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Urban Ecosystems

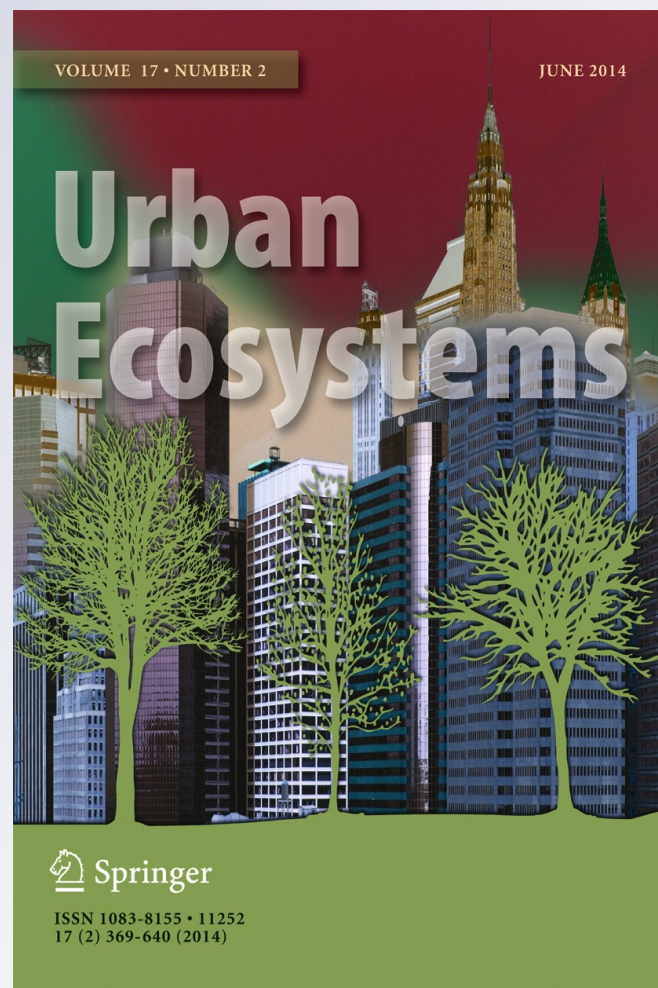
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Local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats

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Abstract Urban green spaces, such as forest fragments, vacant lots, and community gardens, are increasingly highlighted as biodiversity refuges and are of growing interest to conservation. At the same time, the burgeoning urban garden movement partially seeks to ameliorate problems of food security. Arthropods link these two issues (conservation and food security) given their abundance, diversity, and role as providers of ecosystem services like pollination and pest control. Many previous studies of urban arthropods focused on a

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single taxon (e.g. order or family), and examined either local habitat drivers or effects of landscape characteristics. In contrast, we examined both local and landscape drivers of community patterns, and examined differences in abundance, richness, and trophic structure of arthropod communities in urban forest fragments, vacant lots, and community gardens. We sampled ground-foraging arthropods, collected data on 24 local habitat features (e.g., vegetation, ground cover, concrete), and examined land-cover types within 2 km of 12 study sites in Toledo, Ohio. We found that abundance and richness of urban arthropods differed by habitat type and that richness of ants and spiders, in particular, varied among lots, gardens, and forests. Several local and landscape factors correlated with changes in abundance, richness, and trophic composition of arthropods, and different factors were important for specific arthropod groups. Overwhelmingly, local factors were the predominant (80 % of interactions) driver of arthropods in this urban environment. These results indicate that park managers and gardeners alike may be able to manage forests and gardens to promote biodiversity of desired organisms and potentially improve ecosystem services within the urban landscape.

Keywords Community gardens · Conservation · Forest · Habitat characteristics · Landscape · Urbanization · Vacant lots

Introduction

Urban expansion is a large and increasing threat to biodiversity. Over the past century, the human population has increased dramatically within urban centers, and now more than half of all humans inhabit cities (UNPD 2008). Increases in urbanization result in widespread wildlife habitat fragmentation and transformation via paving and roadways, changes in the local climate, pollution, and a loss of species richness, including arthropods (Pyle et al. 1981; Niemelä 1999; McIntyre 2000; Marzluff 2001; McKinney 2002; Miller and Hobbs 2002; Clark et al. 2007). Historically, little research has focused on understanding the biodiversity value of urban habitats for conservation (Miller and Hobbs 2002). However, since the widely heeded call made by McIntyre (2000), research based on understanding the mechanisms and impacts of arthropod biodiversity change in urban areas has boomed. It is now apparent for several groups of arthropods (e.g. spiders, ants, beetles, bees) that urbanization affects biodiversity, abundance, community structure, and interactions among arthropods and their food sources and mutualists (Turner et al. 2004; Shochat et al. 2006; McKinney 2008). Several studies document that habitat characteristics (such as vegetation complexity, leaf litter depth, number and size of trees, amount of impervious surface) affect abundance, richness, and composition of individual arthropod groups (McKinney 2008; Uno et al. 2010). Similarly, landscape-level drivers, such as area of habitat fragments, distance to natural areas, habitat connectivity, and position along the urban to rural gradient, may affect arthropod communities (Rudd et al. 2002; Yamaguchi 2004; Pacheco and Vasconcelos 2007; Magura et al. 2010). Despite the growth in knowledge of conservation and biodiversity of arthropods in urban ecosystems, there are several areas that deserve further study.

First, although individual studies document the impacts of certain habitat or landscape characteristics on abundance and richness of urban arthropods (Faeth et al. 2012), few studies have systematically compared the relative impact of local and landscape factors on urban arthropod communities (but see Bates et al. 2011;

Bennett and Gratton 2012; Wojcik and McBride 2012; Shwartz et al. 2013). Arthropods provide important ecosystem services in urban areas, such as predation and pollination (e.g. Sanford et al. 2008). Thus, understanding those factors that drive abundance and richness may be critically important for managing urban areas to promote both arthropod conservation and provisioning of ecosystem services. Several studies have simultaneously examined the impacts of local and landscape variables on arthropod communities in rural, agricultural landscapes, finding different taxonomic groups respond differently to factors at multiple spatial scales (e.g. Aviron et al. 2007; Carré et al. 2009; Gabriel et al. 2010). Although we know that changes in local and landscape factors impact ecosystem services provided in some ecosystems (Otieno et al. 2011 and references therein), studies in urban habitats are lacking.

Second, there are relatively few studies that take a multi-taxon approach by examining the impacts of urban habitat and landscape change on groups of arthropods that differ in their life histories, trophic status, or dispersal capabilities. Bolger et al. (2000) examined the impacts of habitat fragmentation, fragment vegetation type (native vs. non-native woody vegetation), and fragment age on non-ant arthropods, and again, different arthropod groups responded to different factors. Abundance and composition of multiple arthropod groups vary with changes in fragment size, age, and quality (Bolger et al. 2000; Gibb and Hochuli 2002). But to our knowledge, no study has examined local and landscape impacts of urbanization on multiple arthropod groups.

Third, few studies actually examine the change in trophic groups, or the relative abundance of predators, herbivores, and decomposers in different urban habitats, and the drivers of those changes. Many studies in urban ecosystems focus on detecting alterations in biodiversity or community structure, and make subsequent statements regarding the potential impact on ecosystem services (Faeth et al. 2011). Few actually quantify differences in ecosystem services, and only recently have some observed change in trophic structure and identified the drivers of those changes. For example, urbanization and associated fragmentation may affect the relative abundance of different trophic groups and result in changes in predator composition and trophic structure (Bolger et al. 2000; Gibb and Hochuli 2002). Likewise, the abundance of canopy herbivores, predators, and parasitoids may change depending on the location within sampled fragments (edge vs. interior) (Christie et al. 2010). Natural enemy to herbivore ratios in urban habitats may change due to alterations in local conditions (e.g. water availability) or because of shifts in the strength of predator–prey interactions within urban habitats (Marussich and Faeth 2009). Increases in natural enemy to herbivore ratios may be indicative of enhanced provisioning of ecosystem services. The specific habitat characteristics or the drivers of those changes between habitat edges and interior or in different urban habitat types are less known.

We examined patterns of arthropod abundance, richness, and trophic composition in urban green spaces to investigate whether characteristics of the habitat or of the surrounding landscape were more important determinants of arthropod communities. We worked in forest remnants, gardens, and vacant lots, all prevalent habitat types in an urban setting. Specifically, we addressed four research questions: 1) Does the abundance of arthropods and common arthropod groups differ with habitat type?; 2) Does species richness of common arthropod groups differ with habitat type?; 3) Does the abundance of predators, herbivores, and decomposers differ with habitat type?; and 4) What are the predominant local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats, and are different taxonomic groups related to different factors?

Materials and methods

Study sites

We worked within the city limits of Toledo, Ohio, U.S.A. (41°39'56"N, 83°34'31"W). We selected four replicates each of forest fragments (forests), community gardens (gardens), and vacant lots (lots) for a total of 12 sites (Fig. 1). Study sites were between 0.5 and 13.1 km apart. There were no significant differences in distance between sites; garden sites were located 5.8 ± 1.9 km (SE) apart, lots were located 3.9 ± 0.8 km apart, and forests were located 7.7 ± 1.1 km apart ($F_{2,15} = 1.95$, $P = 0.177$). The forest fragments were located within Toledo City Parks and ranged from 30,750–85,000 m². Garden sites were all linked to ToledoGROWS, an urban gardening outreach program of the Toledo Botanical Garden. All had been vegetable gardens for at least five years prior to the study and ranged in size from 420 to 2688 m². The vacant lots ranged in size from 1299 to 8262 m², were all managed (and owned) by the City of Toledo, and were vacant for at least 9 years prior to the study. Vacant lots represent a significant amount of land area in Toledo (>1 %), with more than 1000 lots distributed in the city (Uno et al. 2010).

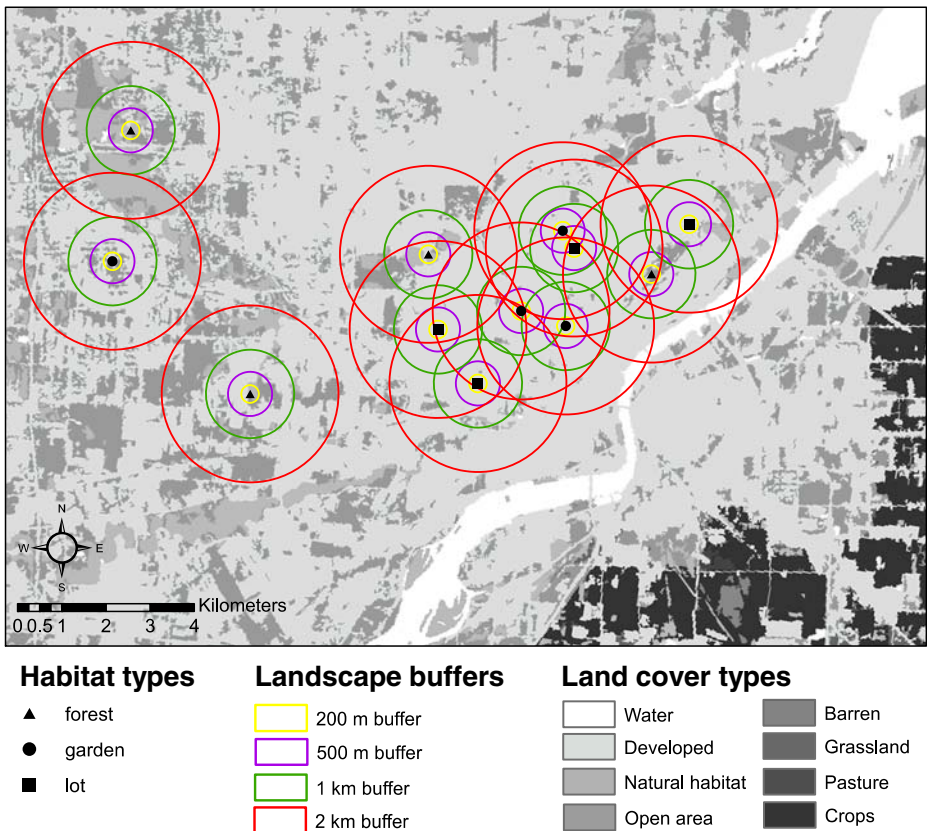


Fig 1 Map of the study sites in Toledo, Ohio

Pitfall sampling and arthropod identification

In each study site, we installed six ground pitfall traps consisting of two nested plastic tubs (11.4 cm diameter \times 7.6 cm deep). We placed two rows of three traps each near the center of each study site. Within rows, each trap was separated by 5 m, and the two parallel rows were separated by 5 m. We buried traps with the rim of each tub flush with the soil level. The tubs were sealed with lids when not in use. The trap size selected is unlikely to capture rare or large invertebrates but acceptably characterizes the dominant fauna active within the ground layer without mammalian and amphibian by-catch (Work et al. 2002).

The traps were open to catch arthropods on 3 days each month during the summer of 2007 (7–10 May, 4–7 June, 2–5 July, 30 July–2 August). We filled traps with 200 ml of a saturated saline solution with a drop of unscented detergent to break the surface tension. Saline solution is a neutral field sampling preservative, with little attractive or repulsive characteristics for most arthropod groups, and preserves important morphological components of the insects (Perner and Schueler 2004; Sasakawa 2007). We placed green plastic plates (7.62 cm diameter, Solo brand) over each trap and elevated plates 7–8 cm above ground with nails. The plates acted to exclude rainwater and non-target taxa (e.g. flies, bees) from falling into traps. On collection days, we filtered trap contents with deionized water to remove the salt solution and then stored specimens in a 70 % ethyl alcohol solution.

We identified arthropods to order and some (e.g. Coleoptera, Hemiptera) to family following Borror and White (1970) and Marshall (2006) and further identified ants, beetles, and spiders to species or morphospecies. We chose these three groups as they were highly abundant in pitfall traps and are among those arthropods that provide ecosystem services in urban and agricultural habitats (Gibb and Hochuli 2002). We identified arthropods with keys for ants (Covert 2005), beetles (White 1983; Marshall 2006), and spiders (Bradley 2004; Ubick et al. 2005). We determined the trophic group (e.g. predator, herbivore, decomposer) of arthropod orders (and families, where trophic group differs within an order) with White (1983) and Marshall (2006).

Habitat sampling

We quantified 24 site characteristics of the habitats across three (nested) spatial scales (100 \times 100 m, 20 \times 20 m, and 1 \times 1 m). We first measured the extent of habitat patch (e.g. contiguous garden, lot, or forest habitat) surrounding pitfall traps. In the 100 \times 100 m plots around pitfall traps we counted all trees (> 30 cm circumference at breast height, cbh) and quantified percent area with a) concrete, b) buildings, c) bare ground, d) grass or forbs, and e) shrubs. In the 20 \times 20 m plots, we sampled canopy cover with a concave vertical densiometer at each corner and the center of each plot. For woody plants we counted, measured circumference (1.37 m above ground), and estimated the height of all trees >30 cm cbh and also identified and measured height and circumference (1 cm above ground) of all tree seedlings and shrubs <2 m tall. Within 20 \times 20 m plots, we randomly placed four 1 \times 1 m plots within which we measured height of the tallest vegetation, counted and identified forbs and grasses, and visually estimated percent cover of a) bare ground, b) grasses, c) forbs, d) rocks/wood panels, e) leaf litter, and f) fallen branches. We collected site data during May–July 2007.

Landscape analysis

We used a geographic information system (GIS) to investigate land-cover types surrounding each study site. We obtained land-cover data for Lucas County, Ohio, from the 2001

National Land Cover Database (NLCD, 30 m resolution) (Homer et al. 2004) and calculated the percentage of land-cover types in buffers surrounding each study site. We divided possible land-cover types into five categories: 1) open water (NLCD value 11), 2) natural habitat (including woody (90) and emergent herbaceous wetlands (95), deciduous (41) and evergreen forest (42)), 3) open space (including lawn grass, parks, and golf courses) (21), 4) developed areas (including low, medium, and high intensity) (22, 23, 24), and (5) barren land (31). We assessed the percent of each land-cover type in 200 m, 500 m, 1 km, and 2 km buffers around each study site with the tabulate area function in the spatial statistics tools in ArcGIS v. 10.1. For all land-cover classes (except water that covered a small [$<10\%$] of land area), there was a wide range (at least a 28 % and up to a 84 % difference in values for different sites) in the percent of land-cover types at each spatial scale (Table S1).

Data analysis

We compared abundance of all arthropods, common arthropod groups, and trophic groups, and compared richness of ants, beetles, and spiders among habitats. We pooled arthropods from all traps and all months from a single site, and used that as the replicate. We defined common arthropod groups as those with more than 250 individuals captured. We excluded flying arthropods (e.g. bees, wasps, flies), springtails, and mites, and included only adult spiders due to difficulty in identifying juveniles. We made comparisons among habitat types with generalized linear models with the `glm.nb` function in the ‘MASS’ package in R (Venables and Ripley 2002; R Development Core Team 2011). Habitat was the main factor. Because the goodness of fit tests showed a lack of fit of the data to a Poisson distribution (significant chi-square tests), we used the negative binomial distribution for the analysis. We followed the `glm` with a Tukey’s HSD test to determine pairwise comparisons between habitats with the `glht` function in the ‘multcomp’ package in R (Hothorn et al. 2008). We used an analysis of similarity (ANOSIM) in PAST to compare the species composition of all arthropods among habitat types (Hämmer et al. 2001).

We used two methods to explore the relevance of the habitat characteristics for abundance and composition of arthropods in urban green spaces. First, we used canonical correspondence analysis (CCA) in PAST (Hämmer et al. 2001) to visually examine differences in habitat types with the local and landscape habitat characteristics, and to view relationships among these same local and landscape characteristics and abundance of arthropod groups, trophic groups, and richness of ants, spiders, and beetles. Our data set included 24 local habitat characteristics and 16 landscape characteristics (Table 1). Because of this large number of predictor variables (40), we first ran a principal components analysis in PAST, followed with Pearson’s correlations in SPSS v. 19. The variables that were significantly correlated with PC1 (at $P < 0.001$ level) were represented in the CCA by PC1. We ran two separate CCA tests; the first examined the distribution of study sites relative to the predictor variables and PC1, and the second examined arthropod groups. We followed CCA tests with permutation tests to determine the significance of the CCA axes in predicting arthropod composition. For this analysis, we used data from each sample month in each site as a replicate to best capture variation across the season.

To determine the significance and relative importance of individual local and landscape factors for arthropod abundance and richness (of ants, spiders, and beetles), we used conditional inference trees with the ‘party’ package in R (Hothorn et al. 2006; R Development Core Team 2011). Classification and regression trees examine the degree to which factors predict a dependent variable, and determine the relative importance of individual factors (Olden et al. 2008; Strobl et al. 2009). Specifically, conditional inference

Table 1 A list of local and landscape variables measured in forest, garden, and lot sites in Toledo, Ohio, and correlations between PC1 and the local and landscape variables

| Habitat characteristic | Pearson's correlations with PC1 |
|---------------------------------------|---------------------------------|
| Habitat extent | -1.000 ^a |
| Measured in 1×1 m plots | |
| Percent cover of bare ground | 0.096 |
| Percent cover of grass | 0.425 ^a |
| Percent cover of forbs | -0.084 |
| Percent cover of rocks | 0.114 |
| Percent cover of leaf litter | -0.540 ^a |
| Percent cover of branches | -0.614 ^a |
| Height of tallest vegetation (cm) | 0.402 ^a |
| No. of forbs | -0.278 |
| Forb richness | 0.339 ^a |
| Measured in 20×20 m plots | |
| No. of trees | -0.894 ^a |
| Tree circumference (cm) | -0.693 ^a |
| Tree height (m) | -0.786 ^a |
| No. of shrubs | -0.490 ^a |
| Shrub circumference (cm) | 0.22 |
| Shrub height (cm) | -0.205 |
| Woody plant richness | -0.768 ^a |
| Canopy cover | -0.559 ^a |
| Measured in 100×100 m plots | |
| Percent cover by concrete | 0.585 ^a |
| Percent cover by buildings | 0.558 ^a |
| Percent cover by bare ground | -0.098 |
| Percent cover by vegetation | -0.612 ^a |
| No. trees | -0.920 ^a |
| No. shrubs | -0.805 ^a |
| Measured with GIS land-cover analysis | |
| Open water (200 m) | NA |
| Open water (500 m) | -0.615 ^a |
| Open water (1 km) | -0.615 ^a |
| Open water (2 km) | -0.164 |
| Open area (200 m) | -0.268 |
| Open area (500 m) | -0.558 ^a |
| Open area (1 km) | -0.776 ^a |
| Open area (2 km) | 0.186 |
| Natural habitat (200 m) | -0.901 ^a |
| Natural habitat (500 m) | -0.776 ^a |
| Natural habitat (1 km) | -0.760 ^a |
| Natural habitat (2 km) | 0.123 |
| Developed (200 m) | 0.766 ^a |
| Developed (500 m) | 0.753 ^a |
| Developed (1 km) | 0.822 ^a |
| Developed (2 km) | -0.169 |

^aSignificant correlation at the $P < 0.001$ level

trees utilize an iterative, binary recursive data-partitioning algorithm to examine each variable, searching for the best predictor, splitting the data for the dependent variable into two distinct groups, and then repeating the variable selection until no more significant predictors are found (Hothorn et al. 2006). We included all 40 predictor variables in the analysis (Table 1). The 16 response variables we tested (in separate analyses) were total arthropod abundance; abundance of ants, beetles, spiders, isopods, orthopterans, true bugs, millipedes, and harvestmen; abundance of predators, herbivores, and decomposers; and species richness of ants, beetles, and spiders. We used natural log (value +1) transformed values for number of shrubs in 20×20 m plots, arcsine square root transformed data for all percent cover readings, including land-cover data, and raw values for all other site characteristics measured. We considered the pooled sample of six traps per a site on a single sample date as a replicate, and the minimum criterion was set to 0.95 ($P=0.05$).

To examine whether the proximity in sample plots (Fig. 1) influenced the conditional inference tree results, we tested for spatial autocorrelation in the dependent variables (Dormann et al. 2007). We examined the degree of spatial autocorrelation in the residuals of the conditional inference trees with (1) spatial correlograms (with the 'nfc' package in R) and (2) the Moran's test for spatial autocorrelation using a spatial weights matrix (with the 'spdep' package in R) (Bjornstad 2009; R Development Core Team 2011; Bivand et al. 2012). For correlograms, we computed 100 permutations using the *resamp* argument in the *correlog* function to examine the distance, if any, at which variables were spatially autocorrelated. For the calculation of Moran's I, we used nearest-neighbor distances as the metric, and used the permutation test option. Only two of the variables examined (beetle abundance and beetle richness) displayed significant spatial autocorrelation (Table S2). For those two variables, we included the location (Longitude and Latitude) as additional explanatory variables in conditional inference trees to account for the role of space in the analysis.

Results

Arthropods in gardens, vacant lots, and forests

Overall, we collected a total of 23,479 arthropods, including 5954 in forests, 13,440 in gardens, and 4085 in vacant lots. These arthropods represented 14 orders. Common orders (>250 individuals collected) included Isopoda (pillbugs, 15,344 individuals or 65.4 % of captures), non-flying Hymenoptera (ants, 4309, 18.4 %), Opiliones (harvestmen, 901, 3.8 %), Diplopoda (millipedes, 818, 3.5 %), Araneae (spiders, 652, 2.8 %), Coleoptera (beetles, 529, 2.3 %), Orthoptera (grasshoppers and crickets, 490, 2.0 %), and Hemiptera (true bugs, 376, 1.6 %). Chelonethida, Chilopoda, Dermaptera, Trichoptera, and Thysanoptera each represented less than 1 % of captures. In terms of overall richness, we found a total of 36 species of ants, 141 species of beetles, and 77 species of spiders.

Overall abundance of arthropods, common arthropod groups (except beetles), and trophic groups (except herbivores), as well as species richness of ants, beetles, and spiders differed with habitat type (Table 2). Arthropod abundance was more than twice as high in gardens than in lots or forests. Spiders, true bugs, and ants were more abundant in vacant lots, followed by gardens, and then by forests. Isopods were more than three times as abundant in gardens than in forests, and 15 times as abundant in forests than in lots. Grasshoppers, crickets, and harvestmen were twice as abundant in forests than in gardens or vacant lots. Millipedes were more abundant in forests than in lots. Beetle abundance did not differ with

Table 2 Mean (\pm SE) total abundance or richness of all arthropods and of different arthropod groups and feeding groups in urban green spaces in Toledo, Ohio

| Arthropod group | Forest | Garden | Lot | df | Deviance | Resid. dev. | <i>P</i> |
|-------------------------|-----------------------|------------------------|-----------------------|-----|----------|-------------|----------|
| Arthropods | 1488.50 \pm 215.26b | 3360.0 \pm 1165.37a | 1021.25 \pm 203.86b | 2,9 | 14.17 | 12.42 | <0.001 |
| Araneae | 27.75 \pm 6.73b | 58.25 \pm 17.93a | 77.0 \pm 4.24a | 2,9 | 14.05 | 12.30 | <0.001 |
| Coleoptera | 35.75 \pm 8.34 | 52.25 \pm 10.73 | 44.25 \pm 8.73 | 2,9 | 1.91 | 12.25 | 0.385 |
| Diplopoda | 111.75 \pm 45.8a | 70.0 \pm 24.2a,b | 22.75 \pm 14.26b | 2,9 | 7.82 | 13.04 | 0.02 |
| Hemiptera | 5.0 \pm 2.38b | 35.5 \pm 24.92a | 53.5 \pm 15.02a | 2,9 | 11.29 | 13.93 | 0.004 |
| Formicidae | 162.0 \pm 45.73b | 316.0 \pm 47.75a,b | 599.25 \pm 159.72a | 2,9 | 15.17 | 12.42 | <0.001 |
| Isopoda | 883.25 \pm 176.35b | 2774.5 \pm 1087.8a | 178.25 \pm 59.67c | 2,9 | 33.56 | 12.70 | <0.001 |
| Opiliones | 179.5 \pm 37.68a | 29.75 \pm 12.09b | 16 \pm 4.26b | 2,9 | 39.53 | 12.70 | <0.001 |
| Orthoptera | 82.0 \pm 27.92a | 12.25 \pm 6.61b | 28.25 \pm 14.09a,b | 2,9 | 9.34 | 13.22 | 0.009 |
| Decomposer | 1010.5 \pm 207.2b | 2859.25 \pm 1098.17a | 211.75 \pm 72.07c | 2,9 | 31.28 | 12.69 | <0.001 |
| Herbivore | 90.25 \pm 27.1 | 60.25 \pm 33.03 | 93 \pm 5.93 | 2,9 | 1.43 | 12.57 | 0.488 |
| Predator | 387.75 \pm 49.44b | 440.5 \pm 74.04a,b | 716.5 \pm 154.78a | 2,9 | 8.14 | 12.19 | 0.017 |
| Beetle species richness | 16.25 \pm 1.89b | 24.25 \pm 3.64a | 22.5 \pm 2.47a,b | 2,9 | 6.44 | 12.11 | 0.039 |
| Ant species richness | 12.5 \pm 0.87a | 7.0 \pm 1.29b | 10.25 \pm 1.03a,b | 2,9 | 6.36 | 4.89 | 0.041 |
| Spider species richness | 9.5 \pm 2.53c | 17.5 \pm 1.66b | 28.0 \pm 2.55a | 2,9 | 38.38 | 15.50 | <0.001 |

Statistical results from generalized linear models comparing dependent variables between habitat types. Small letters indicate significant differences between habitats ($P<0.05$) determined with Tukey's HSD tests

habitat type. Abundance of some trophic groups differed with habitat type. Decomposer abundance was more than twice as high in gardens than in forests, and again more than 13 times as high in forests than in lots. Predator abundance was significantly higher in lots than in forests. In contrast, herbivore abundance did not significantly differ with habitat. Richness of beetles, spiders, and ants differed with habitat type. Spider species richness was highest in lots, followed by gardens, and was lowest in forests. Ant richness was higher in forests than in gardens, but species richness in lots did not differ from forests or gardens. Beetle species richness was higher in gardens than in forests. Arthropod group composition in the three habitat types was significantly different (Global $R=0.4609$, $P<0.001$), and composition differed between each pair of habitat types ($P<0.001$).

Canonical correspondence analysis

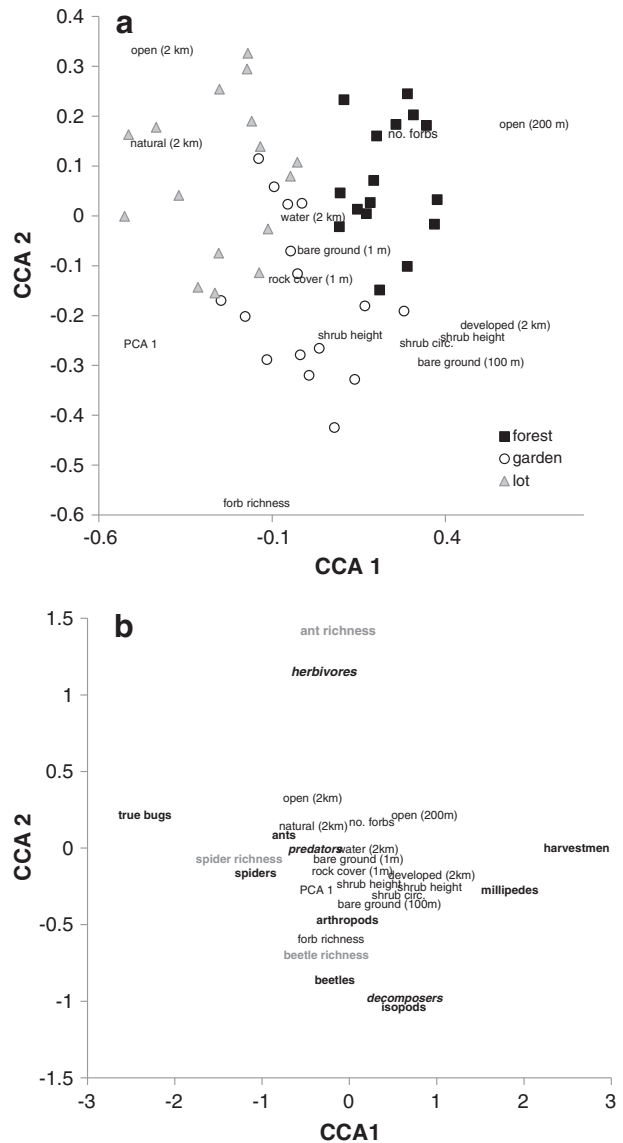
PC1 was correlated with 27 of the habitat variables (eigenvalue = 9.91×10^8 , % of variance explained = 99.996 %; Table 1). PC1 was negatively correlated with several variables associated with vegetation and litter complexity, and increased in open, natural, and water area surrounding the study sites. In addition, PC1 was positively correlated with concrete, building, and grass cover, height of the herbaceous layer, and with increases in developed area. We included PC1 and 13 additional variables (open habitat within 200 m and 2 km, water within 2 km, developed area within 2 km, natural area within 2 km, percent cover of

bare ground and rocks in 1×1 m plots, bare ground in 100 m plots, shrub height, shrub circumference, forb richness, and the number of forbs) as predictors in the CCA. The habitat types clearly separated in the CCA (Fig. 2a). Each habitat corresponded with different habitat characteristics. Forests corresponded with forb abundance and open area within 200 m. Gardens corresponded with PC1, forb richness, and rock cover in 1×1 m plots. Lots corresponded to amount of open area and natural habitat within 2 km. The CCA examining arthropod groups showed four clusters of arthropod groups (Fig. 2b). One cluster of true bugs, ants, and spiders most closely followed the amount of open area and natural habitat within 2 km. The cluster with beetles and isopods tracked forb richness and forb cover in 1×1 m plots. The millipedes and harvestmen cluster corresponded to changes in the amount of bare ground in 100×100 m plots and shrub height. Finally, orthopterans were far removed from any habitat characteristic but were closest to open area within 200 m. The three trophic groups examined also differed strongly in position according to habitat characteristics (Fig. 2b). Predator abundance was aligned with natural habitat within 2 km. Herbivores were most aligned with forb abundance in 1×1 m plots and open area within 2 km. Decomposers corresponded to developed area within 2 km and shrub circumference. Ant, spider, and beetle richness widely differed in the CCA position (Fig. 2b). Ant richness corresponded to open area within 200 m and bare ground in 1×1 m plots. Spider richness corresponded to PC1. Beetle richness corresponded to developed area at 2 km and bare ground in 100×100 m plots.

Local and landscape predictors of arthropod communities

Several local and landscape factors predicted differences in abundance and species richness of different groups of arthropods (Fig. 3). Overall, arthropod abundance was correlated with local factors including rock cover and bare ground (positive correlations), forb cover (a negative correlation), and negatively correlated with one landscape factor, open area within 2 km of study sites (Fig. 4a). Millipede abundance was positively correlated with two local factors, shrub height and forb abundance (Fig. 4b). Grasshoppers and crickets correlated with local factors and were more abundant in plots with more trees, more vegetation cover (in 100×100 m plots), and with taller herbaceous vegetation (Fig. 4c). Pillbugs were affected by both landscape (developed area within 2 km) and local factors (branch cover in 1×1 m plots and the number of shrubs) (Fig. 4d). True bugs increased with more one local factor (building cover) and decreased with one landscape factor (natural habitat area within 200 m) (Fig. 4e). Harvestmen correlated with local factors and were more abundant with higher woody plant and lower forb richness and with taller vegetation (Fig. 4f). Ant abundance increased with one local factor (more building cover (Fig. 5a), and ant richness positively correlated with two local factors (shrub abundance and herbaceous vegetation height (Fig. 5c)). Beetle abundance was significantly higher in the 16 samples with more than 12 species of forbs ($P=0.04$), and beetle richness was significantly lower in the 31 samples with low levels of canopy cover ($P=0.028$). Spider abundance increased with more developed area within 200 m (a landscape factor), with decreases in forb richness and with taller shrubs (both local factors) (Fig. 5b). Spider richness likewise increased with more developed area within 200 m and less open space within 200 m (both landscape factors) and with fewer trees (a local factor) (Fig. 5d). Decomposer abundance increased in sites with more developed area within 2 km (a landscape factor), larger tree circumference, and lower amounts of branch cover (in 1×1 m plots) (two local factors) (Fig. 6a). Herbivore abundance was correlated with local factors and was higher with high grass cover, less concrete cover, and less canopy cover (Fig. 6b). Finally, predator abundance was higher in the 16 samples with more than 15 % of building cover (a local factor) ($P=0.003$).

Fig. 2 Canonical correspondence analysis plots showing the correspondence between 13 local and landscape variables and PC1 with **a** the forest, garden, and lot sites and **b** abundance of common arthropod groups (*bold*), abundance of three trophic groups (*grey letters*), and richness of three common arthropod groups (*bold italics*)



Although abundance and richness of different groups was best predicted by different factors, the majority of the predictor variables of all arthropod groups were local-scale factors (Fig. 3, Table 3). Overall, of the 35 significant correlations between a habitat factor and one of the 15 taxonomic or feeding groups of arthropods, 80 % resulted from local factors measured at 1×1 m, 20×20 m, or 100×100 m scales, and 20 % resulted from landscape factors measured at the 200 m, 500 m, 1 km, or 2 km scales. Furthermore, most of the significant correlations for local factors related to vegetation or ground cover predictors (24 of the 28 local predictors) rather than other characteristics specifically associated with urbanization (e.g. buildings or concrete).

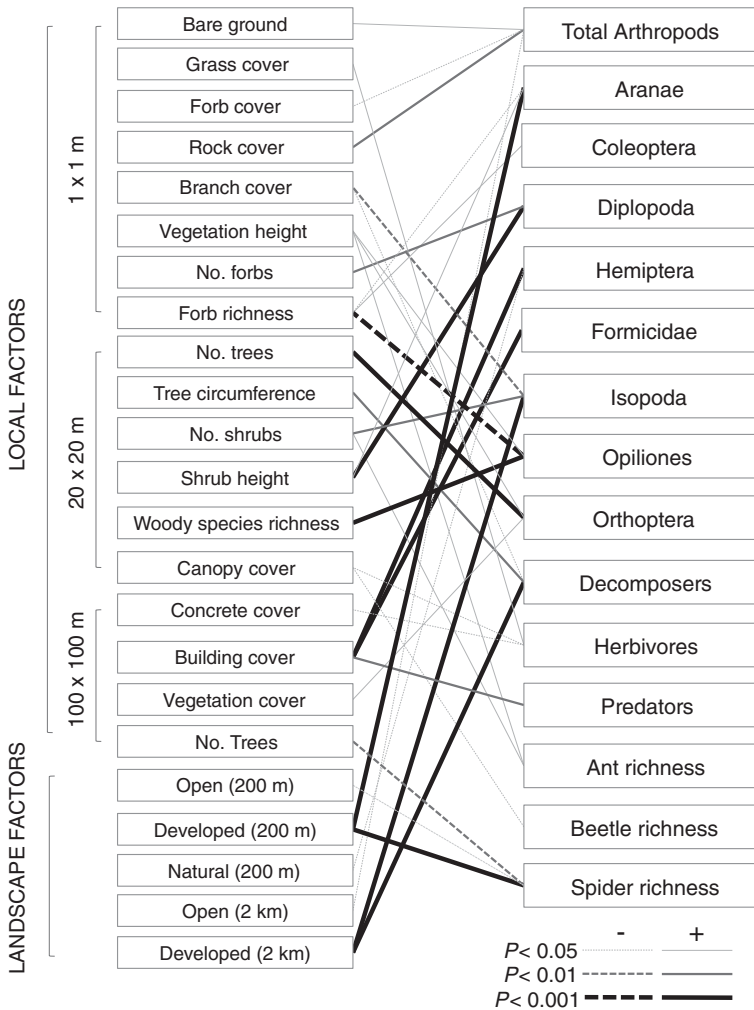


Fig. 3 A schematic figure showing all positive (solid lines) and negative (dashed lines) correlations between local and landscape habitat factors and abundance and richness of arthropods in urban habitats in Toledo, Ohio. All correlations were extracted from the conditional inference tree analysis. The color of the line (black, dark grey, light grey) indicates the level of significance of the relationship

Discussion

We found that the abundance and richness of arthropods varied significantly depending on the urban habitat type, and that the patterns of abundance and richness differed depending on trophic and taxonomic group. A long list of both local habitat and landscape-scale characteristics corresponded to changes in abundance and richness of arthropods in our urban sites, and these effects also differed dramatically for different arthropod groups. As urban populations continue to increase, urban green spaces will be highlighted as potential saviors of biodiversity and an answer to food insecurity. If one aim of preserving green space within cities is to protect and maintain biodiversity in increasingly urban landscapes, understanding

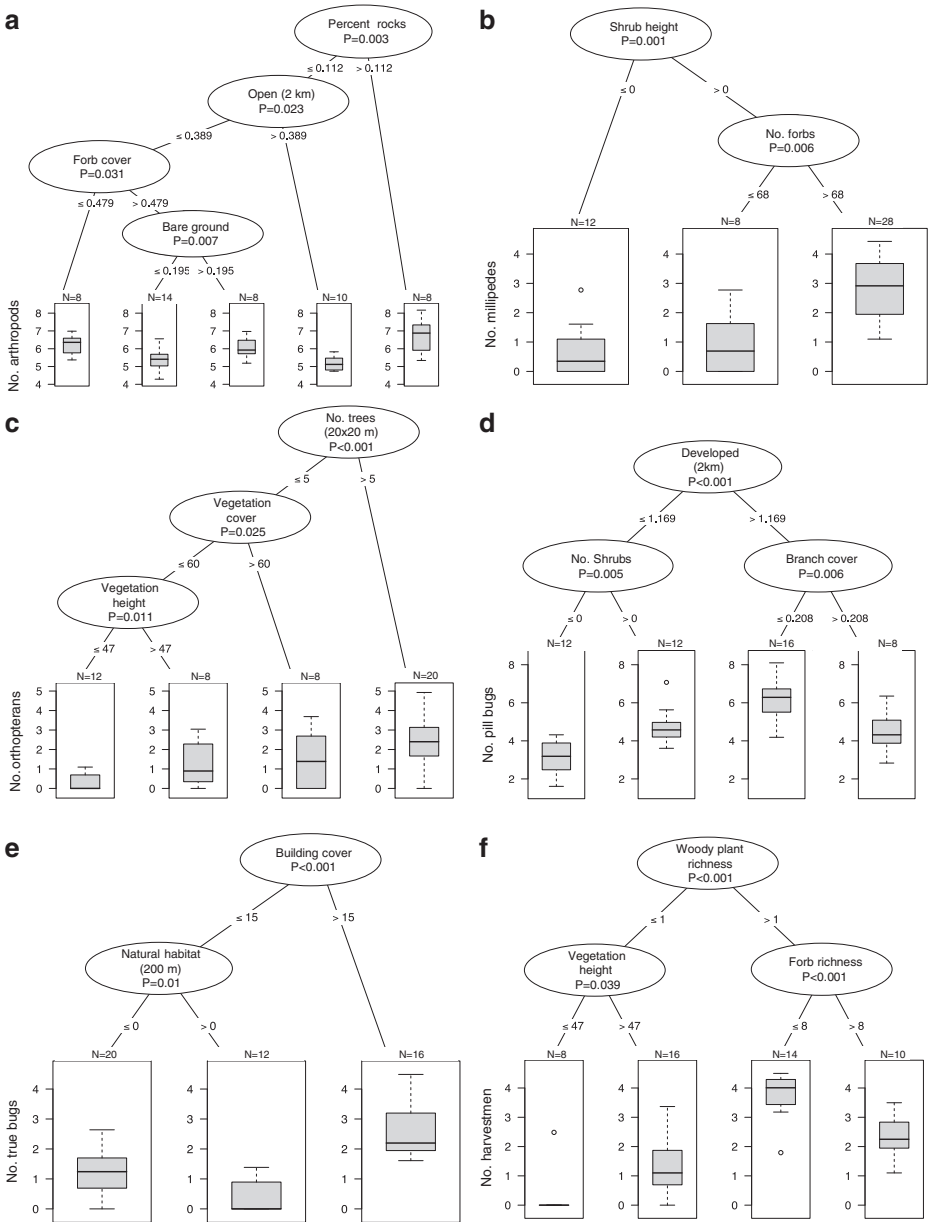


Fig. 4 Conditional inference trees examining relationships between 24 local and 16 landscape factors and abundance of: **a** arthropods, **b** millipedes, **c** orthopterans, **d** pillbugs, **e** true bugs, and **f** harvestmen in forests, gardens, and vacant lots in Toledo, Ohio. Significant predictors of arthropod groups are circled and ranked (top-most variable has highest correlation with dependent variable). P -values indicate the significance at 95 % of confidence in the relationship tested. Box plots include the inner quartiles (grey box), the median values (solid black line), and $1.5 \times$ the inner quartiles (error bars) of the dependent variable associated with each string of predictor variables. The numbers between each significant predictor show the value above or below which the dependent variable is split by the iterative, binary recursive data-partitioning algorithm. Sample sizes at each terminal node show the number of sites in that box plot

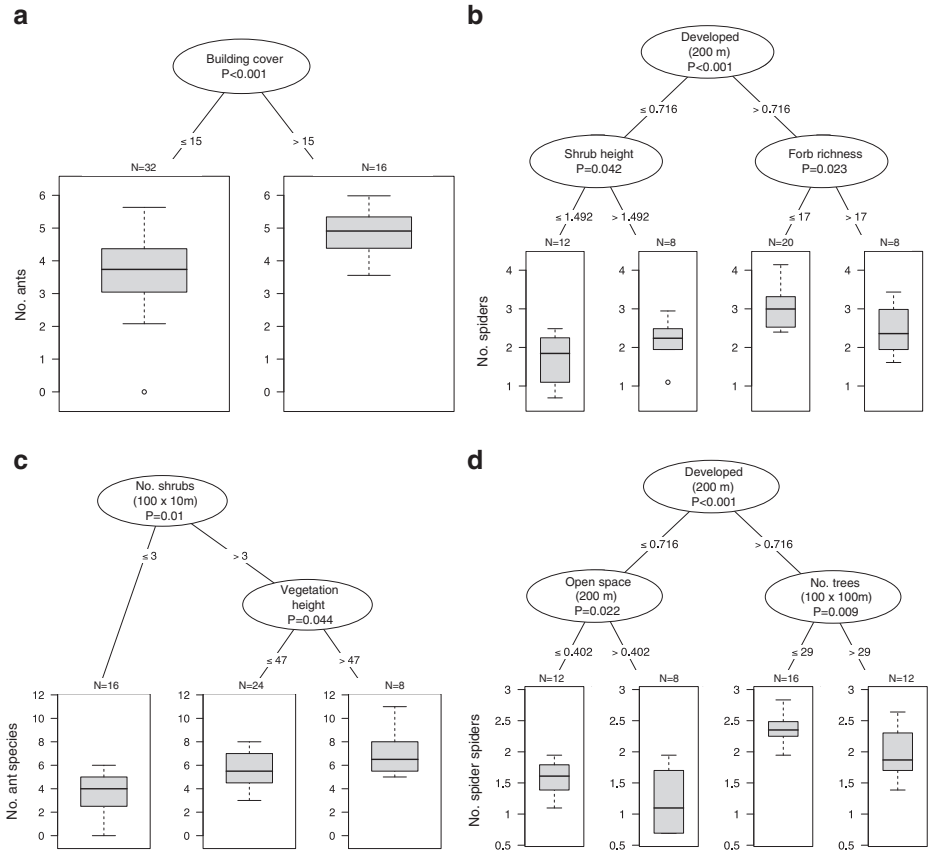


Fig. 5 Conditional inference trees examining relationships between 24 local and 16 landscape factors and: **a** ant abundance, **b** spider abundance, **c** ant richness, and **d** spider richness in forests, gardens, and vacant lots in Toledo, Ohio. Explanation is as for Fig. 4

how different groups respond to different local and landscape drivers will become an important part of urban land management and conservation planning. Likewise, as urban gardens increasingly contribute to urban food security, understanding factors that drive changes in trophic groups in the urban garden will be essential to long-term management. Here, we outline some of the major patterns we observed for different arthropod groups, and then discuss some more general patterns relating to the drivers of arthropod communities in urban areas.

There were differences in abundance between habitat types for all arthropods and for abundance of most common arthropod groups (spiders, true bugs, ants, isopods, grasshoppers, crickets, and harvestmen), and many different habitat factors were reflected in shifts in arthropod abundance. Not surprisingly, different arthropod groups were more abundant in different habitats. Isopods accounted for nearly two-thirds of all arthropods encountered and were as common in other urban arthropod studies (Bolger et al. 2000). Isopods were most abundant in gardens and forests, likely due to high amounts of organic inputs (e.g. manure, grass clippings, recycled wood chips) brought in to enhance soil fertility and to create pathways, and due to higher leaf litter depth (in forests) (Jordan and Jones 2002). Isopod

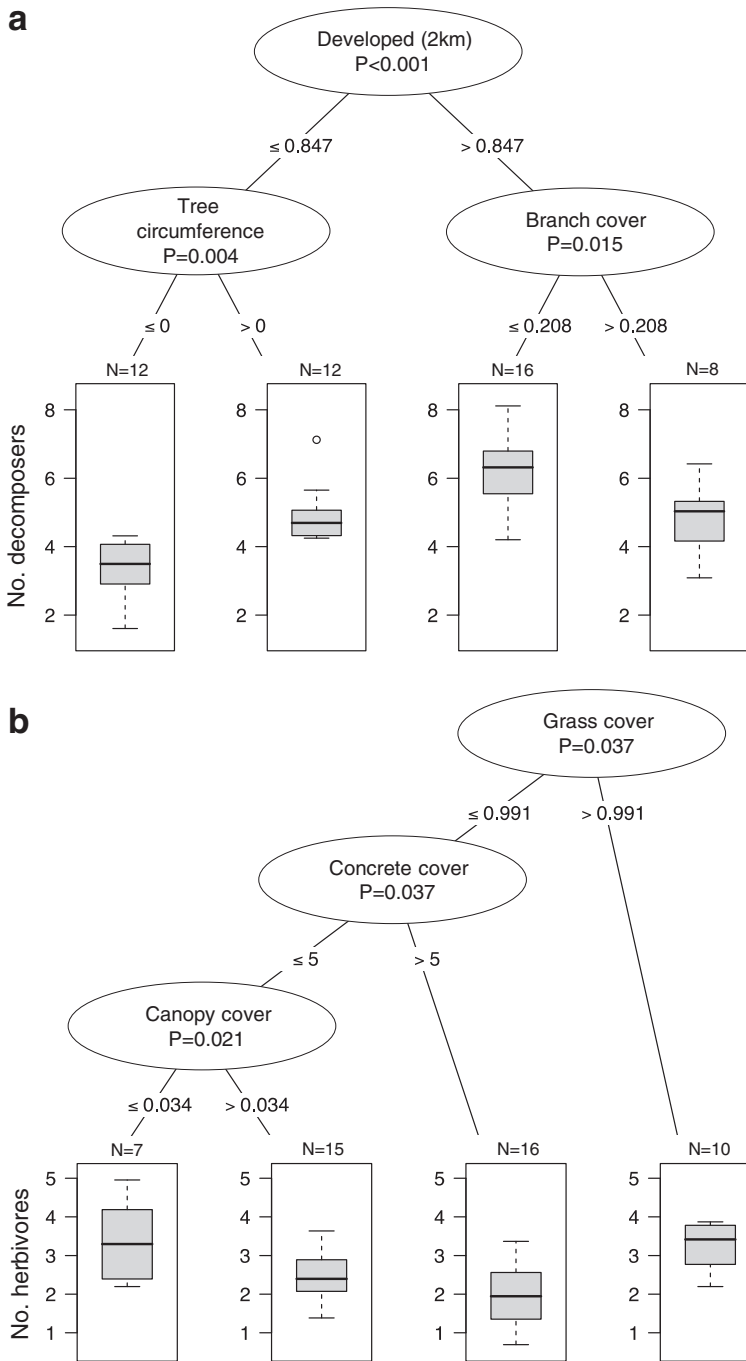


Fig. 6 Conditional inference trees examining relationships between 24 local and 16 landscape factors and abundance of: **a** decomposers and **b** herbivores in forests, gardens, and vacant lots in Toledo, Ohio. Explanation is as for Fig. 4

Table 3 The total number of significant predictors of arthropod abundance and richness at both local and landscape spatial scales

| Arthropod group | 1×1 m plot | 20×20 m plot | 100×100 m plot | 200 m buffer | 500 m buffer | 1 km buffer | 2 km buffer |
|--------------------|------------|--------------|----------------|--------------|--------------|-------------|-------------|
| All arthropods | 3 | 0 | 0 | 0 | 0 | 0 | 1 |
| Araneae | 2 | 0 | 0 | 1 | 0 | 0 | 0 |
| Coleoptera | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diplopoda | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| Hemiptera | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| Formicidae | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Isopoda | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| Opiliones | 2 | 1 | 0 | 0 | 0 | 0 | 0 |
| Orthoptera | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| Decomposers | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| Herbivores | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| Predators | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Ant richness | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| Beetle richness | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Spider richness | 0 | 0 | 1 | 2 | 0 | 0 | 0 |
| Total factors | 14 | 7 | 7 | 4 | 0 | 0 | 3 |
| Percent of factors | 40.0 | 20.0 | 20.0 | 11.42 | 0 | 0 | 8.6 |

abundance positively responded to developed area and decreases in branch cover. Development may alter soil pH and be associated with heavy metal contamination, and branches may decompose, altering soil pH; both pH and metal contamination affect isopod abundance (Smith et al. 2006). Most isopods are important providers of decomposition services in natural and agricultural habitats, but because isopods can be important agricultural pests as root herbivores (e.g. Paoletti et al. 2008), understanding the specific factors that relate to patterns of isopod abundance in gardens, especially where mulch is added, may be important for urban food production. Ants were most abundant in vacant lots, followed by gardens, consistent with results from other studies and different sampling methods (Uno et al. 2010). Ant abundance also increased with increased building cover. The pavement ant, *Tetramorium caspaetum*, and the cornfield ant, *Lasius neoniger*, were the two most common ant species encountered. Both species form large colonies and tend to occur in open, disturbed habitats (Merickel and Clark 1994; Lessard and Buddle 2005). The pavement ant, in particular, may have dramatic impacts on the abundance and richness of other ants in urban areas and may have negative influences on both biodiversity and agricultural production (Uno et al. 2010). Spiders were also more abundant in lots and gardens than in forests, and spider abundance increased with more developed area. Spiders, generally, are more abundant in more disturbed habitats, such as the lots and gardens examined here that experience more mowing and soil manipulation during the summer season (e.g. Samu et al. 1999; Bolger et al. 2000; Pinkus-Rendón et al. 2006).

Species richness of ants, beetles, and spiders differed with habitat type. Ant species richness was higher in forests than in gardens, even though ant abundance was much higher in the lots and gardens than in forests. Differences in the patterns of ant richness and abundance may relate to the presence of the invasive pavement ant in the gardens and lots,

and the lack of this ant in the forest. Other studies have found significant correlations between the abundance of the pavement ant and declines in richness of other ants (Uno et al. 2010). Beetle species richness was higher in the gardens than in forests. This may be due to the relatively larger observed changes in garden vegetation over time, inputs of soil amendments (compost, manure, mulch), or variety of plants for herbivorous beetles. Spider species richness, similar to spider abundance, was higher in the lots and gardens than in forests, was correlated with water and developed areas in the surrounding landscape, and declined with forb richness. Spiders generally are more species-rich in disturbed habitats (e.g. Samu et al. 1999; Bolger et al. 2000; Pinkus-Rendón et al. 2006;). Although spiders may sometimes respond positively to plant richness (e.g. Wise 1993), spider activity density, especially that of hunting spiders likely to be caught in pitfall traps, may increase in physically simpler environments with fewer forb species (Siemann 1998).

Abundance of different trophic groups was strongly affected by habitat type and several habitat factors. Predators were most abundant in vacant lots and in areas with higher building cover. Predator abundance was aligned with increases in natural habitat within 2 km. Increasing the amount of natural habitat in urban areas, even in areas with high housing density, thus could be used in urban gardens to promote ecosystem services. Herbivore abundance, in contrast, did not differ with habitat type, but herbivore abundance increased with more grass cover and decreased in areas with more concrete and more canopy cover. Individual groups of herbivores (true bugs, grasshoppers, and herbivorous beetles) all showed different responses to habitat type and to local and landscape habitat factors, which may have masked broader patterns with habitat. In other studies, herbivores tend to be more common in open or edge habitats (Christie et al. 2010), consistent with our results. Finally, decomposers were more abundant in gardens and forests than in lots, and were more abundant with large amounts of nearby developed land, larger tree circumference, and lower branch cover. This result reflects the responses of isopods, by far the most common group of decomposers. In the CCA, trophic groups were widely separated based on factors with which they associated. This general result is consistent with other studies that have examined trophic structure in urban settings. Previous research has documented that trophic structure of urban arthropods can strongly respond to differences in fragment age and size, management intensity, amount of impervious areas, and water availability (Gibb and Hochuli 2002; Cook and Faeth 2006; Sattler et al. 2010).

Local and landscape drivers were both important predictors of urban arthropods, but the specific drivers differed by taxonomic and trophic group. There is a strong indication that different arthropods respond strongly to different characteristics of the habitat and surrounding landscape, given the relatively low number of predictor variables shared between taxa and trophic groups (Fig. 3). In addition, most of the predictors of arthropod abundance, richness, and trophic structure (80 % of interactions) were local-scale factors, with potentially important consequences for promoting biodiversity and ecosystem services within urban areas. It is easier for park managers, city officials, and gardeners to adjust the local vegetation complexity and composition of individual sites and habitats than it is to restructure urban landscapes. The result that significant predictors specifically related to vegetation, and not to physical components of the environment (e.g. concrete), is especially important. Gardeners and resource managers for city parks might use results such as those outlined here in management plans for increasing biodiversity within urban habitats, or for promoting the abundance of a key garden predator, for example. From a biological standpoint, stronger influences of local factors may be because most arthropods collected in pitfall traps are relatively poor dispersers compared with other more mobile arthropods (e.g. bees, parasitoids), and increased mobility of an organism may result in that organism being more highly

impacted by landscape relative to local factors (Tscharntke et al. 2005). Yet in some urban studies, responses of low and high mobility organisms to local and landscape factors may be somewhat similar, with only slightly larger influences in local management for low-mobility arthropods (Sattler et al. 2010). It is possible that at larger spatial scales (1 km or 2 km) urban habitats become homogenized, with little variation in landscape surroundings between sites. However, the increasing degree of overlap between the 1 km and 2 km buffer zones of our study sites make it more difficult to assess whether or not this is the case. The study sites included here varied in land-cover at larger spatial scales, but the degree of variation was smaller at the two larger scales (1 km and 2 km) than at the 200 m and 500 m scales. Those landscape factors that were important predictors tended to cluster at the 2 km scale, rather than the smaller scales included. The significant relationships at the 2 km scale were correlations between Isopoda abundance and percent of developed area within 2 km of the study sites. Isopods were the most common decomposer and the most abundant arthropod collected, and thus all three significant predictors at this scale are driven by Isopods.

In sum, arthropods in urban areas strongly respond to differences in habitat type, and responses to habitat and to individual habitat characteristic are highly taxon and trophic-level dependent. Overall, local factors tend to better predict the abundance and richness of the many ground-foraging taxonomic groups examined in this study. This finding, in particular, has a highly significant impact for urban planning both for biodiversity conservation and potentially for increasing food production, ecosystem services, and food security within urban areas. Our results indicate that different vegetation and other local factors could be manipulated in order to influence the abundance and richness of certain arthropod groups within urban green spaces both for biodiversity conservation and for provisioning of ecosystem services.

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