds, but not in a spatially-patterned manner. Also, as land use variables were important for these two measures of biodiversity, land use adjacent to a pond may hold the key in determining complex spatial variation in urban pond biodiversity.

## 5. Conclusions

Our main finding was that aquatic insect species richness was primarily determined by their density, water depth and proportion of buildings surrounding the ponds. In contrast, local contribution to beta diversity (LCBD) was primarily related to the proportion of arable land and industry in the surroundings of the ponds. Our results also showed that aquatic insect species richness and LCBD were not structured by spatially-patterned dispersal effects. The results imply that the conservation of insect biodiversity in urban ponds should specifically consider the surroundings of the ponds, and highlight that high-richness ponds are not necessarily ecologically the most unique, since we found that LCBD and species richness were negatively correlated to each other. However, there are a few caveats in our study. For instance, besides being based on a correlative approach, we cannot extrapolate our results to other aquatic groups (e.g. fish, plankton and macrophytes) because they may show patterns different from aquatic insects ([Heino, 2010](#)). In this context, we think that the evaluation of the response of other aquatic groups would be important to increase the generality of

our findings regarding the role of land use variables on pond biodiversity. Finally, from the perspective of sustainability many urban ponds are used in the form of Sustainable Urban Drainage Systems ([Eriksson et al., 2007](#)). Such ponds replace or complement traditionally used sewage systems. The biodiversity and metacommunity patterns we found can therefore be useful when evaluating more applied-oriented issues such as environmental impact assessments (e.g. [Zhao et al., 2006](#)).

## Author Contributions

JA and FJ designed the study. JA performed the field surveys, and JA, JB, UB and FJ did the species determinations. LMB, JH and FJ devised the analytical approach. LMB conducted the statistical analyses. JH, LMB and FJ led the writing, with contributions from all authors.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.10.006>.

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