Fine-scale heterogeneity across Manhattan's urban habitat mosaic is associated with variation in ant composition and richness

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Abstract. 1. Global urbanisation is rapidly expanding and most of the world's humans now live in cities. Most ecological studies have, however, focused on protected areas.

2. To address this issue, we tested predictions from studies of protected areas in urban ecosystems.

3. Because most cities are heterogeneous habitat mosaics which include habitats with varying levels of chronic environmental stress, we focused on predictions from studies of less modified ecosystems about community-wide responses to variation in chronic stress.

4. We sampled ants across Manhattan's urban habitat mosaic, at sites with varying levels of chronic environmental stress.

5. Many predictions derived from less modified ecosystems were supported by our findings: despite being the most intensively sampled habitat, high stress urban medians had less variability in ant composition –both within and among sites – than either urban parks or urban forests, the lowest stress habitat – urban forests-had significantly more accumulated species and a higher number of unique species than higher stress habitats, and urban parks, which have intermediate levels of chronic environmental stress, also had intermediate levels of variation in among-site species composition, accumulated species richness, and the incidence of unique species. The most common species also differed across Manhattan's urban habitat mosaic.

6. Nevertheless, the prediction that exotic species would occur more frequently in higher stress habitats was not supported; exotic species were equally common across all habitats.

7. These findings suggest that fine-scale heterogeneity in the chronic stress of urban habitats may be an underappreciated, but important structuring force for urban animal communities.

Key words. Ants, chronic environmental stress, community structure, diversity, exotic species, *Lasius*, *Tapinoma*, *Tetramorium*, unique species, urban ecology.

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Introduction

The world is becoming increasingly urban. Globally, cities are among the only habitats that are currently expanding (Ellis & Ramankutty, 2008). Between 2005 and 2010,

a fundamental shift in human populations occurred, with >50% of all people on the planet now living in cities that cover just ~3–7% of terrestrial inhabitable land area (Grimm *et al.*, 2008; Martin *et al.*, 2012). Urban ecosystems are predicted to become more widespread in the near future; the spatial extent of cities is estimated to increase by 430 000 km^2 (slightly more than California's land area) to 12 568 000 km^2 (approximately the combined area of the United States and Argentina) by 2030 (Seto *et al.*, 2011). But what is an urban ecosystem and what ecological factors govern which species live in urban ecosystems? To what extent do expectations based upon studies in protected areas accurately predict the structure and dynamics of urban communities? Although reviews about urban ecology have bemoaned the lack of study in urban ecosystems for years (McDonnell, 1997; Pickett *et al.*, 1997; McIntyre, 2000; McDonnell & Hahs, 2008; Martin *et al.*, 2012), cities remain one of the most understudied and poorly understood ecosystems in the world (Martin *et al.*, 2012).

Recent work has begun to elucidate some basic ecological rules of thumb about biodiversity in cities, at least for some organisms. For example, evidence is accumulating that the bird species that thrive in cities have broader environmental tolerances and geographic distributions than congeners that are absent from urban ecosystems (Bonier *et al.*, 2007) and birds and mammals both tend to be less diverse in cities than in surrounding natural habitats (Blair, 1996; Cam *et al.*, 2000; Minor & Urban, 2010; Leveau, 2013; Saito & Koike, 2013; but see Fuller *et al.*, 2009). Historically, studies of urbanisation made progress by treating the urban matrix as if it is a single habitat type (e.g. 'urban, suburban, rural designations'; Ramalho & Hobbs, 2012) or have been conducted at broad spatial scales that blur distinctions among habitats within cities (e.g. Ellis & Ramankutty, 2008). For large mobile organisms, cities may be relatively homogenous ecosystems and such approaches may be both usefully simplifying and reasonable.

Most species, however, are small enough that the finer grain heterogeneity of cities may be relevant to their distribution and composition. We have a poor understanding of the importance of heterogeneity at fine spatial scales to patterns of local diversity. Recently, simple continuous metrics, such as % impervious surface or human population density, have been used as approximations of the multivariate complexity of urban habitats (Pickett & Cadenasso, 2013). Yet, at fine spatial grains, the distributions of habitats within cities are disjunct rather than continuous. Consequently, cities are more accurately described as mosaics of different habitats with a range of human land uses and varying levels of chronic environmental stress that may act as environmental filters for many species (Niemelä *et al.*, 2011; Ramalho & Hobbs, 2012). Chronic stress across urban habitat mosaics can vary along many axes, including – but not limited to – temperature, water availability and intensity, space availability, and pollution levels (see below). The distribution of these habitats within cities is frequently more strongly influenced by human preferences and urban planning than local abiotic conditions (Cilliers, 2010).

Importantly, chronic environmental stress almost certainly simultaneously affects ecological communities across multiple spatiotemporal scales. Different species (Teet & Denlinger, 2014) and even individuals within a given species (Fulton *et al.*, 2013) can respond differently to chronic environmental stress. In this study, we are particularly interested in understanding the relationship between habitat-level chronic environmental stress and its influences on entire communities across urban habitat mosaics.

A rich literature on the effects of chronic environmental stress on diversity of plants and animals in less modified environments provides a starting point for understanding the relationship between chronic environmental stress and diversity in urban ecosystems. In general, work in less modified ecosystems suggests that there is an inverse relationship between native diversity and chronic environmental stress (Menge & Olson, 1990; Fitzgerald *et al.*, 2011). Recently, multivariate measures of simultaneous variation in multiple different components of environmental stress (e.g. temperature, aridity, space constraints, and salts) suggest that mutualism, facilitation, and ecosystem engineering become more important structuring forces for entire ecological communities as multivariate stress increases (He *et al.*, 2013; Pringle *et al.*, 2013; Von Holle, 2013; Watt & Scrosati, 2013). Based on observations of plants and insects living in urban environments, Raupp *et al.* (2010) recently suggested that chronic environmental stress is likely to be important to entire communities of urban plants and arthropods. We still lack empirical tests of this hypothesis, even for otherwise well-studied urban species, however.

Abundant, diverse, widespread, and ecologically important, ants are among the better studied groups of urban invertebrates. For example, previous studies have compared ant diversity across multiple cities in the same geographic region (Stringer *et al.*, 2009; Antonov, 2013; Lutinski *et al.*, 2013). These studies suggest that across broad geographic scales, cities may benefit a few dominant species (perhaps particularly exotic ant species), and create an environmental filter that excludes a large number of native species that occur in less urbanised surrounding areas. Yet, we still do not understand how ant diversity and composition vary across fine-scale urban habitat mosaics within cities.

New York City (NYC) – and Manhattan in particular – is the most urban city in the United States according to a variety of metrics. Compared to 55.2 people per km^2 across the entire United States, NYC's population density is 17,116.7 people per km^2, and Manhattan is home to 44 068.9 people per km^2 (US Census Bureau 2010). Furthermore, NYC was recently ranked as the eighth most populated city in the world (Tokyo was number one; Cox, 2014). In a recent study, Rosenweig *et al.* (2006) found that NYC landscapes had 60.2% (Queens) to 94.3%

(midtown Manhattan) impervious surfaces. Manhattan also has an extensive system of parks, however. City parks and forests cover more than 2700 acres across 367 different parks (~20% of Manhattan's land area; O'Neil-Dunne, 2012) and are complemented by many smaller green habitats, which range from community gardens to urban street medians to street tree pits. A large proportion of these parks and green spaces were engineered in the early 1900s to influence how people moved through and used the city (e.g. Rybczynski, 1999) but they almost certainly also affect how small-bodied organisms use the city.

Here, we assess the diversity of Manhattan's ants across urban medians, which are vegetated but have high levels of chronic environmental stress, urban forests, which are the lowest stress habitats in the urban habitat mosaic and urban parks which have lower stress than urban medians but higher stress than urban forests (e.g. Fig. 1). Ants were an ideal system for addressing our study questions (below) because they are widespread and diverse (Dunn *et al.*, 2007, 2009; Jenkins *et al.*, 2011; Guénard *et al.*, 2012), commonly associate with humans and their structures (Delabie *et al.*, 1995; Klotz *et al.*, 1995; Lessard & Buddle, 2005; Menke *et al.*, 2011), and are an ecologically important group across various spatial scales and multiple habitat types (Folgarait, 1998; Holway *et al.*, 2002; Dostál *et al.*, 2005; Zelikova *et al.*, 2011). With long-lived and sessile colonies (Hölldobler & Wilson, 1990), ants have to cope with both acute and chronic disturbances. In addition, ants have been studied in one of the green habitat types in Manhattan, urban medians (Pećarević *et al.*, 2010). Here, we were interested in assessing ant diversity across habitats with different levels of chronic environmental stress across the urban habitat mosaic in Manhattan. More specifically, we addressed the four following questions, in each case explicitly testing theory developed in more natural habitats.

(1) How does the composition of local ant assemblages vary across Manhattan's urban habitat mosaic?

We predicted that variation in the composition of Manhattan's ant communities would be negatively associated with habitat stress level, with urban forests supporting the most species-rich ant assemblages and urban medians having the fewest ant species. Furthermore, we predicted that the ants living in urban medians and urban parks would be subsets of those found in urban forests.

(2) Is there a relationship between habitat stress level and the incidence of unique species?

Species with restricted nesting, dietary, or temperature restrictions would likely be less able to survive and thrive in high stress habitats. Therefore, we predicted that the number of unique species (those species which occur only in one habitat type) would decline as habitat stress levels increased.

We were also interested in understanding the patterns of occurrence for ant species that were found in multiple habitats with varying levels of environmental stress. Therefore, we asked:

(3) Are the most common ants different in urban habitats with varying levels of stress?

Common species could be the same across habitats, with rare species contributing the most to differences among habitats in compositional diversity. Alternatively, ecological conditions in high stress habitats could be so different from those in low stress habitats that even the most common ants in urban forests or urban parks could become rare in urban medians or vice versa.

Finally, exotic species are generally predicted to have broader tolerances to climatic conditions and less specialised diets than native species (Holway *et al.*, 2002). Therefore, we asked:

(4) How does the occurrence of native and exotic ant species compare across habitats with varying levels of stress?

We predicted that urban medians would have the highest proportion of exotic species and that native species would occur more frequently in urban parks than urban
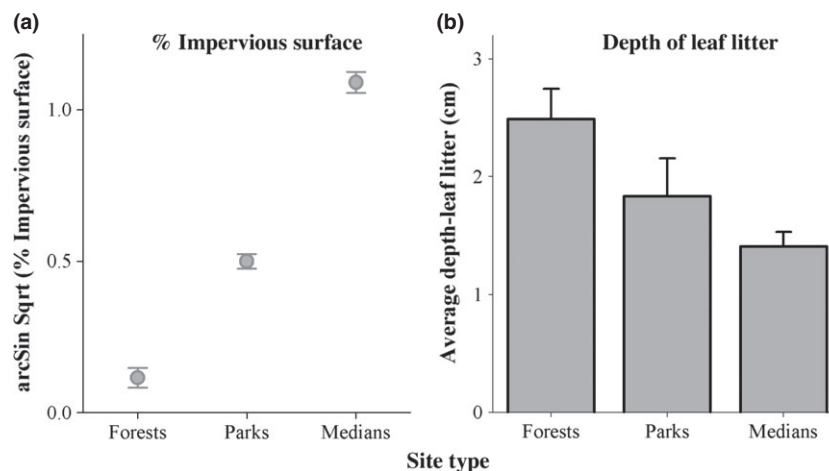

Fig. 1. Comparison of (a) % impervious surfaces and (b) depth of leaf litter across urban medians, urban parks, and urban forests.

medians and more frequently in urban forests than urban parks.

Methods

Study sites and sampling dates

We were interested in assessing the relationship between variation in chronic stress levels across Manhattan's urban habitat mosaic and the structure of local ant communities. We used Barrett *et al.*'s (1976) definition of ecological stress as, 'a perturbation (or stressor) applied to a system (i) which is foreign to that system or (ii) which is natural to that system, but applied at an excessive level'. Chronic stress refers to press disturbances (including increased temperature, exposure to traffic, and regular clearing of the vegetation) rather than pulse disturbances (such as those imposed by extreme weather events; Bengtsson, 2002). We focused on three habitat types that were located in close proximity across our study area in Manhattan. The sites with the highest levels of multivariate chronic environmental stress were urban medians (Fig. 1, Youngsteadt *et al.*, In Press). Urban medians are narrow strips of vegetation located in the middle of major streets. The term 'median' is regional, but is synonymous, or nearly so, with the following terms that are in common usage in other areas: Traffic Island, Boulevard, Neutral Ground, Berm, Mall, Verge, Devil's Strip, Planting Strip,

and Tree Belt (Fig. S1a). The lowest stress habitats were urban forests; managed as forests, these sites had ≥50% tree cover (Fig. S1c). Urban Parks had intermediate levels of chronic stress; managed as community parklands, these sites were dominated by grass, herbaceous plants or concrete, with <50% tree cover (Fig. S1b).

We sampled local ant assemblages in Manhattan, NYC across two consecutive years (Fig. 2). From 14 to 24 June 2011, we sampled a total of 22 sites across habitats with low stress (urban forests; $n = 3$), intermediate stress (urban parks; $n = 7$), and high stress (urban medians; $n = 12$; Pećarević *et al.*, 2010). All of the urban park sites were located in Riverside Park ($n = 7$), while urban forests were in Central Park ($n = 3$; Fig. 2a). Urban medians were all located along Broadway Avenue ($n = 12$; Fig. 2a; Table S1). During the 2011 sampling period, average daily temperatures ranged from 18 to 24 °C (mean = 22 ± 0.59 °C) and daily precipitation ranged between 0 and 6.86 mm (mean = $1.76 \pm .85$ mm; http://www.wunderground.com/history/airport/KNYC/DailyHistory.html). From 20 August–07 September 2012, we sampled a total of 32 sites. As in 2011, all urban medians ($n = 14$) were located along Broadway Avenue (Fig. 2b; Table S1). We expanded our sampling of parks to include greater replication of both urban parks and urban forests. Urban park sites were located in five city parks: Riverside ($n = 2$), Carl Schurz ($n = 2$), Isham ($n = 2$), Morningside ($n = 2$), and Sherman Creek ($n = 2$). Urban forests were located in three city parks: Central ($n = 2$), Fort Tryon
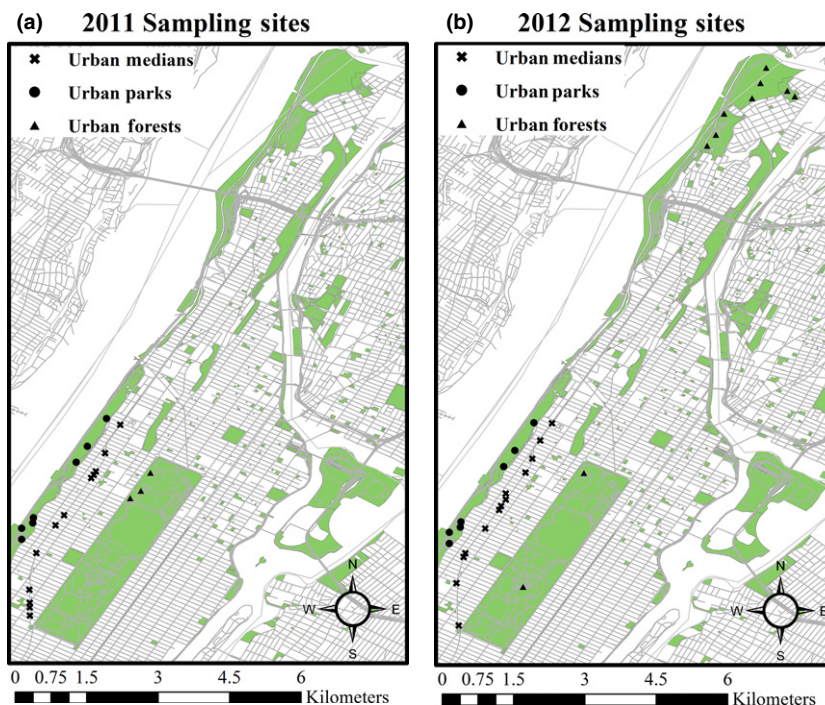

Fig. 2. Sampling sites in (a) 2011 and (b) 2012. Xs represent high stress median sites, circles represent parks, and triangles represent urban forests.

(n = 3), and Inwood Hill (n = 3; Fig. 2b; Table S1). Sites were haphazardly selected within the interior of urban forests and urban parks. During the 2012 sampling period, daily temperatures ranged from 22 to 28 °C (mean = 24.63 ± 0.38 °C); and precipitation ranged from 0 to 15.49 mm (mean = 1.34 ± 0.88 mm; http://www.wunderground.com/history/airport/KNYC/DailyHistory.html).

We collected ants across all sites using a combination of hand collections and Winkler sifting/extraction from 09:00 to 18:00 h. These methods are most effective at assessing ground foraging, day active ant species. These are also the ant species that are most likely to interact with humans (e.g. direct contact or indirectly, as happens when diurnally foraging ants feed on discarded human food). There are, however, likely other ant species that are restricted to plants or underground or that are more active at night. Unfortunately, we were unable to sample at night because of logistical constraints related to accessing sites at night. The specific methods were slightly different between years, and are described below. We measured the dimensions of a subset of Broadway medians (n = 6) to determine the sampling area for urban median, urban park, and urban forest sites. On average, medians were 5.53 ± 0.19 m wide and 56.5 ± 5.98 m long.

2011 Hand collection.   Each sampling site was divided into three sections of equal size for hand collecting. In each section, three workers simultaneously and haphazardly collected ants from the ground, on vegetation, and under rocks for a 5-minute period within each section using aspirators.

2012 Hand collection.   We systematically walked across the sites and collected ants from all of the microhabitats that we could find in 15 min. During these timed collections, we collected ants as described above. We used forceps and/or an aspirator for these collections and subsequently stored all specimens in 95% ethanol. Ants were identified to species in the laboratory using Ellison *et al.* (2012).

2011 Winkler sampling.   We sampled the ground-foraging ant community using the Winkler extraction method (Bestelmeyer *et al.*, 2000). In a previous study, Ribeiro *et al.* (2012) demonstrated that using this method yields a higher diversity of ants than pitfall trapping (which mostly collect multiple workers from colonies of numerically dominant species). Location of the leaf litter sample (1 m^2 patch) was determined based upon leaf litter presence. Winkler extractors were left for 48 h. All extracted arthropods were stored in 95% ethanol. We sorted and identified ants (as described above) from these samples in the laboratory.

2012 Winkler sampling.   Methods for Winkler collections were the same in 2012, except that we used a con-stant volume (1 litre) instead of area for litter collection. The 1 litre of leaf litter was collected throughout the length of each site.

Data analyses

Sampling methods in 2011 and 2012 differed slightly. Therefore, we first conducted non-metric multidimensional scaling (NMDS) ordination and PerMANOVA (as described below) for the subset of sites that were sampled in both years (n = 6 sites). We used sampling year as a factor in a PerMANOVA, which demonstrated that sampling year did not significantly influence ant assemblages in our study (Fig. S2). Therefore, we pooled 2011 and 2012 data for the analyses described below. For sites which were sampled both years, we randomly selected data from either 2011 or 2012 for the following analyses.

In addition, habitats were not distributed evenly across Manhattan's urban habitat mosaic (O'Neil-Dunne, 2012; Fig. 2). Although we could not control the distribution of habitats within the study area, we recognised that spatial relationships among sites could contribute strongly to differences that we detected in species occurrences across our study sites. Therefore, we used partial Mantel tests with 9999 iterations (PASSaGE, V. 2.0.11.6; Rosenberg & Anderson, 2011) to assess the relative importance of distances among sites and habitat type to the composition of local ant assemblages. We found that when distances among sites were held constant, habitat type was still significantly correlated with multidimensional variation in species composition ($P < 0.0001$, $r = 0.2540$). When habitat type was held constant, there was no significant effect of among-site spatial variation on ant composition, however ($P = 0.0727$; $r = 0.1583$). We explored a range of analytic options that yielded qualitatively similar results. Therefore, we focused on the relationship between habitat type and ant composition in the analyses below.

(1) How does the composition of local ant assemblages vary across Manhattan's urban habitat mosaic?

We examined the composition of local ant assemblages in Manhattan using NMDS ordination in Primer-E v.6.1.13 with PerMANOVA ext. 1.0.3 (Clarke & Gorley, 2009). Specifically, we conducted NMDS analyses for each year using 100 restarts and a Type I Kruskal fit scheme. To assess the relationship between habitat type and variation in within-site ant composition, we conducted a permuted multivariate analysis of variance (PerMANOVA) test with habitat type as a fixed factor, 9999 iterations and Type III sums of squares. We assessed the relationship between habitat type and among-site variability using a permuted dispersion test (PermDisp) using distances to centroids, habitat type as a fixed factor and 9999 iterations. In addition, we conducted *post-hoc* pairwise comparisons of within- and between-site dissimilarity for urban medians, urban parks, and urban forests. Finally, we constructed rarefied species accumulation curves using the observed species counts across all site

types and 9999 iterations. We used a one-way ANOVA (with a *post-hoc* Tukey HSD test) to test for differences in accumulated species as a function of habitat type (SAS Institute Inc, 2012).

(2) Is there a relationship between habitat stress level and the incidence of unique species?

To examine this question, we first determined the prevalence of unique species per site. We define the prevalence of unique species to be the frequency of occurrences of those species only found in one type of habitat. We then conducted a one-way ANOVA with habitat type as the independent factor and the number of unique species per site as the response variable. *Post-hoc* tests were conducted as described for species accumulation curves.

(3) Are the most common ants different in urban habitats with varying levels of stress?

We first determined the relative % occurrences in urban medians versus urban parks using the following equation: % Occurrence difference = [(% parks where species was found) − (% medians where species was found)]. We repeated this calculation for all pairwise habitat combinations. We then used SAS v.9.3; SAS Institute, Cary, NC, USA to conduct a one-way ANOVA assessing the relative prevalence of all ant species as a function of habitat type. We conducted a *post-hoc* Tukey HSD test to assess differences among urban medians, urban parks, and urban forests. We excluded singletons and doubletons from the data set. Species were then ranked based upon the magnitude of differences between the two habitat types (encompassing species that were more common in lower stress habitats than they were in higher stress habitats and vice versa) to visualise differences among the most common ants (maximum of 20 species).

(4) How does the occurrence of native and exotic ant species compare across habitats with varying levels of stress?

We used the presence/absence matrices to determine the total number of exotic and native species collected from each habitat type. Next, we conducted a two-way ANOVA with the independent, fixed factors of habitat type, origin, and their interaction using SAS v.9.3 statistical software. Data met assumptions of GLM after log ($n + 0.5$) transformations. Finally, we conducted a *post-hoc* Tukey HSD test to assess the differences among medians, parks, and urban forests.

Results

Overall ant species richness

We collected a total of 42 species from 22 genera across all of our sites. With a total of 18 species from 10 genera, urban medians hosted the fewest ant species, urban parks were intermediate, with 26 ant species from 20 genera, and with 32 species from 22 genera, we collected highest number of ant species from urban forests.

(1) How does diversity of local ant assemblages vary across Manhattan's urban habitat mosaic?

Within-site composition of ant assemblages differed as a function of habitat type (Fig. 3, PerMANOVA, $P_{\text{Habitat type}}$ = 0.0001). Medians differed significantly from parks ($P = 0.0001$) and urban forests ($P = 0.0001$). Although weaker, the within-site composition of ant assemblages in urban parks and urban forests also differed ($P = 0.0324$). The dissimilarity of ant assemblages among sites similarly differed by site type (PermDISP, $P_{\text{Habitat type}} = 0.0001$). These differences were driven by significantly lower among-site variability in medians than in either urban parks ($P = 0.0001$) or urban forests ($P = 0.0016$). There was no significant difference in among-site variation in urban parks and urban forests ($P = 0.2089$; Fig. 4).

The cumulative number of species was lowest in urban medians, intermediate in parks, and highest in urban forests (Fig. 5, ANOVA: $P_{\text{Habitat type}} < 0.0001$). Differences in species richness were driven by lower numbers of accumulated species in urban medians than in either urban parks (Tukey HSD, $P < 0.002$) or urban forests (Tukey HSD, $P < 0.001$). Increased accumulated species counts in urban forests relative to urban parks were not significant (Tukey HSD, $P = 0.1670$).

(2) Is there a relationship between habitat stress level and the incidence of unique species?

We predicted that there would be an inverse linear relationship between habitat stress level and the number of unique species (those that were only found in that habitat type). The fewest unique species occurred in urban medians, intermediate levels of unique species were found in urban parks and the highest number of unique species occurred in urban forests (Fig. 6). As a result, we observed a significant difference among habitat types in the number of unique species per site (one-way ANOVA, $P = 0.0014$). Among-habitat differences were only significant when comparing urban forests to urban medians (Tukey HSD: $P < 0.01$); urban parks were not significantly different from either of the other two habitat types.
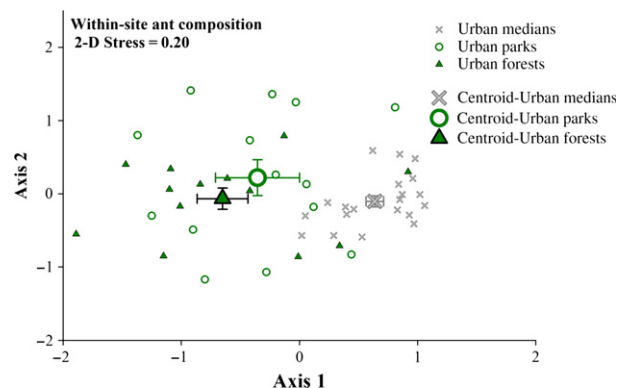

Fig. 3. Within-site (α) compositional differences in ant assemblages in Manhattan's urban habitat mosaic. Ants were sampled in urban medians, urban parks, and urban forests using Winkler sifting and hand collections. The composition of assemblages varied significantly by habitat type (PerMANOVA, $P = 0.0001$).
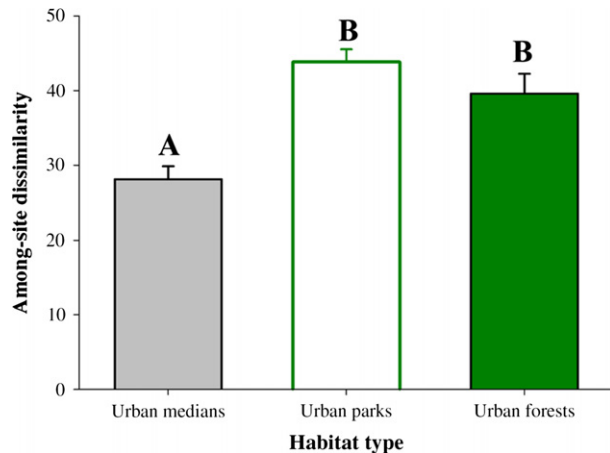
Fig. 4. Among-site compositional differences across habitats with varying levels of chronic stress (measured as the average distances to the centroid for each habitat type-one metric of β-diversity). The dissimilarity of ant assemblages among sites differed significantly by habitat type (PermDisp: $P = 0.0001$). Urban medians tended to be similar to each other, whereas urban parks tended to be relatively different from each other as was also true of urban forests. Error bars represent 1 SE of the mean. Different letters represent statistically different groups ($\alpha < 0.001$).
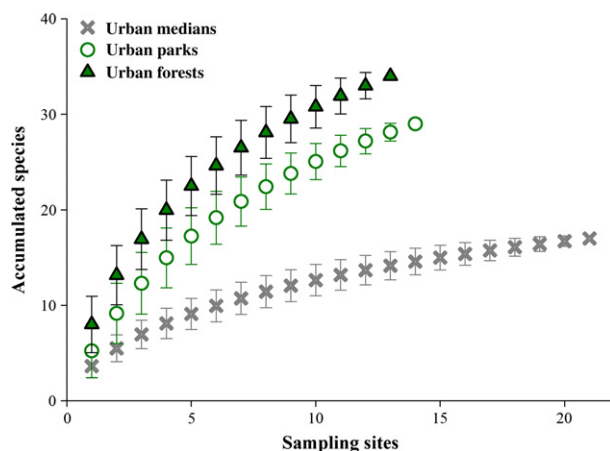

Fig. 5. Rarefied species accumulation curves of ants constructed across all sites by habitat type. Curves show the mean number and ($\pm$1 SD) number of ant species expected for each number of sampled sites given 9999 random draws from the total number of site*species occurrences. Cumulative species differed significantly by habitat type (one-way ANOVA: $P < 0.0001$).

Two species were found solely in urban medians, but were absent from other urban habitats – *Crematogaster cerasi* was found in one median and *Camponotus* sp. was found in two urban medians (Table S2). Half (21/42) of the species collected over 2 years were absent from urban medians. Three species were only found in urban parks: we collected *Strumigenys rostrata* in two urban park sites and both *Crematogaster lineolata* and *Myrmica* cf. *puncti-*
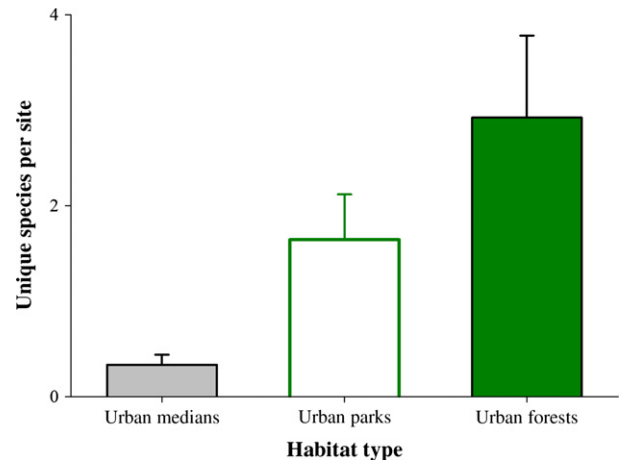

Fig. 6. Incidence of unique species across habitat types with varying levels of chronic stress, where unique species are those that occurred in just one habitat type. Error bars represent 1 SE of the mean. Urban parks did not differ from urban medians or urban forests; however, urban forests had significantly more unique species per site than urban medians (one-way ANOVA: $P = 0.0014$; Tukey HSD: $P < 0.001$).

ventris occurred at a single park site. Eight ant species were found solely in urban forests. *Lasius pallitarsis*, *L. subglaber*, *Proceratium silaceum*, *Stenamma brevicorne*, and *S. impar* were all present in a single urban forest site, while *Strumigenys pulchella* was found in two forested sites and *L. flavus* and *Myrmica americana* were present in three forest sites. There were also 10 species present in both urban parks and forests, but absent from urban medians (Table S2).

(3) Are the most common ants different in urban habitats with varying levels of stress?

There were among-habitat differences in the identity of the most common ant species. The overall prevalence for all species was highest in urban forests, followed by urban parks and was lowest in urban medians (Fig. 7a–c; one-way ANOVA: $P = 0.0018$). Two species were consistently more common in urban medians than they were in either urban parks (Fig. 7a) or urban forests (Fig. 7b). We found the *Tetramorium caespitum* sp. grp (hereafter, *T. caespitum*) in 100% of urban medians ($n = 21$), but in just five urban park sites (36%; Fig. 7a) and nine urban forest sites (69%; Fig. 7b). *Lasius neoniger* was also more common in urban medians (occurring in 62% of all medians) than urban parks (21% of all park sites; Fig. 7a) and was absent from urban forests (Fig. 7b). Across all urban park sites, the most common species were the native species, *Tapinoma sessile,* which occurred in 64% of all urban park sites and the exotic species, *Nylanderia flavipes,* which was found in 57% of all urban park sites. *Nylanderia flavipes* was found in all three habitat types, but was more common in urban parks than in urban medians (43%; Fig. 7a), and less common in urban parks than urban forests (85%; Fig. 7c). Similarly, *T. sessile* was
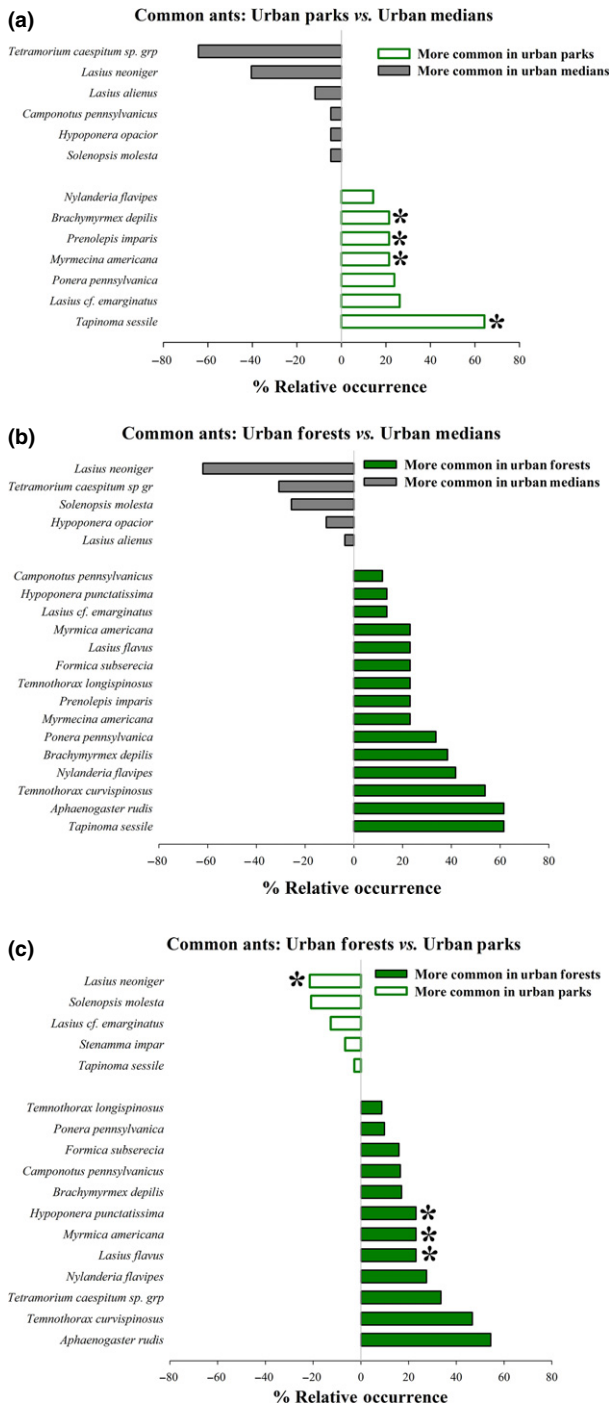
Fig. 7. Relative % occurrences of ants in (a) urban forests versus urban medians, (b) urban parks versus urban medians, and (c) urban forests versus urban parks. Relative occurrences were calculated by subtracting the % occurrence in the higher stress habitat from the % occurrence in the lower stress habitat (e.g. % occurrence in urban forests-% occurrence in urban medians). Asterisks denote species that were only found in one of the two habitat types for each comparison. Overall prevalence varied significantly by habitat type (one-way ANOVA, *P* = 0.0187).

common in urban forests (found in 62% of all forested sites), but absent from all medians (Fig. 7a, b). Finally, both *Temnothorax curvispinosus* and *Aphaenogaster rudis* were relatively common in urban forests (occurring in 54% and 62% of forested sites), but rare in urban parks (with a single record for each species in urban parks; Fig. 7c) and absent from urban medians (Fig. 7b).

(4) How does the occurrence of native and exotic ant species compare across habitats with varying levels of stress?

Exotic and native ant species had different occurrence patterns across high and low stress habitats. Exotic species richness did not vary significantly by habitat type (Fig. 8). Nevertheless, there were ~2 and 3× more native ants collected in urban parks and forests than in urban medians, respectively. There were also ~1.5× more native ants found in urban forests than in urban parks (Fig. 8; two-way ANOVA, $P_{Habitat \times origin} < 0.0001$).

Discussion

Summary

Understanding the ecological factors that underlie variation in the composition of animal assemblages in cities is becoming increasingly important as worldwide urbanisation continues to expand. Yet, we still have limited knowledge on how the features of urban environments shape species composition. The simplest starting point is to assume that urban ecosystems function in the way that less modified ecosystems do; in essence using theory derived from work in forests and grasslands distant from cities to make predictions about the ecological factors that contribute the most to the diversity within cities.
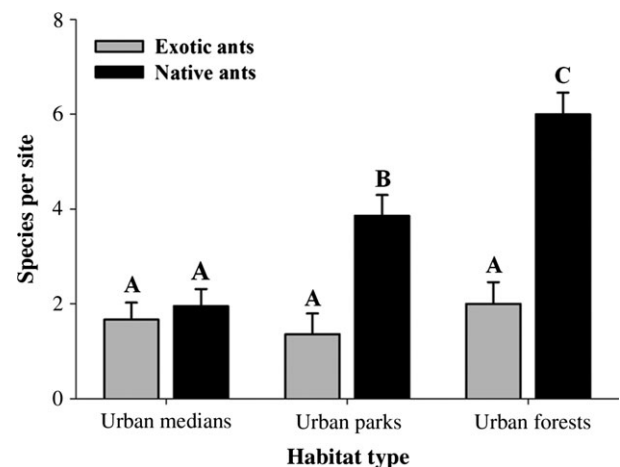

Fig. 8. Number of exotic (grey) and native (black) ants across urban medians, parks, and forests in Manhattan. Error bars represent ±1 SE of the mean and different letters represent significantly different means (Tukey HSD, *P* < 0.05).

In this study, we assessed the structure of local ant assemblages across the medians, parks, and forests of Manhattan's urban habitat mosaic. These habitat types, which vary in chronic stress levels, supported significantly different ant assemblages according to a variety of different metrics. Many predictions derived from less modified ecosystems were supported by our findings: (i) despite being the most intensively sampled habitat type, high stress urban medians had less variability in ant composition – both within and among sites – than either urban parks or urban forests; (ii) the lowest stress habitat (urban forests) had significantly more accumulated species and a higher number of unique species than higher stress urban habitats; and (iii) urban parks, which have intermediate levels of chronic environmental stress, also had intermediate levels of variation in among-site species composition, accumulated species richness, and incidence of unique species. Among-habitat differences in ant assemblages were not driven solely by the presence of rare species in lower stress habitats. The most common species also differed across Manhattan's urban habitat mosaic. In terms of diversity then, the habitats of Manhattan seem to behave similar to what might be expected based on the broader literature (Odum, 1985; Rapport *et al.*, 1985; Menge & Sutherland, 1987; Gray, 1989; Halpern & Spies, 1995; Tilman & Lehman, 2001; Scrosati *et al.*, 2007; Yergeau *et al.*, 2007). Where our results departed from these broader expectations was in terms of non-native species. A large literature on introduced species suggests that more stressed habitats should have more introduced species (Occhipinti-Ambrogi & Savini, 2003; Jimenez *et al.*, 2011; Zerebecki & Sorte, 2011; Bauer, 2012; Diez *et al.*, 2012). Instead, we found that exotic ants were just as likely to occur in low stress and high stress environments, but some native ant species only occurred in lower stress habitats.

Ant diversity was inversely associated with chronic environmental stress levels

The diversity patterns that we detected were qualitatively similar to many patterns found for birds – which are the best studied urban taxon to date (McDonnell & Hahs, 2008; Chamberlain *et al.*, 2009). As levels of chronic environmental stress within Manhattan increased, we observed a reduction in both the incidence of unique ant species and the total number of ant species occurring per site. Similarly, studies of avifauna across urban to rural gradients commonly report that a subset of species ('urban exploiters') tend to thrive in cities, while a different group of birds ('urban avoiders') only persist in protected areas (Blair, 1996; Marzluff, 2005). Studies of urban birds , however, typically show a non-linear relationship between chronic environmental stress and diversity, such that the highest diversity occurs in sites that have intermediate levels of stress (Blair, 1996, 1999;

Clergeau *et al.*, 1998; Palomino & Carrascal, 2006). Although much less intensively studied, our findings mirror similar inverse linear relationships between chronic stress and diversity that have been reported for other terrestrial invertebrates, including butterflies (Blair, 1999), beetles (Ishitani *et al.*, 2003), and bumble bees (Ahrné *et al.*, 2009).

Recent studies in other urban areas have also demonstrated that ant diversity varies across urban habitat mosaics. Slipinski *et al.* (2012) reported that ants living in the urban forests, parks, and medians of Warsaw in the 1970s were completely nested, with all of the ants from parks being a nested subset of those found in forests and all of the ants found in street medians being a subset of those found in parks. In contrast, de Souza *et al.* (2012) sampled medians, parks, and a forest in a suburb of São Paulo, Brazil and found the lowest diversity of ants in urban parks, with medians having intermediate ant species richness and the greatest number of ant species in the forest. Together with our results, these findings suggest that the relationship between chronic environmental stress and ant diversity is generally negative, although this relationship is complex and likely to be influenced by other factors in urban ecosystems. Nonetheless, previous work by Pećarević *et al.* (2010) demonstrated that the ant diversity in Manhattan's urban medians was high in absolute terms. Our work adds context to this result by showing that the diversity of species in urban forests and parks is actually much higher; while some species persist in medians, it is also true that most species fail to persist in these habitats with high levels of chronic environmental stress. Whether this scenario leads to greater stability in urban forests and parks relative to medians remains still unclear; future studies that assess ant diversity across urban habitat mosaics and spanning >2 years will be needed to assess the relationship between chronic stress and stability.

Furthermore, chronic environmental stress can also operate at finer scales, with different species (Teet & Denlinger, 2014) and even different individuals of the same species (Fulton *et al.*, 2013) displaying variable responses to chronic environmental stress. In this study, we focused on habitat-level, community-wide responses of Manhattan's ants to variation in chronic environmental stress across urban habitat mosaics. The degree to which this variation, however, affects ants at the level of species or even individual colonies is still unresolved. There is some evidence in the literature that such variation may be important to ant communities. For example, in a recent review, Kingsolver *et al.* (2013) showed that across multiple different habitats and broad geographic scales, ant species can have dramatically different sensitivities to temperature stress. More detailed studies at the scale of species and colonies will help elucidate the relationship between the habitat-level stress we examined here and finer scale effects of chronic environmental stress on urban ants.

Habitat type was more predictive of patterns of ant diversity than spatial relationships

One explanation for the differences among sites in Manhattan is that dispersal is limiting, leading to compositional patterns in which nearby sites are more similar to one another than they are to distant sites, regardless of habitat type. Urban parks and forests are non-randomly distributed in Manhattan (O'Neil-Dunne, 2012). Consequently, differences in species composition across Manhattan's urban habitat mosaic could have been driven by variation in these among-site distances. We did not find this. Instead, most of the variation in ant species composition among sites was due to habitat type. The species found in medians were largely nested subsets of the species found in urban parks and forests, while those found in urban parks were largely a subset of the species that were collected in forested sites. Furthermore, many of the most common ants in urban parks and forests occurred in both of these lower stress habitats, but were absent from medians. These findings indicate that some microhabitat variation in urban parks and urban forests maintain species absent from medians. One potentially important ecological trait that varies across urban habitat mosaics is habitat area. Carpintero and Reyes-López (2013) found that the area of parks within two cities in Spain strongly influenced ant diversity. Street medians in our study had the smallest habitat area. Therefore, space constraints (as opposed to spatial autocorrelation described above) may be an important factor structuring urban ant communities more generally.

The absence of variation in the occurrence of exotic ants among habitat types suggests that these species are not likely to be driving patterns of native ant diversity in our sites. Nonetheless, the newly discovered invasive ant, *Pachycondyla chinensis,* has recently been observed elsewhere in New York State (B. Guénard & R.R. Dunn, unpubl. manuscript). Although this species was absent from our samples, it may arrive in NYC in the near future and may have very different influences on co-occurring ants than the exotic species detected here. Future studies examining variation in the relative abundance of exotic ants across urban habitat mosaics could help inform these results. A recent study of ants in highway medians in Perth, Australia demonstrated that, while the number of exotic species was much lower than native species richness, ~72% of all individual workers collected were exotic species (Heterick *et al.*, 2013).

The only exceptions to this pattern were the occurrences of one native species, *Lasius neoniger*, and one introduced species, *Tetramorium caespitum*. These two species appear to benefit from the conditions of the medians. Both of these species have been previously documented to avoid forests (Wilson & Hunt, 1966; Clarke *et al.*, 2008) and prefer high stress urban environments (Uno *et al.*, 2010; Menke *et al.*, 2011). Overall, our composition results are reconcilable with a model wherein some features of urban parks and forests allow persistence of a large number of species. Those features are absent or greatly reduced in medians, where a small set of relatively fecund or tolerant species live. But medians are dominated by species able to take advantage both of medians and of the cement-covered space around them, as appears to be the case for both *L. neoniger* and *T. caespitum*. We suspect that in the majority of NYC – where the habitat is even more chronically stressed than in medians (e.g. sidewalks, buildings, and streets) – ant assemblages are a nested subset of those reported here for medians.

Are ants in cities different from ants in less modified habitats?

We used studies of mostly protected areas as a starting point to make predictions about the diversity of local ant assemblages across Manhattan's urban habitat mosaic. Some of these predictions were supported by our data (e.g. parks had a more diverse native ant assemblage than medians), suggesting that many of the same processes underlie community structure in urban and rural protected landscapes. Other predictions were, however, notably unsupported by our data (e.g. the prediction that exotic species would occur more frequently in habitats with higher stress). Manhattan represents a uniquely urban landscape – for example, the largest tract of forest in our study – Inwood Hill –includes land that was previously farmland and country estates, in addition to Manhattan's last remaining 'natural forest' and salt marsh (NYCParks.org). Overall, the structure of the Manhattan ecosystem – a structure set in place through sociopolitics, history, and one of the most ambitious urban green space initiatives in the history of cities (thanks to Olmstead) – has a strong effect on the composition of smaller societies in the city. Somewhat to our surprise, the green spaces of the island seem to be islands in and of themselves more so than might be predicted for an organism that flies to reproduce. Future work (currently underway) to assess genetic diversity of Manhattan's ant communities will allow us to test these predictions.

Acknowledgements

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12098:

Figure S1. Photographs of (a) urban medians, (b) urban parks, and (c) urban forests.

Figure S2. Non-metric multidimensional scaling plot of the sites that were sampled in both 2011 and 2012. There were no significant differences in species composition between years either within (PerMANOVA, *P* = 0.6012) or among (PermDISP, *P* = 0.2140) sites.

Figure S3. Within-site (α) compositional differences in ant assemblages in Manhattan's urban habitat mosaic. Ants were sampled in urban medians, urban parks, and urban forests using Winkler sifting and hand collections. This plot is identical to Fig. 3, except that sites are labelled.

Table S1. GPS coordinates and site classifications for all study sites.

Table S2. Number of occurrences of each species in median and park habitats across both years of the study. Exotic species are denoted with asterisks.

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