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Research

Niche use and co-occurrence patterns of zooplankton along a strong urbanization gradient

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Community composition in a given landscape is a complex product of the constituent species' niche requirements, geographic connectivity, environmental properties, species interactions and drift. In this study, we examined niche use of 16 cladoceran species in 81 zooplankton communities that inhabit environmentally variable sites along a strong urbanization gradient. We tested to what extent niche shifts occurred along the urbanization gradient. We also quantified to what extent niche overlap can explain co-occurrence patterns and tested whether alternative processes such as dispersal limitation or environmental heterogeneity impact co-occurrence patterns. Niche use in the study region was size-mediated, with larger species preferring nutrient-rich environments while smaller species were more specialized on distinct niche axes. Our analyses also revealed that mainly generalist species were able to establish in urban sites. While the average niche position for most species was conserved from rural to urban sites, the niches of those species occurring in both rural and urban areas remain partly unfilled in the urban populations. We observed that a relatively small proportion (13%) of species pairs co-occurred more or less often than expected by chance, but also that niche overlap was the only predictor that was strongly and significantly associated with co-occurrence scores in our study. While most of these species pairs showed evidence for a role of environmental filtering, a few common, generalist species pairs displayed segregated co-occurrence patterns and high niche overlap, suggesting a role of limiting similarity relationships as well. Our study highlights the damaging effects on biodiversity of urbanization through biotic homogenization benefitting generalist species, as well as the difficulty species may face in occupying available niche space in urbanized habitats.

Keywords: co-occurrence, niche, niche overlap, spatial statistics, urbanization, zooplankton

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Introduction

One of the main goals in community ecology is to link observed patterns in community structure to the processes driving community assembly. Diamond (1975) proposed to analyze species co-occurrence patterns in geographical space and hypothesized that such patterns could reveal general rules of community assembly. He claimed that non-random patterns of co-occurrence could be the product of shared niches and of competitive interactions between species that resulted in some taxa occurring together more often, while others occurred less often than expected by chance. Species that compete for the same niche requirements cannot coexist due to competitive exclusion, and would therefore exhibit patterns such as checkerboard distributions. Though Diamond's approach has been assessed, criticized and refined over the years (Gotelli and McCabe 2002, Leibold and Mikkelson 2002), the basic idea that locally co-occurring species might have less niche overlap compared to random assemblages from the regional species pool because they undergo niche partitioning to minimize interspecific competition has endured (MacArthur 1972, Boulangeat et al. 2012). Ecologists now understand that non-random co-occurrence patterns can arise from competition as well as shared environmental preferences, the degree of environmental heterogeneity in the landscape, species differences in their geographic distributions, and also due to drift (Bell 2000, Hubbell 2005, Heino et al. 2017, Leibold and Chase 2017).

Despite the historical importance of co-occurrence patterns in community ecology, numerous studies have focused on metacommunity-wide analysis to identify the processes that structure community assembly (Gotelli and Ulrich 2010, Chase and Myers 2011). These analyses focus on metrics that identify dominant processes structuring the entire community and thus offer less power to identify how assembly mechanisms can vary among species of the same community. However, species in a community may not all respond to the environment or to one another in an aggregate way that can be determined from analysis of the entire composition matrix. This may be the case, for example, if the group of species in a sampled region does not represent a single discrete regional community (Veech 2014). Furthermore, species can be distinguished by their functional traits and the relationship between functional traits and abiotic and biotic environmental properties can play an important role in determining community structure (McGill et al. 2006, Lessard et al. 2012, Violle et al. 2012, Siefert et al. 2013). For this reason, the ecological niche is often the main focus in species distribution modelling (Kearney 2006, Soberón 2007, Pearman et al. 2008). Different subsets of species can also show distinct community assembly patterns. For instance, rare and common species (Hanski 1982, Magurran and Henderson 2003, Siqueira et al. 2012, Umaña et al. 2017) and generalists and specialists (Pandit et al. 2009, Liao et al. 2016) can have distinct metacommunity structure. Species with specialized niche requirements can be more sensitive to environmental perturbations than generalist species (the specialization-disturbance hypothesis: Futuyma and Moreno 1988, Bergamini et al. 2009, Boulangeat et al. 2012, Slatyer et al. 2013). It is therefore important to evaluate community structure for different functional groups and subsets or pairs of species, to identify which groups are structured by different processes. In addition, many analyses of community structure consider the effects of abiotic environment and geographic space for species distributions, but not species interactions (Violle and Jiang 2009, Cazelles et al. 2016). Despite the recent call to incorporate joint species distribution models and co-occurrence patterns to explain community assembly (Clark et al. 2014, Pollock et al. 2014, Harris 2015, Ovaskainen et al. 2017), the role of biotic interactions in structuring species distributions is still debated (Gotelli and Ulrich 2010, Boulangeat et al. 2012). Analyses of metacommunity structure should ideally distinguish among biotic interactions and response to abiotic and spatial gradients (Fournier et al. 2017, García-Girón et al. 2020, Thompson et al. 2020).

The goal of our study was to evaluate species niche use and co-occurrence patterns across a spatially and environmentally heterogeneous landscape that is influenced by anthropogenic land use. Urban centers are hotspots of anthropogenic disturbance that profoundly affect urban ecosystems (Sattler et al. 2010), and urbanization is predicted to affect the realized niche of a species as well (Bowler et al. 2015). Niche conservatism, the tendency of a species to retain its ecological niche in space or time, is an important premise to predict species responses to environmental change, and is likely to be influenced by urbanization. Environmental change can affect both the shape and position of a species in multidimensional niche space (Warren et al. 2008, Broennimann et al. 2012, Petitpierre et al. 2012). Species can respond by shifting their mean position (centroid) in niche space, by expanding their niche (adapting to new environments) or by only partially filling their existing niche space in the new habitat (niche unfilling). We expect that environmental conditions differ between urban and natural sites (Brans et al. 2018), and that this differentially influences species niches via effects on competition and resource availability. Based on the urbanization-tolerance hypothesis (Croci et al. 2008, Sih et al. 2011), we also expect a subset of mainly generalist species from the regional species pool, with broad environmental tolerances, to occur in and dominate highly disturbed environments. Species have diverse ways of coping with disturbed environments, and it is therefore important to examine how different species and different functional groups respond to human disturbance.

In this study, we evaluated species distributions and co-occurrence patterns of 81 cladoceran zooplankton communities that inhabit freshwater ponds in Belgium. The 81 sites span environmental and spatial gradients, with variability in the degree of urbanization of surrounding land as a main structuring gradient, and have been the focus of a metacommunity analysis along urbanization gradients (Gianuca et al. 2018). We used the same data set to analyse niche use patterns along the urbanization gradients, to 1) assess differential niche use among cladoceran species, 2) assess differential

niche use for contrasting functional groups linked to body size) and 3) evaluate niche shifts within species associated with urbanization pressure. Additionally, 4) we examined the relative contribution of niche differentiation compared to other (environmental and spatial) processes in explaining community assembly patterns and species coexistence. We hypothesized that larger species would occupy niche space in favourable environments (high productivity) because they are stronger competitors (Brooks and Dodson 1965, Burns 1969, Gliwicz 1990, Shurin et al. 2009). We also hypothesized that mainly generalist species would persist in urban environments due to the high disturbance level, based on the specialization-disturbance/urbanization-tolerance hypothesis (Preston 1962, Futuyma and Moreno 1988, Vázquez and Simberloff 2002). We expected zooplankton to show non-random, segregated patterns due to strong interspecific competition in zooplankton communities. We also hypothesized that co-occurrence patterns would be structured more by limiting similarity (favoring co-occurring species with dissimilar niche use; MacArthur and Levins 1967) than by geographic properties or by the observed site environmental properties.

Material and methods

Occurrence and environmental data

The dataset used in this study is previously described in Gianuca et al. (2018). It contains information for 81 zooplankton pond communities from a field survey in the northern part of Belgium (Supporting information). Briefly, sites were selected using an a priori GIS analysis of percentage built-up area (%BUA, percentage of area covered by buildings) from polygons around the cities of Ghent, Brussels, Antwerp and Leuven. Sites were chosen according to a stratified hierarchical design, with 27 regional scale (3 × 3 km) plots chosen at each of three classes of built-up area (high: > 15% BUA, medium: 5–10% BUA and low: < 3% BUA), and a total of three ponds from each of these categories sampled within each regional plot. The scores for percentage built-up area used for each site were calculated a posteriori by combining ground building value and biologically valuable area, for both a 50 and 3200 m radius around each pond (Brans et al. 2017, 2018). Ponds were surveyed in a randomized manner (at the among-plot level) between May and July 2013, and a suite of physical, chemical and morphometric pond properties were measured (Supporting information). Standard water properties (pH, oxygen concentration, conductivity, sneller depth) were measured and water samples were collected to determine the concentration of chlorophyll A, total and available phosphorus and nitrogen, suspended matter, dissolved organic carbon, alkalinity and sulphate ions. At each site, maximum water depth was measured using a graduated stick along an orthogonal transect of the pond, sludge depth and surface area were measured, and the properties of percent shade cover, percent cover by submersed, floating, emergent and overhanging vegetation were visually assessed. At each site, the cladoceran zooplankton community was sampled by collecting a 40 l water sample with a depth-integrated water sampler (8 sample locations per pond, using a 7.5 cm diameter tube sampler, collecting 5 l per sample) in both the pelagic and littoral zones of the pond. This water was filtered over a 64 µm sieve and fixed with 7% formalin for subsequent identification. For each sample, a minimum of 300 individuals were identified to species and counted. Counting continued until no new species were observed in the last 100 individuals. Densities were calculated as the number of individuals per L, and body length (mm) was measured for 15 individuals from each species in each sample (30 individuals for *Daphnia magna*). More information on the study site selection and environmental variables studied can be found in Brans et al. (2017) and Gianuca et al. (2018).

The occurrence dataset consisted of 28 species in total, but some species were more commonly observed than others. The rarest species do not provide enough information to separate niche use from occurrence, so we restricted our niche analysis to the 16 species in the dataset with at least 5 occurrences. We measured available environmental (niche) space using the 21 abiotic, biotic and morphometric pond measures (Supporting information). These variables represent water quality requirements and other important aspects of pond environment that have been shown to structure zooplankton communities (Davies et al. 2010, Casas et al. 2011, Pinel-Alloul and Mimouni 2013, Hassall 2014).

Niche volume

A principal component analysis was performed on the entire environmental dataset (21 variables) after standardization of the variables to zero-mean and unit variance. For each species, niche volume was quantified as the convex hull volume, or the volume of the smallest convex set in the first two PC axes (which explain 34.2% of total variance) that contained all the sites where the species was present (using the Quickhull algorithm in 'convhulln' implemented in the R package 'geometry', Habel et al. 2019, in R ver. 3.5.0, 2018). As such, niche volume represents the environmental conditions that a species occupies, i.e. the realized niche. Niche volume ranged from 7.06 to 48.80 (Table 1), out of a maximum of 58.36 which represents the niche volume of the entire available environmental niche space (in the first two PC axes).

Analysis of generalists versus specialists and large versus small species

Species with large niche volumes (> 30, upper quartile) were categorized as generalist species, while species with small niche volumes (< 10, lower quartile) represent specialists with narrow environmental tolerances. In addition, species were categorized based on body size, quantified as the mean body size found across all communities where the species was present (Table 1; Brans et al. 2017). Body size is a major structuring factor in zooplankton communities and large bodied species generally are competitively superior to

Table 1. Niche volume, number of site occurrences (for all sites, and for urban and rural sites – values are given at the 50 and 3200 m spatial scale for urban sites), and functional properties (habitat specialization and body size) of species that occur in 5 or more sites.

Species	Niche volume	Site occ.	Urban occ. (50, 3200 m)	Rural occ.	Habitat specialization	Body size category	Body size (mm)
Alona guttata	28.81	15	4,3	5,4	/	Small	0.26
Alona rectangula	20.27	13	2,6	7,3	/	Small	0.35
Bosmina longirostris	21.02	17	2,5	8,3	/	Small	0.33
Ceriodaphnia sp.	26.57	20	7,7	5,7	/	Small	0.53
Chydorus sphaericus	48.80	64	21,19	19,18	Generalist	Small	0.26
Daphnia longispina c.	38.26	36	12,13	7,10	Generalist	Large	0.76
Daphnia magna	9.23	7	1,2	1,4	Specialist	Large	1.8
Daphnia obtusa	27.02	16	5,6	2,3	/	Large	1.14
Daphnia pulex	31.09	23	7,9	5,8	Generalist	Large	1.37
Graptoleberis testudinaria	7.06	6	0,1	4,1	Specialist	Small	0.38
Leydigia quadrangularis	12.29	5	2,2	2,0	/	Small	0.52
Pleuroxus aduncus	8.35	8	0,1	2,2	Specialist	Small	0.41
Pleuroxus truncatus	8.41	10	0,1	6,4	Specialist	Small	0.46
Scapholeberis mucronata	18.13	24	4,8	8,9	/	Small	0.51
Simocephalus exspinosus	30.97	22	11,10	2,4	Generalist	Large	0.95
Simocephalus vetulus	12.46	14	4,1	4,6	/	Large	1

smaller-bodied species (size-efficiency hypothesis; Brooks and Dodson 1965, Gliwicz 1990, Tessier et al. 2000). We used a complete linkage clustering algorithm (implemented in the 'base' R package) to classify species into small and large body size categories.

Niche overlap

We quantified niche overlap between species pairs (aim 1) and between urban and rural populations of the same species (aim 3) using the framework of Broennimann et al. (2012). We first reduced the available environmental space to the first two axes of a principal component analysis that includes the environmental properties of all sites within the study area, and those sites associated with species occurrences (PCA-env; Broennimann et al. 2012). These axes explained 34.2% of the variation in PC-env space (Supporting information). We then divided this environmental space into a 100 × 100 grid of cells. For each cell, we calculated the density of occurrences of each species (o_{ij}, the kernel density estimation of the number of occurrences of the species at sites with the environment given in cell *ij*, where *i* and *j* refer to the cell corresponding to the *i*th and *j*th bins of the environmental space), the density of available environments (e_{ij}, the kernel density estimation of the number of sites with the environment given in cell *ij*), and the occupancy of the environment by each species (z_{ij}, which is o_{ij}/e_{ij}, scaled by the maximum *o*/*e* value in the community occurrence dataset). The smoothed density of occurrences and available environments are estimated using a Gaussian kernel density function. The occupancy of the environment by each species (z_{ij}) ranges between 0 and 1 and provides a measure of environmental occupancy that is independent of sampling effort and of the unequal availability of environments across study areas (Broennimann et al. 2012 eq. 3a; we generally refer the reader to Broennimann et al. 2012 for more information about how these indices are calculated). We used this value, z_{ij}, as a measure of niche occupancy. We then calculated a measure of niche overlap, the *D* metric (*Dscore*; Schoener 1970, Warren et al. 2008), using the z_{ij} values obtained for each species. *D* quantifies the overlap in niche occupancy between two species across the entire environmental space, and is independent of any difference in availability of the environments between the subsets of sites occupied by each species being compared, as well as of the resolution of the environmental grid chosen. *D* ranges from 0 (no niche overlap) to 1 (complete overlap).

To determine the change in niche use of species in response to urbanization (aim 3), we compared niche occupancy for each species in a subset of the total dataset with sites in an urban setting or in a rural setting. Different spatial scales of urbanization may influence species niche shifts, so we calculated urbanization using percentage of built-up area for an area within 50 m radius around the pond (local scale, n = 45), and for an area of 3200 m radius around the pond (regional scale, n = 47) and calculated niche overlap between rural and urban populations at these two scales separately (urban setting: n = 21 using 50 m radius, 23 using 3200 m radius; rural setting: n = 24 sites). Metrics were calculated using the 'ecospat' package (Broennimann et al. 2018) in R.

Co-occurrence patterns

Based on the occurrence dataset, pairwise species co-occurrences were calculated using normalized checkerboard scores (*Cscore*, Stone and Roberts 1990). Non-random co-occurrences (whether or not species co-occurred more or less than expected by chance) were assessed via a standard null model approach (Gotelli 2000, Gotelli and Ulrich 2010). This 'fixed-equiprobable' null model uses an algorithm that reshuffles species occurrences across sites while keeping the number of occurrences for each species over all sites constant. This analysis was repeated for 10 000 iterations (using ecospat.Cscore in 'ecospat' package), producing the mean of predicted null *Cscore* distribution, the observed *Cscore* for

each species pair, and the standardized effect size of *Cscore* (*CscoreSES*). Standardized effect sizes are calculated by subtracting the *Cscore* values under the null distribution from the observed values and dividing them by the standard deviation of the null distribution (Cohen's d; Supporting information). Positive *CscoreSES* values suggest segregated co-occurrence patterns, while negative values represent more aggregated co-occurrence patterns than expected from a random distribution (Broennimann et al. 2012).

Drivers of co-occurrence patterns

To determine the importance of niche differentiation compared to other environmental and spatial drivers of co-occurrence patterns (aim 4), we considered four potential explanatory variables of the *CscoreSES* for each species pair in a linear model following Bar-Massada and Belmaker (2017). The first was similarity in niche use (pairwise niche overlap; *Dscore*). The second was a measure of the likelihood that species co-occur based on the geographic proximity of sites occupied by each species, *Geomean*. To calculate this, for each species we estimated an occurrence probability using geographic proximity to other occupied sites using a Gaussian kernel density smoother (following Belmaker et al. 2015). This probability was calculated using spatial interpolation (using R packages 'adehabitatMA', 'adehabitatHR', 'raster' and 'SDMTools'; Calenge 2006, VanDerWal et al. 2019, Hijmans 2020). For each species, we split the record of presence-absence across the 81 sites into a training and testing dataset depending on the number of occurrences of that species (80:20 training:testing of the 81 sites for species with $N > 25$ occurrences, 60:40 for $25 \geq N \geq 13$ and no split for $N < 13$). The occurrence probability for species with $N < 13$ occurrences was taken as the average across all 81 sites, and for species with $N \geq 13$ occurrences, the value for each site was taken as the average across 100 repetitions of the training and testing procedure. The mean probability of occurrence of each pair of species (*Geomean*) thus measures the probability of species co-occurrences predicted solely on geographic proximity (i.e. independent of environmental suitability), where low values correspond to species that are likely to be found in different geographic regions. The third explanatory variable was the overall suitability of the landscape in terms of environmental properties for a species pair, *Habmean*. This pairwise measure of joint habitat suitability expresses how suitable sites are for a certain species pair as a measure of location along environmental gradients. We estimated *Habmean* by creating a species distribution model (SDM) using MaxEnt (Phillips et al. 2006; implemented in R using the 'dismo' package; Hijmans et al. 2017) to quantify the suitability of each site for each species based on their occurrences in environmental space. This generates values between 0 and 1, where zero values are sites that are highly unsuitable for that species and sites with values of 1 are highly suitable habitats for that species (additional information for SDMs and model assessment are given in the Supporting information). An overall estimate of habitat suitability for each species pair was calculated by taking the mean environmental suitability value of the two species over all sites (Bar-Massada and Belmaker 2017), where low values of *Habmean* represent a species pair that is found in sites further away from their environmental niche optimum. The fourth explanatory variable was a measure of environmental heterogeneity for the regions in which each species pair occurred, *Volsum*, calculated as the convex hull volume that contains all sites where both species were present in the space of the first two PC-env axes (following Bar-Massada and Belmaker 2017).

Statistical tests

Niche use

To evaluate niche differentiation in the metacommunity of Cladoceran zooplankton (aim 1), we assessed significance of niche overlap scores (*D*) using niche equivalency and niche similarity tests for all pairs of species (Broennimann et al. 2012). The niche equivalency test compares the niche overlap (*D*) of a pair of species to overlaps between random niches, created by randomly reallocating occurrences for each species among all possible sites and computing the corresponding *D* value (Warren et al. 2008; 100 random reallocations were used). The niche similarity test determines the relationship between the niche of one species and the occurrence of a second species. It compares the observed niche overlap between the first and second species in a pair to the overlap between the first species and random niches available in the range of the second species (obtained by randomly re-allocating occurrences of the second species; Warren et al. 2008). Significance was assessed by randomly reallocating occurrences 100 times, changing the order of the species in the pair (so that both species have their occurrences randomly reallocated 100 times), and calculating the number of times the observed value was greater than or equal to the randomized values.

Functional groups

We tested for an association between species body size and niche use (aim 2), first by applying a discriminant function analysis (using R package 'MASS', Venables and Ripley 2002) to determine the percent of species successfully reassigned to the correct body size class based on their position in niche space, then by testing the significance of differential niche use between large and small species using a multivariate analysis of variance (MANOVA). To evaluate niche differentiation among generalist and specialist species, we compared *D* scores for all pairs of species in the bottom (< 10, $n = 4$) and top (> 30, $n = 4$) quantile of niche volume. We used ANOVA to determine whether *D* values differed for pairs of the four most generalist species, for pairs of the four most specialized species, and for the generalist versus specialist species pairs and used post-hoc t-tests to determine which sets had significantly different *D* scores.

Urban niche shifts

We used niche equivalency and similarity tests (on *D* scores) to determine whether the urban and rural niches of species were

more diverged than expected by chance (Broennimann et al. 2012; aim 3). We also quantified and tested for three aspects of niche shifts from rural to urban habitats: niche stability, niche expansion and niche unfilling (i.e. niche contraction; Petitpierre et al. 2012). Niche stability measures the shift in mean niche position in environmental space from rural to urban habitats (quantified as the proportion of the species' densities in the urban environmental distribution that overlap with the rural distribution). Niche expansion is the proportion of the urban niche that is not overlapping with the rural niche (measured as the proportion of the densities in the urban distribution located in different environmental conditions than the rural distribution, 1 − stability) and niche unfilling is the proportion of the rural niche that is located outside the urban niche (measured as the proportion of the densities in the rural distribution located in different conditions than the urban distribution). For all three indices, the analysis was performed including the 90% percentile of the environmental densities, in order to exclude some of the marginal environmental habitat values (Petitpierre et al. 2012). Niche expansion and unfilling of more than 10 percent are considered to be substantial niche shifts (Petitpierre et al. 2012). These analyses were performed only for the subset of species that occurred in more than four urban and more than four rural sites. Most species showed fewer occurrences than this in at least one habitat type. Only four taxa met the requirement at the local (50 m) urbanization scale, and five taxa (the same subset from the local scale with one additional species) were retained at the regional (3200 m) scale. To better understand the differences in available niche space between rural and urban sites, we tested for homogeneity of group dispersions for rural versus urban sites at the 50 and 3200 m scale (using the euclidean distances among sites based on centered and scaled environmental variables; Anderson 2006; implemented in the R package vegan; Oksanen et al. 2020). We also compared environmental variation in rural and urban sites using a principal component analysis (one analysis for the n = 45 sites at the 50 m scale of urbanization, and a second analysis for the n = 47 sites at the 3200 m scale of urbanization).

To evaluate whether species at urban or rural sites formed nested subsets of one another, we calculated the nestedness temperature, *T* of the species presence-absence matrix (Atmar and Patterson 1993, Rodríguez-Gironés and Santamaría 2006). This temperature is normalized to scale from 0 to 100 where 0 is a perfectly nested matrix and 100 is a maximally unnested matrix and is calculated by permuting rows and columns of the presence–absence matrix to maximize nestedness and then calculating the distance of the observed matrix to an isocline representing a perfectly nested matrix. We compared the observed *T* to a null distribution by randomly reordering the community matrix while preserving the number of presences and the site frequencies and asked whether our observed *T* differed from values expected by chance.

Occurrence and co-occurrence patterns

To assess whether spatial isolation influenced species occurrence patterns, we tested whether the species occurred in sites that were closer together than expected by chance using Monte Carlo randomization tests. For each species, we preserved the number of occupied sites, randomly permuted the identity of these sites 1000 times, and calculated the number of times the observed average distance between pairs of occupied sites was greater than or equal to the randomly generated values (Pantel et al. 2011).

Drivers of co-occurrence patterns

To determine whether niche use was the most important driving process behind the species co-occurrence patterns (aim 4), we analyzed the relative contribution of each of the drivers to explain the entire set of species co-occurrence scores (*CscoreSES*). We used a linear least squares model with niche overlap (*Dscore*), geographic proximity (*Geomean*), overall environmental suitability (*Habmean*) and environmental heterogeneity (*Volsum*) as explanatory variables. Significance of these predictors was assessed using likelihood ratio tests (we compared the log likelihoods of models with each individual predictor to a null model with no predictors, and added subsequent predictors if their log-likelihood significantly differed from the model with fewer predictors). To investigate the relationship between niche overlap and co-occurrence, we conducted a post-hoc evaluation of the relationship between the *CscoreSES* and *Dscore* of species pairs with nonrandom co-occurrence patterns. This was done by comparing the *Dscore* of species pairs with lower and higher *CscoreSES* values than expected by chance using a t-test. All statistical analyses were performed using R statistical software (R Development Core Team, ver. 3.5.0., 2018).

Results

Occurrence and environmental data

The occurrence dataset consisted of 28 species in total, with species richness varying from 0 to 8 species (Supporting information; measures for alpha, gamma and beta diversity, estimated using Shannon entropy, were $\alpha = {}^1D_\alpha = 3.98$, $\gamma = {}^1D_\gamma = 15.87$ and $\beta = {}^1D_\beta = 3.98$; Jost 2007). Species occur on average in 11.39 ± 2.62 (average ± SE) sites, and the number of occurrences ranges from 1 to 64 sites (Supporting information, Table 1).

Niche use

Niche equivalency tests indicated 15 out of 120 species pairs that significantly differed in their niche use (aim 1). 10 species pairs had equivalency lower than expected by chance and 5 species pairs had higher niche equivalency than expected by chance (Supporting information). Similarity tests indicated no species pairs with significantly lower similarity than expected by chance and 3 species pairs with higher similarity than expected by chance (Supporting information). Niche overlap (*Dscore*) did vary depending on whether species in the pair were both generalists, generalists versus specialists

and both specialists ($F_{2,25}=18.85$, $p < 0.001$; Supporting information). Generalist species pairs had on average higher niche overlap with other generalist species (mean ± standard deviation of D scores: 0.65 ± 0.06, n = 6) than they did with specialist species (0.33 ± 0.09, n = 16; $t_{14.14}=10.26$, $p < 0.001$) and compared to niche overlap among pairs of specialist species (0.27 ± 0.22, n = 6; $t_{5.65}=4.12$, $p=0.007$). Niche overlap did not significantly differ between generalist–specialist and specialist–specialist species pair comparisons ($t_{5.59}=-0.63$, $p=0.55$). These relationships may be influenced by the observed strong association between z_{ij}, which quantifies how a species occupies environmental niche space, and the total number of sites occupied in the region. We found that a species' average niche overlap with other species (D, where D is calculated using the difference in each species' z_{ij} values) is positively associated with the number of sites it occupies (Supporting information). The niche space occupied by generalist and specialist species is seen in the Supporting information.

Functional groups

The clustering algorithm indicated that the threshold of 0.76 mm best divided species into small and large body size groups. Linear discriminant analysis was successful in sorting cladoceran taxa into the broad body size categories of small (< 0.76 mm, 8 of 10 successfully re-assigned) and large (≥ 0.76 mm, 5 of 6 successfully re-assigned) based on their niche use (aim 2, Fig. 1 and 2). Multivariate analysis of variance indicated a non-significant trend (Wilks' $\lambda=0.66$, $F_{2,13}=3.38$, $p=0.07$) for the difference in environmental niche space between large and small bodied species. The direction of association for environmental variables with the first linear discriminant axis (LD1; Supporting information) indicates that small species are associated with high levels of oxygen, pH and submerged vegetation cover, whereas large species are associated with high levels of phosphorus, nitrogen, suspended matter and a high amount of chlorophyll a. However, one large species, *Simocephalus vetulus*, does not follow the general trend for large species and is instead more associated with environments with high oxygen, pH and submerged vegetation cover.

Urban niche shifts

Species in habitats spanning both rural and urban habitats (> 4 occurrences in each; n = 4 species at the 50 m and n = 5 species at the 3200 m scale) were mainly widespread (n = 20–64 ponds) species with relatively large niche volumes (volume > 18) (Table 1). Niche overlap (D) between rural and urban ranges of each species (aim 3) was high (between 49 and 59%) for the four species evaluated at the local scale, though most values were not significant after comparison to the randomized distribution of D scores (Supporting information; Fig. 3). The exception was *Chydorus sphaericus*, which had a significantly higher niche similarity than expected by chance. At the regional scales, most species had high niche overlap, and niche similarity was significantly greater for *Daphnia pulex* ($p=0.03$) than expected by chance. However, *Scapheloberis mucronata* had a low niche overlap with a significantly lower niche equivalency than expected by chance ($D=0.14$, $p=0.05$). Three of the four species evaluated at

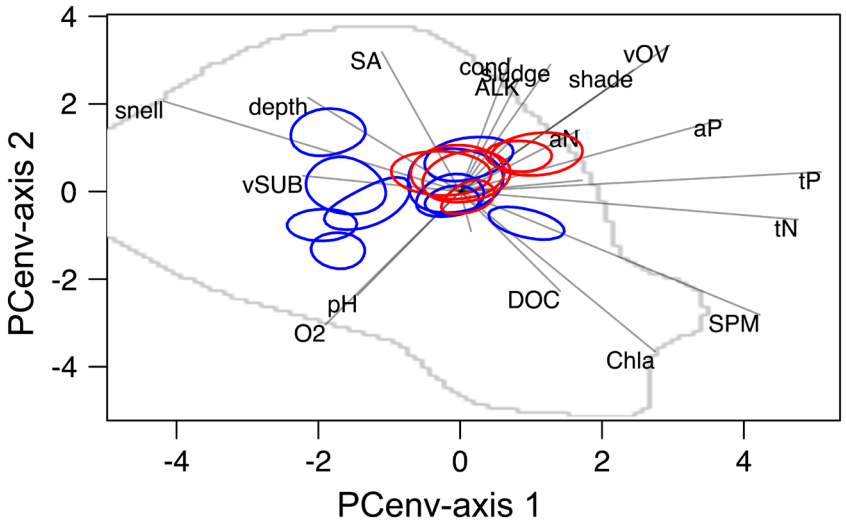

Figure 1. Niche use of cladoceran zooplankton in Belgian ponds. Ellipses are the 97.5% percentile of a species' density in the environmental space and lines indicate the scores of each environmental property for each PC-env axis. Large species are indicated by red ellipses and small species are indicated by blue ellipses. Text labels for some environmental variables were suppressed for readability (PC-env scores for each environmental variable are given in the Supporting information). The environmental variables and their associated labels are: percent shade cover (shade), sludge depth (sludge), sneller depth (sneller), conductivity (cond), pH (pH), maximum water depth (depth), oxygen concentration (O2), concentration of chlorophyll A (Chla), suspended matter (SPM), alkalinity (ALK), dissolved organic carbon (DOC), total and available nitrogen concentration (tN and tA), total and available phosphorus concentration (tP and tA), surface area (SA), submersed vegetation (vSUB) and overhanging vegetation (vOV). The suppressed variables are sulphate ions, floating and emergent vegetation.

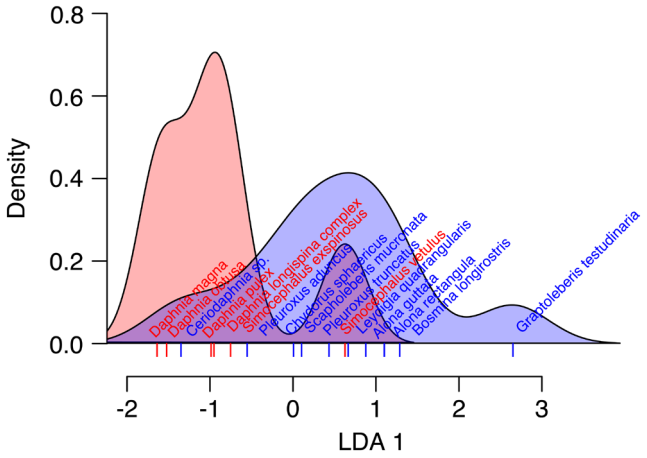

Figure 2. Density plot of species associations with a single linear discriminant axis (LDA1) that separates small and large-bodied cladoceran zooplankton. The density of small (blue) and large (red) species groups are depicted, as well as the position of individual species along the LDA1 axis.

the local scale and four of the five species assessed at the regional scale exceeded the 10% threshold for niche unfilling, i.e. only part of the rural niche was filled in the urban niche. *Scapheloberis mucronata* had an especially strong signal of niche unfilling: 78% of the rural niche was unfilled in the urban niche environment at the regional scale, and this species also displayed strong expansion as 41% of the urban niche did not overlap with rural niche. *Ceriodaphnia* sp. was the only other species with niche expansion exceeding the 10% threshold, observed at both the local and regional scale (Fig. 3). Tests of homogeneity of group dispersions for rural versus urban sites, which were based on euclidean distances among sites for all 21 environmental variables, did not indicate that available environmental niches differed significantly depending on site urbanization (50 m: $F_1 = 0.09$, $p = 0.77$; 3200 m: $F_1 = 2.05$, $p = 0.16$; see Supporting information for PCA biplots comparing rural and urban sites at the 50m and 3200 m scale).

The community presence–absence matrix was nested ($T = 33.75$) and the observed nestedness temperature was significantly less than values generated under null expectations ($p = 0.001$). However, we did not observe clear evidence that the site nestedness patterns corresponded to urbanization values observed at each site (Supporting information).

Occurrence and co-occurrence patterns

Only three of the sixteen species occurred at sites that were closer together than expected by chance and these were not limited to rare species that occurred in few sites (*Alona rectangula*, $p = 0.025$, $n = 13$; *Bosmina longirostris*, $p = 0.003$, $n = 17$; *Leydigia quadrangularis*, $p = 0.026$, $n = 5$; Supporting information). For co-occurrence patterns, tests for checkerboard scores (*Cscore*) indicate that checkerboard patterns cannot be distinguished from random null distributions for many pairs of species. Of 120 species pairs considered, 8 co-occur significantly more (6.67%) and 8 co-occur significantly less (6.67%) than expected by chance (Supporting information).

Drivers of co-occurrence patterns

We used a linear model, with predictors added if their log-likelihood significantly differed from a model with fewer predictors, to determine drivers of co-occurrence (*CscoreSES*). The best-fit model (AIC = 392.31) included niche overlap (*Dscore*: $\beta = -3.19$, SE 0.46) and environmental heterogeneity (*Volsum*: $\beta = 0.04$, SE 0.011), and significantly differed from a null model with no predictors (null model AIC = 415.83; $\chi^2_2 = 27.52$, $p < 0.001$; see Table 2 for AIC values and likelihood ratio test results for the other, non-significant predictors). Species co-occurrence patterns were thus significantly less segregated as niche overlap increased (a strong negative relationship between *CscoreSES* and *Dscore*) and significantly more segregated as environmental heterogeneity increased (a weak positive relationship between *CscoreSES* and *Volsum*). For the pairs of species with *Cscore* values that significantly differed from the score expected by chance (using randomization tests; red points in Fig. 4), those with higher *Cscore* values had significantly lower *Dscore* values than pairs with lower *Cscore* values ($t_{11.13} = 2.49$, $p = 0.03$).

Discussion

We quantified niche use for 16 cladoceran zooplankton species inhabiting ponds and small shallow lakes in Northern Belgium and found that species demonstrated distinct niche use. Niche use patterns were strongly associated with body size class and with species being generalists or specialists. Urbanization also structured species niche use as well. Generalist species were better able to establish in urban sites, and niches in urban sites compared to rural ones were largely conserved but with substantial volumes of niche space remaining unfilled. We also found a strong significant negative relationship between niche overlap and pairwise species co-occurrence (indicating that increased niche overlap leads to decreased segregation), a weaker positive relationship with environmental heterogeneity, and no significant relationship with geographic proximity (the co-occurrence patterns expected if species inhabit sites based solely on their spatial proximity to one another) or habitat suitability (the matching between a species' occurrence pattern and their environmental preferences). The fact that species with higher niche overlap tend to be more aggregated suggests that processes such as environmental filtering may be reflected in our study, and that competitive interactions may either be less important or may not be captured in our occurrence-based analysis (with exceptions for some pairs of species). Our study highlights the importance of evaluating niche use and assembly patterns

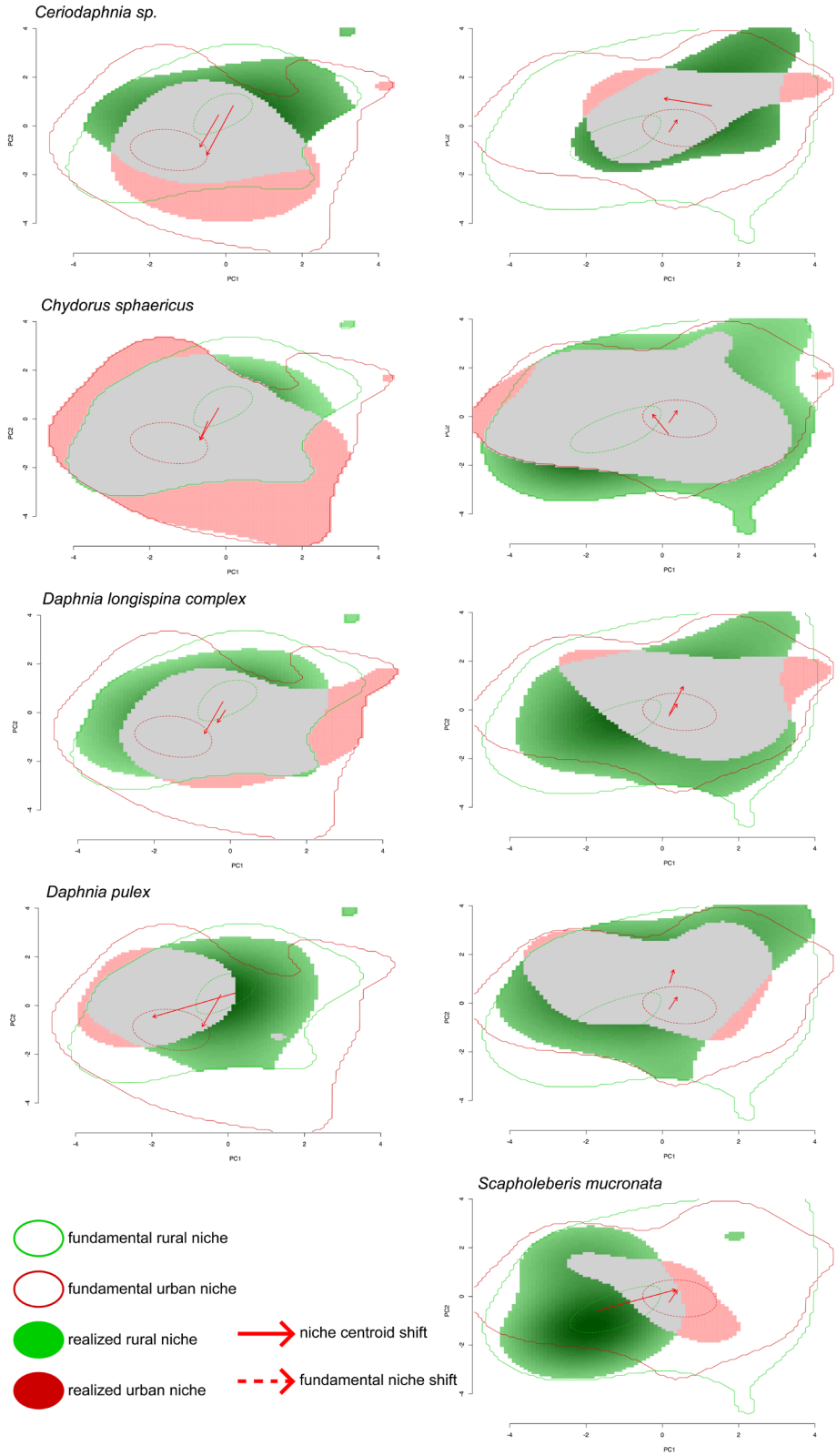

Figure 3. Niche shifts for zooplankton species from rural to urbanized habitats. Analysis at the local (50 m) scale is pictured at left and for the regional (3200 m) scale at right. The available rural niche space (the fundamental rural niche) is outlined in green and each species' realized rural niche is shown by the filled green contour. The available local urbanized niche space (the fundamental urban niche) is outlined in red and each species' realized local urban niche is shown by the filled red contour. Niche overlap between rural and urban habitats is colored in grey. Species' niche centroid shifts going from their rural to urban ranges are indicated with a solid arrow. The dashed arrow shows how the fundamental niche centroid shifts from the rural to urban habitats in the landscape.

Table 2. Model comparison of drivers of co-occurrence patterns (*CscoreSES*) using the Akaike information criterion. Models with log-likelihood values significantly higher than a null model with no predictors, or higher than a model with fewer predictors, are indicated in bold.

Predictors	AIC	χ^2	df	p	Comparison
1 (null model)	415.827	/	/	/	
Full model	**393.539**	**30.288**	**4**	**< 0.001**	Null
Dscore	**404.864**	**12.964**	**1**	**< 0.001**	Null
Geomean	417.514	0.314	1	0.575	Null
Habmean	417.824	0.003	1	0.953	Null
Volsum	**408.929**	**8.899**	**1**	**0.003**	Null
Dscore + Geomean	406.656	0.208	1	0.649	Model with Dscore
Dscore + Habmean	405.346	1.518	1	0.218	Model with Dscore
Dscore + Volsum	**392.310**	**14.554**	**1**	**< 0.001**	Model with Dscore
Dscore + Volsum	**392.310**	**27.517**	**2**	**< 0.001**	Null

not only for the entire metacommunity, but for subsets of species with functional or other properties in common.

Body size is an important effect and response trait in cladocerans, as it affects competitive ability and grazing efficiency of a species (Brooks and Dodson 1965, Burns 1969, Romanovsky and Feniova 1985), and in turn is affected by predation, nutrient limitation, temperature and other factors (Thompson et al. 2015, Gianuca et al. 2016). Zooplankton body size is considered a key functional trait in freshwater systems and is important in ecosystem functioning, as it directly impacts the top–down control on algae and indirectly maintains a clear-water state (Scheffer 1998, Carpenter et al. 2001). We found that body size categories were associated with broad niche use patterns, but that individual taxa still displayed variation in their particular niche preferences. Larger species were associated with high nutrient levels and high amounts of chlorophyll a, which matches expectations from studies indicating that larger zooplankton species are more sensitive to low food quality (phosphorus content) and quantities compared to smaller species (Hessen and Lyche 1991, Gulati and Demott 1997, Nelson et al. 2001, Weider et al. 2008). The small species on the other hand occupied a more diverse range of the environmental niche, and were also strongly associated with the amount of submerged vegetation at a site (Fig. 1). The clustering of *S. vetulus*, a relatively large-bodied cladoceran that lives associated with macrophyte surfaces, with the small-bodied taxa, many of which benthic or epiphytic, suggests that the small-bodied species group to some degree also represents alternate feeding habits compared to the pelagic cladocera in the large-bodied group (Stansfield et al. 1997). The study of Gianuca et al. (2018) did find that metacommunity structure varied for these general body size classes in urban and rural environments, but did not define the niche preferences of the individual species nor did it evaluate the potential for biotic interactions to structure occurrence patterns in rural and urban habitats. We also note that our survey was focused on ponds without visual predators such as fish. In systems with fish, large bodied species are expected to be absent not only from low quality habitats but also from habitats with strong predation pressure by visual predators (Brooks and Dodson 1965, Boven and Brendonck 2009, Drenner et al. 2009).

Our analysis on the most generalist and specialist species also indicated niche use differences. Specialist species were distinct in their niche use patterns both from generalists and from other specialists (Supporting information), which suggests that they are sorting to use particular niche axes. This result aligns with findings in other studies that local environmental properties are important for structuring specialist species (Pandit et al. 2009, Liao et al. 2016). However, these studies have suggested that regional spatial processes are more important for community assembly in generalist species. In this study, we find evidence suggesting that body size segregation, species interactions inferred through co-occurrence patterns, and the increased ability of generalist species to persist in disturbed urbanized habitats are important for the regional coexistence of specialists with high niche overlap.

Niche overlap between species in rural and urban subsets of ponds was high for four of the five taxa that occurred in enough sites to evaluate niche shifts associated with urbanization, and this overlap was significantly higher than expected by chance for two species (*C. sphaericus* for urbanization at the local 50 m level and *D. pulex* at the regional 3200 m level), indicating niche centers were largely conserved across the environmental shift. However, three of these four taxa showed strong patterns of niche unfilling, where species in the urban sites occupied only a subset of the niche space available in the rural sites. A fifth species, *S. mucronata*, displayed significant niche divergence between urban and rural ponds at the regional level, induced by both niche expansion of the urban niche as well as partial niche unfilling compared to the rural niche. *Ceriodaphnia* sp. displayed niche expansion as well. Taken together, these results indicate that niches are not fixed in urbanized habitats. We also observed that mainly widespread species with relatively large niche volumes were found in urban habitats (Table 1 and Supporting information). Our data suggest that mainly generalists are able to occur in urban habitats, with substantially unfilled (*Ceriodaphnia* sp., *D. longispina complex*, *D. pulex*) or diverged (*S. mucronata*) niches. Two taxa (*Ceriodaphnia* sp., *S. mucronata*) expanded their niche use in the urban sites. The lower occurrence of specialized taxa in urban ponds, known to be highly unstable, thus matches the specialization-disturbance hypothesis (Preston 1962, Vázquez and Simberloff 2002). Under this theory, species with a limited environmental range are more sensitive to environmental disturbances than generalists (Boulangeat et al. 2012, Slatyer et al. 2013, Carboni et al. 2016). Stochastic extinction also influences establishment patterns in disturbed environments. Rare species that go locally extinct due to chance may not recolonize sites for much longer time periods than common species because of the lack of colonizers from surrounding habitats (Volkov et al. 2003, Leibold and Loeuille 2015). Our study adds to an increasing number of studies that observe increased urbanization causing biotic homogenization and

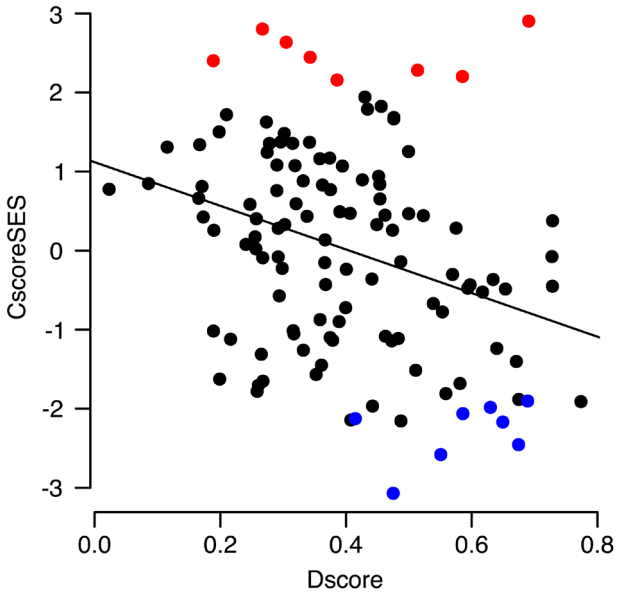

Figure 4. Scatterplot of niche overlap (Schoener's D metric, *Dscore*) against standard effect size of checkerboard score (*CscoreSES*). Species pairs with significantly greater or lower *Cscore* values than expected by chance are highlighted in red and blue, respectively.

species loss (Rahel 2002, Olden and Poff 2003, McKinney 2006), drawing further attention to this threat to natural biodiversity patterns. High disturbance, urban habitats can favour generalists, causing them to become widespread and locally abundant. Increased urbanization may thus increasingly threaten rare species in aquatic systems.

Species co-occurrence patterns in a given landscape emerge as a product of a number of factors, including geographic connectivity and other spatial properties, environmental properties, species interactions and drift. Our finding that pairs of species with aggregated occurrences tended to have higher niche overlap than segregated pairs of species (low *CscoreSES* and high *Dscore*) did not match our expectations based on the principle of limiting similarity (MacArthur and Levins 1967). In this hypothesis, interspecific competition should produce coexistence of species with dissimilar niches. Our results indicate the opposite pattern, suggesting that environmental filtering (where species are limited by their matching to local environmental conditions; i.e. the species sorting concept of Leibold et al. 2004) is operating for many species pairs in our study system. Environmental filtering selects for species that are best adapted to the local environment, hence co-occurring species have more similar niches than expected by chance (Leibold 1997, Mayfield and Levine 2010). However, it is important to note that this pattern is not responsible for the co-occurrence patterns of all pairs of species. Some species pairs displayed classic limiting similarity relationships as well (points in the top right of Fig. 4). *Chydorus sphaericus* and *D. pulex*, *C. sphaericus* and species of the *D. longispina* complex, and *A. guttata* and *D. pulex* all had high niche overlap and co-occurred in fewer sites than expected by chance, indicating that competition may have led to exclusion of one of the two species in mutually favorable sites (Supporting information). These co-occurrence patterns align with the expectation under Diamond's (1975) assembly rules when species interactions structure community composition. It is also important to note that the relationship between niche overlap and co-occurrence patterns is unlikely to capture other mechanisms for coexistence of competing species (e.g. in a temporally fluctuating environment, Chesson 1994; due to a spatial storage effect, Chesson 2000), and that the process of community assembly may fundamentally differ for sites that lie along an urbanization gradient (Magura et al. 2018). Our findings of variable structure across all species pairs highlight the importance of understanding that a variety of processes structure co-occurrence in metacommunities on a landscape scale. It is unlikely that any single assembly mechanism is adequate to summarize the complexity that arises when multiple abiotic, biotic and spatial processes in a landscape combine to structure community composition. Analysis of individual pairs of species can reveal patterns not possible in surveys that use sites as the unit of observation (i.e. studies of communities that use variation partitioning, Cottenie 2005).

The zooplankton communities in this survey contained many rare species and many species pairs had co-occurrence patterns that were not clearly distinguished from patterns expected by chance. Of the 120 species pairs included in the co-occurrence analysis (12 of the 28 species were not considered because they occurred in three or fewer sites), 15 co-occurred at 0 sites and 16 had non-random co-occurrence. These attributes are quite common in community ecological surveys. Most community assemblages contain many rare species and a few common species (Magurran and Henderson 2003) and our observed distribution of co-occurrences (Supporting information) is similar to those found in many surveys of animal communities (Horner-Devine et al. 2007). The pairs of species that appear to be structured by limiting similarity (e.g. strong niche overlap and strong checkerboard patterns) were actually some of the most common species, as well as the broadest habitat generalists, in our survey (Table 1). These observations for the rare and specialist versus common and generalist species is in line with expectations of the core-satellite hypothesis (Hanski 1982). This theory predicts that occurrences of satellite (rare) species are driven by dispersal and associated co-occurrence patterns should display random or aggregated patterns, while core (common) species should lead to more segregated patterns due to competition (Diamond 1975, Ulrich 2004). Although there are no spatial aggregations in co-occurrence patterns found for abundant species, we should be careful inferring processes such as dispersal limitation, because the lack of significant co-occurrence patterns may also result from the reduced power to detect patterns inherently associated with rare species.

The nature of our survey precludes analyses that take other potential structuring mechanisms into account. For example, our taxon-based co-occurrence analysis does not consider whether aggregated patterns result from co-occurring species with distinct functional traits that enable coexistence within the same habitat without sharing the same niche (within-site

niche partitioning), thereby reducing competitive interactions between them (Davies et al. 2007). Furthermore, our analysis does not allow us to incorporate indirect species interactions. As such, some pairwise patterns can be disguised because of the interference of a third species (Cazelles et al. 2016). Finally, our empirical data provides a snapshot in time. Ponds may not be at equilibrium when sampled and likely show temporal variation (Araújo et al. 2011, Tulloch et al. 2016). However, our approach of taxon-based pairwise co-occurrence analysis does provide an opportunity to consider patterns of community assembly that cannot be observed when focusing on analysis of among-site variation in composition. Here we can isolate particular species that are structured by particular attributes of the landscape around them (see Warren 2012 for more insight into the usefulness of taxon-based occurrence modeling), which presents insights about species niche use as well as the impacts of niche overlap with other species and of stressors such as urbanization.

In addition to describing niche volume and occupancy for the different cladoceran species in the region, our study provides information about the impact of urbanization for freshwater invertebrates. Our results showing that specialist species may be unable to colonize urban sites reflects other studies indicating increased biotic homogenization for invertebrate taxa (Deguines et al. 2016, Knop 2016, Merckx and Van Dyck 2019). Previous studies of birds have shown evidence of niche expansion (Pagani-Núñez et al. 2019), but we observed that niche unfilling – where the species only partially occupies its environmental niche – was the dominant pattern for species inhabiting both rural and urban habitats. This pattern has been commonly observed when comparing niche use for invasive species with their native ranges, across various vertebrate (Strubbe et al. 2013, Tingley et al. 2016, Cardador and Blackburn 2020), invertebrate (Polidori et al. 2018) and plant (Petitpierre et al. 2012) taxa. However, niche filling has not been studied as commonly in the context of urbanization. Given common responses to urbanization observed across diverse taxonomic groups (Merckx et al. 2018, Piano et al. 2020), an interesting area of future research will be to identify whether niche unfilling is a general phenomena for species that occupy urbanized environments.

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Author contributions

Jelena H. Pantel: Conceptualization (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Jessie M. T. Engelen**: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Luc DeMeester**: Funding acquisition (lead); Investigation (supporting); Project administration (equal); Resources (lead); Supervision (lead); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data and R code are available from Github (<https://github.com/jhpantel/zoop-niche>) (Pantel et al. 2022) and the Zenodo Repository (<https://doi.org/10.5281/zenodo.5914941>) (Pantel 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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