Habitat and species identity, not diversity, predict the extent of refuse consumption by urban arthropods

ELSA YOUNGSTEADT[1], RYANNA C. HENDERSON[1]*, AMY M. SAVAGE[2],
ANDREW F. ERNST[1], ROBERT R. DUNN[2] and STEVEN D. FRANK[1]

[1]*Department of Entomology, North Carolina State University, Raleigh, NC 27695-7613, USA*, [2]*Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695-7617, USA*

Abstract

Urban green spaces provide ecosystem services to city residents, but their management is hindered by a poor understanding of their ecology. We examined a novel ecosystem service relevant to urban public health and esthetics: the consumption of littered food waste by arthropods. Theory and data from natural systems suggest that the magnitude and resilience of this service should increase with biological diversity. We measured food removal by presenting known quantities of cookies, potato chips, and hot dogs in street medians (24 sites) and parks (21 sites) in New York City, USA. At the same sites, we assessed ground-arthropod diversity and abiotic conditions, including history of flooding during Hurricane Sandy 7 months prior to the study. Arthropod diversity was greater in parks (on average 11 hexapod families and 4.7 ant species per site), than in medians (nine hexapod families and 2.7 ant species per site). However, counter to our diversity-based prediction, arthropods in medians removed 2–3 times more food per day than did those in parks. We detected no effect of flooding (at 19 sites) on this service. Instead, greater food removal was associated with the presence of the introduced pavement ant (*Tetramorium* sp. E) and with hotter, drier conditions that may have increased arthropod metabolism. When vertebrates also had access to food, more was removed, indicating that arthropods and vertebrates compete for littered food. We estimate that arthropods alone could remove 4–6.5 kg of food per year in a single street median, reducing its availability to less desirable fauna such as rats. Our results suggest that species identity and habitat may be more relevant than diversity for predicting urban ecosystem services. Even small green spaces such as street medians provide ecosystem services that may complement those of larger habitat patches across the urban landscape.

Introduction

Urbanization is a leading cause of biodiversity loss and environmental change on local and global scales (Grimm *et al.*, 2008; McDonald *et al.*, 2008; McKinney, 2008). Despite their reduced diversity, urban ecosystems provide services, such as air purification and pollination, to city residents (Nowak *et al.*, 2006; Gardiner *et al.*, 2013). Research over the past two decades has sought to incorporate ecosystem services into urban planning, with efforts to categorize, map, and assess the economic and cultural value of these services (McDonnell *et al.*, 1997; Bolund & Hunhammar, 1999; Gómez-Baggethun & Barton, 2013; Larondelle & Haase, 2013). However, management of ecosystem services is hindered by a poor understanding of how they are shaped by biodiversity and the abiotic environment

(Kremen, 2005; Cardinale *et al.*, 2012). This knowledge gap is especially pronounced in cities, where ecological studies have lagged behind those in natural areas (Elmqvist *et al.*, 2008; Swan *et al.*, 2011; Martin *et al.*, 2012), and where forces of future ecological change may be extraordinarily complex. Urban systems are subject not only to local stresses typical of urbanization itself (e.g., habitat fragmentation, urban warming, introduced species) but also to broader global and regional climate changes, including warming and extreme weather (Shochat *et al.*, 2006; Karl *et al.*, 2008; Bender *et al.*, 2010; McCarthy *et al.*, 2010). An understanding of how these forces interact with urban biodiversity to shape ecosystem services is needed.

In this study, we assess the influence of biotic and abiotic factors on a novel urban ecosystem service: animal consumption of littered food waste. Littering (improper disposal) of food waste is a public health concern because littered environments discourage human physical activity and sustain populations of organisms – such as rats, pigeons, and filth flies – that

*Present address: Teach for America, North Carolina Piedmont Triad, Raleigh, NC 27695-7617, USA

Correspondence: Elsa Youngsteadt, tel +1 919 515 1661, fax +1 919 515 7746, e-mail: eyoungsteadt@gmail.com

harbor or transport human pathogens (Colvin *et al.*, 1996; Graczyk *et al.*, 2001; Haag-Wackernagel & Moch, 2004; Ellaway *et al.*, 2005; Himsworth *et al.*, 2013; Feng & Himsworth, 2014). Litter also raises the cost of urban waste management. In 2008, the US spent an estimated $11.5 billion on litter abatement, with large cities disposing of 10.6 kg of litter per person per year (KAB, 2009b). Despite these efforts, the same study found 1.5 pieces of litter per linear foot of urban roadway, and, in some settings, up to 26% of littered items were food (KAB, 2009b). Even if this waste could be efficiently diverted to landfills, it would contribute to a different environmental problem: Landfilled urban food waste produces 8% of global anthropogenic emissions of methane, a powerful greenhouse gas (Adhikari *et al.* 2006).

Because many scavenging and decomposing arthropods are common in cities, this group of organisms has the potential to reduce the public health, esthetic, and financial burden of littered food waste by diverting it from undesirable vertebrates and from landfills. This potential likely varies across the urban landscape, because arthropod diversity and species composition are sensitive to urbanization and to habitat type within the urban matrix (e.g., McIntyre *et al.*, 2001; Sanford *et al.*, 2009; Kotze *et al.*, 2011; Savage *et al.*, in press).

We expected urban refuse consumption to follow patterns of ecosystem function known from ecological theory and nonurban systems. Specifically, the efficiency and stability of resource capture generally increase with biological diversity, and this pattern is attributed to the presence in diverse systems of greater biomass and complementary forms of resource use (Frank & McNaughton, 1991; Tilman *et al.*, 1996; Cardinale *et al.*, 2006, 2012). For example, in marine mesocosms, diverse communities of invertebrate grazers (six species) consumed more algae than did less-diverse communities (1 to 3 species) (Duffy *et al.*, 2003). Where invasive species become common, however, their effects can counter diversity-based predictions. Invasive species tend to reduce biodiversity, but their extraordinary abundance and tolerance of disturbance may increase the rate and stability of ecosystem processes (Marvier *et al.*, 2004; Pejchar & Mooney, 2009; Vilà *et al.*, 2009; Ehrenfeld, 2010; McGeoch *et al.*, 2010; Schlaepfer *et al.*, 2011; Strayer, 2012). For example, invasive earthworms, despite reducing the diversity of soil fauna, appear to increase rates of leaf-litter decomposition (Pouyat *et al.*, 1997; Migge-Kleian *et al.*, 2006). Finally, the abiotic environment itself shapes ecosystem function, not only by determining diversity and community composition of organisms but also by affecting their metabolism and behavior (Gray, 1989; Haddad *et al.*, 2008; McKinney, 2008). For example, even when species composition remains constant, whole-ecosystem metabolism (respiration) increases with temperature (Enquist *et al.*, 2003). Thus, ecosystem function may be largely determined by species composition, but further tuned by effects of local abiotic factors on those species.

Here, we assess the magnitude and stability of the food-waste consumption service in green spaces of New York City (NYC), the most populous city in the United States (US Census Bureau, 2012) and the eighth most populous in the world (United Nations Department of Economic & Social Affairs, Population Division, 2014). We focus on the role of arthropods and consider their consumption both in absolute terms and relative to that of vertebrates, with which they may compete for food waste. Previous work showed that NYC parks (open or forested habitats) supported greater native ant diversity than did street medians (vegetated islands between lanes of traffic), while the two habitat types supported a similar diversity of introduced ants (Pećarević *et al.*, 2010; Savage *et al.*, in press). In October 2012, Hurricane Sandy struck NYC, flooding a subset of parks and medians and potentially disrupting animal assemblages and ecosystem processes.

In this context, we ask: (i) Does the magnitude of the food waste consumption service vary between parks and medians? We predicted that the more diverse park arthropods would use resources more efficiently, removing more food waste per day. (ii) Did flooding alter the magnitude of service in either site type? On the basis of biodiversity, we expected parks to provide the more stable service, that is, that food removal would be similar in flooded and unflooded sites. Alternately, medians, dominated by disturbance-tolerant invasive species, may also remain stable. (iii) What is the relative importance of physical habitat, biodiversity, species introductions, species traits, and species identity in predicting the magnitude of service across sites? We explored the predictive power of these biotic and abiotic factors to suggest future directions in the mechanistic study and rapid assessment of urban ecosystem services. To address these questions, we measured the amount of food refuse (cookies, potato chips, and hot dogs) removed by arthropods and vertebrates in each site type, and interpreted the results in light of the arthropod assemblage, habitat characteristics, and flood history.

Materials and methods

Study sites and environmental data

We sampled ground arthropods and gathered environmental data at 59 sites in green spaces across the borough of Manhattan in New York City, New York, USA. Manhattan is

one of the most urbanized areas in the United States with about 27 500 people/km² and 91% impervious land cover (University of Vermont, 2012; US Census Bureau, 2014). We focused on two categories of green space, parks, and street medians (Fig. 1). Median sites ($n = 15$ unflooded, 14 flooded) were a randomly selected subset of those previously sampled by AMS on Broadway, and a randomly selected subset of all existing medians in the corridor formed by West St., 11th Ave, and 12th Ave. Park sites (19 unflooded sites, 11 flooded, located in 14 parks) were selected based on their inclusion in previous studies, their exposure to flooding, and recommendations of park staff. When multiple sites were selected within a single park, they differed in habitat or flood history and were separated by at least 65 m.

Temperature and humidity were monitored at each site using a DS1923 hygrochron iButton data logger (Maxim Integrated, San Jose, CA, USA). iButtons were attached to tree branches 2–3 m above ground level using an iButton wall mount (Maxim Integrated) housed inside a 3-cm deep translucent plastic cup (Dart, Mason, MI, USA) and attached to the branch with a cable tie. iButtons were installed in March 2013; data were downloaded and missing iButtons replaced in May–June and in August 2013. Here, we analyze July temperature and humidity because they represent summer conditions (under which ecosystem services were measured), and because July is the month for which the most sites had complete data.

In May–June 2013, we measured leaf-litter depth every 4 m along a 20 m transect at each site using a sharpened dowel marked with 1-cm graduations, as described in (Kostel-Hughes *et al.*, 1998). For each site, the value used in analyses was the mean of the six measurements. Site exposure to flooding during Hurricane Sandy (November 2012) was determined using a 1-m resolution storm-surge map made by the U.S. Federal Emergency Management Agency (available at http://services.femadata.com/arcgis/rest/services/2012_Sandy/SurgeBoundaries_Final_0214/MapServer). Sites were further characterized using a 0.9 m resolution land cover map of New York City, in which surfaces are classified as tree canopy, grass/shrub, bare earth, water, roads, buildings, or other impervious surface (University of Vermont, 2012). We overlaid this map with site coordinates in ArcMap 10.0 (ESRI, Redlands, CA, USA) and extracted the percent tree canopy cover and percent impervious surface in a circle of 30-m radius centered on each site. We also used the map to measure the longest and shortest straight-line distances to habitat edge, where edge was defined as an expanse of impervious surface at least 9 m wide, or a body of water. Nine meters is the width of impervious surface that separates one street median from the next; we used the same distance to define habitat edges for parks. Of the 59 study sites, complete environmental data were ultimately available for 53 – those where iButtons successfully recorded data for the entire month of July.

Arthropod sampling

We used Winkler extractors and hand collections to sample ground arthropods from May 30–June 9, 2013. At each site, we established a 20 m transect in an area where leaf litter was present (avoiding lawns and bare dirt). We collected leaf litter every 4 m along the transect, sifted it through a litter reducer (4 mm mesh), and extracted arthropods from 1 l of sifted litter per site using a Winkler extractor. Litter remained in the extractor for 48 h and all arthropods were stored in 95% ethanol.

Hand collections targeted ants only. We searched sites for 15 min and collected worker ants from all microhabitats found within ~6 m of the transect on the ground and up to 2 m high. We collected ants with an aspirator or moist paintbrush and stored them in 95% ethanol. All arthropods were identified to class or order, all adult hexapods to family, and all ants to species according to (Ellison *et al.*, 2012) and confirmed by comparison to reference specimens in the lab of RRD. Vouchers of ants are deposited in the North Carolina State University Insect Museum (Raleigh, NC, USA) and the American Museum of Natural History (New York, NY, USA).

Details of overall arthropod composition will be addressed elsewhere; here, we use specific attributes of the arthropod assemblage to test hypotheses about how species diversity and traits should affect ecosystem function. These attributes were: (i) hexapod family diversity (measured as family density, that is, number of families encountered per site); (ii) ant species diversity [measured as species density, that is, number of species encountered per site, (Gotelli & Colwell, 2001)]; (iii) proportion of ant species that were nonnative, and (iv) proportion of ant species that were 'nuisance' ants. We classified a species as a nuisance ant if it possessed the trait of foraging for human-provided food in kitchens or garbage cans, as reported in (Vander Meer *et al.*, 1990; Klotz, 2008; Ellison *et al.*, 2012; MacGown, 2013) as well as in AntWeb (http://www.antweb.org, accessed 14 February 2014) and AntWiki (http://www.antwiki.org, accessed 14 February 2014). Ultimately, complete data on arthropod assemblages were available for 57 of the 59 study sites (information from two sites was lost during sample processing).
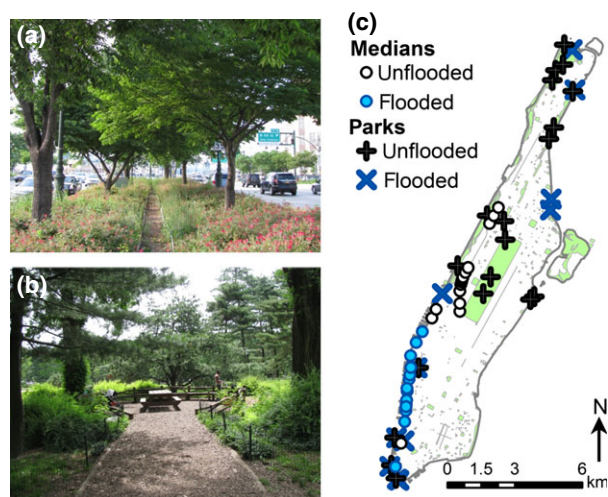

Fig. 1 Examples of sites in (a) a street median and (b) a park. The map of Manhattan (c) indicates locations of 59 sites where arthropods were sampled. Sampling sites are marked by symbols, and green fill indicates park areas, for reference.

Ecosystem service

To measure removal of littered food waste by urban animals at a subset of study sites, we presented three commonly dropped food items expected to attract fat-, sugar-, and protein-feeding animals: potato chips (Ruffles Original, Frito-Lay, Dallas, TX, USA), cookie (Nabisco Nilla Wafers, Mondelez International, Chicago, IL, USA), and hot dogs (Oscar Mayer Extra Lean Franks, Kraft Foods, Northfield, IL, USA). Food items were preweighed, and removal was measured as dry weight of food items removed. Foods were not dehydrated prior to presentation in the field; to determine initial dry weights of foods offered, we reserved 3–5 reference samples of each food type every time foods were prepared for the field. We dried these reference samples at 65 °C in a drying oven until stable weight was reached. We used the ratio of dry: wet weight of these samples to calculate the expected dry weight of food pieces placed in the field on the same day. Foods were moistened when presented in the field to improve palatability and minimize effects of variable dew or light rain.

We placed two sets of foods at each site: One set of the three items was caged to exclude vertebrates and to reveal the contribution of arthropods to the ecosystem service. The second set was uncaged; food removal in this treatment represented the combined activity of arthropods and other animals, primarily vertebrates. We note that mollusks (i.e., slugs) may also consume littered food waste; immature individuals could have accessed caged foods while adults would have been restricted to uncaged foods. However, we observed slugs or their slime trails in the vicinity of our cages at only two study sites and assume that arthropods and vertebrates were the principal consumers of foods in this study.

Cages were assembled on site by first placing on the ground a 22 cm square of hardware cloth (0.6 cm mesh). Preweighed food items were placed on the mesh and covered by an inverted, round, wire culinary basket (20.3 cm diameter at open base, 15 cm diameter at top, 16 cm tall, 0.6 cm mesh, WINCO, Lodi, NJ, USA) from which the handle had been removed and to which a polystyrene plate (15 cm diameter) had been glued as a shield from light rain or debris (Fig. 2a). The hardware-cloth base and the culinary-basket dome were secured to one another and to the ground using cable ties and landscape staples.

Uncaged foods were placed on an identical square of hardware cloth. Instead of a cage dome, we installed only a rain shield by mounting a 15-cm polystyrene plate on a bolt (0.6 × 15.2 cm) using a washer and a small cable tie to form an umbrella, which we inserted into the ground through the center of the hardware-cloth square (Fig. 2b).

We returned to sites ~24 h after food was presented to retrieve leftover food, which we dried at 65 °C until stable weight was reached. Final dry weights of leftovers were subtracted from calculated initial dry weights of the same items to determine the dry weight of each food removed at each site.

We performed this experiment twice. In Experiment 1, we used small amounts of food to simulate portions accidentally dropped by people, and assessed its removal at 45 sites (13 unflooded medians, 11 flooded medians, 13 unflooded park sites, and eight flooded park sites). Cookies, hot dogs and potato

Fig. 2 Cage (a) and uncaged shelter (b) used to present food in refuse-consumption experiments.

chips were presented in similarly sized pieces (roughly 1/3 chip, 1/5 cookie, 1/40 hot dog), but due to differing densities, dry weights varied (mean ± SD for each food item, in mg): chip 554 ± 206; cookie 889 ± 223, hot dog 319 ± 77, total food 1762 ± 321. Food exposure time was (mean ± SD) 24 ± 1.2 h. We tested 6–12 sites per day, such that the whole experiment took 6 days to complete (May 29–June 2 and June 4–5, 2014).

Because a large proportion of total food was removed in the first experiment, we increased the amount of food offered in Experiment 2 to assess maximum food removal. Experiment 2 included 20 sites (5 unflooded medians, 5 flooded medians, 5 unflooded park sites, and 5 flooded park sites) and was executed in a single 24 h period beginning on June 8. Amounts of food offered were (mean ± SD for each food item, in mg): 1 large chip (1664 ± 528); 1 cookie (3635 ± 200), 1/10 hot dog (950 ± 167), total food 6249 ± 633. Exposure time was (mean ± SD) 24 ± 0.4 h.

Analysis of environmental data

iButtons recorded relative humidity (RH), but vapor pressure deficit (VPD) is the humidity measure most directly related to evaporation rates and thus to desiccation in animals (Monteith

& Unsworth, 2013). Vapor pressure deficit was calculated from temperature and relative humidity as follows: Saturation VP over liquid water was calculated from temperature using the sixth order polynomial of (Flatau *et al.*, 1992), and VPD was derived from saturation VP and RH according to (Shuttleworth, 2012). Average July VPD (mean of 248 values recorded for each site in the month of July) was the value used in analyses. Similarly, average July temperature was the mean of 248 July temperature readings for each site.

To compare the physical habitat across sites, we conducted a principal components analysis (PCA) on the correlation matrix of the seven environmental variables (July temperature, July VPD, leaf litter depth, percent canopy, percent impervious surface, shortest distance to edge, longest distance to edge). We analyzed the correlation matrix, rather than the covariance matrix, to equalize the contributions of all variables regardless of their scale of measurement. We applied data transformations to reduce skewness and improve linearity of relationships among variables prior to PCA. Percent impervious surface and percent canopy cover were arcsine transformed, and leaf litter depth and distances to edge were log transformed. PCA was performed in JMP v. 10.0.0 (SAS Institute, Cary, NC, USA).

Analysis of ecosystem service data

Effects of site type and flooding. First, we asked whether arthropod food removal differed by site type (median or park), flooding (flooded or unflooded during Hurricane Sandy), or their interaction, using the GLM procedure of SAS v. 9.3 for Windows (SAS Institute, Cary, NC, USA). We pooled all food types and analyzed total removal because arthropod preferences for different foods did not differ across site types (Data S1, Figure S1). In Experiment 1, we included two covariates in the analysis: the number of hours the food was available at each site and the temperature during the ~24 h that food was presented at each site (mean of 12 iButton readings). These covariates were not included in analyses of food removal in Experiment 2, since exposure times were highly consistent, and all sites were exposed on the same dates.

Removal by arthropods relative to other animals. To determine whether arthropods and vertebrates compete for the same food resources, we asked whether more food was removed when other animals also had access. To test for effects of exclusion cages on the dry weight of food removed in both site types, we used the MIXED procedure in SAS 9.3 to fit a mixed model with fixed effects of site type (median or park) and cage treatment (caged or open) and a random effect of site nested in site type.

Predictive power of arthropod and environmental variables. Since we detected a strong categorical effect of site type on arthropod food removal in both experiments, we further explored which aspects of habitat and arthropod composition were most predictive of the magnitude of food removal services. In the following analyses, we used only the subset of sites where complete data for food removal, community composition, and environmental variables were available: 39 sites (21 medians, 18 parks) in Experiment 1, and 15 sites (8 medians, 7 parks) in Experiment 2.

At the species level, we tested for effects of four generalist species previously identified as more common in medians than in parks (Savage *et al.*, in press). For each species, we used a 1-tailed *t*-test to ask whether species presence was associated with greater food removal. When this categorical test was significant, we further used the subset of sites where the species was present in Winkler samples to test for effects of its abundance on food removal using linear regression in JMP 10.0.

At the assemblage level, we used multiple regression to compare the relative importance of six arthropod and environmental variables: hexapod family diversity, ant species diversity, proportion of introduced ants, proportion of nuisance ants, and environmental PCA axes 1 and 2. For Experiment 1, we also included two potential covariates, the number of hours food was available and mean site temperature on the day of the experiment. Prior to analysis, number of ant species per site was log transformed, and proportional data transformed using a variation in the arcsine transformation that performs better at extremes (near 0 and 1) (Zar, 1999). For a proportion X/n, the transformed value is $p' = \arcsin \sqrt{[(X + 3/8)/(n + 3/4)]}$. For Experiment 1, we considered all 255 possible models constructed from these eight variables. For Experiment 2, we considered six predictor variables for a total of 63 candidate models. We used AIC_c (Akaike information criterion corrected for small sample size) to rank models and to compute Akaike weights (w_i) for all models and predictor variables (Symonds & Moussalli, 2011). This information theoretic selection process can be compromised if full-model R^2 values are poor, or if included variables are highly collinear. Before performing the analysis, we confirmed that full-model R^2 values were high (0.43 and 0.55 for Experiments 1 and 2, respectively) and multicollinearity was low (mean tolerance = 0.54 and 0.41 in Experiments 1 and 2). All multiple regressions were conducted in the REG procedure of SAS 9.3.

Finally, to synthesize the results of individual species effects with assemblage and environmental effects, we used a general linear model in the GLM procedure of SAS 9.3 to partition variance between our top categorical and continuous predictors from the two preceding analyses. (Individual species data could not be included in the multiple regression analysis because a dummy variable representing species presence/absence greatly reduced the tolerance among variables in the full model to a mean of 0.23 (minimum 0.07), compromising the results.)

Results

Habitat

We detected distinct environmental differences between medians and parks. Sampled sites in medians were hotter, drier, closer to habitat edges, and surrounded by more impervious surface and less tree canopy than were those in parks (Table 1). These

Table 1 Mean and 95% confidence intervals for seven environmental variables measured in parks and medians

	Median (n = 27)		Park (n = 26)	
Variable	Mean	95% CI	Mean	95% CI
July temperature (°C)	27.7	27.6–27.9	26.6	26.4–26.8
July VPD (hPa)	14.7	14.4–15.0	11.7	11.1–12.2
% Canopy	15.2	12.2–18.3	58.3	43.3–72.6
% Impervious	80.5	77.5–83.4	10.8	5.4–17.8
Distance to nearest edge (m)	2.2	1.8–2.5	12.8	7.6–21.5
Distance to farthest edge (m)	76.1	50.3–115.1	347.9	261.9–462.3
Litter depth (cm)	0.7	0.5–1.0	0.8	0.5–1.2

Note that all variables that were transformed for analysis are back-transformed here for ease of interpretation.

highly correlated differences were reflected in PCA axis 1, which completely separated park and median sites and explained 66.7% of the measured environmental variation among sites (Fig. 3, Table S1, Table S2). PCA axis 2 captured an additional 13.6% of the variation and was associated primarily with leaf litter depth, which varied across a similar range in both site types (Table 1; Fig. 3).

Arthropod assemblage

From leaf-litter samples, we extracted a total of 16 294 arthropods from seven classes. Ninety three percent of all individuals were either insects (20% of individuals, 48 families) or other hexapods (Entognatha, 73% of individuals, eight families) (Table S3). Ants were the most abundant insect family (71% of all individual insects). Leaf-litter samples included 1926 worker ants of 27 species, and hand collections captured five

additional species for a total of 32 ant species (Table 2, Table S4). Park sites supported more diverse arthropods than did medians, with an average of two additional hexapod families and two additional ant species per site. The greater ant diversity in parks was driven by the presence of more native, nonnuisance species (Table 2). Parks and medians did not differ in the number of introduced or nuisance species encountered per site.

Ecosystem service

Across all sites, arthropods removed 59% of available food within 24 hours in Experiment 1 (small portions) and 32% in Experiment 2 (large portions). Counter to our prediction that diverse arthropod assemblages would consume the most food, we found that arthropods in medians removed 2.1 times more food than arthropods in parks in Experiment 1 (small portions; $P < 0.001$, Fig. 4, Table 3), and 3.3 times more in Experiment 2 (large portions; $P < 0.001$, Fig. 4, Table 3). We detected no main or interactive effect of flooding on the
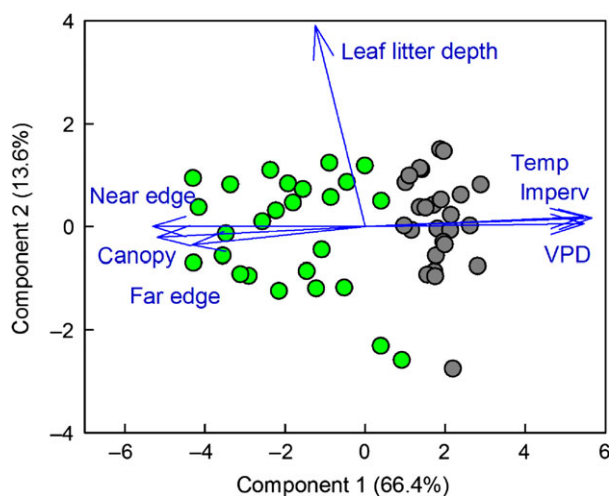

Fig. 3 A PCA separates parks (green circles) from medians (gray circles) on Axis 1, which is strongly loaded with six highly correlated habitat variables (blue arrows).

Table 2 Characteristics of arthropod assemblages in parks and medians

	Median (n = 28)		Park (n = 29)	
Variable	Mean	95% CI	Mean	95% CI
Class diversity	4.8	4.5–5.1	4.4	4.0–4.9
Hexapod family diversity	9.0	8.1–10.0	11.0	9.5–12.4
Ant species diversity	2.7	2.2–3.4	4.7	3.8–5.8
Introduced ant diversity	1.6	1.3–1.9	1.6	1.3–1.8
Native ant diversity	1.1	0.7–1.6	2.8	1.9–4.0
Nuisance ant diversity	2.2	1.8–2.5	2.6	2.2–3.1
Other ant diversity	0.6	0.3–0.9	1.9	1.3–2.8

Note that all variables that were transformed for analysis are back-transformed here for ease of interpretation; the measure of diversity used is taxon density.
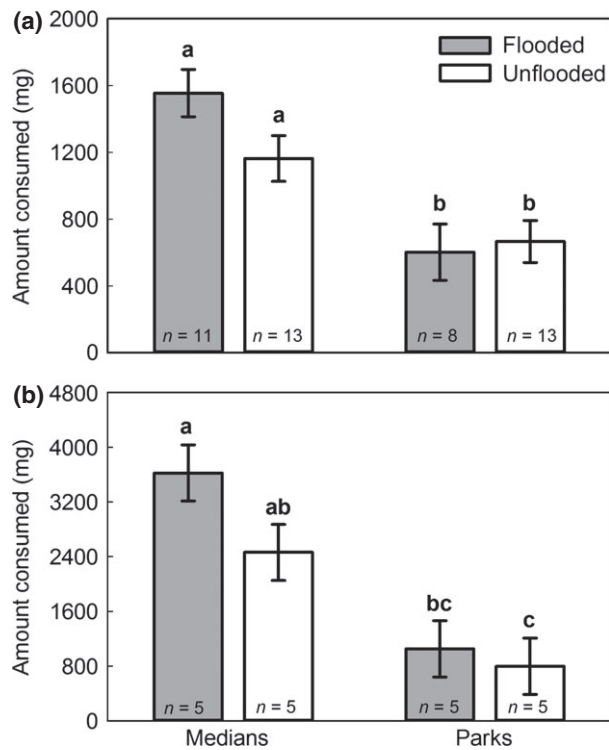
Fig. 4 Arthropod communities in medians consistently consumed more than those in parks in Experiment 1 (a) and Experiment 2 (b). We detected no effect of flooding on food consumption in either site type. Bars indicate least-squares means ± SE.

amount of food refuse removed by arthropods, and variance in removal was not greater among flooded sites than among unflooded sites (Fig. 4, Table 3).

Where food was left, hot dogs were the most likely to be left, while chips and cookies were equally preferred (Data S1, Figure S1).

Removal by arthropods relative to vertebrates. When all animals, including vertebrates, had access to food, 93% of available food was removed in Experiment 1 and 80% in Experiment 2; that is, arthropods and other animals together (uncaged treatment) removed 1.5–2.5 times more food than arthropods alone (caged treatment) (Fig. 5, Table 4), indicating that both groups of animals use the same food resources. In Experiment 1 (small portions), arthropods ate much less than all animals in parks, but ate only slightly less than all animals in medians (site type × cage interaction, Table 4). Arthropods removed 100% of the caged food at 1/3 of our median sites and no park sites.

To determine the upper limit of arthropod consumption, we offered ~3.5 times more food in Experiment 2. Together, arthropods and other animals continued to regularly remove 100% of the food (from 60% of sites), but arthropods no longer did so on their own. Maximum removal by arthropods was 85% (4.9 g) in a median site. With the larger amounts of available food, arthropods consistently ate less than that did all animals in both site types (no site type × cage interaction, Table 4).

Effects of individual ant species. More food was eaten by arthropods at sites where *Tetramorium* species E [formerly known as *Tetramorium caespitum* (Schlick-Steiner *et al.*, 2006)], was present (Experiment 1 $t = 3.53$, $P = 0.0005$; Experiment 2 $t = 4.2$, $P = 0.0003$, see also

Table 3 Results of ANOVAS testing for effects of site type, flooding, and their interaction on the amount of food refuse removed by arthropods in Experiments 1 and 2; covariates included in the Experiment 1 model controlled for food exposure time and site temperature on the day of the experiment; P values < 0.05 are bold

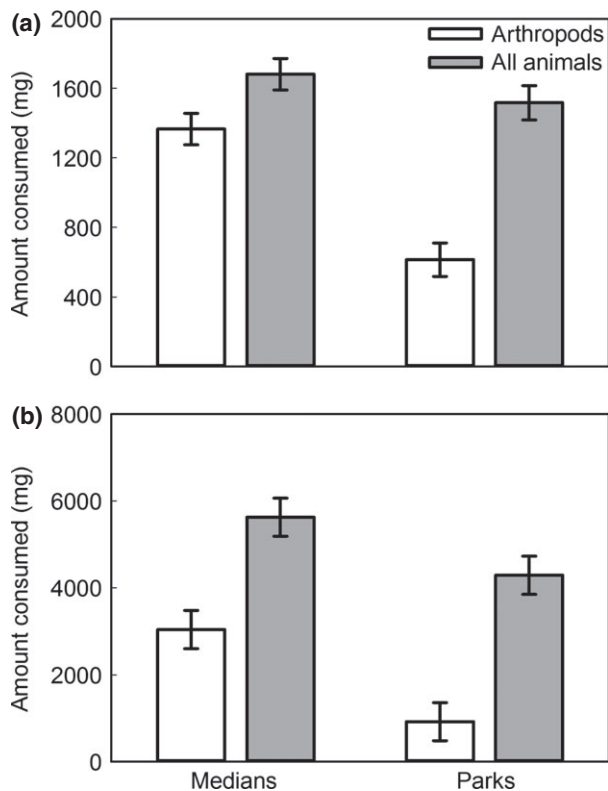| Source	df	SS	MS	F	P	R^2
(a) Experiment 1						
Model	5	7305778	1461156	7.07	**<0.001**	0.48
Site type	1	6323722	6323722	30.61	**<0.001**	
Flooding	1	135726	135726	0.66	0.42	
Site type x flooding	1	508818	508818	2.46	0.12	
Hours	1	87725	87725	0.42	0.52	
Temperature	1	249786	249786	1.21	0.28	
Error	39	8056579	206579			
Corrected total	44	15362357				
(b) Experiment 2						
Model	3	25999913	8666638	10.27	**<0.001**	0.66
Site type	1	22463521	22463521	26.61	**<0.001**	
Flooding	1	2504904	2504904	2.97	0.10	
Site type x flooding	1	1031488	1031488	1.22	0.29	
Error	16	13504992	844062			
Corrected total	19	39504905				

Fig. 5 More food refuse was removed in medians and parks when both arthropods and vertebrates had access in Experiment 1 (a, $n = 24$ medians and 21 park sites) and Experiment 2 (b, $n = 10$ medians and 10 park sites). Bars represent least-squares means ± SE.

Table S5 and Figure S2). Given *T*. sp. E presence, however, its abundance in Winkler samples did not predict food removal (Experiment 1 $F_{1,18} = 2.66$, $P = 0.12$; Experiment 2 $F_{1,8} = 0.02$, $P = 0.90$). *T*. sp. E was more common in medians than in parks: It was present in 91% of medians and 40% of park sites used in Experiment 1; and in 100% of medians and 22% of park sites used in Experiment 2. However, its abundance in Winkler samples was not correlated with PCA axis 1 (Figure S3). No other ant species was positively associated with food removal (Table S5).

On the basis of these results, we estimated how much food the arthropods of a single block-long median strip could remove per year. We assumed that a single 400 m² median encompasses about 9 *T*. sp. E foraging territories, within each of which additional food would have been removed independently (Brian *et al.*, 1967) – that is, within each of which ~3 g of food waste could be removed per day (Fig. 4, Experiment 2). This amounts to 27 g removed per median per day. Assuming a 5–8 month activity period for arthropods in NYC, the arthropods of a single block-long median strip could remove about 4–6.5 kg (dry weight) of food

refuse per year or on the order of 600–975 kg per year for the full ~150-block extent of the Broadway and West St. medians we studied. We made no attempt at a similar estimate for parks because of their greater size and habitat heterogeneity.

Predictive power of arthropod and environmental variables. To explore the categorical effect of site type (more food removed in medians) in greater detail, we considered food removal as a function of arthropod and environmental variables that varied continuously across sites (Table 5, Table S6). We expected to find that some measure of arthropod composition, or a combination of arthropods and habitat, would be most predictive. Instead, when we examined all possible combinations of arthropod and environmental variables, only environmental PCA axis 1 was strongly supported in both experiments as a predictor of the amount of food removed by arthropods (Table 5; w_i values near 1 indicate a high probability that PCA axis 1 is a component of the best model). The highest food removal was associated with high scores on PCA axis 1, that is, with median-like conditions (Fig. 6). A negative effect of the proportion of introduced species was weakly supported in both experiments (Table 5, Table S6).

In summary, our analysis of individual species found that the presence of *T*. sp. E predicted high consumption, and our multiple regression of arthropod and environmental variables found that 'medianness' (large values on habitat PCA axis 1) also predicted high consumption. Although *T*. sp E was more frequently collected in medians, these two results were not strictly redundant: After accounting for *T*. sp. E, environmental conditions (PCA axis 1) still accounted for an additional 12% of the variation in the food consumption in Experiment 1 (Table 6, Fig. 6). A similar trend was evident in Experiment 2 (Table 6, Fig 6).

Discussion

People in cities add food refuse to the environment by accidentally dropping or intentionally discarding it (KAB, 2009a). If left uneaten – or if eaten by animals that harbor human diseases – this littered food waste becomes a public health, environmental, and financial burden. We show that arthropods in green spaces of New York City, the most populous city in the United States, contribute to the ecosystem service of removing littered food waste such as potato chips, hot dogs, and cookies. When food portions were small (<2 g), similar to accidentally dropped pieces of larger food items, arthropods alone were capable of removing 100% of the food from many of our sites in street medians. When food portions were larger (~6 g, whole cookies and

Table 4 Results of ANOVAs testing for differences in food removal in caged (arthropods-only) vs. uncaged (all animals) treatments in Experiments 1 and 2; *P* values < 0.05 are bold

Source	Numerator df	Denominator df	SS	F	P
(a) Experiment 1					
Main effects					
Site type	1	45.66	4925454	38.28	**<0.0001**
Cage	1	42	7635405	28.70	**<0.0001**
Interactions					
Site type × Cage	1	42	1665386	6.26	**0.016**
Simple effects of cage					
in parks	1	42	7531636	4.48	**0.040**
in medians	1	42	1192906	31.66	**<0.0001**
Random effects					
Site (site type)	43		5445099		
Residual	42		11173023		
Corrected total	90		39568909.2		
(b) Experiment 2					
Main effects					
Site type	1	18	29816656	15.92	**<0.001**
Cage	1	18	88681862	44.56	**<0.0001**
Interactions					
Site type x Cage	1	18	1543311	0.78	0.390
Random effects					
Site (site type)	18		33706144		
Residual	18		35821931		
Corrected total	39		189569904		

chips, large pieces of hot dog), arthropods were unable to completely remove them within 24 h. In other words, when more waste is present, arthropod consumption is saturated and a greater proportion inevitably feeds vertebrates. We estimated that arthropods in the medians of Manhattan's Broadway and West St. could remove 600–975 kg (dry weight) of food waste per year–equivalent to approximately 60 000 hot

Table 5 Akaike weights (*w*$_i$, larger values indicate greater support) and model-averaged parameter estimates (values near 0 have the least influence) for variables included in competing models to explain the amount of food consumed in Experiments 1 and 2

	Experiment 1		Experiment 2	
Predictor	w_i	Estimate	w_i	Estimate
PCA axis 1	0.99	1.28	0.87	14.10
PCA axis 2	0.59	−0.71	0.15	0.75
Hexapod family density	0.26	−0.04	0.15	−0.11
Ant species density	0.42	0.78	0.21	2.24
Proportion of introduced ants	0.41	−1.59	0.30	−18.01
Proportion of nuisance ants	0.25	0.55	0.26	18.01
Hours food was available	0.23	0.03		
Short-term temperature	0.31	0.05		

dogs, 200 000 Nilla Wafers, or 600 000 Ruffles potato chips. Relative to the litter disposal rate of 10.6 kg per person per year in large cities, of which 0.4–2.8 kg per person may be food waste (KAB, 2009b), the potential contribution of arthropods to total waste removal is modest but notable. Without these animals, more littered food waste would accumulate in cities.

The magnitude of the food removal service varied across habitats, but not in the direction that we predicted. On the basis of diversity theory, we expected that the more diverse arthropod assemblages in parks should consume more food waste. Although we confirmed that park sites supported more ant species and more hexapod families than did median sites (Table 2, Savage *et al.*, in press), park arthropods ate 2–3 times *less* food than those in medians.

Our analyses point to the importance of species identity and habitat characteristics, rather than diversity, as predictors of food removal. Of the 13 most common generalist ant species we collected, only one, the pavement ant *Tetramorium* sp. E, was associated with greater food removal (Fig 6, Table S5, Figure S2). This Palearctic species was introduced to North America more than 100 years ago, is common in urban areas, and – consistent with its occurrence in medians – prefers to nest near pavement (Smith, 1943; e.g., King & Green, 1995; Pećarević *et al.*, 2010). Its large colonies, averaging
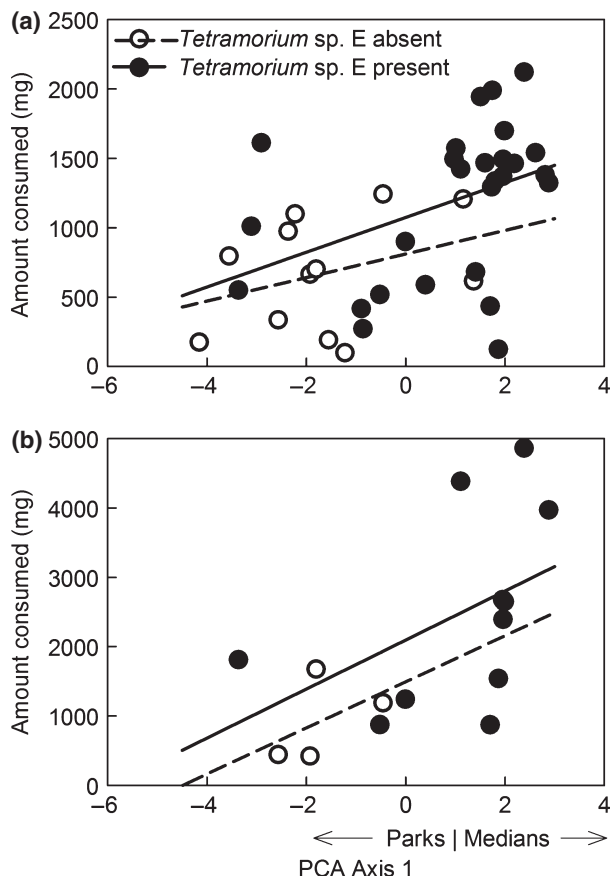
Fig. 6 Scatterplots illustrating the relationship between PCA Axis 1 and arthropod food consumption at sites with and without *T.* sp. E in experiments 1 (a) and 2 (b). More food is eaten as sites become hotter, drier, closer to habitat edges, more impervious and less covered with tree canopy. Lines represent model fits (Table 6).

Table 6 Results of ANCOVA partitioning variance between the best categorical and continuous predictors identified in previous analyses; *P* values < 0.05 are bold

Source	df	SS (Type I)	MS	F	P	R^2
(a) Experiment 1						
Model	3	3661628	1220543	5.1	**0.005**	0.30
T. sp. E	1	2169627	2169627	9.07	**0.005**	
PCA1	1	1455592	1455592	6.08	**0.019**	
T. sp. E x PCA1	1	36408	36408	0.15	0.700	
Error	35	8374400	239269			
Corrected total	38	12036028				
(b) Experiment 2						
Model	3	11274596	3758199	2.50	0.113	0.41
T. sp. E	1	7026475	7026475	4.68	0.053	
PCA1	1	4247316	4247316	2.83	0.121	
T. sp. E x PCA1	1	804	804	0.00	0.982	
Error	11	16504479	1500407			
Corrected total	14	27779075				

10,000 workers, quickly recruit to and dominate food sources (Brian *et al.*, 1967; King & Green, 1995). Although we did note other species at foods (including *Solenopsis molesta*, *Monomorium minimum,* and *Lasius neoniger*), *T.* sp. E appears to have the largest direct effect on food removal, whether because of its abundance, activity levels, dietary preferences, or some combination thereof. Where *T.* sp. E was present, 2–3 times more food was removed by arthropods than when it was absent. This result is consistent with the idea that high abundance of introduced species can trump the effects of biodiversity itself on rates of ecosystem function (Ehrenfeld, 2010; Strayer, 2012).

Urban habitat characteristics alone were also strong predictors of food removal (Table 5, Table S6), and still explained additional variation after accounting for the presence of *T.* sp. E (Table 6). Arthropods consumed more food in sites that were hotter, drier, closer to habitat edges, and surrounded by more impervious surface, and less tree canopy. Although animals are the arbiters of food removal, environmental variation could predict – or improve predictions of – food consumption because of its influence on animals. The environmental variables we measured may have been a proxy for arthropod abundance or species composition, including aspects that were missed in our sampling, such as the presence or activity of nocturnal organisms or mollusks such as slugs. Environmental differences may also alter arthropod metabolism and demand for food, such that similar arthropods consume more in hotter, drier sites (Howard & Tschinkel, 1981; Vogt & Appel, 1999; Kingsolver, 2009). Our July average site temperatures, represented by PCA axis 1, represent a biologically significant [e.g., (Kingsolver, 2009; Meineke *et al.,* 2013)] range of 2.6 °C across sites. The differences in food removal between parks and medians raise additional questions regarding the availability of both 'natural' and anthropogenic foods across urban green spaces: To what extent is littered food waste a dietary staple for urban wildlife inhabiting parks, medians, or even paved areas? On a practical level, our results point to the possibility that urban planners may be able to predict the magnitude of some ecosystem services by using rapid habitat measures rather than more laborious biological sampling.

Our results indicate that vertebrates compete with arthropods for littered food waste in Manhattan. Overall, 1.5–2.5 times more food was removed when vertebrates had access to food than when they did not. However, vertebrate consumption comes at a cost to public health because urban vertebrate populations can transmit diseases to humans, while ants and most arthropod scavengers do not (except under unusual circumstances such as hospitals) (Beatson, 1972; Haag-Wackernagel &

Moch, 2004; Himsworth *et al.*, 2013). Three species of nonhuman vertebrates were noted in medians: rats, house sparrows, and starlings. Parks are more diverse; for example, seven species of mammals and ~275 species of birds are known from Manhattan's Central Park (Roach, 2003; Kakutani, 2008). Among them are consumers of food waste, including rats, raccoons, opossums, squirrels, pigeons, and crows (Feinstein, 2011). Competition between vertebrates and ants has also been documented in desert ecosystems, where the removal of either taxon resulted in increased abundance of – and seed consumption by – the other within a year (Brown *et al.*, 1979; Valone *et al.*, 1994). At a few of our sites, just as much or more food was taken from the caged treatment as from its paired uncaged treatment. At least under some circumstances, then, the arthropod contribution to food removal is dominant. This could occur, for instance, where rat poison is used. Future work should further explore the conditions that favor the competitive advantage of arthropods as food removers in cities. Urban habitat management that favors ants over rats may benefit public health.

Although a growing number of studies have assessed community composition of urban ground arthropods (e.g., McIntyre *et al.*, 2001; Clarke *et al.*, 2008; Uno *et al.*, 2010), few have examined their ecological function. One study found that the rate of seed dispersal by ants was nearly twice as fast in urban forests as in natural areas, despite reduced diversity and density of ants in urban sites; this shift was attributed to the presence in urban sites of only the most efficient and dominant foragers (Thompson & McLachlan, 2007). Another study used ant species composition along an urbanization gradient to predict that both decomposition and soil aeration would decline with urbanization, although these functions were not measured (Sanford *et al.*, 2009). These results, together with the dominant role of introduced pavement ants in our study, are consistent with a key role for species identity, over diversity, in predicting the function of urban arthropod communities. This pattern may be particularly pronounced in cities because urbanization favors animal communities dominated by a few species of highly efficient foragers whose contributions to ecosystem function may outweigh those of other species Shochat *et al.* (2010).

We detected no effect of flooding from Hurricane Sandy, 7 months prior to the study, on the level of service provided by arthropod communities in parks or medians. Since our flooded sites were inundated with up to ~1.5 m of saltwater during the storm, with severe consequences for urban vegetation (Gregory, 2013), we expected this disturbance to also affect the function of arthropods. The lack of effect does not distinguish between our alternative predictions that stability of function would be provided by diversity effects in parks, or by disturbance tolerance of species in medians. Instead, our results suggest that either *both* predictions were correct and both habitat types were resilient for different reasons, or that the storm surge was less devastating to arthropods than we anticipated.

Few other studies have addressed ground arthropod response to transient saltwater flooding. In the most relevant example, a hurricane storm surge reduced abundance of *Solenopsis invicta* fire ants (but not other arthropods) in agricultural fields, leading to decreased ant predation on caterpillars (Beuzelin *et al.*, 2009). After Hurricane Katrina, ant and termite populations were reduced in New Orleans, LA, but (at least for termites), only in sites that remained inundated for 2–3 weeks (Hooper-Bùi *et al.*, 2007; Osbrink *et al.*, 2008). Resilience to flooding among arthropods is generally attributed to their ability to flee, reduce metabolism, or occupy air-filled cavities in soil or vegetation during floods (Hoback & Stanley, 2001; Meeson *et al.*, 2002; Osbrink *et al.*, 2008). During Hurricane Sandy, peak flooding was catastrophic but transient, and we estimate that our flooded sites were inundated for 2–12 h (NOAA, 2012). This is a time period during which many arthropods may withstand hypoxia (Hoback & Stanley, 2001; Schowalter, 2012). Thus, most of the species contributing to removal of food waste may have survived flooding at our sites. The tolerance or resilience of arthropod function to this acute perturbation is promising for urban ecosystems facing increased frequency of extreme weather events.

Successfully managing urban ecosystem services will depend on understanding the entire portfolio of services provided by different habitat types. Here, we provide such an ecological analysis for one service, the removal of littered food waste. Both arthropods and vertebrates contribute to this service, and do so at a higher rate in street medians than in parks. This result emphasizes the ecological value of even very small urban green spaces, whose functions may complement those of larger, more diverse habitats across the urban landscape. It is also clear from this and other studies of urban arthropod communities that, especially in urban faunas dominated by a few highly efficient species, the identity of key service providers may be more relevant than whole-assemblage characteristics for understanding and predicting ecosystem services.

References

Adhikari BK, Barrington S, Martinez J (2006) Predicted growth of world urban food waste and methane production. *Waste Management & Research*, 24, 421–433.

Beatson S (1972) Pharaoh's ants as pathogen vectors in hospitals. *The Lancet*, 299, 425–427.

Bender MA, Knutson TR, Tuleya RE, Sirutis JJ, Vecchi GA, Garner ST, Held IM (2010) Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science*, 327, 454–458.

Beuzelin J, Reagan T, Akbar W, Cormier H, Flanagan J, Blouin D (2009) Impact of Hurricane Rita storm surge on sugarcane borer (Lepidoptera: Crambidae) management in Louisiana. *Journal of Economic Entomology*, 102, 1054–1061.

Bolund P, Hunhammar S (1999) Ecosystem services in urban areas. *Ecological Economics*, 29, 293–301.

Brian M, Elmes G, Kelly A (1967) Populations of the ant *Tetramorium caespitum* Latreille. *Journal of Animal Ecology*, 36, 337–342.

Brown JH, Davidson DW, Reichman O (1979) An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist*, 19, 1129–1143.

Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443, 989–992.

Cardinale BJ, Duffy JE, Gonzalez A et al. (2012) Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Clarke KM, Fisher BL, LeBuhn G (2008) The influence of urban park characteristics on ant (Hymenoptera, Formicidae) communities. *Urban Ecosystems*, 11, 317–334.

Colvin BA, Degregorio R, Fleetwood C (1996) *Norway rat infestation of urban landscaping and preventative design criteria*. In: *Proceedings of the Seventeenth Vertebrate Pest Conference* (eds Timm RM, Crabb AC), pp. 165–171. University of California, Davis.

Duffy JE, Richardson JP, Canuel EA (2003) Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters*, 6, 637–645.

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, 41, 59–80.

Ellaway A, Macintyre S, Bonnefoy X (2005) Graffiti, greenery, and obesity in adults: secondary analysis of European cross sectional survey. *BMJ*, 331, 611–612.

Ellison AM, Gotelli NJ, Farnsworth EJ, Alpert GD (2012) *A Field Guide to the Ants of New England*. Yale University Press, New Haven and London.

Elmqvist T, Alfsen C, Colding J (2008) Urban systems. In: *Encyclopedia of Ecology* (eds Jorgensen SE, Fath B), pp. 3665–3672. Elsevier, Oxford.

Enquist BJ, Economo EP, Huxman TE, Allen AP, Ignace DD, Gillooly JF (2003) Scaling metabolism from organisms to ecosystems. *Nature*, 423, 639–642.

Feinstein J (2011) *Field Guide to Urban Wildlife*. Stackpole Books, Mechanicsburg, PA, USA.

Feng AYT, Himsworth CG (2014) The secret life of the city rat: a review of the ecology of urban Norway and black rats (*Rattus norvegicus* and *Rattus rattus*). *Urban Ecosystems*, 17, 149–162.

Flatau PJ, Walko RL, Cotton WR (1992) Polynomial fits to saturation vapor pressure. *Journal of Applied Meteorology*, 31, 1507–1513.

Frank D, McNaughton S (1991) Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos*, 62, 360–362.

Gardiner MM, Burkman CE, Prajzner SP (2013) The value of urban vacant land to support arthropod biodiversity and ecosystem services. *Environmental Entomology*, 42, 1123–1136.

Gómez-Baggethun E, Barton DN (2013) Classifying and valuing ecosystem services for urban planning. *Ecological Economics*, 86, 235–245.

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391.

Graczyk TK, Knight R, Gilman RH, Cranfield MR (2001) The role of non-biting flies in the epidemiology of human infectious diseases. *Microbes and Infection*, 3, 231–235.

Gray JS (1989) Effects of environmental stress on species rich assemblages. *Biological Journal of the Linnean Society*, 37, 19–32.

Gregory K (2013) Bare trees are a lingering sign of Hurricane Sandy's high toll. *The New York Times*, August 19.

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu JG, Bai XM, Briggs JM (2008) Global change and the ecology of cities. *Science*, 319, 756–760.

Haag-Wackernagel D, Moch H (2004) Health hazards posed by feral pigeons. *Journal of Infection*, 48, 307–313.

Haddad NM, Holyoak M, Mata TM, Davies KF, Melbourne BA, Preston K (2008) Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters*, 11, 348–356.

Himsworth CG, Parsons KL, Jardine C, Patrick DM (2013) Rats, cities, people, and pathogens: a systematic review and narrative synthesis of literature regarding the ecology of rat-associated zoonoses in urban centers. *Vector-Borne and Zoonotic Diseases*, 13, 349–359.

Hoback WW, Stanley DW (2001) Insects in hypoxia. *Journal of Insect Physiology*, 47, 533–542.

Hooper-Bùi LM, Wiltz BA, Seymour MA, Womack LA (2007) FAST prevention: fire ants in New Orleans post-Katrina. *Louisana Agriculture*, 50, 22–23.

Howard DF, Tschinkel WR (1981) The flow of food in colonies of the fire ant, *Solenopsis invicta*: a multifactorial study. *Physiological Entomology*, 6, 297–306.

KAB (2009a) *Littering Behavior in America: Results of a National Study*. Keep America Beautiful, Inc, Stamford, CT, USA.

KAB (2009b) *National Visible Litter Survey and Litter Cost Study*. Keep America Beautiful, Inc, Stamford, CT, USA.

Kakutani M (2008) A night stalker in the center of Manhattan, spying on owls and moths. *The New York Times*, July 1.

Karl T, Meehl G, Miller C (2008) *Weather and Climate Extremes in a Changing Climate*. NOAA National Climatic Data Center, Washington, DC.

King T, Green S (1995) Factors affecting the distribution of pavement ants (Hymenoptera: Formicidae) in Atlantic coast urban fields. *Entomological News*, 106, 224–228.

Kingsolver JG (2009) The well-tempered biologist. *American Naturalist*, 174, 755–768.

Klotz JH (2008) *Urban Ants of North America and Europe: Identification, Biology, and Management*. Cornell University Press, Ithaca and London.

Kostel-Hughes F, Young TP, Carreiro MM (1998) Forest leaf litter quantity and seedling occurrence along an urban-rural gradient. *Urban Ecosystems*, 2, 263–278.

Kotze J, Venn S, Niemelä J, Spence J (2011) Effects of urbanization on the ecology and evolution of arthropods. In: *Urban Ecology: Patterns, Processes, and Applications* (ed. Niemelä J), pp. 159–166. Oxford University Press, New York.

Kremen C (2005) Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters*, 8, 468–479.

Larondelle N, Haase D (2013) Urban ecosystem services assessment along a rural-urban gradient: a cross-analysis of European cities. *Ecological Indicators*, 29, 179–190.

MacGown J (2013) Ants (Formicidae) of the southeastern United States. Available at: http://mississippientomologicalmuseum.org.msstate.edu/ (accessed 14 February 2014).

Martin LJ, Blossey B, Ellis E (2012) Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. *Frontiers in Ecology and the Environment*, 10, 195–201.

Marvier M, Kareiva P, Neubert MG (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis*, 24, 869–878.

McCarthy MP, Best MJ, Betts RA (2010) Climate change in cities due to global warming and urban effects. *Geophysical Research Letters*, 37, L09705.

McDonald RI, Kareiva P, Forman RT (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, 141, 1695–1703.

McDonnell MJ, Pickett ST, Groffman P et al. (1997) Ecosystem processes along an urban-to-rural gradient. *Urban Ecosystems*, 1, 21–36.

McGeoch MA, Butchart SH, Spear D et al. (2010) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, 16, 95–108.

McIntyre N, Rango J, Fagan W, Faeth S (2001) Ground arthropod community structure in a heterogeneous urban environment. *Landscape and Urban Planning*, **52**, 257–274.

McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, **11**, 161–176.

Meeson N, Robertson A, Jansen A (2002) The effects of flooding and livestock on post-dispersal seed predation in river red gum habitats. *Journal of Applied Ecology*, **39**, 247–258.

Meineke EK, Dunn RR, Sexton JO, Frank SD (2013) Urban warming drives insect pest abundance on street trees. *PLoS ONE*, **8**, e59687.

Migge-Kleian S, McLean MA, Maerz JC, Heneghan L (2006) The influence of invasive earthworms on indigenous fauna in ecosystems previously uninhabited by earthworms. *Biological Invasions*, **8**, 1275–1285.

Monteith J, Unsworth M (2013) *Principles of Environmental Physics: Plants, Animals, and the Atmosphere*. Boston, Elsevier/Academic Press, Amsterdam.

NOAA (2012) Tides and Currents: Tides/Water Levels 8518750 The Battery, NY. Available from http://tidesandcurrents.noaa.gov (accessed 7 June 2014).

Nowak DJ, Crane DE, Stevens JC (2006) Air pollution removal by urban trees and shrubs in the United States. *Urban Forestry & Urban Greening*, **4**, 115–123.

Osbrink WL, Cornelius ML, Lax AR (2008) Effects of flooding on field populations of Formosan subterranean termites (Isoptera: Rhinotermitidae) in New Orleans, Louisiana. *Journal of Economic Entomology*, **101**, 1367–1372.

Pećarević M, Danoff-Burg J, Dunn RR (2010) Biodiversity on Broadway – Enigmatic diversity of the societies of ants (Formicidae) on the streets of New York City. *PLoS ONE*, **5**, e13222.

Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution*, **24**, 497–504.

Pouyat RV, McDonnell MJ, Pickett ST (1997) Litter decomposition and nitrogen mineralization in oak stands along an urban-rural land use gradient. *Urban Ecosystems*, **1**, 117–131.

Roach J (2003) 'BioBlitz' Finds 800-Plus Species in New York Park. *National Geographic News*. July 8. Available from http://news.nationalgeographic.com/news/2003/07/0708_030708_bioblitzresults.html (accessed 29 June 2014).

Sanford MP, Manley PN, Murphy DD (2009) Effects of urban development on ant communities: implications for ecosystem services and management. *Conservation Biology*, **23**, 131–141.

Savage AM, Hackett B, Guénard B, Youngsteadt E, Dunn RR (in press) Fine-scale heterogeneity across Manhattan's urban habitat mosaic is associated with variation in ant composition and richness. *Insect Conservation and Diversity*, doi: 10.1111/icad.12098.

Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. *Conservation Biology*, **25**, 428–437.

Schlick-Steiner BC, Steiner FM, Moder K *et al.* (2006) A multidisciplinary approach reveals cryptic diversity in Western Palearctic *Tetramorium* ants (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, **40**, 259–273.

Schowalter T (2012) Insect responses to major landscape-level disturbance. *Annual Review of Entomology*, **57**, 1–20.

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, **21**, 186–191.

Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, competition and biodiversity loss in urban ecosystems. *Bioscience and Microflora*, **60**, 199–208.

Shuttleworth WJ (2012) *Terrestrial Hydrometeorology*. John Wiley & Sons, Hoboken, NJ.

Smith MR (1943) Ants of the genus *Tetramorium* in the United States with the description of a new species. *Proceedings of the Entomological Society of Washington*, **45**, 1–5.

Strayer DL (2012) Eight questions about invasions and ecosystem functioning. *Ecology Letters*, **15**, 1199–1210.

Swan CM, Pickett ST, Szlavecz K, Warren P, Willey KT (2011) Biodiversity and community composition in urban ecosystems: coupled human, spatial, and metacommunity processes. In: *Urban Ecology: Patterns, Processes, and Applications* (ed. Niemelä J), pp. 179–186. Oxford University Press, New York.

Symonds MR, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, **65**, 13–21.

Thompson B, McLachlan SP (2007) The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada. *Urban Ecosystems*, **10**, 43–52.

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718–720.

United Nations Department of Economic and Social Affairs, Population Division (2014) World Urbanization Prospects: The 2014 Revision, CD-ROM Edition.

University of Vermont (2012) *New York City Landcover 2010 (3 ft Version)*. University of Vermont Spatial Analysis Laboratory and New York City Urban Field Station, Burlington and New York.

Uno S, Cotton J, Philpott SM (2010) Diversity, abundance, and species composition of ants in urban green spaces. *Urban Ecosystems*, **13**, 425–441.

US Census Bureau (2012) 2010 Census Urban and Rural Classification and Urban Area Criteria. Available at: https://www.census.gov/geo/reference/ua/urban-rural-2010.html (accessed 2 August 2014).

US Census Bureau (2014) State and County QuickFacts: New York (city), New York. Available at http://quickfacts.census.gov/qfd/states/36/3651000.html (accessed 2 August 2014).

Valone TJ, Brown JH, Heske EJ (1994) Interactions between rodents and ants in the Chihuahuan Desert: an update. *Ecology*, **75**, 252–255.

Vander Meer R, Jaffe K, Cedeno A (1990) *Applied Myrmecology: A World Perspective*. Westview Press Inc, Boulder, CO.

Vilà M, Basnou C, Pyšek P *et al.* (2009) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, **8**, 135–144.

Vogt JT, Appel AG (1999) Standard metabolic rate of the fire ant, *Solenopsis invicta* Buren: effects of temperature, mass, and caste. *Journal of Insect Physiology*, **45**, 655–666.

Zar JH (1999) *Biostatistical Analysis*. Pearson Education, Upper Saddle River, NJ.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Analysis of arthropod food preferences.

Figure S1. Arthropod food preferences did not differ significantly by site type, flooding, or their interaction.

Table S1. Eigenvalues and percent of variance explained by components 1–7 of the principal components analysis of environmental variables measured at park and median sites.

Table S2. Correlations (loadings) between each measured variable and each component in the principal components analysis of environmental variables measured at park and median sites.

Table S3. List of hexapod families detected in leaf-litter samples collected in Manhattan parks and medians.

Table S4. List of ant species detected in leaf-litter samples and timed hand collections in Manhattan parks and medians.

Table S5. Mean amount of food removed at sites categorized by presence or absence of each of the most common generalist ants.

Figure S2. At sites where *Tetramorium* species E was present, arthropods removed more food than at sites where *T.* sp. E was absent; all animals together still consumed, on average, more food than any arthropod assemblage alone.

Figure S3. Given *T.* sp. E presence (more likely in medians), site score on environmental PCA axis 1 was not a statistically significant predictor of *T.* sp. E abundance.

Table S6. Best competing models identified to explain food removal in Experiments 1 and 2.