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Diversity, abundance, and species composition of ants in urban green spaces

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Abstract Urbanization threatens biodiversity, yet the number and scope of studies on urban arthropod biodiversity are relatively limited. We sampled ant communities in three urban habitats (forest remnants, community gardens, vacant lots) in Detroit and Toledo, USA, to compare species richness, abundance, and species composition. We measured 24 site characteristics to examine relationships between richness and composition and habitat patch size, vegetation, and urban features. Ant richness was higher in forests (26) than in gardens (14) and intermediate in vacant lots (20). Ant richness in gardens and vacant lots negatively correlated with abundance of an exotic ant species (*Tetramorium caespitum*); thus this ant may affect native ant richness in urban habitats. Ant composition differed with habitat type, and abundance was lowest in forests. Site characteristics varied with habitat type: forests were larger, had more woody plants, higher woody plant richness, more branches, and leaf litter whereas lots and gardens had more concrete and buildings. Vacant lots had taller herbaceous vegetation, and gardens had higher forb richness, density, and more bare ground. Differences in vegetation did not correlate with ant richness, but several vegetation factors (e.g. patch size, number and size of trees, leaf litter, and amount of concrete and buildings) correlated with differences in ant species composition. Additional factors relating to soil, nests, or microclimatic factors may also be important for urban ant communities. Implications for biodiversity conservation in urban ecosystems are discussed.

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Introduction

Urbanization is a major threat to biodiversity (Kowarik 1995; McIntyre 2000; Marzluff 2001; McKinney 2002; Miller and Hobbs 2002). Urbanization involves conversion of natural habitat to buildings, sealed surfaces, and roads (McKinney 2002), resulting in habitat loss and fragmentation, changes in local climate and hydrology, and pollution (Pyle et al. 1981; Jones and Clark 1987; Niemelä 1999; Speight et al. 1998). Additionally, urbanization favors introduction of exotic species, which in turn results in biotic homogenization and reductions in the biological uniqueness of local ecosystems (Blair 2001). Urban areas cover approximately 4% of Earth's land surface (UNDP et al. 2000). Further, about half of the world's population lives in urban areas today, and urban populations are rapidly expanding (UNPD 2008) thus urban land use may even expand faster than the population. For example, between 1950 and 1990, the urban population of the United States increased from 65% to 75% and urban land use doubled (PRB 1998). Understanding the characteristics of urban habitats that lead to biodiversity loss, and the potential contributions of different urban habitats to biodiversity conservation is critical given the expansion of urban areas at large scales.

Although the need for biodiversity conservation in urban ecosystems is increasingly recognized, studies on urban biodiversity, especially in multiple habitat types, are a minor focus of conservation biology (McIntyre 2000; McKinney 2002; Miller and Hobbs 2002; Turner et al. 2004). For example, of 217 studies published in *Conservation Biology* between 1995 and 1999, less than 6% were conducted in urban ecosystems (Miller and Hobbs 2002). Several more recent studies have examined relationships between biodiversity and urbanization (e.g. Turner et al. 2004; Shochat et al. 2006; McKinney 2008). However, most studies have examined biodiversity in a single urban habitat type (McIntyre 2000; Yamaguchi 2004; Rango 2005; Sadler et al. 2006; Smith et al. 2006; Thompson and McLachlan 2007), and comparisons of different habitat types within urban areas are rare (see McIntyre et al. 2001). A variety of habitats can be found within urban areas, generally categorized into four types: 1) built habitat with buildings and sealed surfaces; 2) managed vegetation; 3) unmanaged green spaces such as vacant lots and abandoned farmland, and 4) natural remnant vegetation (McKinney 2002). Managed and unmanaged green spaces, such as urban gardens and vacant lots are ubiquitous in many U.S. cities. For example, New York City contains more than 1,000 community gardens (Monroe-Santos 1998) and 10,000 vacant lots (Freeman 2004). Relatively little is known about the degree to which common urban habitats may promote biodiversity conservation.

Arthropods are ideal organisms for examining biodiversity in urban habitats for a variety of reasons. First, they represent a range of trophic levels and perform a variety of ecological functions, thus are a particularly advantageous target for biodiversity studies (e.g. McIntyre 2000). Further, arthropod generation time is relatively short, making responses to environmental changes more rapidly detectable (McIntyre 2000; McIntyre et al. 2001). Arthropod diversity is affected by various habitat characteristics such as vegetation structure, herb cover, tree canopy cover, plant species richness, area of canopy vegetation, soil moisture, soil penetrability, leaf litter depth, habitat age, patch size, and degree of habitat disturbance (Andersen 1986; McIntyre et al. 2001; Lassau and Hochuli 2004; Yamaguchi 2004; Philpott et al. 2006; Sadler et al. 2006; Smith et al. 2006). Furthermore, arthropod communities can be strongly influenced by presence of competitive dominants such as exotic invasive species that are increasingly common in urban areas (Gibb and Hochuli 2002; Holway and Suarez 2006). Arthropods have several functions in ecosystems including as herbivores, predators, decomposers, and nutrient cyclers, among others (e.g. Fisher 1998). Along the urban to rural gradient, urban cores generally support few species of plants, birds, mammals, and insects (Denys and Schmidt 1998; Mackin-Rogalska et al. 1998; McIntyre 2000; Blair 2001; Marzluff 2001). For some arthropods, in contrast, species richness may be higher in more urbanized areas (see review by McIntyre 2000). Due to these various reasons, arthropods are useful study organisms for investigating those habitat characteristics that lead to biodiversity loss in urban habitats.

Among arthropods, ants are an important target group, but are underrepresented in studies of urban biodiversity in comparisons to other insect orders such as Lepidoptera and Coleoptera (McIntyre 2000). Ants are ubiquitous, diverse, abundant, and fairly well described (Alonso and Agosti 2000). Ants respond to a variety of disturbances and have served as bioindicators to assess effects of forest clearing (King et al. 1998; Gascon et al. 1999), fire (Andersen 1991; Izhaki et al. 2003), road construction (Samways et al. 1997; Lassau and Hochuli 2003), mining (Majer 1984), and agriculture (Perfecto and Snelling 1995; Philpott et al. 2006). Ecological studies of urban ants have documented changes in species richness and species composition in urban habitat fragments of different size or age, or along urban to rural gradients (Gibb and Hochuli 2002; Yamaguchi 2004; Lessard and Buddle 2005; Pacheco and Vasconcelos 2007). Ant species richness often declines in smaller and older natural habitat fragments in urban areas (Yamaguchi 2004), from rural to urban forests along gradients (Lessard and Buddle 2005), or from urban edges to the inner city (Pacheco and Vasconcelos 2007). However, some studies have found that decreasing size of habitat fragments does not affect ant richness within fragments in urban areas (Gibb and Hochuli 2002). Nearly all studies, however, do find clear changes in ant species composition in urban habitats compared with nearby, rural natural areas. There is little knowledge, however, of differences in ant communities among urban green spaces common within cities.

We conducted ant surveys in three urban green spaces (community gardens, vacant lots, and forest fragments) in two U.S. cities, Detroit, Michigan, and Toledo, Ohio, to address this lack of information about ant biodiversity in urban areas. Specifically we studied ant communities in the three types of urban green spaces to examine the following questions: 1) How do urban habitats differ in terms of ant abundance, richness, and species composition? and 2) Which habitat characteristics correlate with ant biodiversity and species composition in urban areas?

Methods

We worked in two cities, Detroit, Michigan (42°19′54″N 83°2′51″W), and Toledo, Ohio (41°39′56″N 83°34″31′W). Detroit is slightly larger (370.2 km^2) than Toledo (217.8 km^2). In both cities, vacant lots represent a significant habitat type. In Detroit, there are at least 66,000 vacant lots totaling 103 km^2, or about 28% of land area (SEMCOG 2003). In Toledo data are there are at least 1,000 vacant lots representing at least 1.5% of land area (W. Perryman, pers. com.). In each city, we selected 4 replicates each of forest fragments (forests), community gardens (gardens) and vacant lots (lots) for a total of 12 sites in each city (Fig. 1). Study sites were separated by between 1.8 to 28.0 km in Detroit and 0.5 to 13.1 km in Toledo, meaning that sites in Detroit were distributed over a larger area (Fig. 1). Forests were located within city parks, the oldest of which was established in the late 1800's, and size of forest fragments within parks ranged between 28,500 m^2 and 737,500 m^2. All community gardens had been in production for at least 6 years and were organically managed. Size of gardens ranged between 353 m^2 and 2,688 m^2. Vacant lots used in this study were all formerly residential properties now under city management and had been vacant for at least 9 years in Toledo and 15 years in Detroit. Size of vacant lots ranged between 706 m^2 and 8,750 m^2.

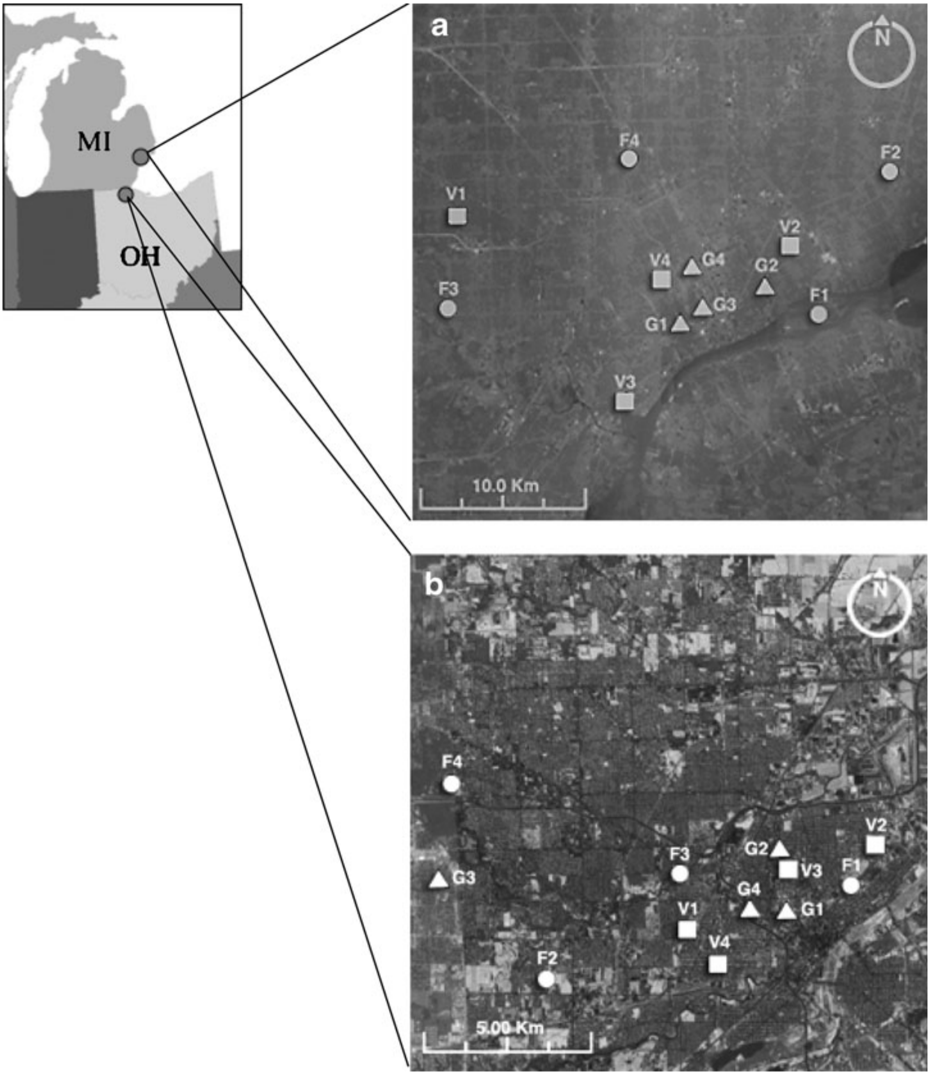


Fig. 1 Location of urban study sites in Detroit, MI (**a**) and Toledo, OH (**b**). Sites sampled included natural forests (F), community gardens (G), and vacant lots (V)

Ant sampling

We sampled ants with tuna baits placed directly on the soil. At each site we established 49 baiting stations distributed in a square grid with each bait separated by 2 m. This is a standard technique that has been used to sample ant richness and activity in a variety of habitats and locations (e.g. Andersen and Patel 1994; Perfecto and Vandermeer 2002; Ratchford et al. 2005). The baiting grid was set up roughly at the center of each habitat patch. We inspected baits 30 min. after placing them, recorded the ant species present at the bait, and collected ants for later identification. When ants were present we recorded activity levels defined as follows: level 1 (1 to 3 ants), level 2 (4 to 9 ants), and level 3 (≥10 ants). We sampled ants monthly from May to July 2007, for a total of three sampling events at each site, with all samplings conducted between 9:00 AM and 2:00 PM. Ants were identified to species with keys in Coovert (2005) and by comparing specimens to those found at the Cleveland Museum of Natural History. Although observations of ants at food baits may be affected by ecological dominance of a subset of the ant assemblage, any community is defined by the method used. Therefore, we tried to minimize competitive exclusion at baits by sampling ants as soon as a majority of baits showed occupation by ants.

Habitat characterizations

At each site, we measured 24 habitat and vegetation characteristics to investigate potential influences on ant richness and abundance (Table 1). First, we measured the size of habitat containing the ant baiting area. To examine factors most related to urbanization (concrete and buildings), we established 100×100 m plots centered on the ant baiting areas. Within each plot we estimated the percent of the area covered with a) concrete, b) buildings, c) bare ground, d) grass or herbs, and e) shrubs, and counted the number of trees >30 cm circumference at breast height (cbh). To examine additional vegetation characteristics we established 20×20 m plots centered on the ant sampling area. Within the 20×20 m plots, we sampled canopy cover with a concave vertical densiometer at each corner and the center of each plot. We counted and identified all trees >30 cm cbh, measured tree circumference at 1.37 m above the ground, and estimated tree height. We also counted and identified all tree seedlings and shrubs <2 m height, and measured seedling and shrub circumference (1 cm above ground) and height, and calculated total woody plant richness at each site. Finally, within 20×20 m plots, we randomly placed four 1×1 m plots to examine herbaceous vegetation and ground cover. Within each 1×1 m plot, we estimated percent cover from a) bare ground, b) grasses, c) forbs and herbs, d) rocks/wood panels, e) leaf litter, and f) fallen branches. We also recorded a) height of the tallest non-woody vegetation, b) number of individuals of forbs and herbs, and c) number of species of forbs, herbs, and grasses. The habitat data were collected during May–July 2007 in Toledo and May–September 2007 in Detroit.

Analyses

To examine ant richness, we plotted species accumulation curves for each habitat type with EstimateS (Colwell 2005) and determined significant differences between habitat types by comparing overlap in 95% confidence intervals (CIs). We treated individual baits as samples and used sample-based rarefaction curves standardized to the number of occurrences to compare species richness between cities and habitat types, as bait occupation differed among sites (Gotelli and Colwell 2001). We examined both observed

Table 1 Vegetation and habitat characteristics measured in forests, gardens, and vacant lots in Detroit, MI, and Toledo, OH

Vegetation or habitat characteristic	Forest	Garden	Vacant Lot	$F_{2, 18}$	p
Size of habitat patch	0.204±0.089a	0.001±0.0003b	0.002±0.001b	22.53	<0.001
100×100 m plots					
Concrete cover (%)	1.00±0.681b	18.5±3.47a	17.12±3.34a	27.79	<0.001
Building cover (%)	0±0b	16.63±3.61a	15.75±5.07a	16.31	<0.001
Bare ground cover (%)	7.75±2.40	6.88±2.78	2.5±0.60	3.26	0.062
Grass and herb cover (%)	49.38±10.95	46.38±7.84	63.75±5.73	2.36	0.123
Shrub cover (%)	36.88±4.623a	5.25±1.70b	9.49±5.07b	23.15	<0.001
No. of trees	295.25±28.34a	35.5±4.23b	35.38±5.44b	108.98	<0.001
20×20 m plots					
Canopy cover	92.80±1.53a	8.62±3.22b	20.88±6.71b	129.99	<0.001
No. of trees	59.25±25.53a	0.75±0.62b	4.38±1.99b	22.99	<0.001
No. of shrubs and seedlings	39.38±15.73a	7.13±2.18a,b	0.75±0.75b	7.66	0.004
Tree circumference (cm)	62.21±13.57	12.39±8.44	35.53±19.52	3.38	0.057
Tree height (m)	10.03±1.80a	1.14±0.88b	4.05±1.67b	14.50	<0.001
Shrub and seedling circumference (cm)	3.46±0.75	6.95±3.11	2.4±2.4	1.33	0.29
Shrub and seedling height (m)	1.61±0.36a	1.53±0.40a	0.39±0.39b	3.78	0.043
No. of woody plant species	6.21±1.39a	2.40±0.72b	1.0±0.87b	10.43	0.001
1×1 m plots					
Height of tallest vegetation (cm)	25.58±3.25b	39.09±5.89a,b	53.08±9.13a	6.05	0.01
No. of herb and forb species	4.69±1.44b	20.06±1.87a	9.0±0.66b	38.15	<0.001
No. of herb and forb individuals	200.62±83.24	288.19±97.00	206.19±35.40	2.98	0.076
Bare ground cover (%)	5.05±2.75b	26.23±8.15a	5.94±2.68b	6.35	0.008
Grass cover (%)	1.09±0.76c	12.91±5.64b	77.99±3.30a	104.43	<0.001
Forb and herb cover (%)	33.16±10.46	44.69±7.69	14.91±3.09	3.37	0.057
Rock and wood cover (%)	3.12±3.13	1.81±0.69	0.89±0.61	0.36	0.702
Leaf litter cover (%)	65.91±12.30a	9.89±5.91b	38.86±15.72a	13.02	<0.001
Branch cover (%)	8.30±1.05a	0.72±0.72b	1.08±0.36b	28.42	<0.001

Values for forests, gardens and lots are mean ± standard error, small letters designate significant differences between habitats (Tukey's, $p<0.05$)

richness and estimated species richness (Chao2) for each habitat type. Given that ants are social insects, we used occurrence rather than abundance-based data for diversity analysis (Longino et al. 2002).

We compared ant abundance in the different habitats based on ant activity and proportions of baits occupied by ants in different habitat types. We calculated ant activity for each site by taking the sum of the activity levels for each species across all baits during one sampling month. Then, we calculated mean activity levels for each site across the three sampling periods. Likewise, we took the mean of proportion of baits occupied in each site across the three sampling dates. Then, we examined differences between cities and habitat types for activity level and occupied baits with univariate analysis of variance (ANOVA) and determined pair wise differences with Tukey's post-hoc tests. Where city by habitat type interactions were significant, we followed with individual ANOVAs for each city separately. Comparisons of ant abundance were conducted with SPSS v. 16.0.

We compared species composition of ants in the three urban habitats with three methods. First, we used non-metric multi-dimensional scaling (NMDS) and analysis of similarities (ANOSIM) to visually and statistically compare species composition of ants in the two cities and three habitat types. We considered each site as a replicate, summed all occurrences of each species over three sample months, and compared similarity with the Bray-Curtis similarity index. ANOSIM produces a global *P*-value to indicate any differences in species composition and also reports pair-wise comparisons between particular sites. Third, we used a non-parametric MANOVA (NPMANOVA) to compare the relative differences in species composition in sites of the same habitat type (spread of the points). All composition analyses were conducted with PAST (Hämmer et al. 2001).

Finally, we compared site characteristics in the different habitat types and investigated potential influences of the site characteristics on the ant richness and composition within the urban habitats. To examine differences in the site characteristics in the three different habitats, we used a multivariate ANOVA (MANOVA) with each of the 24 site variables as dependent variables and city and habitat type as factors. We followed significant MANOVA with individual ANOVA to determine which individual factors differed among the three habitat types. To examine relationships between the site characteristics and ant communities, we first used a Principal Components Analysis (PCA) to reduce the 24 vegetation variables into two principal components. Then we correlated PCA axis 1 and axis 2 with individual vegetation variables with Pearson's correlations to determine which variables were significantly explained by the two principal components. We used three multivariate regressions to examine whether PCA axes 1 and 2 and other remaining variables predicted total observed ant richness, NMDS dimension 1, or NMDS dimension 2. Variables representing percent ground cover at the 100×100 m and 1× 1 m scales were arcsine-square root transformed; counts of trees, shrubs, and herbs were natural log (+1) transformed, and habitat size was square-root transformed to meet conditions of normality before any analysis. Finally, we calculated distance between each site, and correlated these distances to Bray-Curtis similarity values. All vegetation, PCA, and regression analyses were conducted with SPSS v. 16.0.

Results

Ant richness, abundance, and species composition

We collected 33 species, 27 in Detroit and 30 in Toledo. Overall, we collected 26 species from forests, 20 from vacant lots, and 14 from gardens. In Detroit, we found 17, 8, and 16 species in forests, gardens, and vacant lots, respectively, while 23, 12, and 15 species were collected from Toledo (Table 2). Across both cities, the most common ant species was *Lasius neoniger*, accounting for 29.3% of 3,350 total ant occurrences, followed by *Tetramorium caespitum* (28.2%). In Toledo, *T. caespitum* was the most frequently encountered ant (30.9% of 1,820 ant occurrences), followed by *L. neoniger* (26.2%). In Detroit, *L. neoniger* (32.9% of 1,530 occurrences) was most common, followed by *T. caespitum* (25.1%).

Overall, observed richness was greater in forests than in gardens, but ant richness in vacant lots did not differ from the other habitat types (Fig. 2a). In Detroit, both forests and vacant lots had significantly more species than gardens (Fig. 2b). In Toledo, richness patterns were consistent with overall patterns, with significantly greater richness in forests

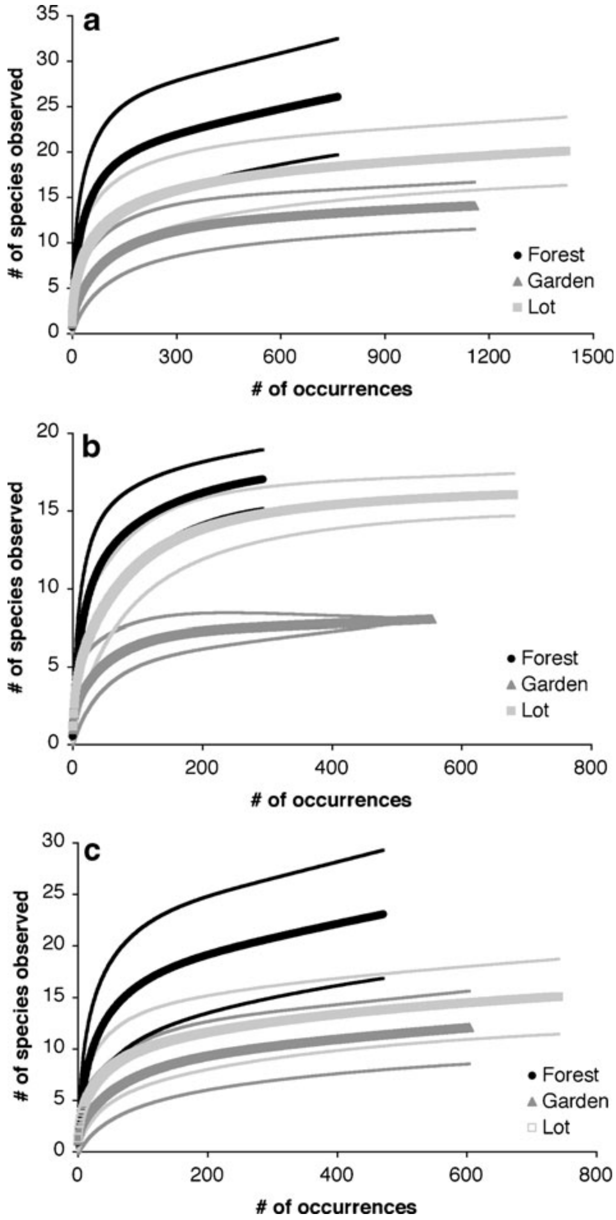
Table 2 Ant species list for three urban habitats in Detroit and Toledo

Species	Detroit			Toledo		
	Forest	Garden	Lot	Forest	Garden	Lot
Aphaenogaster picea	17	0	0	106	0	0
Aphaenogaster rudis	0	0	0	22	0	25
Aphaenogaster tennesseensis	0	0	0	17	0	0
Brachymyrmex depilis	0	0	0	1	0	0
Camponotus americanus	2	0	0	7	1	0
Camponotus caryae	1	0	0	0	0	0
Camponotus chromaiodes	1	1	0	0	11	0
Camponotus nearcticus	3	0	0	2	1	1
Camponotus pennsylvanicus	70	0	13	65	6	3
Crematogaster cerasi	0	7	2	0	0	0
Crematogaster lineolata	0	0	6	0	0	0
Forelius pruinosus	0	0	0	0	0	1
Formica fusca	0	0	11	1	0	0
Formica glacialis	0	0	0	1	0	0
Formica nitidiventris	0	0	10	0	32	35
Formica suscericea	0	0	14	8	2	13
Lasius alienus	35	0	0	25	0	0
Lasius flavus	2	0	4	0	0	2
Lasius neoniger	0	194	310	0	141	335
Leptothorax curvispinosus	12	0	0	1	0	0
Leptothorax longispinosus	28	0	0	1	0	0
Myrmecina americana	5	0	1	7	0	0
Myrmica americana	16	0	121	5	0	16
Myrmica fracticornis	4	0	12	28	0	0
Myrmica punctiventris	14	0	0	63	0	0
Paratrechina faisonensis	0	6	0	0	1	0
Paratrechina flavipes	0	0	0	6	5	4
Prenolepis imparis imparis	17	9	72	64	11	8
Solenopsis molesta	0	30	9	0	7	21
Stenamma impar	7	0	0	8	0	0
Stenamma schmittii	60	0	4	23	0	1
Tapinoma sessile	0	12	4	10	0	104
Tetramorium caespitum	0	296	88	1	387	174
Total occurrences	294	555	681	472	605	743
Total species richness	17	8	16	23	12	15

Numbers are total number of occurrences per habitat type

than in garden, and no difference between vacant lots and other habitats (Fig. 2c). Estimated richness (Chao2) for forests was 33.49 species overall, 30.49 species in Toledo, and 17.33 species in Detroit. Estimated richness in gardens was 14.5 species overall, 13.5 species in Toledo, 8 species in Detroit. Estimated richness in lots was 21.5 overall, 16.5 species in Toledo, and 16 species in Detroit. Patterns for accumulation curves and 95% CI for

Fig. 2 Rarefaction curves for ant species richness observed in urban forests, community gardens, and vacant lots sampled in Detroit, MI (**b**), Toledo, OH (**c**), and across both cities (**a**). *Thin lines* show upper and lower 95% confidence intervals for symbols of the same color

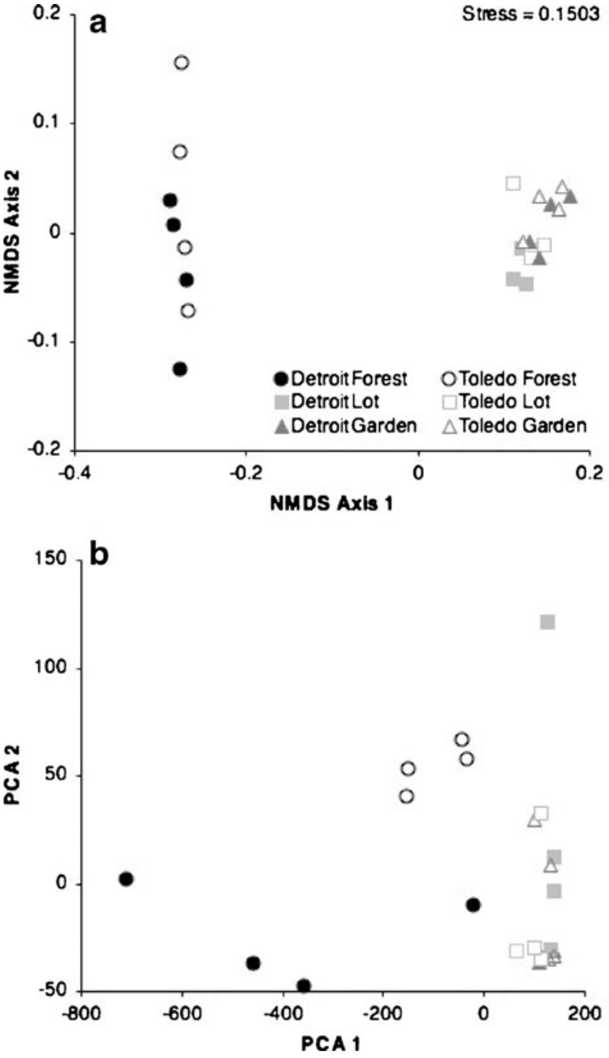


estimated richness (Chao2, not shown) were similar to observed richness except that richness in Toledo forests and gardens did not significantly differ.

Ant abundance differed between the two habitat types. Ant activity levels were more than twice as high in lots (135.8±5.9) and gardens (114.3±8.7) than in forests (48.9±8.8) ($F_{2,18}$=35.632, p<0.001, Tukey's pair-wise tests p<0.001). There were no differences in activity levels in Toledo and Detroit ($F_{1,18}$=3.272, p=0.087), nor did ant activity in different habitats vary with city ($F_{2,18}$=0.807, p=0.462). Ants occupied a higher proportion of baits, on average, in lots (0.91±0.02) and gardens (0.81±0.04) than in forests (0.48±0.07) ($F_{2,18}$=26.058, p=0.024, Tukey's pair wise tests p<0.001). Further, ants occupied more baits in Toledo (0.80±0.05) than in Detroit (0.69±0.07) ($F_{1,18}$=26.056, p<0.001); however, differences in habitats did not vary by city ($F_{2,18}$=1.899, p=0.178).

Overall species composition differed significantly between habitat types as observed visually (Fig. 3a) and statistically (ANOSIM, Global R=0.560, p<0.0001). All three habitat types in Detroit differed from one another (forest-garden, p=0.023; forest-lot, p=0.026; garden-lot, p=0.030). Likewise, ant composition in Toledo forests differed from Toledo gardens (p=0.029) and lots (p=0.028), but Toledo gardens and lots did not differ (p=0.120). Across cities, forest sites, garden sites, and vacant lot sites had similar species composition (P>0.05), but Detroit lots differed from Toledo gardens (p=0.027) and Toledo forests (p=0.025). Furthermore, forest sites tended to be more dissimilar than garden or lot sites for both Toledo and Detroit (F=5.823, p<0.001). The composition of Detroit and Toledo forest sites was more widely distributed than garden or lot sites in Detroit and

Fig. 3 Ordinations of ant communities (**a**) and site characteristics (**b**) in forests, gardens, and vacant lots in Detroit, MI and Toledo, OH. Ant community ordination is the result of non-metric multi-dimensional scaling (NMDS) analysis with Bray-Curtis as the similarity index. The ordination of site characteristics is a principal components analysis (PCA) for 24 variables measured in all sites. In both panels, *circles* are forests, *triangles* are gardens, and *squares* are lots. *Closed symbols* are sites in Detroit and *open symbols* are sites in Toledo



Toledo (all pair-wise comparisons, $p<0.05$). Composition in Toledo garden sites was more dissimilar that composition in Detroit lots ($p=0.028$).

Habitat characteristics and ant richness and composition

There were several differences in habitat and vegetation characteristics measured in the three habitat types ($F_{4,36}=28.08$, $p=0.003$), but no differences in vegetation between cities ($F_{1,18}=5.361$, $p=0.329$), or a city by habitat type interaction ($F_{4,36}=2.011$, $p=0.262$). Generally, forests were larger, had more shrubs and trees, larger shrubs and trees, higher richness of woody plants, and more branches and leaf litter (Table 1). Vacant lots and gardens had more nearby area covered in buildings and concrete (Table 1). Vacant lots had taller non-woody vegetation than the other habitat types, and gardens typically had higher forb richness, density, and ground cover, and more bare ground (Table 1).

The PCA predicted a large fraction of the variation in the vegetation and habitat characteristics and the characteristics of different habitat types were distinct (Fig. 3b). The PC1 explained 94.09% of the variation and PC2 explained 3.67% of the variation in the data. A total of 13 individual factors significantly correlated with PC1 and an additional two factors correlated significantly with PC2 (Table 3). Although additional components (e.g. PC3, PC4) significantly explained additional variation in the data, they did not correlate with remaining site characteristics. Thus the PCA reduced the number of factors included in the multiple regressions from 24 variables to 11.

Ant composition but not richness correlated with measured site characteristics. PC1, PC2, and other vegetation factors explained 86.3% of the variation in the NMDS dimension 1 ($F_{11,23}=6.848$, $p=0.001$). Individually, PC1 ($t=3.859$, $p=0.002$) and the percent cover of grass and herbs at the 100×100 m scale ($t=-2.172$, $p=0.051$) correlated with NMDS dimension 1. However, NMDS 2 was not correlated with the measured site characteristics that explained only 65.4% of the variation ($F_{11,23}=2.066$, $p=0.114$). Similarly, observed ant species richness was not significantly correlated with the site characteristics measured ($F_{11,23}=1.147$, $p=0.407$).

Within each city, forest sites were distributed at greater distances from one another (12.52±2.03 km) than lots (8.44±1.68) or gardens (4.71±0.98). However, there were no significant correlations between distance separating sites and Bray-Curtis similarity for forests ($R^2=0.002$, $p=0.883$), lots ($R^2<0.001$, $p=0.967$), or gardens ($R^2=0.24$, $p=0.108$).

Discussion

Overall, we found the highest ant richness in forests and lowest richness in the gardens, but patterns differed in the two cities. Generally, there is support for two main groups of factors that influence species richness and composition of ants in urban areas: habitat and landscape factors, and competitive interactions. Size of habitat patches (MacArthur and Wilson 1967) and habitat heterogeneity (McCoy and Bell 1991) are important determinants of biodiversity and ant communities respond to both habitat size (Gibb and Hochuli 2002; Yamaguchi 2004) and habitat complexity (Andersen 1986; Lassau and Hochuli 2004; Philpott et al. 2006). Dispersal limitation may be important in community assembly in urban areas, as founding queens may not arrive in urban centres from source populations (Pacheco and Vasconcelos 2007). Additionally, plant diversity positively affects animal diversity as greater resources are provided for consumers (Siemann et al. 1998). Site

Table 3 Principal components analysis loadings for 24 vegetation and habitat characteristics measured in forests, community gardens, and vacant lots in Detroit, MI, and Toledo, OH

Vegetation or Habitat Characteristic	PC1	PC2
Size of habitat patch	−1.000**	−0.021
100×100 m plots		
Concrete cover (%)	0.678**	−0.125
Building cover (%)	0.619**	−0.351
Bare ground cover (%)	−0.060	0.364
Grass and herb cover (%)	0.364	0.385
Shrub cover (%)	−0.630**	0.127
No. of trees	−0.709**	0.193
20×20 m plots		
Canopy cover	−0.727**	0.312
No. of trees	−0.689**	0.367
No. of shrubs and seedlings	−0.376	0.212
Tree circumference (cm)	−0.342	0.922**
Tree height (m)	−0.406*	0.830**
Shrub and seedling circumference (cm)	0.142	0.043
Shrub and seedling height (m)	−0.139	0.136
No. of woody plant species	−0.267	0.462*
1×1 m plots		
Height of tallest vegetation (cm)	0.290	−0.109
No. of herb and forb species	0.492*	−0.390
No. of herb and forb individuals	0.601**	−0.011
Bare ground cover (%)	0.360	−0.073
Grass cover (%)	0.466**	0.010
Forb and herb cover (%)	0.152	−0.107
Rock and wood cover (%)	0.254	−0.053
Leaf litter cover (%)	−0.514**	0.251
Branch cover (%)	−0.708**	0.283

Pearson correlations significant to *$p<0.05$, >0.01, and **$p<0.001$

characteristics measured in this study identified important differences between habitat types (Table 1); however, they explained a limited amount of variability in ant richness. None of site variables that we measured (habitat patch size, ground cover, density, richness, or size of woody plants, or herbaceous diversity and density) significantly correlated with ant richness in this study. Of course, other physical or biological aspects of the environment that we did not measure may also affect ant richness. For example, food and nest resources, temperature, light availability, and soil conditions may affect ant richness within disturbed urban sites. Disappearance of necessary nesting resources may affect specialist ant species. For example, due to a decline in the abundance of rotting wood resources, generalists dominate such nesting resources excluding dead wood specialists from urban areas of Helsinki (Vepsäläinen et al. 2008). Increased soil temperature and decreased soil moisture may enhance the establishment potential of some invasive species and reduce the abilities of some native species to persist (Yamaguchi 2004), and drops in soil moisture correlate with lower ant richness in urban areas (Clarke et al. 2008). Specifically, gardens experience regular soil disturbance and practices such as tilling negatively affect ants and other invertebrate diversity (Peck et al. 1998; Altieri 1999).

A second factor mediating diversity in urban areas may be competitive interactions. Competitive interactions between exotic and native ant species, in particular, may be disassembling urban ant communities as has been demonstrated in other systems (Sanders et al. 2003). Ants that persist in urban habitats tend to be generalist and opportunistic species, competitive dominants, and have large, aggressive colonies (Carpintero et al. 2003). Additionally, factors that drive the loss of native species may facilitate the invasion of non-native "tramp" species in urban areas, further driving homogenization (Holway and Suarez 2006). One of the two exotics collected, *Tetramorium caespitum*, was overwhelmingly abundant in the garden and lot sites, especially in Toledo, where richness in both lot and garden sites was lower. *T. caespitum* is native to Europe was introduced to North America in the 1700's (Brown 1957; Weber 1965). It is a tramp species and is largely restricted to urban and disturbed habitats (Merickel and Clark 1994; Lessard and Buddle 2005). Although little is known about its ecology, *T. caespitum* is highly competitive (King and Green 1995), affects invertebrates (Antonelli and Glass 2006; Katayama and Suzuki 2003), and can locally displace native ant species (Merickel and Clark 1994). In the study sites, number of *T. caespitum* occurrences negatively correlated with ant richness (observed richness, $R^2=0.314$, $p=0.004$), leaving open the possibility that *T. caespitum* alter native ant richness within more open urban habitats. However, exotic species do not always affect native diversity in urban areas (Clarke et al. 2008), thus the influence of *T. caespitum* should be examined experimentally in the future.

Both vegetation characteristics and ant species composition significantly differed between all habitat types (Fig. 3), and several of the site characteristics correlated with changes in the ant composition. Similarly, others have documented differences in ant composition in different urban habitats in Brazil (Pacheco and Vasconcelos 2007) and San Francisco (Clarke et al. 2008). Ant composition was more similar in gardens and lots than in forests, and forest sites were spread over significantly larger areas of the coordinate space. Forests differed from gardens and lots for the majority of site characteristics. One reason for larger differences among forest plots might be the physical distance separating habitats. Forest plots, especially in Detroit, were more dispersed than the other habitats (Fig. 1). However, there were no significant correlations between species similarity and physical distance between sites of the same habitat type, within each city. The greater spread in the forest points may also be due to higher beta-diversity in forested habitats, compared with more open areas. Gardens and lots had more similar composition, likely because the vegetation characteristics were largely similar. Out of the 24 factors sampled, gardens and lots only differed in that lots had shorter shrubs, fewer herb species, less bare ground, and more leaf litter and grass cover (Table 1). That differences in the ant composition result from site differences were further supported by the significant correlations between the first NMDS dimension and PC1 and percent grass and herb cover in 100×100 m plots. Thus several habitat factors including habitat patch size, cover of buildings, concrete and shrubs, number of trees and tree height, canopy cover, forb richness, density, and grass, litter, and branch cover likely influence ant composition in urban habitats.

According to both metrics, ant abundance was significantly lower in forests than gardens and lots. Greater canopy cover and higher tree density in forests likely maintained cooler temperatures in forests than the other habitat types; this suggests lower ant activity and may explain lower bait occupations in forests, as many ant species are thermophilic (Hölldobler and Wilson 1990). Additional important factors explaining differences in ant abundance in the three habitat types are the respective foraging behaviors and colony sizes of species present in each habitat. Whereas the colony size of the frequently encountered *T. caespitum* averages between 7,000 and 14,000 (up to 31,000) individuals and *L. neoniger* colonies are large and vigorous, colonies of the less numerous *C. pennsylvanicus* only include up to 2,500 individuals, and likewise *A. picea* colonies are moderately large (Coovert 2005; Antonelli and Glass 2006). While *L. alienus*, another species with large colony sizes, was present in forests and accounted for 9% of occurrences, *T. caespitum* was mostly absent from forests. Lower prevalence or absence of strong recruiters such as *L. neoniger* and *T. caespitum* in forests were likely important in explaining lower ant abundance in forests. Furthermore, Lassau and Hochuli (2004) suggested that more complex ground cover might hinder ant foraging. The greater variety of plant types (e.g. forbs, shrubs, trees) and leaf litter represented in forest sites with greater woody plant richness likely increased the structural complexity of the understory. Significant negative correlations of fallen branches and rocks with ant abundance may reflect negative effects of ground complexity on foraging activity of ants (Lassau and Hochuli 2004). Ants also used fallen branches and logs as foraging pathways, and this may have lowered their chance of bait discovery (S. Uno, personal observation). Finally, ant abundance was higher in sites with greater grass cover (e.g. lots), likely due to indirect effects of grass on ants. First, continuous grass cover of vacant lots might provide protection (e.g. hiding places) from predators and thus contribute to higher ant abundance in this habitat type. Alternatively, the high abundance of ants could be explained by the absence of ant predators due to the lack of resources in sites dominated by grass.

Our results provide some evidence for negative effects of urbanization on ant communities, and provide some directions for future work on ants in urban habitats. We documented differences in ant richness, abundance, and composition in three urban habitats, with forests generally richer than more open habitats. Between the two cities, richness was slightly greater in Toledo and the number of occupied baits was higher in Toledo. Effects of urbanization can also be manifested as a reduced beta diversity or biotic homogenization (Blair 2001). Species compositions in the same habitat types in Detroit and Toledo did not differ significantly, indicating homogenization at a regional scale. Because the distance between sites did not correlate significantly with similarity in species composition, physical distribution of study sites appears to be a less important determinant of ant assemblages compared with habitat differences.

A number of conservation implications can be drawn from our results. The main objectives of this study were to compare richness and determine possible drivers of ant diversity and abundance in urban areas. Maintaining urban forests is clearly important as they harbor greater ant richness and are less frequently inhabited by exotic species than other urban habitats. Less-developed urban habitats such as urban forests support rare native species in general (McKinney 2002), and may be considered as potential source habitats for the more disturbed urban habitats. However, urban habitats are exposed to pressures from the urban matrix (McKinney 2002) and improving urban matrix and providing sufficient connectivity among urban habitats may play an important role for the overall biodiversity conservation within a city (Rudd et al. 2002). Responses to urban land-use types can be taxon-specific (McIntyre et al. 2001; McKinney 2008) and a range of land-use types, including little-studied urban habitats such as gardens and vacant lots, need to be evaluated for conservation values. Although our results showed ant richness was lower in gardens and vacant lots than forests, species composition in the three habitat types was distinct, thereby contributing to the maintenance of ant diversity in general. Generally speaking, ant communities were quite distinct in the different urban green spaces studied.

Although individual vegetation or habitat characteristics did not correlate with increased ant richness, changes in species composition correlated with changes in woody plant and herb richness, and other structural characteristics. Thus to best conserve high species richness in urban areas, across all habitats, maintaining a variety of habitat types may be most beneficial. Vacant lots are often seen as underutilized resources to be converted to economically or socially beneficial uses such as community gardens in an effort to improve food provision to urban populations (Brown and Carter 2003). However, the manner by which the conversion is executed may benefit from consideration of the resident organisms and their contribution to biodiversity. Finally, further studies are needed to fully understand the ecology of exotic species such as *T. caespitum* and their potential role in limiting native ant diversity in urban areas.

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