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Stable isotopes reveal links between human food inputs and urban ant diets

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The amount of energy consumed within an average city block is an order of magnitude higher than that consumed in any other ecosystem over a similar area. This is driven by human food inputs, but the consequence of these resources for urban animal populations is poorly understood. We investigated the role of human foods in ant diets across an urbanization gradient in Manhattan using carbon and nitrogen stable isotopes. We found that some—but not all—ant species living in Manhattan's most urbanized habitats had $\delta^{13}C$ signatures associated with processed human foods. In particular, pavement ants (*Tetramorium* sp. E) had increased levels of $\delta^{13}C$ similar to $\delta^{13}C$ levels in human fast foods. The magnitude of this effect was positively correlated with urbanization. By contrast, we detected no differences in $\delta^{15}N$, suggesting *Tetramorium* feeds at the same trophic level despite shifting to human foods. This pattern persisted across the broader ant community; species in traffic islands used human resources more than park species. Our results demonstrate that the degree urban ants exploit human resources changes across the city and among species, and this variation could play a key role in community structure and ecosystem processes where human and animal food webs intersect.

1. Introduction

The average person living in a city will produce nearly half a metric ton of rubbish this year [1], and of that, 15% will be food waste [2]. With over half the world's population now living in cities [3], this amounts to 250 million tons of food thrown out in cities each year. While much of this waste will eventually make it into landfills, it represents a massive potential resource for urban animal populations before it is disposed or when it accumulates as litter [4]. By consuming food as litter or in collection bins before it leaves the city, animals can gain valuable resources to fuel their population growth and, in turn, reduce the amount of rubbish that accumulates in urban areas [5]. But to what extent do animals actually exploit these resources, and how do these novel foods affect trophic structure within urban animal communities?

Generally, urban animal communities are characterized by lower diversity but increased abundance of select species that are able to thrive in and around built environments [6,7]. These select species, sometimes called 'urban exploiters' [4], are thought to possess a range of behavioural and physiological traits that facilitate their success, including the ability to incorporate human foods into their diets [4]. Species of mammals and birds that are successful in cities often switch from natural food sources in rural populations to human-derived foods in urban populations [8–11]. Some of the most common species in city centres, like brown rats and feral pigeons, may depend heavily on human foods and reach their highest population densities in areas where access to human rubbish is most available [12,13].

The effects of human foods on animal populations are not only influenced by when and how much food is unintentionally provided, but also what kind of food. Over the past 50 years, human diets have changed significantly, especially within cities [14]. With increased urbanization, humans tend to consume more animal-based foods and feed at a higher trophic level [14]. This shift has occurred in tandem with increased consumption of fast foods [15]. In North America, suppliers of fast food and other processed foods rely on corn-based agricultural systems to

raise beef and chicken [15,16], and corn-based sweeteners are commonly added to foods and beverages [17]. This increased consumption of meat and corn-based foods leaves a conspicuous signature in the composition of nitrogen and carbon isotopes present in humans [18], and we predict that these changes could be apparent in wild animals that feed on human foods.

Stable isotopes of carbon and nitrogen have been used to infer information about the diets of many animals [19]. As trophic level increases from primary producers (e.g. plants) to top predators, isotopes of nitrogen are increasingly enriched, such that carnivores have higher nitrogen isotope ratios ($\delta^{15}N$) than herbivores, which in turn have a higher ratio than plants. If urban species are feeding at a higher trophic level because of the consumption of animal products in rubbish, then they should have higher nitrogen isotope ratios than individuals living more distant from human influence. Carbon isotopes, on the other hand, provide information about the base of a food web; higher $\delta^{13}C$ values are found in C_4 photosynthesizing plants (primarily grasses) compared with more common C_3 plants. Because North American diets include a higher proportion of C_4-derived foods (corn or sugarcane-based), $\delta^{13}C$ values can serve as a metric to indicate how animals are using human food sources in cities and to what extent they rely on these resources across their range [9,20].

Working in New York City, we used stable isotopes to investigate the diets of ants (Hymenoptera: Formicidae) across an urban habitat mosaic in Manhattan. New York is one of the largest and oldest urban centres in North America, and its ant fauna has been recently described [21,22]. Globally, ants are widespread and abundant in both natural [23,24] and urban ecosystems [25], and they commonly recruit to human food sources [26–28]. Within Manhattan, distinct ant communities are found in highly urban areas (e.g. traffic islands) compared with forested city parks [22]. This pattern is driven, in part, by a loss of species that cannot persist in highly urban areas, while a subset of species ('urban exploiters') reach their highest abundances in these urban habitats.

We focused first on the pavement ant, *Tetramorium* sp. E (hereafter *Tetramorium*), which is one of the most common ants in cities in the USA and in other temperate cities around the globe [29]. We sampled stable isotopes in *Tetramorium* workers from city parks, traffic islands and pavements across Manhattan to test whether isotopes could be used to quantify the relative contribution of human foods to animal diets (electronic supplementary material, figure S1). We predicted that ants would rely more heavily on human-derived foods in areas where they came into closest contact with humans (i.e. pavements and traffic islands) and that these differences would be reflected in stable isotopes of carbon. Next, we applied this technique across ant communities living in city parks and traffic islands to test whether urban specialist species relied more heavily on human foods and how switching to a human-derived diet affected trophic position. Combining these results, we evaluated how human foods contribute to ant diets differently across species and how access to these foods may influence community composition generally.

2. Material and methods

(a) Habitat descriptions

We collected ants from a range of habitats in Manhattan (New York, NY, USA) to compare how ant diets changed across an urban landscape (electronic supplementary material, figure S1). The habitats we sampled ranged from heavily trafficked pavements (highest human contact) and traffic islands (medium human contact) to forested park sites (least human contact).

Pavements represented the most extreme urban environment, with ant colonies nesting in pavement cracks or within tree pits. Tree pits are small, landscaped plots of soil along the road edge that were generally planted with a single tree. Pavements were adjacent to numerous shops and restaurants, received heavy foot traffic, and were hosts to rubbish bins and accumulated litter. Traffic islands (sometimes called street medians, neutral ground or malls) along Broadway represented an intermediate level of urbanization and consisted of landscaped plots (average size: 312 m^2 [22]) bordered by three traffic lanes on either side. The traffic islands were planted primarily with eight tree species (pin oak (*Quercus palustris*), crab apple (*Malus* sp.), honey locust (*Gleditsia triacanthos*), London plane (*Platanus acerifolia*), Callery pear (*Pyrus calleryana*), red oak (*Quercus rubra*), gingko (*Gingko biloba*) and hawthorn (*Crataegus* sp.)) and two common understory plant species (English ivy (*Hedera helix*) and yew (*Taxus* sp.)). A subset of the tree species planted in traffic islands were also among those planted in tree pits along the pavement. At the end of each traffic island was a seating area with benches and a rubbish bin that was accessible to colonies nesting in traffic islands. Finally, park sites represented the least urbanized environment. Parks ranged from landscaped greenways adjacent to pedestrian pavements to forested areas with less human impact. Within parks, we deliberately sampled sites with tree and ground cover rather than open fields or sites directly adjacent to pavements (electronic supplementary material, figure S1). The park sites we sampled, therefore, had limited access to human foods.

(b) Study species and sample collection

Ant communities within Manhattan have been recently described [21,22] and represent a mixture of native species characteristic of the New England fauna [30] as well as introduced species. Among the introduced species, some of them are common to urban environments generally (e.g. *Tetramorium*), while others appear to be most abundant in New York compared with other cities (e.g. *Lasius cf. emarginatus*).

We focused first on the pavement ant, *Tetramorium* sp. E (formerly *T. caespitum* Linnaeus 1758). Foragers of *Tetramorium* were collected from across all three habitats described above: city parks, traffic islands and pavements. Between 22 May and 27 May 2013, we collected workers from 12 traffic islands and 12 pavement locations along Broadway in Manhattan (electronic supplementary material, figure S1). The traffic island and pavement sites were sufficiently separated to ensure that independent colonies were sampled for each collection (minimum of 50 m apart). Additionally, *Tetramorium* workers were collected from nine sites in eight city parks (Battery, Carl Moore, Carl Schurz, Central (two sites), Highbridge, Morningside, Nelson A. Rockefeller and South Cove) between 30 May and 6 June 2013.

In parks and traffic islands, we also sampled the broader ant community (electronic supplementary material, table S1) between 22 May and 27 May 2013. Ants were collected from 12 traffic islands and 12 park sites within six parks (Central (four sites), Fort Tryon, Inwood Hill (two sites), Isham, Morningside (two sites), Riverside (two sites); electronic supplementary material, figure S1). Hand collections were made haphazardly, and involved collecting ants nesting under rocks, inside logs, in the leaf-litter and foraging. This sampling protocol was designed to capture the largest diversity of ant species present at each site, and our collections, though less extensive, were comparable in composition to previous studies of ant species diversity in New York City [21,22].

3

From traffic islands and parks, we collected additional arthropod species that represented known predators (Araneae, Coleoptera: Coccinellidae), herbivores (Hemiptera: Aphididae, Cicadellidae, Miridae, Pseudococcidae) and detritivores (Isopoda: Oniscidea) to provide a relative comparison for stable isotope values from ant samples. While some studies have standardized stable isotope values across habitats based on soil $\delta^{15}N$ [31,32], we chose not to do so in this study. The habitats sampled in Manhattan are characterized by allochthonous input [33], and using localized soil samples to standardize isotope values would not accurately reflect the base of the food web in these systems.

(c) Stable isotope analysis

Our methods followed well-established protocols for stable isotope studies in ants [34,35]. In the field, all arthropods were collected live and frozen at $-20°C$ until preparation for isotope analysis. Ants were identified to species based on morphology [30], and after identification, specimens were placed in a drying oven at $50°C$ for 48 h. Non-ant arthropods were identified to order, or to family when possible, and dried under similar conditions.

After specimens were dried, we removed the gaster (abdominal portion) of each ant, because the storage of recent food items in the crop and relative differences in fat reserves among individuals can introduce bias into isotopic comparisons [35,36]. Next, we weighed out 0.1–1.5 mg of tissue for each sample into a 5×9 mm tin capsule (Costech Analytical Technologies Inc., Valencia, CA, USA) using an analytical balance (A&D Instruments, HR-202i, precise to 0.01 mg). Small ant species required pooling individuals to reach a minimum weight, while larger species needed to be crushed so that only a portion of each individual was used per sample. After reaching the appropriate weight, the capsules were crushed using sterilized forceps and placed individually into a 96-well plate for shipment to the Stable Isotope Facility at the University of California, Davis.

The ratio of heavy to light isotopes of carbon (^{13}C–^{12}C) and nitrogen (^{15}N–^{14}N) were measured using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The ratio is reported as a delta (δ) value and expressed in permil units (‰) with respect to ^{13}C and ^{15}N. Higher levels of $\delta^{13}C$ are found in plants that use the C_4 photosynthesis pathway rather than C_3, and elevated $\delta^{13}C$ values of consumers indicate the acquisition of a higher proportion of basal resources from C_4 plants. With respect to nitrogen, $\delta^{15}N$ increases with trophic position, and there is generally a 3–4‰ enrichment per trophic level [19]. The delta value is calculated by comparing the ratio of heavy to light isotopes in the sample (R_{sample}) to the ratio found in a specific standard ($R_{standard}$) using the following formula:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 1000.$$

(d) Statistics

Assumptions of normality or equal variance (Bartlett's test, $p < 0.05$) were not met for parametric tests of stable isotope data, and standard transformations did not improve normality. Therefore, we used non-parametric tests to compare rank differences among groups. For *Tetramorium*, the Kruskal–Wallis test was used to determine whether differences in isotope ratios were present among habitats, and the Mann–Whitney U-test was used for pairwise comparisons between habitats. For community-wide tests, we analysed isotope differences between all species in parks versus traffic islands as well as average isotope values for independent park sites versus traffic island sites. For species that occurred in at least four park sites and in four traffic islands, we tested within-species differences between parks and traffic islands using the Mann–Whitney U-test. All tests were performed using Prism 6 statistical software (GraphPad Software, Inc. 2013). Two-tailed tests were used for all analyses, and alpha was set at $p < 0.05$.

3. Results

(a) Shift in pavement ant diets

With increasing levels of urbanization, *Tetramorium* displayed higher body values of $\delta^{13}C$ indicating a shift from carbon derived from C_3 sources towards carbon derived from C_4 sources (Kruskal–Wallis: $\chi^2 = 22.9$, $p < 0.0001$; Mann–Whitney pairwise comparisons, $N_{parks} = 9$, $N_{traffic\ islands} = 12$, $N_{pavement} = 12$, (pavement versus parks, $U = 1$, $p < 0.0001$), (pavement versus traffic islands, $U = 2$, $p < 0.0001$), (traffic islands versus parks, $U = 25.5$, $p = 0.043$); figure 1a). This change corresponded with higher $\delta^{13}C$ values found in human fast foods (table 1). The trophic feeding position of *Tetramorium* (as measured by $\delta^{15}N$) did not change across habitat types (Kruskal–Wallis: $\chi^2 = 0.76$, $p = 0.68$; figure 1b), which indicates that *Tetramorium* colonies fed on similar proportions of plant and animal-based foods in park, traffic island and pavement populations.

The increase in $\delta^{13}C$ values in *Tetramorium* from park to pavement populations (mean difference: 2.72‰) was comparable (figure 1c) to the shift observed between rural to urban populations of kit foxes in California, USA (mean difference: 2.4‰, calculated from Newsome *et al*. [9]). Differences of similar magnitude were also observed between human populations in North America and Europe, which differ with respect to the proportion of corn-derived foods in their diets (mean difference: 2.56‰, calculated from Bol & Pflieger [18]). Among foods available to ants, the highest $\delta^{13}C$ was found in human fast foods compared with arthropod prey (table 1). Unlike ants, other arthropods did not shift to higher $\delta^{13}C$ values in traffic islands compared with parks (mean ± s.d.: traffic islands $= -28.08 \pm 3.3$, parks $= -26.75 \pm 2.6$; Mann–Whitney, $N_{parks} = 9$, $N_{traffic\ islands} = 6$, $U = 22$, $p = 0.58$).

(b) Shift in ant community diets

Across all habitats we sampled, 21 ant species were collected (electronic supplementary material, table 1) with an average of 5.3 species per park site (range: 4–7 species) and 3.1 species per traffic island (range: 1–5 species). Our samples included the 12 most common species in Manhattan, which collectively account for 88% of ant occurrence in the city [22]. Of these 21 species, five were collected in both parks and traffic islands.

We compared differences in stable isotopes between park and traffic island populations using two methods. First, we compared differences between parks and traffic islands based on average values of $\delta^{13}C$ and $\delta^{15}N$ for each species. When species occurred in both parks and traffic islands, populations in each habitat were treated separately (i.e. we calculated average stable isotope values for park populations of a species and their traffic island populations separately). Overall, species in traffic islands had higher $\delta^{13}C$ values compared with park species (Mann–Whitney U-test, $N_{parks} = 71$, $N_{traffic\ islands} = 37$, $U = 472$, $p < 0.0001$; figure 2a,b). Additionally, traffic island species exhibited slightly higher values of $\delta^{15}N$ (Mann–Whitney U-test, $N_{parks} = 71$, $N_{traffic\ islands} = 37$, $U = 922$, $p = 0.011$; figure 2c), an indication of a relative
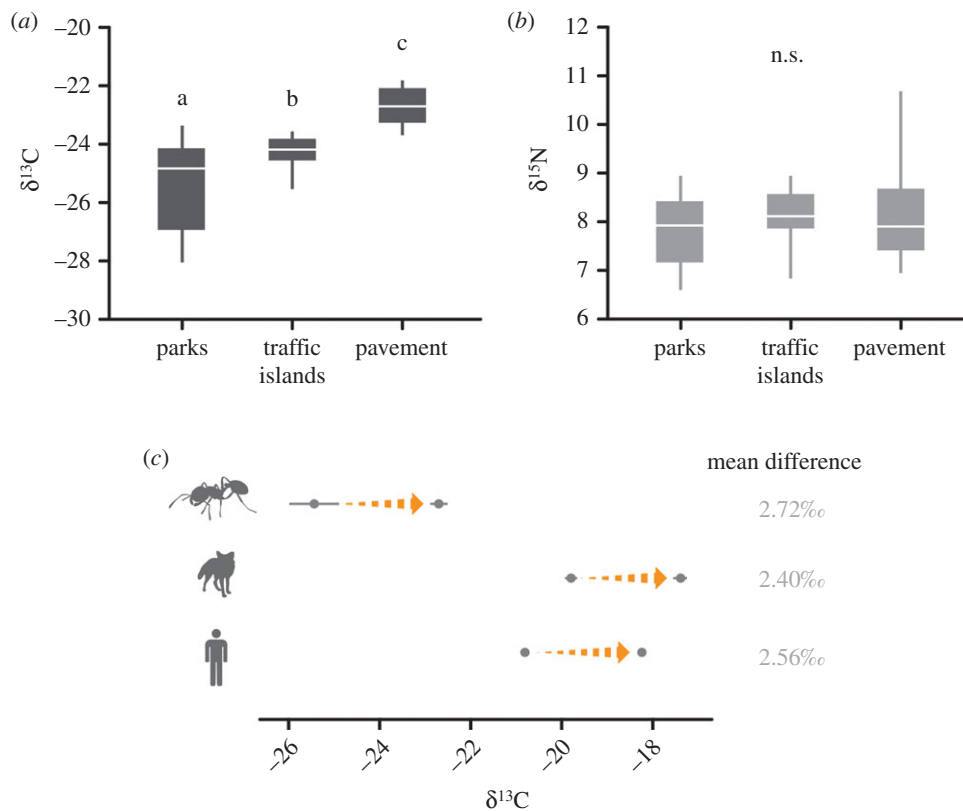
Figure 1. Changes in *Tetramorium* diet across urban habitats. Box plots show stable isotope values (median, 25–75%, and range) of (*a*) carbon and (*b*) nitrogen for *Tetramorium* workers collected from parks, traffic islands and pavements. *Tetramorium* workers exhibit a shift towards higher $\delta^{13}C$ values in habitats with increasing urbanization, but levels of $\delta^{15}N$ show no change (letters indicate significant differences). (*c*) Comparison of the shift in $\delta^{13}C$ values (mean $\pm$ s.e.m.) from relatively rural to urban populations of *Tetramorium* ants and kit foxes [9], as well as the difference in $\delta^{13}C$ from human populations in Europe and North America [18]. While mean values of $\delta^{13}C$ differ among groups, the relative change in $\delta^{13}C$ values (indicated by the direction of the arrow) is similar. (Online version in colour.)

Table 1. Stable isotope content of potential food items.

potential food	n	$\delta^{13}C$	s.d.	$\delta^{15}N$	s.d.
arthropod predators	7	−25.6	0.5	7.1	1.86
arthropod herbivores	5	−30.6	2.3	1.8	1.7
arthropod detritivores	3	−24.9	1.9	6.2	0.1
fast-food beef[a]	162	−18.0	2.9	6.5	0.4
fast-food chicken[a]	161	−17.5	0.5	2.3	0.3

[a]Adapted from Jahren & Kraft [15].

shift away from herbivory towards carnivory. For our second comparison, we analysed differences between parks and traffic islands based on average values of $\delta^{13}C$ and $\delta^{15}N$ for each site (i.e. species were pooled within sites to produce a single site-based average). Average $\delta^{13}C$ values for traffic islands were significantly higher than average $\delta^{13}C$ values for park sites (Mann–Whitney U-test, $N_{parks} = 12$, $N_{traffic\ islands} = 12$, $U = 6$, $p < 0.0001$; figure 2*d,e*). However, average $\delta^{15}N$ values did not differ between habitats on a site-by-site basis (Mann–Whitney U-test, $N_{parks} = 12$, $N_{traffic\ islands} = 12$, $U = 50$, $p = 0.22$; figure 2*f*).

The trophic breadth of ant communities differed between parks and traffic islands. The range in $\delta^{15}N$ values from species found in parks (2.26–11.70‰, difference: 9.44‰) was greater than the range observed in traffic islands (4.73–11.96‰, difference: 7.23‰). The average span of $\delta^{15}N$

values for each park site (3.0‰) was nearly double the average found per traffic island (1.6‰). This pattern was largely driven by a greater presence of herbivorous ant species in parks (indicated by lower $\delta^{15}N$). Overall, the minimum $\delta^{15}N$ for park sites (median 6.6‰) was lower than the minimum in traffic islands (median 7.7‰), and this difference was significant (Mann–Whitney U-test, $N_{parks} = 12$, $N_{traffic\ islands} = 12$, $U = 33$, $p = 0.024$). The maximum $\delta^{15}N$ per site (which is associated with more carnivorous ant species) did not significantly differ between parks and traffic islands (Mann–Whitney U-test, $N_{parks} = 12$, $N_{traffic\ islands} = 12$, $U = 66.5$, $p = 0.77$).

In addition to *Tetramorium*, two species (*Nylanderia flavipes* and *Lasius cf. emarginatus*) were collected in large enough numbers to compare within-species differences in isotope values between habitats. While *Tetramorium* exhibited an increase in $\delta^{13}C$ and no change in $\delta^{15}N$ (figure 3), the other two species investigated showed slightly different patterns. Similar to *Tetramorium*, *N. flavipes*, a ground-foraging species, displayed an increase in $\delta^{13}C$ in traffic islands (Mann–Whitney U-test, $N_{parks} = 11$, $N_{traffic\ islands} = 4$, $U = 4$, $p = 0.018$; figure 3*a*), but *N. flavipes* also exhibited a marginally significant increase in $\delta^{15}N$ in traffic islands (Mann–Whitney U-test, $N_{parks} = 11$, $N_{traffic\ islands} = 4$, $U = 7$, $p = 0.056$; figure 3*b*). By contrast, *L. cf. emarginatus*, an ant species that forages chiefly in trees (where it feeds on plant exudates and the honeydew of plant-feeding insects), did not show any difference in $\delta^{13}C$ or $\delta^{15}N$ between habitat types (Mann–Whitney U-test, $N_{parks} = 5$, $N_{traffic\ islands} = 5$; $\delta^{13}C$: $U = 11$, $p = 0.802$; $\delta^{15}N$: $U = 12$, $p = 0.944$; figure 3).
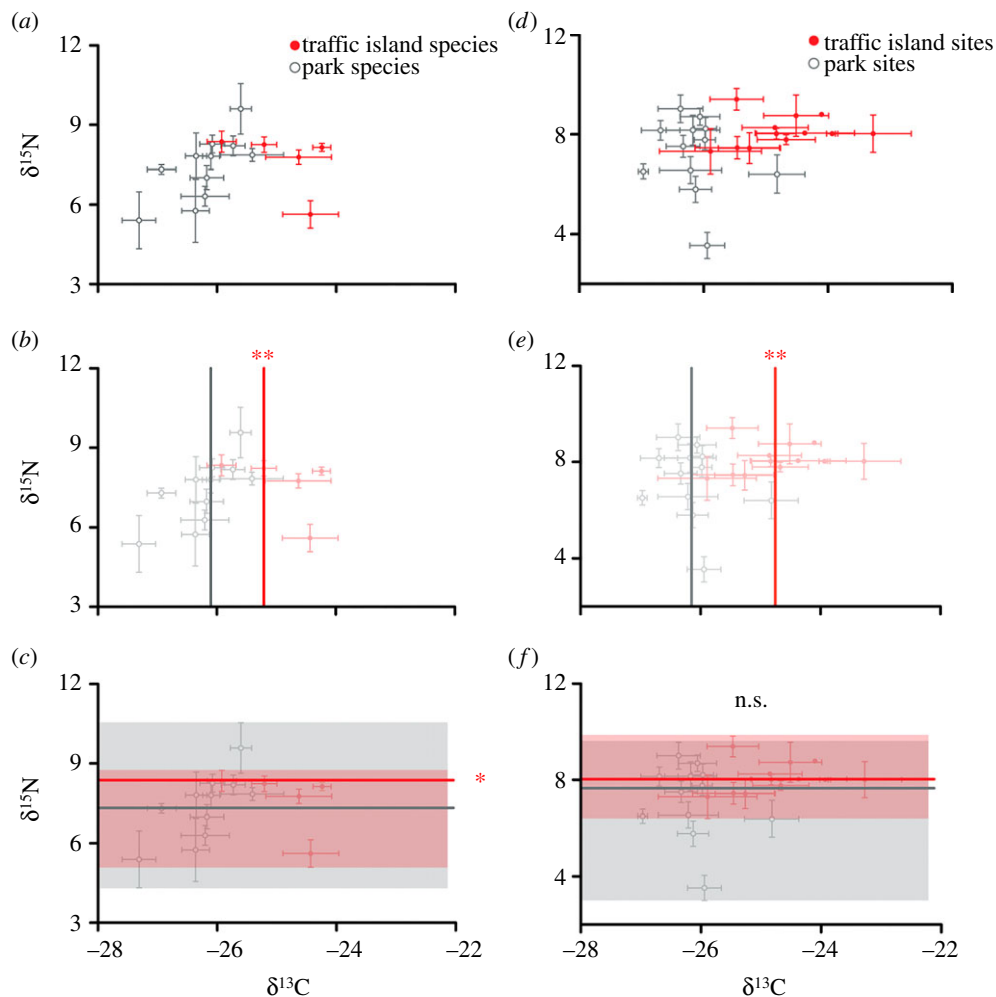
Figure 2. Community-level differences in stable isotope values between parks and traffic islands. ($a-c$) Values of $\delta^{13}C$ and $\delta^{15}N$ (mean $\pm$ s.e.m.) for individual species collected from parks and traffic islands; only species collected from at least three park sites or three traffic islands are included. The median $\delta^{13}C$ (b) and $\delta^{15}N$ (c) are indicated by solid lines for species collected in parks or traffic islands. Shaded areas indicate the trophic breadth based on $\delta^{15}N$ values (min to max s.e.m. for individual species). ($d-f$) Values of $\delta^{13}C$ and $\delta^{15}N$ (mean $\pm$ s.e.) for individual park sites or traffic islands. Lines indicate the median $\delta^{13}C$ (e) and $\delta^{15}N$ (f) for park sites and traffic islands, and the shaded areas represent trophic breadth based on $\delta^{15}N$ values (min to max s.e.m. for individual sites). Asterisks indicate *$p < 0.05$ and **$p < 0.0001$. (Online version in colour.)

(c) Trophic position of urban ants and arthropods

To provide context for stable isotope values obtained for ants, additional arthropods of known trophic guild (herbivores, predators and detritivores) were sampled. In line with predictions, herbivores had lower $\delta^{15}N$ values than either predators or detritivores (table 1). The mean difference in $\delta^{15}N$ values between herbivores and predators was 5.3‰, which was higher than the generally measured range of 3–4‰ [19]. However, the most abundant insect herbivores present during the sampling period were plant-sucking herbivores, and these have been previously shown to have lower $\delta^{15}N$ values compared with other arthropod herbivores [37]. With respect to ants, specialist predators, such as *Ponera pennsylvanicus* and *Pyramica pulchella*, had among the highest $\delta^{15}N$ values (median values above 9‰), while known herbivores, such as members of the genus *Camponotus* [38], had among the lowest $\delta^{15}N$ values (median values below 6‰; electronic supplementary material, figure S2). Overall, most ant species had a median $\delta^{15}N$ within or above the range associated with predators (14 species). Traffic islands were biased towards predatory species, where eight of the nine species (89%) found in traffic islands were ranked among predators.

By contrast, only 11 of 18 species (61%) found in parks were ranked among predators.

4. Discussion

Urban ants are tapping into the human food web. Across Manhattan, ant species in highly urban areas displayed evidence of increased consumption of human-derived foods compared with park species. This pattern was based on carbon isotope signatures, where higher $\delta^{13}C$ values were associated with urban populations. This was clearest in the pavement ant, *Tetramorium*, which lives across all habitats in the city including parks, traffic islands and pavements. For species such as *Tetramorium*, which are broadly distributed, we predicted that the influence of human food is greatest where human populations are most dense. Correspondingly, *Tetramorium* workers had the highest $\delta^{13}C$ values in pavement populations and the lowest values in parks. A similar pattern was mirrored at the community level, with ant species in traffic islands exhibiting higher $\delta^{13}C$ values compared to park-dwelling species.
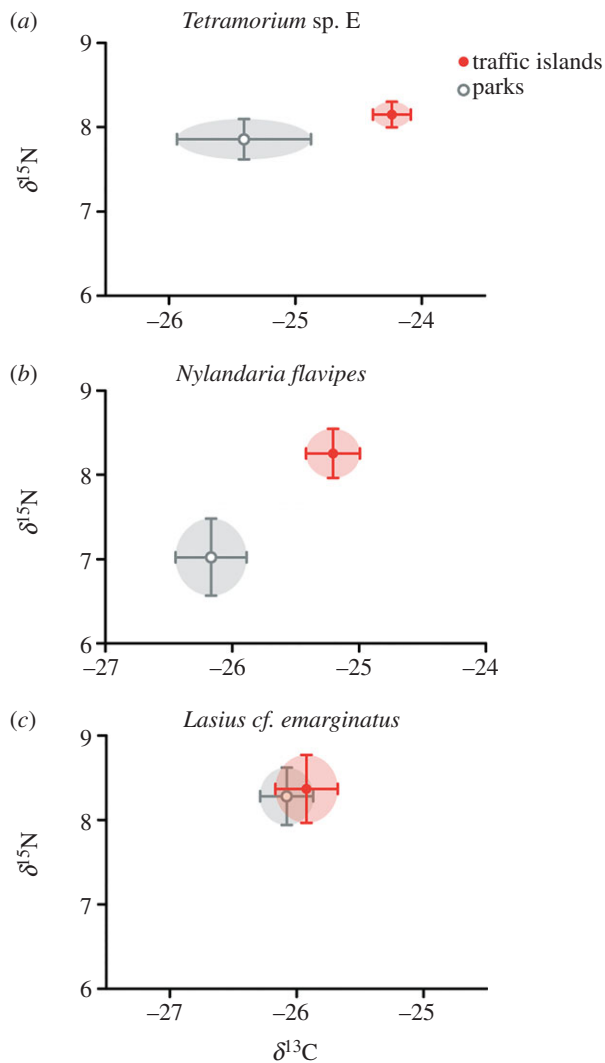
Figure 3. Within-species changes in stable isotopes between parks and traffic islands. Comparisons of $\delta^{13}C$ and $\delta^{15}N$ (mean $\pm$ s.e.m.) between park populations and traffic island populations of three species that were consistently found in both habitats ((a) *Tetramorium* sp. E, (b) *Nylanderia flavipes* and (c) *Lasius cf. emarginatus*). Results for *Tetramorium* are presented again from figure 1 for reference. Note that isotopic patterns for *L. cf. emarginatus* did not differ between sites. (Online version in colour.)

Differences in $\delta^{13}C$ across urban habitats probably reflected the availability of human foods in these environments. Elevated $\delta^{13}C$ can be caused by higher levels of fats in a sample [36] or by increased feeding on resources derived from C_4 photosynthesizing plants [19]. Because we removed the gaster from our samples, where most fat is stored in ants [35], it is unlikely that differences in fat content caused the changes in $\delta^{13}C$ we observed. Instead, the differences we observed most probably reflect changes in diet associated with consumption of resources derived from C_4 photosynthesizing plants. The most common C_4 plants in the wild are grasses, but grasses were not common in traffic islands or pavements (see Material and methods), where $\delta^{13}C$ was increased. Potential arthropod prey collected from traffic islands also did not have elevated $\delta^{13}C$. Therefore, the most probable source contributing to elevated $\delta^{13}C$ was from human foods, which have elevated $\delta^{13}C$ from the contribution of corn and sugarcane to fast foods [15]. Ants living in traffic islands and on pavements have greater access to human foods compared with park species. Also, park species may be less likely to feed on human foods even when they

are available. This was suggested by the increased number of specialist herbivores found in parks compared with traffic islands. Both of these factors probably contribute to differences in $\delta^{13}C$ we observed among populations, and both are related to consumption of human foods.

Our results suggest that carbon isotopes could provide a general method to assess the relative contribution of human-derived foods to animal diets, especially in North America. Like New York's ants, urban kit foxes also exhibit an increase in $\delta^{13}C$ [9], and humans living in North America have higher $\delta^{13}C$ values compared with European or Asian populations, where corn-based foods are less prevalent [18]. The relative differences in $\delta^{13}C$ values between populations of ants, kit foxes and humans were consistent when all groups shifted to North American-style diets (represented by a $\delta^{13}C$ increase of approx. 2.5‰). This pattern is largely driven by the corn-based agricultural system in North America, especially with respect to fast foods [15]. Using carbon isotopes alone, it is difficult to determine the exact proportion of a species' diet that is made up of human-derived foods, but $\delta^{13}C$ can provide a relative measure for the extent to which certain species use these resources. What is more interesting is that this relationship appears to hold up for both mammals and insects.

While carbon isotope signatures revealed a shift in *Tetramorium* diets, their trophic position remained stable as indicated by $\delta^{15}N$. This suggests that *Tetramorium* colonies were able to balance the types of foods they consumed (i.e. the proportion of animal to plant derived foods) whether they were foraging on natural or human food sources. Social insects display an impressive ability to regulate their nutritional intake, and they can make these decisions at the colony level [39–41]. This stands in interesting contrast to human populations in which dietary balance is strongly influenced by regional factors associated with food availability [14]. This is not to say social insects never shift their trophic level in response to resource changes. When Argentine ants (*Linepithema humile*) invaded California, early populations drove down prey species in their introduced range and became more herbivorous over time compared with native populations [42]. Perhaps the contrast between the case for Argentine ants and that of *Tetramorium* is that Argentine ants were dealing with the absence of a typical food while urban *Tetramorium* populations confront the addition of new foods. With an abundance of food choices, *Tetramorium* may be able to select their preferred diet among sugars, oils and animal-based foods present in human rubbish. This is evidenced by the fact that *Tetramorium* will recruit to both animal- and plant-based food baits when either are provided [28,43].

Among humans, fast foods and other processed foods in North American diets generally have negative impacts on health [44,45], but at least some urban animals appear to benefit from these diets. Kit foxes that subsist on human foods in urban habitats exhibit some diagnostic differences from rural populations, such as higher cholesterol levels [46], but there is no evidence that these differences are associated with negative health consequences. Instead, kit fox populations are more stable in urban areas compared with rural populations, and female kit foxes have increased fecundity relative to their rural counterparts [9]. Likewise, *Tetramorium* reach their highest occurrences in urban sites compared with parks [22]. Nevertheless, we cannot exclude the possibility that there are subtle costs to shifting to human diets, such as micronutrient deficiencies or toxic effects of preservatives or

pesticide residues. Questions about how consumption of human foods affects the health of urban animal populations remains open to further research.

At the community level, traffic island and park species displayed differences in trophic composition. Ant communities in these two habitats are distinct, with higher diversity found in parks [22]. This was in line with trophic information based on δ^{15}N, where park species covered a larger trophic breadth compared with traffic island species. This pattern was largely driven by a loss of specialist herbivores in traffic islands, such as *Lasius flavus*, which feed on honeydew produced by root aphids [47]. This corresponds with a shift from specialized to generalist arthropods observed in another urban ecosystem, Phoenix, AZ [25]. Traffic islands, unlike parks, were landscaped and lacked most native plants, and this lack of native vegetation may explain why some park species were excluded. By contrast, all species found in traffic islands also occur in parks to some extent, but a subset of these species, including *Tetramorium*, reach their highest abundances in traffic islands [22]. It is possible that access to anthropogenic foods could disproportionately favour these species. In city-dwelling rats, for example, the local abundance of urban populations may be regulated by availability of human food sources [13]. Our results show that human food inputs could be important to urban ants as well, but other factors, like temperature and soil moisture, may also influence the success of city-dwelling species [48].

The exotic species *N. flavipes* and *L. cf. emarginatus* were successful in both park and traffic island habitats like *Tetramorium*, but their stable isotope signatures were quite different. *Nylanderia flavipes* shifted towards consuming human foods in traffic islands, but unlike *Tetramorium*, their trophic feeding position changed as well; higher δ^{15}N values indicated that *N. flavipes* were consuming more animal-based foods in traffic islands compared with park populations. Our *a priori* prediction was that insect prey would be less common in traffic islands while there would be greater access to sugar sources in human foods, but the pattern in *N. flavipes* as well as the ant community as a whole suggests this is not the case. *Nylanderia flavipes* reaches their highest occurrence in parks [22], and it would be interesting to investigate how trophic differences between these populations affect their performance in urban versus park habitats.

Lasius cf. emarginatus, in contrast to both *Tetramorium* and *N. flavipes*, showed no change in either δ^{13}C or δ^{15}N across habitats. *Lasius cf. emarginatus* was only recently documented

in New York and is becoming common across the city [22]. It was the only species in addition to *Tetramorium* that we observed on pavements during our collections, but rather than foraging on the ground, their foraging trails extended into trees planted in tree pits (C. A. Penick 2013, personal observation). Planted trees are common in urban landscapes and represent an open resource for species that forage arboreally. Based on these observations and our stable isotope results, it appears that *L. cf. emarginatus* is largely avoiding human food sources and exploiting an arboreal food web.

In short, not all ants in cities feed on our rubbish, and there are multiple strategies that can lead to successful introductions in urban habitats. Identifying distinct food webs in cities is necessary to understand how interactions among species can affect community composition. Even in this context, our results indicate that human resources play a large role in urban food webs. The unusual abundance of these resources [49] may change trophic dynamics and alter processes controlling population size in these systems [50]. Our work focused on a single city, but it would be interesting to compare how human foods contribute to ant diets in different urban habitats or even within houses, where ants may feed on human foods before they are thrown out as waste. The contribution of human foods to urban diets could also vary by season and play a larger role during periods when natural prey is scarce (e.g. cooler months). Future work on trophic relationships in urban communities should provide additional insight into how these novel resources influence species interactions and affect community structure.

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