



# Moving targets: determinants of nutritional preferences and habitat use in an urban ant community

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## Abstract

Urban environments are often associated with reduced biodiversity, presumably because they are typically more fragmented, warmer, and drier than nearby non-urban environments. However, urban landscapes offer significant complexity that have allowed some taxonomic groups to flourish. Understanding how urban-exploiting animals navigate this spatiotemporal heterogeneity is important given the continued global urban land expansion. Here, we examined the factors influencing resource-use in an urban community of ants, which represent a widespread and important taxon in urban ecosystems. In particular, we sought to integrate ants' nutritional, thermal, and spatial niches to better understand how urban animals successfully access critical resources throughout their active season. Meteorological season (spring, summer, and fall) and/or species ( $n = 9$ ) influenced ants' preferences for nutrition (ratio of ingested protein-to-carbohydrate ratio), as well as the temperature, type (impervious vs. non-impervious), and shade status (shaded vs. non-shaded) of surfaces used during activity. Our data also indicate links among habitat variables, as well as between nutritional preferences and habitat use. Together, our results suggest that species and seasonality influence ecological (combined nutritional, thermal, and spatial) niches in an urban community. We encourage future work in urban ecosystems that continues to integrate more features of the ecological niche, and to examine the outcomes of variation in niches (e.g., non-overlapping niches may explain both the persistence of some native animals and the success of invaders).

**Keywords** Food · Foraging · Geometric framework · Niche · Resource · Temperature

## Introduction

Urban environments are complex and characterized by a diversity of interconnected microhabitats where patches of modified, nutrient-rich vegetation (e.g., grass lawns or cultivated fruit trees) are often interspersed among matrices of paved, impervious surfaces (e.g., sidewalks and roads) (Sukopp 2008; Parris 2016). Urban landscapes are not only fractured; they are also often embedded in warmer and drier local climates due to the urban heat island effect (Sukopp 2008; Forman 2014). Likely due to these spatial and climatic

constraints, urbanization is typically associated with a reduced biodiversity of native plants and animals (McKinney 2008). This is problematic because most humans now live in cities (UN 2014), and the global urban land expansion is expected to continue (Seto et al. 2011). Therefore, it is important to understand how animals navigate the spatial complexity of urban environments to successfully access resources they need to persist.

Food is a critical resource for animals, and spatiotemporal variation in food availability drives the geographic distribution and activity patterns of many animals (Raubenheimer 2010).

The abundance and energetic (caloric) value of food strongly influences animal ecology (Stephens and Krebs 1986; Karasov and Martinez del Rio 2007; Brown et al. 2011). The nutrient composition of food is also important because an animal with access to an abundance of high-energy food may still be food insecure if the food is of low quality (e.g., lacking essential nutrients). Nutrient imbalance, in turn, affects the behavior, physiology, and interspecific

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interactions of animals (reviewed in Simpson and Raubenheimer 2012). Therefore, animals—from insects to humans—adaptively defend a macronutrient intake target (the optimal amount of protein and carbohydrates to ingest) via foraging decisions (Simpson et al. 2003; Behmer 2009; Simpson and Raubenheimer 2012; Gosby et al. 2014). In urban environments, a range of animal taxa exploit and, possibly, depend upon human-derived food to meet their nutritional requirements (Penick et al. 2015, but see Penick et al. 2016). Although nutrient regulation by urban animals may vary across species and seasons, the factors influencing macronutrient intake targets of an urban community have not been explored.

Similar to food, thermal resources are important to animals given the profound effects of temperature on all levels of biological organization (reviewed in Angilletta 2009). As in other ecosystems, thermal resources or microclimates exhibit spatiotemporal variation in urban landscapes (Hansen et al. 2001; Gaffin et al. 2008). For example, many animals experience and respond to diurnal and seasonal variation in temperature where microhabitats are generally warmer in the afternoon and summer, respectively. Thermal microclimates also vary spatially (e.g., shaded microhabitats are cooler than those that are unshaded; reviewed in Greene and Millward 2017), and temperatures in urban microhabitats may be particularly variable. Urban environments are often a patchwork of impervious and vegetated surfaces, which vary dramatically in temperature and together influence the surface heat island effect (Hwang et al. 2014; Coutts et al. 2016). Therefore, accessing thermal resources requires animals to integrate a range of environmental inputs—from micro- and macro-weather conditions (e.g., shade and cloud cover, respectively) to surface types (impervious vs. non-impervious surfaces)—across time scales ranging from minutes to months.

Interspecific variation in resource use (e.g., nutrition and temperature) can indicate or lead to niche differentiation (or partitioning) whereby competing species use environmental resources differently, which results in species coexistence. Niche differentiation has been shown in urban environments (Heltai et al. 2015), and it can be important for the persistence of native species in response to invasive species. For example, overlapping climatic (thermal and hydric) and nutritional niches explain the successful invasions by multiple species of fruit flies and the concomitant decline in a native species of fruit fly (reviewed in Duyck et al. 2006, 2008). Further, dietary preferences can also vary among coexisting urban animals (Hanley et al. 2014; Penick et al. 2015), and non-overlapping nutritional niches may be important for maintaining urban ecosystem stability. Yet, the spatiotemporal dynamics of (including links between) nutritional preferences and thermal habitats in urban communities are poorly understood.

Here, we examine the effects of species and season on nutrient intake targets and microhabitat preferences in an

urban community of ants. Ants (Family Formicidae) are abundant and important components of terrestrial ecosystems (Crist 2009; Del Toro et al. 2012; Parr et al. 2016), including urban ecosystems (Guenard et al. 2015; Penick et al. 2015; Savage et al. 2015). Some ant species have proven to be useful models for investigating questions related to urban, nutritional, thermal, and/or spatial ecology (e.g., Crist and Haefner 1994; Angilletta et al. 2007; Penick et al. 2015; Savage et al. 2015; Gippet et al. 2017). Our study seeks to build upon these studies to understand how an urban ant community effectively accesses key resources across its active season. To meet this aim, we characterized nutritional preferences and the use of micro-climates and habitats individually, as well as collectively—that is, the integration of nutritional, thermal, and spatial niches.

## Materials and methods

### Study site

Our study site, the main campus of the University of the Pacific (UOP), is situated within the city of Stockton (current estimated population > 300,000; U.S. Census Bureau) in California's Central Valley (Fig. S1). The UOP campus represents an established urban ecosystem as it was built in 1923. It exhibits several features characteristic of urban ecosystems in the western U.S., including cultivation of non-native plants, an abundance of impervious surface cover (e.g., roads, sidewalks, and parking lots), and regular irrigation (Parris 2016). The Calaveras River runs east-west through the UOP campus (0.7 km<sup>2</sup>), effectively dividing the campus into a smaller area north of the river and a larger area south of the river. For our study, we divided the campus into nine zones of similar size: three zones north of the river, and six zones south of the river (Fig. S1).

### Experimental design

For two years (2016 and 2017), we sampled ants using bait stations (see below) throughout the three seasons during which ants were most active: spring, summer, and fall (April, July, and October, respectively). During each season, we sampled our study site for three days. We sampled three non-adjacent zones (see above) during each sampling day. On each sampling day, we searched for surface-active ants and placed eight bait stations in each zone (i.e., a total of 72 bait stations each season in both years) near ants. To avoid pseudoreplication (i.e., sampling the same colony at >1 bait station), we ensured that bait stations were > 25 m from one another and ants from nearby bait stations were not the same species.

Each bait station consisted of four baits that varied in protein:carbohydrate (p:c) ratio: high p (p:c = 34), 2p:1c (p:c = 2), 1p:2c (p:c = 0.5), and high c (p:c = 0.032). Thus, the average macronutrient content of bait options at each station was p:c = 9.133. Because ant feeding preferences may be influenced by nutrients other than protein or carbohydrate (e.g., salt: Kaspari et al. 2008), all four baits were isocaloric (4 kcal/g dry mass), isolipid (3% wt/wt dry mass), and isomineral. Baits were a mixture of egg powder, whey protein, casein, sucrose, and Wesson salts. We added dH<sub>2</sub>O to dry ingredients to create a batter-like consistency because (1) ants (including at least one of our focal species) prefer wet baits (Tennant and Porter 1991; Nyamukondiwa and Addison 2014) and (2) wet baits eliminate variation due to species-specific preferences for food particle size (Hooper-Bui et al. 2002).

At each bait station, we used a 30 ml syringe to place a dollup of bait (1.5–2.0 cm in diameter) at each corner of a 15 cm × 15 cm square (sensu Cook and Behmer 2010), the orientation of which was randomly determined. After 60 min, we counted the number of ants (n) recruited to each bait, and we used a mixing model to estimate the preferred p:c of ants at each bait station (Eq. 1).

$$\begin{aligned} \text{Preferred } p : c = & 34 \left( \frac{n_{\text{high } p}}{n_{\text{total}}} \right) + 2 \left( \frac{n_{2p:1c}}{n_{\text{total}}} \right) \\ & + 0.5 \left( \frac{n_{1p:2c}}{n_{\text{total}}} \right) \\ & + 0.032 \left( \frac{n_{\text{high } c}}{n_{\text{total}}} \right) \end{aligned} \quad (1)$$

For example, if a colony of ants recruited strongly to the high p and 2p:1c baits, we determined a strong protein bias in macronutrient preference for this colony. We identified ants at bait stations, or we collected ants and identified them later under a dissection microscope. We did not use data from bait stations that attracted <10 ants (indicative of poor recruitment). We also excluded data from bait stations with >1 species because, for example, a subordinate species may shift to a bait with a non-preferred p:c if it is excluded from its preferred bait by a dominant species. However, recruitment of multiple species to the same bait station was rare (<0.5% of bait station sampling points). We performed  $\chi^2$  tests on the observed and expected number of ants recruited to each bait for each species every season, which allowed us to confirm that p:c choices were non-random (all  $p < 0.01$ ).

To estimate the temperatures used by ants, we measured the surface temperature ( $T_{\text{surface}}$ ) at the center of each bait station at 0 min and 60 min using an infrared thermometer (model 62 MAX, Fluke Corp., Everett, WA, USA). We also recorded the type of surface (1: impervious; 0: non-impervious) and shade status (1: shaded; 0.5: mix of shaded and non-shaded; 0: non-shaded) at which bait stations were positioned, as well as the cloud cover (number of oktas) during each 60 min sampling period.

## Statistical analyses

To determine the effects of species and seasonality on specific metrics of nutritional and microhabitat use, we used several linear models in SPSS (v.22 IBM Corp., Armonk, NY). We transformed data when necessary, and we determined two-tailed significance at  $\alpha = 0.05$ . We used linear mixed models to determine the factors influencing macronutrient intake target (p:c),  $T_{\text{surface}}$ , shade status, cloud cover, and time-of-day. We used a binary logistic generalized linear model to determine factors influencing surface type. For these linear and binary logistic models, we included season, species, and season×species as fixed effects, and year as a random effect.

## Results

We observed nine species of ants during our study: *Cardiocondyla mauritanica*, *Linepithema humile*, *Liometopum occidentale*, *Monomorium ergatogyna*, *Monomorium pharaonis*, *Paratrechina longicornis*, *Pogonomyrmex californicus*, *Prenolepis imparis*, and *Tetramorium immigrans* (Table 1). Macronutrient intake target (preferred p:c) was influenced by season (spring > summer > fall;  $F_{2,307} = 30$ ;  $p < 0.001$ ) and species ( $F_{8,318} = 2.6$ ;  $p = 0.0081$ ) but not by a season×species interaction ( $F_{11,317} = 0.88$ ;  $p = 0.56$ ) (Fig. 2). The  $T_{\text{surface}}$  at which ants were observed (and, thus, bait stations were placed) was influenced by season (summer > fall > spring;  $F_{2,267} = 5.5$ ;  $p = 0.0047$ ), species ( $F_{8,318} = 12$ ;  $p < 0.001$ ), and a season×species interaction ( $F_{11,317} = 2.0$ ;  $p = 0.027$ ) (Fig. 3a). The surface type (impervious vs. non-impervious) upon which ants were observed was influenced by species ( $\chi^2 = 16$ ,  $df = 8$ ,  $p = 0.037$ ) but not by season ( $\chi^2 = 1.8$ ,  $df = 2$ ,  $p = 0.40$ ) (Fig. 3b). The shade status at which ants were observed was influenced by season (more shaded during summer;  $F_{2,318} = 4.4$ ;  $p = 0.014$ ), species ( $F_{8,318} = 4.0$ ;  $p < 0.001$ ), and a season×species interaction ( $F_{11,318} = 2.1$ ;  $p = 0.020$ ) (Fig. 3c). The amount of cloud cover during which ants were observed was influenced by season (less cloudy during summer;  $F_{2,298} = 24$ ;  $p < 0.001$ ) but not by species or a season×species interaction (all  $p > 0.22$ ). Neither season, species, nor season×species influenced the time-of-day ants were observed (all  $p > 0.05$ ).

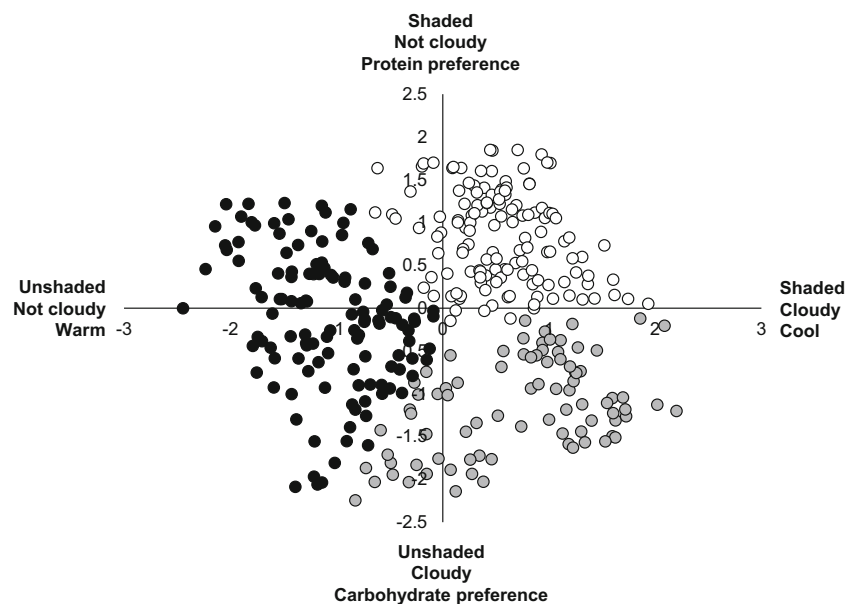
To determine the effects of species and seasonality on correlative patterns of nutritional preferences and microhabitat use, we used a multivariate approach in SPSS (v.22 IBM Corp., Armonk, NY). First, we performed a principal components analysis (PCA) on the dependent variables described above. We removed two variables (impervious surface and time-of-day) due to poor correlation with other variables and to improve the Kaiser-Meyer-Olkin measure of sampling adequacy. The resultant PCA generated two principal components (PCs) with eigenvalues greater than 1. The first PC explained >37% of the total variance, and it

**Table 1** The visitation rate to bait stations and most common niche cluster (see Fig. 1 for details) for each of nine focal ant species surveyed across three seasons in Stockton, CA

	Bait station visits (%)	Most common niche cluster
<i>Cardiocondyla mauritanica</i>	3.5	3
<i>Linepithema humile</i>	29.4	1
<i>Liometopum occidentale</i>	1.5	2, 3 (tie)
<i>Monomorium ergatogyna</i>	8.2	3
<i>Monomorium pharaonis</i>	0.3	3
<i>Paratrechina longicornis</i>	5.0	1
<i>Pogonomyrmex californicus</i>	0.6	3
<i>Prenolepis imparis</i>	15.0	1
<i>Tetramorium immigrans</i>	36.5	3

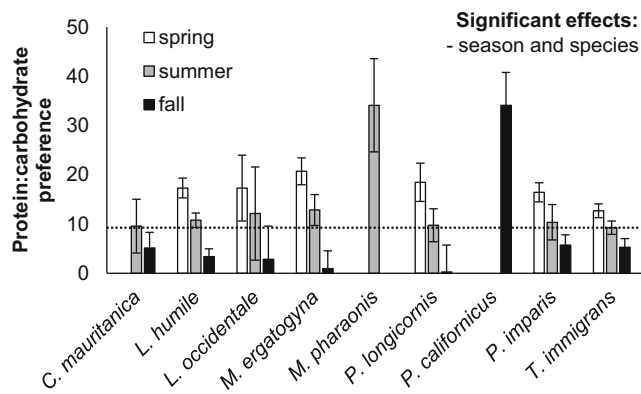
loaded positively on to shade status (0.80) and cloud cover (0.28) and negatively on to  $T_{\text{surface}}$  (−0.87) and only weakly on to preferred p:c (−0.08). Thus, a bait station data point with a high PC 1 value indicated that ants were observed at a shaded, cool bait station during cloudy conditions. The second PC explained >28% of the total variance, and it loaded positively on to shade status (0.80) and preferred p:c (0.65) and negatively on to cloud cover (−0.87) and only weakly on to  $T_{\text{surface}}$  (−0.02). Thus, a bait station data point with a high PC 2 value indicated that ants exhibited a protein-bias at a shaded bait station during sunny (not cloudy) conditions. Second, we plotted our bait station data, and we determined that these data best fit into three clusters (indicative of different nutritional, thermal, and spatial niches) by entering PC 1 and PC 2 into a hierarchical cluster analysis

using Ward's method (Fig. 1). Niche cluster 1 signified lower  $T_{\text{surface}}$ , more shade, and a protein bias. Niche cluster 2 signified lower  $T_{\text{surface}}$ , more clouds, and a carbohydrate bias. Niche cluster 3 signified less shade, less cloudy, and higher  $T_{\text{surface}}$ . Third, we performed a k-means cluster analysis (where  $k = 3$ ) to assign each bait station data point to one of the three niche clusters. Last, we performed an ordinal logistic generalized linear model to determine the effect of season, species, and season×species on niche cluster assignment (e.g., data from bait stations in summer may have been more likely to fall within niche cluster 3 if ants haphazardly chose microhabitats during activity). Based on this approach, season ( $\chi^2 = 25$ ,  $df = 2$ ,  $p < 0.001$ ) and species ( $\chi^2 = 34$ ,  $df = 8$ ,  $p < 0.001$ ) influenced whether a given bait station's data was assigned to niche cluster 1, 2, or 3 (Fig. 1).



**Fig. 1** Niche cluster graph of data from bait stations (i.e., locations at which individuals were observed;  $n = 340$ ) across three seasons for nine species of ants in Stockton, CA. The x-axis represents PC 1, which characterized shade status, cloudiness, and surface temperature, and the y-axis represents PC 2, which characterized shade status, cloudiness, and

macronutrient preference (see text for details). Cluster analysis indicated three niche clusters—cluster 1 (white symbols), cluster 2 (gray symbols), and cluster 3 (black symbols)—each of which indicates a different ecological (combined nutritional, thermal, and spatial) niche

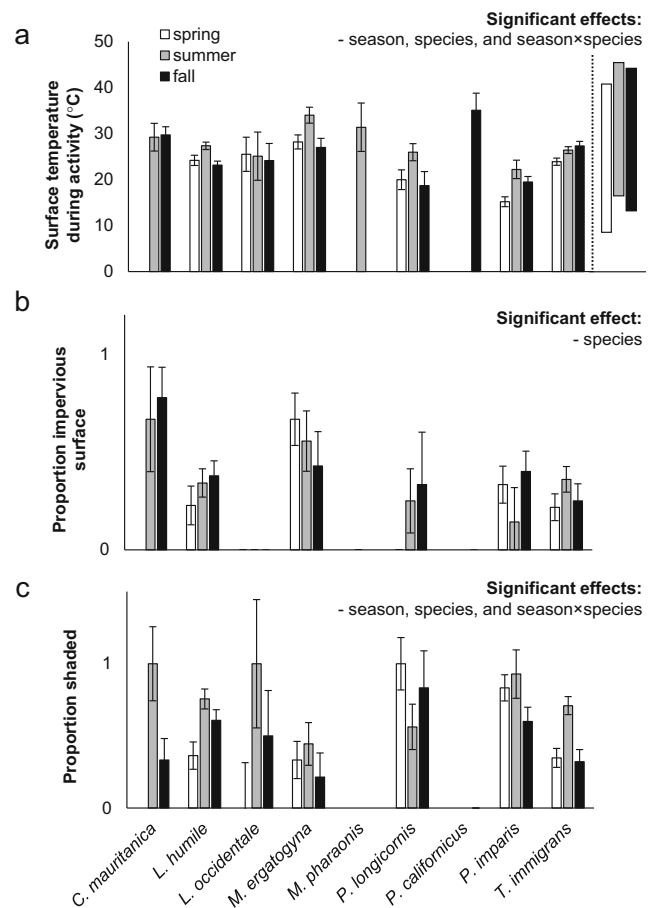


**Fig. 2** Effects of season and species on macronutrient intake target (preferred protein:carbohydrate [p:c] ratio; dotted horizontal line represents average p:c ratio of bait options at each station; see text for details) for an ant community in Stockton, CA sampled over two years. Significant effects are listed, and two-tailed significance was determined at  $\alpha = 0.05$  (see text for full statistical results)

## Discussion

Temporal and interspecific variation drive community dynamics across ecosystems. Here, we specifically detected strong effects of season and species on nutritional preferences and microhabitat use in an urban ant community (Figs. 2 and 3). Seasonality and species-level differences independently influenced aspects of animals' nutritional niches (e.g., species exhibited different macronutrient intake targets, and protein bias shifted to carbohydrate bias from spring to fall; Fig. 2) and thermal niches (e.g., ants exhibited activity on warmer surfaces during the summer; Fig. 3a). We further show that seasonality and species can exhibit interactive effects on resource use. For example, the  $T_{\text{surface}}$  of active ants in several species was not warmest in summer—rather,  $T_{\text{surface}}$  was often similar between the fall and summer, or across all three seasons (Fig. 3a). Our data also indicate links among microhabitat variables, as well as between nutritional preferences and microhabitat use (Fig. 1). Together, our results suggest that species and seasonality influence ecological (combined nutritional, thermal, and spatial) niches in an urban community.

Animals adaptively forage to ingest their optimal amounts of macronutrients, such as protein and carbohydrate, and nutrient intake targets are variable across species (reviewed in Simpson and Raubenheimer 2012). With the exception of two species (*M. pharaonis* and *P. californicus*, the latter of which is a specialist for seeds, a high-protein food item), ants in our study exhibited similar p:c preferences (Fig. 2); thus, there appears to be significant overlap in nutritional niches within this urban ant community. Further, seasonal shifts in nutritional preferences have been demonstrated by a range of animal taxa—from invertebrates (ants: Cook et al. 2011; Abbott et al. 2014; Frizzi et al. 2016; our study [Fig. 2]) to vertebrates (fish: Rubio et al. 2008; birds: Wheelwright 1988; mammals: Felton et al. 2009; Irwin et al. 2015; Coogan et al. 2018). Two, non-mutually



**Fig. 3** Effects of season and species on **a.**) surface temperature during activity (floating bars to the right of the dotted line represent the range of surface temperatures during activity measured for each season), and use of **b.**) impervious surface and **c.**) shaded microhabitats for an ant community in Stockton, CA sampled over two years. Values represent mean  $\pm$  s.e.m. Significant effects are listed for each dependent variable, and two-tailed significance was determined at  $\alpha = 0.05$  (see text for full statistical results)

exclusive explanations have been offered for seasonal shifts in macronutrient intake targets (Cook et al. 2011; Abbott et al. 2014; Frizzi et al. 2016). First, the intrinsic needs of an animal (or colony) may shift with season. For example, if reproduction requires an abundance of protein (e.g., to produce yolk proteins, such as vitellogenin), then protein would be preferred during the reproductive season. In ants, carbohydrates are used by workers and protein is consumed by the larvae (reviewed in Dussutour and Simpson 2009), which suggests that brood care during the spring in our study system may drive protein-bias during this season and then transition to carbohydrate-bias as brood develop into adults (workers) through the summer and into the fall (Fig. 2). Second, environmental variability in macronutrients due to season may drive seasonal shifts in macronutrient intake targets (Abbott et al. 2014; Frizzi et al. 2016). For example, if protein is limited in the environment during a given season, then protein would be preferred during this season. We lack information about the relative availabilities of protein and

carbohydrates in the environment in our system. However, urban ecosystems may exhibit less seasonality in p:c than non-urban ecosystems due to anthropogenic food subsidization. As examples, some urban animals have nutritional ecologies that are modified by or reliant upon food from humans (Penick et al. 2015, but see Penick et al. 2016), which may exhibit minimal seasonality in macronutrient composition.

Thermoregulation exhibits phylogenetic and biogeographic variation, and the vast majority of animals rely on behavior to thermoregulate (>99% of animals are ectothermic: Angilletta 2009). Urban environments offer significant thermal heterogeneity, which creates a diversity of thermal niches that animals can exploit on a species- or season-specific basis to facilitate thermoregulation (Hwang et al. 2014; Coutts et al. 2016; Greene and Millward 2017). Temperature influences community interactions, such as competition, in many ant communities (Savolainen and Vepsäläinen 1988; Cerdá et al. 1998; Diamond et al. 2017), and our results in an urban ant community suggest a range of variation in thermal niche overlap across species—from non-overlap (*M. ergatogyna* and *P. imparis*) to significant overlap (*L. occidentale* and *T. immigrans*) (Fig. 3a). Thermoregulatory strategies can be important in biological invasions (e.g., Duyck et al. 2006, 2008), and we demonstrate that the native *P. imparis* is active in significantly cooler temperatures than the invasive *L. humile* (Fig. 3a). Notably, *P. imparis* is one of few ants that can co-exist with *L. humile* in some parts of the invasion range of *L. humile* (Vonshak and Gordon 2015). Thus, thermal niche non-overlap during an invasion may explain both the persistence of some native ants and the success of invasive ants. Our results also demonstrate that  $T_{\text{surface}}$  was affected by season—ants were generally active on warmer surfaces during the summer (Fig. 3a). For example, the lower surface temperatures used by *P. imparis* in the spring may not be available in the summer (Fig. 3a). Two explanations may underlie the effect of season on  $T_{\text{surface}}$  in our study system. First, ants may shift their preferred temperatures with season (as in lizards: reviewed in Clusella-Trullas and Chown 2014) allowing them to maintain an optimal body temperature across seasons. Second, ants' preferred temperatures may not change, but the range of thermal resources in the summer are non-ideal (i.e., too warm) resulting in ants using warmer surfaces than they would prefer (i.e., imprecise thermoregulation). In our system, future work is required to determine which of these explanations best describes the seasonal patterns of behavioral thermoregulation we observed.

To facilitate behavioral thermoregulation, animals may integrate and respond to non-thermal information from their environments. For example, behavioral thermoregulation in lizards requires that they successfully navigate the spatial arrangement of shaded and non-shaded patches representing low- and high-temperature thermal resources (Sears et al. 2016). Shade is a valuable resource in urban environments

given the effect of shade (e.g., due to vegetation or nearby buildings) on local microclimates and in mitigating the urban heat island effect (Swaid 1993; Armson et al. 2012). The thermal benefits of vegetation shade are likely pronounced in hotter, drier cities (Shashua-Bar et al. 2009; Wang et al. 2016), such as Stockton, which is characterized by a hot-summer Mediterranean climate (Köppen). The use of shade by ants in our study was associated with reduced active temperatures ( $T_{\text{surface}}$ ) during the warmest season (Fig. 3a,c; mixed model on summer  $T_{\text{surface}}$  data with shade status as a fixed effect and species as a random effect:  $F_{2,114} = 25.4$ ,  $p < 0.001$ ; mean temperatures on shaded and unshaded surfaces were 25.6°C and 32.0°C, respectively). Specifically, several species (*C. mauritanica*, *L. occidentale*, and *T. immigrans*) were more likely to be found in shade during the summer (Fig. 3c) and this summer shade use was associated with a  $T_{\text{surface}}$  during activity in the summer that was not warmer than other seasons for these species (Fig. 3a). At our site, the hourly  $T_{\text{surface}}$  collected by a surface temperature probe (HOBO U23, Onset Computer Corp., Bourne, MA, USA) during sampling was (mean  $\pm$  s.d.) 24.9  $\pm$  4.7°C, 36.4  $\pm$  5.9°C, and 28.4  $\pm$  3.8°C for spring, summer, and fall, respectively. Thus, using shade in warmer seasons likely allows urban animals to maintain a relatively constant body temperature across seasons that vary significantly in surface temperature. In addition to clarifying the links between vegetation and temperature in cities (e.g., cooling effects of grass versus trees, or small versus large patches of trees: Armson et al. 2012; Jiao et al. 2017), urban ecologists should continue to account for seasonality to comprehensively understand how and why animals use shade patches within the mosaic of the urban landscape.

Urban habitat types (e.g., urban medians, parks, semi-natural areas, and forests) vary in temperature and in the amount of impervious surface and leaf litter, as well as in animal biodiversity (Hwang et al. 2014; Savage et al. 2015; Vonshak and Gordon 2015; Parris 2016). The amount of impervious surface, in particular, has been linked to a reduced abundance of bees, birds, and bats (Dixon 2012; Luck et al. 2013; Geslin et al. 2016). Yet, impervious surfaces may benefit communities of ground-dwelling species with smaller home ranges (e.g., ants) because these surfaces may offer advantages related to locomotion (an energetically costly activity) and thermal biology. For example, arboreal ants run faster on smoother tree surfaces than on rougher surfaces (Yanoviak et al. 2017), and urban ants may similarly improve locomotion by using smoother impervious surfaces rather than rougher non-impervious surfaces. Further, impervious surfaces retain heat longer than non-impervious surfaces, and using impervious surfaces could facilitate more precise thermoregulation (Pincebourde et al. 2016) and/or prolong foraging later into the day. Together, these features may benefit some species and, in turn, facilitate spatiotemporal niche non-overlap in

urban ant communities. In support, impervious surfaces were used differently by our focal species. For example, *L. occidentale*, *M. pharaonis*, and *P. californicus* were never observed on impervious surfaces while over 70% of our observations of *C. mauritanica* were on impervious surfaces (Fig. 3b). We encourage continued work examining how this ubiquitous feature of urban landscapes mediates interspecific variation in resource use (Dixon 2012; Luck et al. 2013; Savage et al. 2015; Geslin et al. 2016).

Animal niches are important for understanding trophic interactions and animals' responses to climate change, and they are often characterized reductively where individual aspects, such as thermal niche (e.g., Sinervo et al. 2010) or nutritional feeding niche (e.g., Behmer 2009), are considered independently. However, the ecological niche is multidimensional (Chase and Leibold 2003) and, thus, ecologists should characterize comprehensive niches that span several biotic and abiotic factors (Kearney et al. 2010). Here, we integrate nutritional, thermal, and spatial niches in an urban ant community (Fig. 1). We demonstrate that species' niche clustering within this integrated framework varied across the active season—thus, seasonality must be considered when characterizing the dynamics of niche differentiation or partitioning. Future work in urban ecosystems should continue to integrate more features of the ecological niche, such as an improved understanding of the nutritional niche (e.g., use of stable isotopes to determine how much of urban animals' diets are reliant on human food waste: Penick et al. 2015, 2016), spatial niche (e.g., use of geographic information mapping to characterize space-use patterns at local, landscape, and regional levels: Parrish and Hepinstall-Cymerman 2012), and thermal niche (e.g., comparative studies linking micro-climate to organismal performance across taxa: Pincebourde et al. 2016).

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