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Covariation between local and landscape factors influences the structure of ground-active arthropod communities in fragmented metropolitan woodlands

Matthew A. McCary · Emily Minor · David H. Wise

Abstract

Context The world is becoming increasingly urbanized, with more than half of the global population now living in cities. Understanding the factors impacting natural communities in fragmented landscapes is therefore crucial for predicting how the remaining ecosystems will respond to global change. Ground-active arthropods, which are important in nutrient cycling, are likely sensitive to habitat changes resulting from urbanization.

Objectives We addressed two questions: (1) What is the relative importance of local and landscape factors in shaping ground-active arthropod communities in urban woodlands? (2) How does body size (as a surrogate for dispersal ability) affect sensitivity to landscape-level factors?

Methods In the summers of 2010 and 2011, we sampled ground-active arthropod communities in 19 woodlands in the Chicago metropolitan region using pitfall traps. We also assessed local plant and soil characteristics, as well as landscape-level variables using GIS.

Results Redundancy analyses and variation partitioning revealed that local factors, particularly invasive woody-plant cover and soil nitrate, had the most influence on arthropod communities, explaining 12% of the total variation. Of the landscape-level variables, landscape richness, which is one measure of landscape fragmentation, explained the most variation; however, the shared variance between landscape and local variables was responsible for half (16%) of the total explained variation (32%). Landscape factors alone explained only 4% of variation. No relationship between arthropod body size and landscape variables was observed, but several groups (e.g. ants and ground beetles) were correlated with landscape-level factors.

Conclusions Our research shows that both local and landscape variables are important in influencing ground-active arthropods, but the majority of explained variance is attributed to the covariation between landscape richness, invasive woody-plant cover, and soil nitrate. We therefore conclude that landscape fragmentation is likely affecting the ground-active arthropods through its positive influence on invasive woody plants and soil nitrogen.

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Introduction

More than half of the world's human population lives in cities and this number is expected to reach over 70% by 2050 (Heilig 2012). Urban development fragments landscapes and reduces available habitats for many plant and animal species (Pauchard et al. 2006; McKinney et al. 2008). In particular, urbanization leads to changes in the structure of local communities (Bolger et al. 2000; McDonald et al. 2008), disruptions in ecosystem functioning and dynamics (Alberti 2005; Hutyra et al. 2011), and species extinctions (Pimm and Raven 2000; Fattorini 2011). Understanding the mechanisms by which urbanization elicits these ecological changes is critical for predicting how the remaining ecosystems will respond to fragmentation and global change.

One fundamental debate relating to how urbanization impacts ecological communities is whether the local or landscape scale is more important in structuring urban ecosystems (i.e. the local- vs. landscape-scale debate; Wright et al. 2003). Local factors include abiotic (e.g. soil moisture and nutrients) and biotic characteristics (e.g. plant structure and composition), and are often referred to as a resource-related question (Niemelä et al. 1996; Donovan et al. 1997). In contrast, landscape-level factors are factors that occur at the broader scale and are typically associated with dispersal limitation (Dauber et al.2005; Purtauf et al. 2005). Previous findings are inconclusive in determining which scale is more important (Schmidt et al. 2005; Bergman et al. 2008), and the answer appears to be strongly related to the taxon of choice (Tscharntke et al. 2012; Kennedy et al. 2013). For instance, spider and ground-beetle diversity in agricultural grasslands is more affected by landscape-level processes than local factors, with increased complexity in the broader landscape generally leading to increased species richness (Clough et al. 2005; Gardiner et al. 2009). Other arthropod groups such as ants and millipedes have been found to be mostly affected by local factors (Dauber et al. 2005; Philpott et al. 2014), which has been attributed to the access and quality of resources occurring at the local scale. While there have been important advances in the local versus landscape debate (Donovan et al. 1997; Tscharntke et al. 2007), such inconsistent findings have made it difficult to select the appropriate scale when managing vulnerable communities.

An important, yet often overlooked, aspect of the local- versus landscape-scale debate is the question of how much covariation occurs between the two spatial scales. Most research separates the scales into discrete units, which allows for a 1-to-1 comparison, but does not account for the potential covariance between local and landscape factors. In reality the boundaries of the two scales differ depending on the focal taxon, and it is likely that factors that occur at one scale may influence the processes of another. For instance, a large contiguous forest spanning > 25 square kilometers will likely affect the local temperature and moisture conditions by offering shading and creating a barrier for wind (Pielke and Avissar 1990; Chen et al. 1995). Similarly, intensive agricultural management practices at the local scale can result in reduced arthropod diversity and community composition at the landscape-level scale due to land-cover homogenization (Hendrickx et al. 2007; Gámez-Virués et al. 2015). One potential reason for inconsistent findings in the local versus landscape debate is that most studies have ignored the covariance, consideration of which might have helped tease apart the unique contribution of each scale. Thus, to advance the debate in determining which scale is more important in structuring ecological communities, there must be an evaluation for how the local versus landscape scales co-vary in time and space.

Ground-active arthropods, which are important players in litter decomposition and terrestrial food-web dynamics (Bardgett 2005), comprise one group of organisms likely to be affected by both local and landscape-level factors. At the local scale, plant structure and diversity in urban habitats influence arthropod diversity and community composition, with increasing plant diversity correlating with increased arthropod diversity (McIntyre et al. 2001). Landscape-level factors can also be important for ground-active arthropod communities in urban woodlands, as the surrounding matrix is generally impassible (e.g. concrete/urbanized land-cover types) and thereby reduces connectivity between patches. For instance, increasing cover of developed land typically resulted

in decreasing abundance of ground spiders in the broader landscape (Magura et al. 2010a; Vergnes et al. 2014). Given their important role in terrestrial ecosystems and sensitivity to both local and landscape factors, understanding the relative influence of local versus landscape scale in structuring ground-active arthropod communities will make an important contribution for the local- versus landscape-scale debate.

An additional reason ground-active arthropods are ideal for investigating the impacts of local and landscape variables is that they include a spectrum of body sizes, and thus possibly, quite different dispersal abilities (Coleman et al. 1999; Bardgett and Wardle 2010). Previous research has suggested that body size can be used as a surrogate for mobility and/or dispersal capability (Hoekstra and Fagan 1998; Kuussaari et al. 2014). For example, studies have reported positive correlations between dispersal ability and body size in which the larger the body, the greater the ability to disperse to new habitats (Jenkins et al. 2007; Warzecha et al. 2016). In a habitat with limited resources, larger species with greater dispersal abilities are more likely to encounter the matrix in pursuit for more favorable patches, and therefore, are more likely affected by landscape configuration and composition (Holland et al. 2005; Thornton and Fletcher 2014). On the contrary, smaller arthropods are less likely to reach and cross the patch's edge, rendering them more susceptible to factors operating at the local scale. Hence, body size of ground-active arthropods should be associated with sensitivity to local versus landscape-scale factors.

In this study, we evaluated the influence of local versus landscape factors in shaping ground-active arthropod communities in fragmented woodlands within the greater Chicago metropolitan region. We addressed two questions: (1) What is the relative importance of local and landscape factors in shaping ground-active arthropod communities in metropolitan woodlands? (2) How does body size affect sensitivity to landscape-level processes? To address these questions we took advantage of a "natural experiment" established by the Chicago Wilderness Land Management Research Program (Heneghan et al. 2012; McCary et al. 2015), which includes patches of woodland differing in size, surrounding habitat, and restoration/management history. We hypothesized that local factors will be more important in determining the structure of ground-active arthropod

communities relative to the landscape factors. Furthermore, we predicted that increasing arthropod body size will lead to an increased influence of the landscape-level variables.

Methods

Study sites

We conducted this study in the greater Chicago metropolitan region in northern Illinois, USA (Fig. 1). The region contains a wide variety of land-cover types, from densely built-up residential and industrial areas to large publicly owned green natural spaces. Each study site ($n = 19$) was a 1-ha section of woodland in the Chicago Wilderness Land Management Research Program (CWLMRP; McCary et al. 2015). Composition and structure of the vegetation varied among sites, ranging from dense understories of invasive shrubs to open woodlands with scattered herbaceous vegetation (McCary et al. 2015). Most sites were densely forested; only two were open enough to be classified as "savanna".

Arthropod sampling and local-variable dataset

Details of arthropod sampling and the collection of local environmental variables are described elsewhere (McCary et al. 2015). We used pitfall traps to sample the arthropod community in the summers of 2010 and 2011, but only data from 2011 was reported in McCary et al. (2015). Four pitfall traps were installed on each site for fifteen days in 2010 and for two 10-day intervals in 2011. To make data between years comparable, we calculated the average number of arthropods trapped per day (activity-density). For this study arthropods were sorted into 15 taxonomic units, from family to class depending upon the organism. The major groups were: Araneae, Carabidae, Collembola, Diplopoda, Formicidae, Isopoda, Opiliones, and Staphylinidae (see Supplemental Material Appendix 1 in Electronic Supplementary Material for full details). We decided to analyze these particular arthropod groups because they occupy numerous trophic levels and serve many different functions (Bardgett 2005). This grouping of taxa also includes varied means of locomotion as well as different body sizes and mobility. Median body size of each taxon was taken

Fig. 1 The distribution of sites across the greater metropolitan Chicago region. Dark grey shading indicates urban developed areas (i.e. developed open space, low intensity, medium intensity, and high intensity), and black shading denotes forested regions (i.e. deciduous, evergreen, and mixed forests). Names denote Illinois counties. Forest and developed land covers are from the 2011 National Land Cover Database (NLCD)
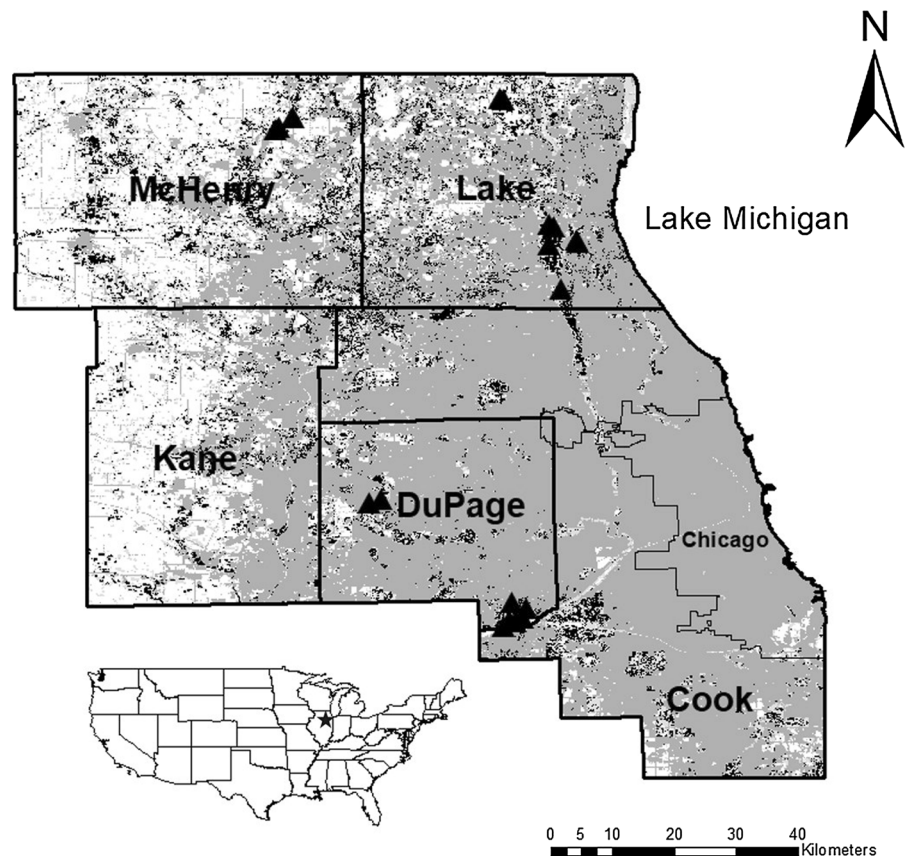
from Medel ([1995](#)), Coleman et al. ([1999](#)), and Bardgett ([2005](#)), and was used to define different size classes.

The CWLMRP research team sampled the plant community and measured soil characteristics on each of the 1-ha sites in 2010 or 2011 (McCary et al. [2015](#)). For this study we limited analyses to rates of uptake by plant-root simulators of nitrate (NO_3^-), phosphate ($H_2PO_4^-$), and calcium (Ca^{2+}), as our previous study (McCary et al. [2015](#)) suggested that variation in these soil nutrients was correlated with variation in activity-densities of ground-active arthropods. Plant cover was estimated according to functional group using the Braun-Blanquet cover classification system within nine 4-m^2 quadrats (McCary et al. [2015](#)). Plant-cover estimates included percent cover of trees, moss, invasive woody plants, invasive herbaceous plants, and leaf litter (Table [1](#)). Canopy cover was measured using a Nikon camera with a hemispherical fisheye lens (183° image), which was taken at breast height and at the ground layer. The resulting image was then analyzed using Gap Light Analyzer (Frazer et al. [1999](#)). Here, canopy cover was used to get an estimate of canopy denseness; all other plant-cover categories were used to estimate plant composition.

Landscape-variable dataset

No landscape-level factors were investigated in McCary et al. ([2015](#)). For the current study we measured five landscape-level variables hypothesized to be important to ground-active arthropods: (1) average distance to the edge of the woodland patch in which each 1-ha site was embedded; (2) landscape richness; and proportions of (3) developed land, (4) water, and (5) woodland in the surrounding landscape. Distance-to-edge was calculated by taking the distance from the center of the woodland patch to the edge along each of the four cardinal directions, and then averaging these values to get an estimate of patch edginess. The remaining four landscape-level variables were measured from the 2011 National Land

Table 1 Environmental datasets used to assess the influence of local and landscape variables on ground-active arthropod community structure

Variable	Description	Mean (min–max)
Local		
Ca^{2+}	Mean calcium uptake from soil	1726 (858–3432)
Canopy	Proportion of canopy cover in a 1-ha site	86 (76–91)
Invasive herbaceous	Mean invasive-herbaceous cover	6 (0–26)
Invasive woody	Mean invasive woody-plant cover	17 (0–45)
Leaf litter	Proportion of leaf-litter cover	61 (9–88)
Moss	Mean ground-moss cover	10 (0–49)
NO_3^-	Mean nitrate uptake from soil	64 (5–456)
$H_2PO_4^-$	Mean phosphate uptake from soil	4 (1–12)
Tree	Mean tree cover	2 (0–5)
Landscape		
Developed land	Proportion of developed land	36 (2–90)
Distance-to-edge	Mean distance to edge of woodland patch	317 (84–893)
Landscape richness	Total number of land-cover types	7 (4–11)
Water	Proportion of water cover	0.04 (0–0.1)
Woodland	Proportion of woodland habitat	66 (14–100)

Percent cover ranges from 0 to 100; uptake rates for soil nutrients are reported as μg nutrient/10 cm^2/month ($\sim$30 days). The units for distance-to-edge are meters

Cover Database (NLCD) at a 30-m resolution (Homer et al. 2015) using ArcGIS 10.3 (ESRI, Redlands, CA, USA). Because each site was dominated by forest cover, we did not use a diversity metric that included relative proportions of land-cover types in the calculation. Instead, we calculated landscape richness as the total number of land-cover types in the surrounding landscape (Wu et al. 2012). We considered the 16 different land-cover classes in the NLCD database to be the maximum possible number of land-cover classes. To calculate the proportion of developed land, water, and woodland habitat, the area of each land cover was divided by the total area at a specified radius. All developed land-cover types in the NCLD (developed open space, low intensity, medium intensity, and high intensity) were combined in the calculation for proportion of developed land. Similarly, forest land-cover types in the NLCD (deciduous, evergreen, and mixed forests) were combined to calculate proportion of woodland habitat.

Landscape richness and the proportion of developed land, water, and woodland habitat were initially calculated at four spatial scales (100, 200, 400, and 1600-m radii). These spatial scales were used because they represent scales in which ground-active arthropods are most responsive (e.g. Schmidt et al. 2005; Braaker et al. 2014; Barton et al. 2017). Although some buffers overlapped to some degree at the 1600-m radius, empirical and theoretical evidence suggest that

overlapping of landscapes does not contribute to spatial autocorrelation (Zuckerberg et al. 2012). However, we did test the major arthropod taxa for spatial autocorrelation and found that no arthropods were in violation (i.e. $P > 0.05$, Appendix 2 in Electronic Supplementary Material). After buffers were calculated, we then performed a redundancy analysis (RDA) on arthropod community structure with spatial scale as the predictor variable to determine which radius was most appropriate for the rest of our analyses (Braaker et al. 2014), defined as the radius with the highest adjusted R^2 (Borcard et al. 2011).

Statistical analyses

Two sets of analyses were performed: one to examine how local and landscapes variables correlated with the overall structure of the ground-active arthropod community (i.e. our dependent variable), and a second set to evaluate the relationships between activity-densities of individual arthropod groups and the landscape dataset. For the first set of analyses we used RDAs to determine which local and landscape variables explained the most variance in arthropod community structure. Arthropod activity-densities were Hellinger-transformed to minimize the effect of extreme values and double zeroes in the taxon-by-site matrix (Borcard et al. 2011). We used a square-root

transformation on all landscape variables and those local variables that exhibited a right-skew. We first tested both local and landscape-level environmental datasets for multicollinearity by calculating the variance inflation factor (VIF) for each variable; we found no evidence of substantial collinearity, as all variables displayed a VIF < 10 (Borcard et al. 2011). A stepwise selection procedure was then employed to identify those environmental variables explaining a reasonable proportion of variation in community composition for each dataset; variables with P values < 0.1 were retained in the respective local or landscape model. To help visualize the relationship between the predictor variables and arthropod community structure, we present a separate Principal Coordinate Analysis (PCoA) ordination plot with the retained environmental variables overlaid on top. This plot was performed on a Bray–Curtis dissimilarity matrix based upon ground-active arthropod activity-densities (Anderson et al. 2008).

Following the RDA for the complete arthropod dataset we used variation partitioning to differentiate the relative effects of local and landscape factors in structuring the ground-active arthropod community. Variance partitioning uses partial RDAs to calculate the amount of variation in community structure explained uniquely by each explanatory matrix (i.e. either the local or landscape dataset), as well as the shared variance explained by both explanatory matrices (Legendre et al. 2005; Peres-Neto et al. 2006). Variation partitioning is generally used to disentangle the impact of local and landscape processes on variation in community composition (Borcard et al. 2011). For this analysis only pure fractions are capable of being tested for statistical significance (i.e. a P value can be calculated only for the complete local or landscape fractions). After detecting the large amount of variation jointly explained by local and landscape-level variables, we further investigated the relationship among these explanatory variables using simple linear regressions.

To examine how landscape-level variables affect arthropod activity-density as a function of body size (the second set of analyses), we performed stepwise multiple regression for each arthropod taxon against the five landscape variables (Table 1). As with the entire arthropod dataset, to determine which spatial scale was most appropriate we first performed a stepwise multiple regression at each spatial scale (i.e.

100, 200, 400, and 1600 m) for each arthropod group, and then selected the radius resulting in the highest adjusted R^2 value. We also used linear regressions and scatterplots to further evaluate individual relationships between arthropod taxa and the explanatory variables that were retained in each respective multiple regression model. Only the arthropod taxa that represented $> 5\%$ of the total collection were used for our analyses.

For each test (i.e. RDA, variation partitioning, stepwise multiple regression, and simple linear regression), we present data for 2010 and 2011 averaged together, as arthropod community composition did not differ between the two years. Statistical analyses were performed using the 'vegan' package in R version 3.3.0 (R Development Core Team 2016), and the PCoA ordination was generated using the PRIMER-E/PERMANOVA + software (Anderson et al. 2008).

Results

Over 68,000 arthropods were collected. Springtails (Collembola) and woodlice (isopod suborder Oniscidea) had the highest activity-densities, respectively representing 38 and 34% of total arthropods trapped. The beetle families Curculionidae and Nitidulidae, and centipedes (Chilopoda), were the least-frequently sampled groups. Refer to Appendix 1 Electronic Supplementary Material for details.

What is the relative influence of local versus landscape factors in shaping arthropod communities in metropolitan woodlands?

For the local environmental dataset, the RDA analysis revealed that invasive woody-plant cover ($P = 0.01$) and nitrate uptake estimated from root simulators ($P = 0.025$) were the most important local variables for the ground-active arthropod community. In the RDA of the landscape dataset, landscape richness in a 400-m radius ($P = 0.011$) and the proportion of woodland in a 100-m radius ($P = 0.09$) were the only landscape variables explaining an important proportion of variation in arthropod composition, although the proportion of woodland was less influential compared to landscape richness. The PCoA ordination shows that invasive woody-plant cover, nitrate uptake, and landscape richness were all correlated with PCO
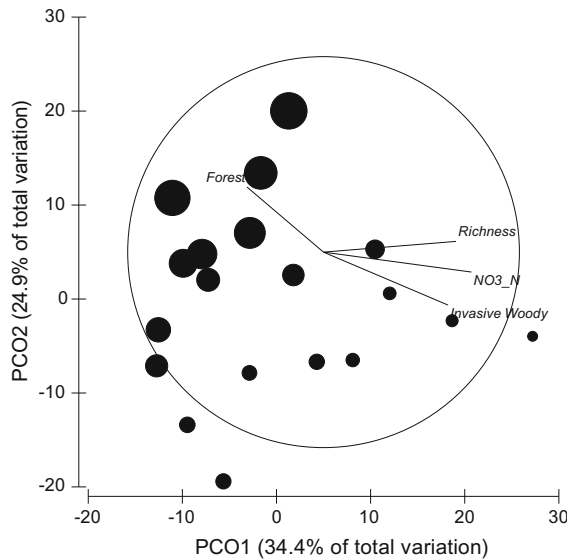
Fig. 2 Principal Coordinate Analysis (PCoA) for ground-active arthropod community structure. Pearson's correlation vector overlays show the relationship between sites and the four most-important environmental variables. Symbol size indicates the abundance of springtails (the most abundant group); the bigger the symbol the higher the abundance. Forest = forest cover in a 100-m buffer; Invasive. Woody = invasive woody plant cover; NO3_N = nitrate uptake; Richness = landscape richness in a 400-m buffer

Axis 1 (Fig. 2); forest cover was weakly correlated with PCO Axis 1 and 2 (Fig. 2).

Variation partitioning revealed that the combined environmental dataset (i.e. the reduced local and landscape datasets) explained about one-third (32%) of the total variance in arthropod community structure. The local-variable fraction alone explained 12% of the total variation ($P = 0.006$), whereas the landscape fraction uniquely explained only 4% of the total variation in arthropod community composition ($P = 0.14$). The variance shared between the local and landscape variables explained half (16%) of the total explained variance, more than either the local or landscape dataset considered separately. Simple linear regressions showed that landscape richness was positively correlated with invasive woody plants ($r = 0.62$, $P(F_{1,17}) < 0.01$, adj. $R^2 = 0.35$), as well as soil nitrate ($r = 0.52$, $P(F_{1,17}) = 0.02$, adj. $R^2 = 0.22$) (Fig. 3). See Appendix 2 Electronic Supplementary Material for additional analyses of the ground-active arthropod community, which includes a separate model selection procedure for the environmental variables.
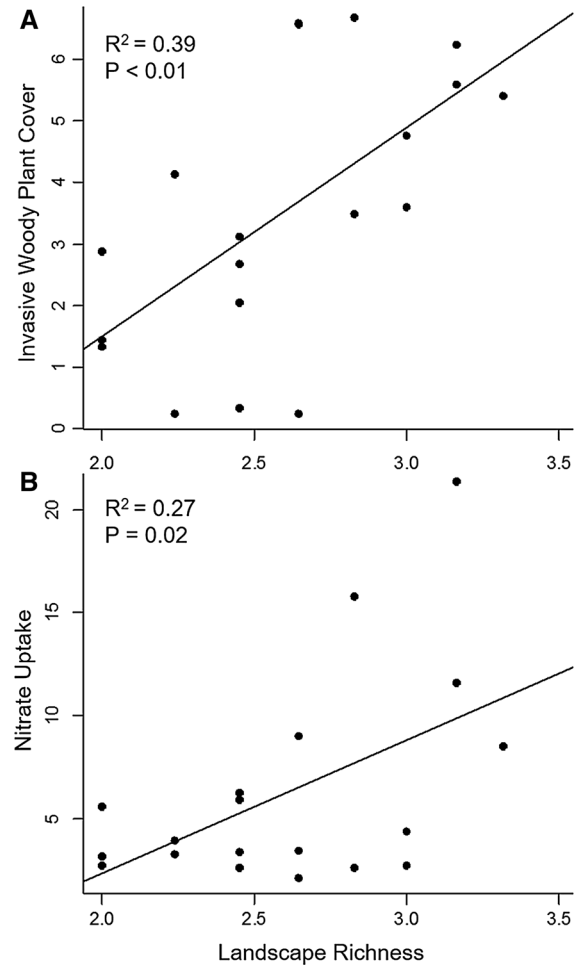

Fig. 3 Scatterplot showing the relationship between landscape richness at 400 m and **a** invasive woody-plant cover and **b** nitrate uptake rates estimated by root simulators. These patterns illustrate covariation between the landscape variable and two local variables that exhibited the strongest relationships with arthropod community structure

How does arthropod body size affect sensitivity to landscape-level factors?

Among the most abundant arthropod taxa collected, multiple regression analyses indicated no consistent patterns between arthropod size class and the relative influence of the landscape variables (Fig. 4). However, even though there was no pattern with body size, a number of arthropod groups were influenced by the landscape variables (Table 2). Activity-densities of all taxa except for the two arachnid orders (spiders (Araneae) and harvestmen (Opiliones)) were affected by landscape variables to some degree (Fig. 4). In
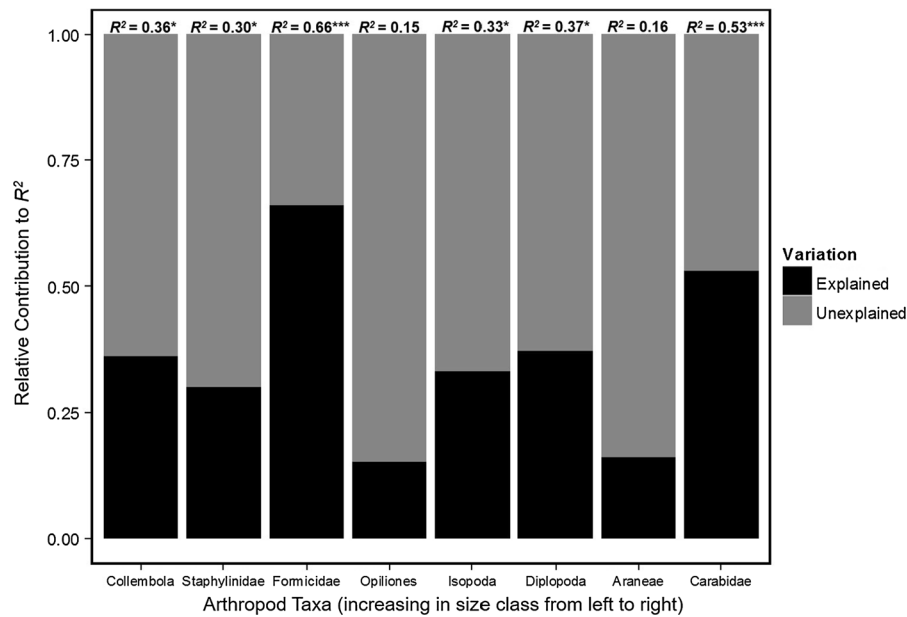
Fig. 4 Bar graph indicating the absence of a clear relationship between size class of each arthropod taxon and the amount of variation explained/unexplained by the landscape-variable dataset. The arthropod taxa are shown in increasing size classes from left to right on the x-axis. Despite the absence of a relationship with body size, a substantial amount of variation in activity-density is explained by landscape-level variables for several taxa, particularly ants (Formicidae) and carabid beetles (Carabidae). (***) indicates $P < 0.001$; (*) denotes $P < 0.05$ for the multiple regression model. The adjusted R^2 is provided

**Table 2** The relative influence of landscape variables on each individual arthropod taxon

	Landscape variables					
	Median size (mm)	Developed land	Distance-to-edge	Richness	Water	Woodland
Arthropod taxa						
Collembola	0.5					$0.004_{(100)}$
Staphylinidae	1			$0.013_{(1600)}$		$0.060_{(1600)}$
Formicidae	1.25	$0.087_{(1600)}$		$0.061_{(1600)}$		$0.030_{(400)}$
Opiliones	5			$0.074_{(100)}$		
Isopoda	5.5				$0.005_{(1600)}$	
Diplopoda	6			$0.004_{(400)}$		
Araneae	7.5					$0.051_{(400)}$
Carabidae	8			$0.007_{(400)}$		

Open spaces indicate that the variable was not retained in the model ($P \geq 0.10$). Values represent P values for model-selected variables

particular, activity-densities of ants (Hymenoptera, Formicidae) and carabid beetles (Coleoptera, Carabidae) were strongly correlated with the landscape dataset (multiple regression: Ants: $F_{4,14} = 9.86$, $P < 0.001$; Carabids: $F_{2,16} = 11.18$, $P = 0.001$). Follow-up linear regressions revealed that the activity-density of ants was negatively correlated with landscape richness ($r = -0.33$, $P(F_{1,17}) = 0.09$, adj. $R^2 = 0.11$, Fig. 5a). In contrast, numbers of carabids trapped were positively correlated with landscape richness ($r = 0.72$, $P(F_{1,17}) < 0.001$, adj. $R^2 = 0.49$, Fig. 5b). Collembola activity-density had a positive

Fig. 5 The relationship between landscape richness at 400 m and the activity-density of **a** ants, **b** ground beetles, **c** millipedes, and **d** springtails. Landscape richness was the most important landscape variable
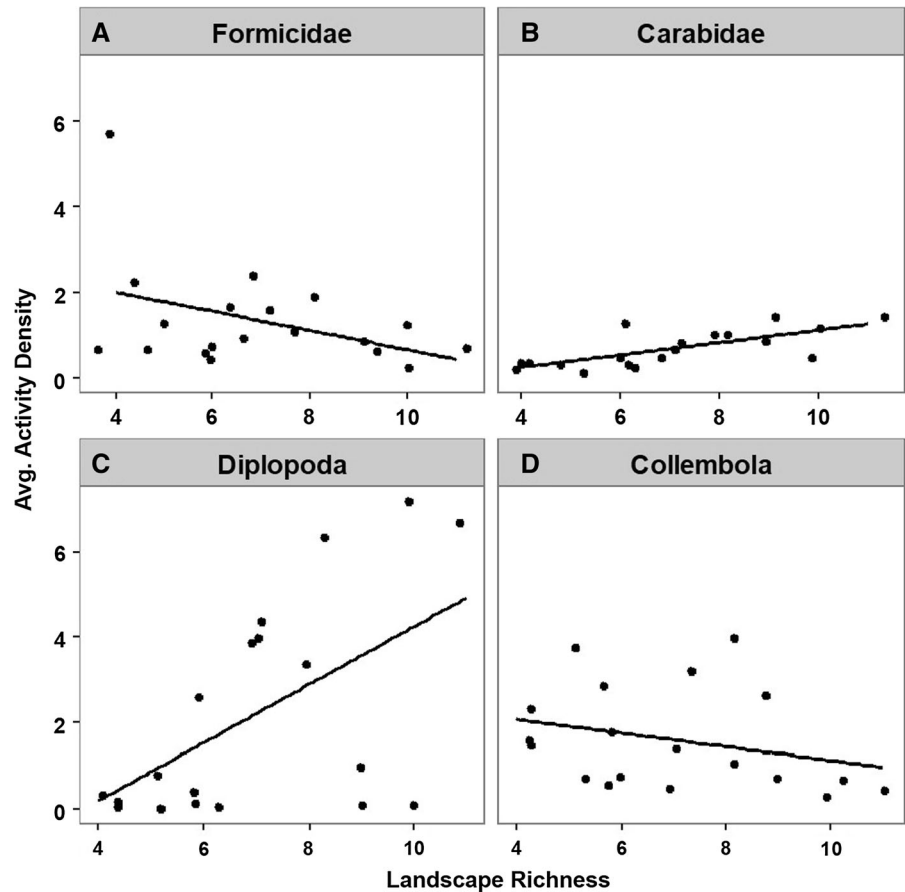
relationship with forest cover in a 100-m buffer ($r = 0.62$, $P(F_{1,17}) < 0.01$, adj. $R^2 = 0.39$, Fig. 6d). Overall, the landscape variables that appeared to have the greatest effect on the number of arthropod taxa trapped were landscape richness and proportion of woodland habitat (Table 2).

Discussion

In support of our first hypothesis, we found that differences in local habitat features are more influential than landscape factors in shaping ground-active arthropod communities in fragmented metropolitan woodlands. We also reveal that the two scales shared a large amount of variation, suggesting that both local and landscape factors are important when considering the structure of ground-active arthropod communities. Furthermore, there was no relationship between arthropod body size and landscape-level factors,

indicating that body size may not be a good predictor for dispersal for ground-active arthropods. We did, however, find that landscape factors strongly influenced certain groups, particularly ants, ground beetles, and springtails. Overall, these findings contribute to our understanding of how spatial scales can influence urban arthropod communities by illustrating the importance of covariation between local and landscape factors.

The overall influence of local versus landscape factors in shaping arthropod communities

We found that the total amount of variation explained in ground-active arthropod community structure was 32%, with the local scale alone explaining 12%, but 16% jointly with landscape factors. The total amount of variance explained in this study is comparable with the findings of other urban studies (e.g. Sattler et al. 2010 (20–37%); Bates et al. 2011 (15%); Braaker et al.

Fig. 6 Additional scatterplots showing the correlation between woodland habitat at 100 m and activity-density of **a** ants, **b** ground beetles, **c** millipedes, and **d** springtails. Of all the landscape-level variables, woodland habitat cover was second-most influential
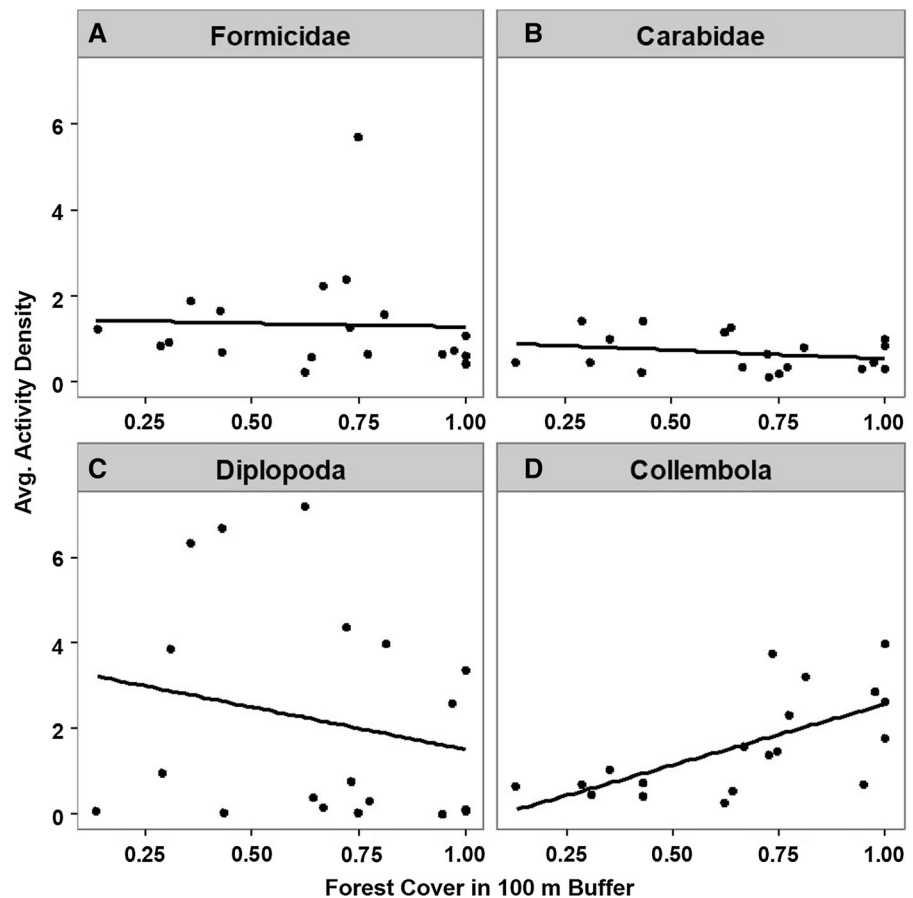
2014 (8–26%)). Potential reasons for the relatively low fraction of variance explained in our study are the different management practices across sites (McCary et al. 2015) and inherent differences between plots. Despite these limitations, we found that local invasive woody-plant cover and nitrate uptake estimated from root simulators were correlated with the community structure and abundances of ground-active arthropods, which is in agreement with previous research (Carvalheiro et al. 2010; Fickenscher et al. 2014; Loomis and Cameron 2014; van Hengstum et al. 2014). For instance, Kuebbing et al. (2014) demonstrated that invasions by two co-occurring shrubs, *Lonicera maakii* and *Ligustrum sinense*, indirectly altered ground-active arthropod communities via changes in soil pH and chemistry. Changes in communities of ground-active arthropods will likely have important implications for food-web dynamics and ecosystem functioning (Moore et al. 1988; Wright et al. 2014; McCary et al. 2016).

Covariation between local and landscape factors explained an unexpected high amount of variation. We found positive correlations between landscape richness—the most important landscape-level variable explaining arthropod community composition—and invasive woody-plant cover and soil nitrate. Given that landscape richness is a measure of heterogeneity and fragmentation, this finding suggests that highly heterogeneous landscapes also harbor higher rates of invasive woody plant species and soil nitrogen in urban regions. Other studies have also shown increased rates of plant invasion (Dukes and Mooney 1999; Yates et al. 2004; Vilà and Ibáñez 2011) and nitrogen deposition (Aber et al. 2003; Gregg et al. 2003; Bettez and Groffman 2013) in fragmented woodlands. The accumulation of invasive plants and soil nitrogen in small urban fragments will likely lead to shifts in the structure of communities of ground-active arthropods compared to larger, more contiguous woodlands (Gibb and Hochuli 2002; McCary et al.

2015). Numbers trapped of some arthropod groups (e.g. entomobryid and sminthurid Collembola (springtails)) were negatively correlated with invasive woody plants, whereas numbers of other groups (e.g. carabid beetles and millipedes) were positively correlated (Appendix 2 Electronic Supplementary Material). Given the relatively coarse taxonomic resolution used in this study, it is difficult to discern if there was a correlation between non-native plants and exotic arthropod species.

The proportion of woodland habitat surrounding each site at 400 m explained only 4% of variance in ground-arthropod community structure. This small amount was surprising, as we expected from previous research that the proportion of woodland in the landscape would account for more variation (Burke and Goulet 1998; González et al. 2015). Several studies have reported a positive relationship between the portion of woodland habitat and arthropod species richness and/or diversity (Meyer et al. 2009; Dainese et al. 2015). One possible reason we found a much weaker pattern is that we examined variation in community structure rather than a univariate response metric such as species richness or diversity. Because individual species within a community will likely differ in their sensitivity to the local habitat (e.g. habitat specialists vs generalists), the differential responses across species can either hide or exasperate patterns. For example, we found habitat-sensitive species such as springtails to be highly correlated with the proportion of woodland; in contrast, generalist predators such as spiders and harvestmen were not.

Arthropod body size and relative influence of landscape variables

We found no relationship between arthropod body size and the relative importance of landscape-level factors in determining numbers trapped. There are several reasonable explanations for this finding. First, because we restricted our study to arthropods that are active primarily on the ground surface, it is likely that the relative differences in mobility between these taxa are not large due to their small body size and similar method of dispersing (i.e. walking across a complex forest floor). Studies that reported differences in the relationship between arthropod body size and landscape configuration usually separated ground-active from flight-dispersing arthropods (e.g. Sekar 2012;

Kormann et al. 2015). Secondly, body size may not be a good indicator of ground-active arthropod mobility given their often complex life-history traits and foraging strategies. For example, sit-and-wait predators, such as crab spiders (Thomisidae), can be rather large yet relatively immobile for long periods of time. Conversely, numerous species of smaller spiders are capable of dispersing long distances aerially via ballooning (Crawford et al. 1995). One last possible reason we did not see a strong correlation between body size and landscape-level variables is that our range of dispersal abilities was too narrow to detect a difference. Previous research that revealed patterns between dispersal capabilities and the influence of landscape factors included a wider range of dispersal abilities, such as the differences between sessile plants and mobile vertebrates (Gonthier et al. 2014).

Even though we found no relationship between arthropod body size and the landscape-variable dataset, activity-densities of many groups were affected by landscape-scale factors. In fact, of the eight major groups of ground-active arthropods sampled in this study, activity-densities of six (ants, ground and rove beetles, springtails, millipedes, and the woodlice) were correlated with landscape-level variables. For instance, 66% of the variability in the activity-density of ants was explained by the landscape-variable dataset. Ants were negatively correlated with landscape richness and the proportion of developed land, in agreement with findings from other studies in urban ecosystems (Lessard and Buddle 2005; Thompson and McLachlan 2007). For example, Sanford et al. (2009) demonstrated that ant species richness and abundance decreased dramatically with increasing rates of landscape fragmentation. The authors attributed these declines to loss of habitat and decreasing patch size (Sanford et al. 2009). Carabid beetles can also be sensitive to landscape-level factors (e.g. Dauber et al. 2005; Fujita et al. 2008; Kormann et al. 2015), though several studies have demonstrated that carabids are just as impacted by variation in the local habitat as by the broader landscape because of reduced resources in fragmented habitats (Magura et al. 2010b). Other arthropod groups correlated with landscape-level factors in our study, such as the isopods, staphylinid beetles, springtails, and millipedes, have also been shown to be affected by landscape factors (Dauber et al. 2005; Hornung et al.

2007; Magura et al. 2013; Santorufo et al. 2014; Bogyó et al. 2015).

Conclusions

With the projected increase in urbanization across the globe, it is critical to understand the factors impacting the remaining ecosystem patches across metropolitan landscapes. Our findings illustrate the importance of examining local- and landscape-level factors not only individually, but also jointly, when predicting how natural communities will respond to future global change. Using variance partitioning we found that landscape factors influenced ground-active arthropod community structure primarily through their impact on local factors. Increasing landscape heterogeneity (i.e. landscape richness) was correlated with increased rates of invasive woody plants and nitrate uptake, which were the local factors most strongly correlated with differences in arthropod community structure. We observed no relationship between arthropod body size and the relative importance of landscape variables; however, activity-densities of several groups were strongly correlated with landscape-level factors. Overall, this research suggests that although processes that occur at the local scale predominate in shaping ground-active arthropod communities in fragmented metropolitan woodlands, landscape-level factors also have an influence, but primarily through their impact on local environmental factors that influence arthropod community structure.

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