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The role of temperature in competition and persistence of an invaded ant assemblage

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Abstract. 1. To achieve numerical dominance, an ectotherm consumer requires a sizeable abiotic window in which it can forage. Here we explore how one abiotic factor, temperature, provides opportunity and regulates the impact of the invasive red imported fire ant, *Solenopsis invicta*, on an urban ant assemblage.

2. We first quantified *S. invicta*'s ability to outcompete native species by contrasting its foraging biomass to that of its potential competitors. In doing so, we found that *S. invicta* deployed more ant biomass at baits than the estimated whole colony biomass of three of the four co-occurring native species. It did so across *c.* 75% of the hours in a summer day, those hours below its thermal maximum of 49 °C. Higher thermal maxima allowed two native species to avoid encountering workers of *S. invicta*.

3. Exclosure experiments revealed that a third species, *Dorymyrmex flavus*, more similar in body size and thermal tolerance to *S. invicta*, was competitively suppressed by the invasive. Carbon and nitrogen stable isotope analysis suggests that *D. flavus*' persistence is likely due to dietary differences.

4. Although thermal and dietary traits help predict how species coexist in this invaded assemblage, one key to *S. invicta*'s success is likely to be its ability to forage in all but 6 h of a summer's day.

Key words. Fire ant, invasive species, stable isotopes, thermal tolerance, temperature, traits.

Introduction

The composition and relative abundance of species in an assemblage arises in part from the match of their individual abiotic and biotic requirements to environmental availability – their niche (Grinnell, 1917; Elton, 1927; Hutchinson, 1957; Chase & Leibold, 2003). In a warming world, temperature is one factor that regulates where species live and when they are active (Janzen, 1967; Huey & Stevenson, 1979; Adolph & Porter, 1993; Sanders *et al.*, 2007). And although the abiotic environment may fundamentally limit where species can live, alone it does not necessarily determine if certain species live there because both intra- and interspecific interactions can be important factors in structuring communities (Paine, 1969; Tilman, 1977; Schoener, 1983; Parr, 2008; Diamond *et al.*, 2016).

A potential invader whose niche space encompasses an ecosystem's abiotic centre (the suite of common abiotic conditions for a given environment) can achieve numerical dominance and subsequently disrupt community structure through competitive displacement and behavioural dominance (Holway, 1999; Mooney & Cleland, 2001; Simberloff, 2013). However, opportunity for native species may occur on the abiotic periphery. For example, many dominant species are limited more so by abiotic conditions than interspecific interactions (e.g. the amount of soil moisture required by the Argentine ant, *Linepithima humile*; Holway *et al.*, 2002). Thus, if invasive species are limited by extreme physical conditions, a diversity of traits and tolerances is one way that native species can specialize and promote coexistence. Here we explore how differences in functional traits such as thermal tolerance and diet combine to predict biotic interactions in an invaded urban ant assemblage.

Ants are an ideal clade to explore how the abiotic environment and biotic interactions shape the niches of species within an assemblage. Ants are abundant and widespread, with over

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200 introduced species throughout the world – five of which occupy spots on the IUCN's top 100 worst invasive species list (Bertelsmeier *et al.*, 2017). Ant species vary widely in diet (Blüthgen *et al.*, 2003; King, 2016; Roeder & Kaspari, 2017), and species differences in thermal tolerance in the laboratory (Diamond *et al.*, 2012; Baudier *et al.*, 2015; Kaspari *et al.*, 2015; Bishop *et al.*, 2017; Penick *et al.*, 2017) frequently reflect overlap in ant activity in the field (Talbot, 1934; Kaspari, 1993; Cerdá *et al.*, 1998; Bestelmeyer, 2000; Stuble *et al.*, 2013). Yet we know of no studies that have looked at the combined effects of diet and thermal tolerance on the impact of an invasive ant.

The red imported fire ant, *Solenopsis invicta* (hereafter RIFA), is a devastating invasive that dominates disturbed landscapes across the southeastern United States (Porter & Savignano, 1990; Tschinkel, 2006; Resasco *et al.*, 2014). We explore how RIFA impacts an urban ant assemblage by first quantifying its potential power to outcompete native species by contrasting its foraging biomass to that of its potential competitors. Next, we measure how both native and invasive ant species array their foraging activities across a 41 °C range in temperature during a 24-h summer cycle. We use two functional traits – thermal tolerance and body size – to predict the most likely competitor with RIFA. Finally, we use an experimental exclosure to test for competition among these two species and show evidence for dietary divergence using carbon and nitrogen stable isotope values.

Materials and methods

Study site

All samples were collected at the University of Oklahoma Biological Station (hereafter UOBS; OK, U.S.A., 33.88° N, 96.80° W, 204 m a.s.l.) in July and August, a period of peak activity for RIFA in Oklahoma (Vogt *et al.*, 2003). Yearly air temperatures range from −16.1 to 44.4 °C, with a mean annual rainfall of 1027.94 mm (Oklahoma Climatological Survey). Most of the area surrounding the UOBS has been modified into pastures, row crop agriculture, or human residences with disturbed habitats being occupied by the monogyne form of RIFA.

Foraging biomass of fire ant colonies

We estimated the foraging biomass of RIFA colonies across a range of naturally occurring temperatures by baiting twenty nests at four different times of the day (06:00, 12:00, 18:00 and 24:00 hours Central Daylight Time). During each of these time periods and for each colony, we first placed a 3.55 ± 0.05 g piece of Bar-S® hotdog into a 50 ml centrifuge bait tube. We then positioned four of these bait tubes at the cardinal points, 0.5 m from the edge of each RIFA nest, retrieving one vial at 10, 20, 30 and 60 min after the start of each trial. Workers were dried to constant mass at 60 °C for 48 h and weighed to the nearest 0.01 mg using a R 200D electronic semi-microbalance (Sartorius Research, Gottingen, Germany). We report activity per colony as the total dry mass of collected individuals at 06:00, 12:00, 18:00 and 24:00 hours. Surface temperature was recorded every minute, and then averaged per hour, at the top of each RIFA nest using HOBO temperature loggers for 2 days (Onset Computer Corporation, Bourne, MA, U.S.A.).

Temperature as a structuring mechanism of ant assemblages

In late July/early August, we tested how temperature regulated the activity patterns of ants during a daily cycle in two ways. First, we set out 100 1.5-ml micro centrifuge vials (VWR International, Radnor, PA, USA) filled with cotton that was saturated with a 10% sucrose solution. Vials were evenly distributed along five 40-m transects that were spaced 40 m apart. This was done 24 times over a 3-week period on the lawn of the UOBS. Each temporal replicate represented a different hour of the day with sampling periods spaced at least 12 h apart. We recorded activity by counting the number of vials that were occupied by ants after a 1 h period. Individuals were then identified to species to quantify foraging activity, as a proportion of the total number of vials, for both invasive and native ants. Surface temperature was recorded every 5 min, and then averaged per hour, for each sampling period using a HOBO temperature logger for 20 days (Onset Computer Corporation).

Second, we located five colonies for all collected species to test if thermal tolerance was a mechanism behind the observed foraging patterns. For each colony, we performed thermal tolerance assays on five individual workers within 2 h of collection to see when individuals lost muscle control and reached their critical thermal maximum, or $CT_{\max}$. Assays were conducted by first placing an individual into a 1.5-ml micro centrifuge tube that had been modified with modelling clay to remove a potential thermal refuge in the cap (as in Bujan *et al.*, 2016). Vials were than randomly placed into a Thermal-Lok two-position dry heat bath (USA Scientific, Orlando, FL, U.S.A.; advertised accuracy ± 0.2 °C) that was prewarmed to 36 °C. Three additional vials per colony were kept at ambient temperature during thermal assays as a control, all of which survived. Every 10 min, individuals were checked to see if they had reached their $CT_{\max}$ by rotating the tubes and looking for a righting response (as in Diamond *et al.*, 2012). The dry bath temperature was then increased by 2 °C and this process was repeated until all ants had reached their $CT_{\max}$. For each run, the interior temperature of one unused vial was confirmed using a thermocouple attached to an Extech MN35 Digital Mini MultiMeter (Extech Instruments, Waltham, MA, U.S.A.). Ants were then dried to constant mass at 60 °C for 48 h and weighed to the nearest 0.001 mg on a Cahn microbalance (Cahn Instruments, Cerritos, CA, U.S.A.).

Competitive interactions between invasive and native ant species

The $CT_{\max}$ of each individual was plotted against that ant's dry mass as species which overlap in trait space may be more likely to compete for resources. For the two species with the largest trait overlap, we set up 20 exclosure/20 nonexclosure replicates (i.e. a total of 40 colonies for each species were used) on the lawn of the UOBS to test if the observed activity patterns were in part driven by competitive interactions. For each exclosure, we modified a Sterilite® plastic container (height = 177.8 mm, width = 361.95 mm, length = 444.5 mm) by removing the bottom, then positioning the container around an ant's nest. Four tent stakes were placed near the outside corners of the container and then connected, diagonally, with bungie cords to apply downward pressure to keep the container flush with the ground. As an additional measure of control, a light coat of Johnson's® baby powder was applied at the bottom of the container to prevent exterior ants from entering. When the temperature stabilized at 25 °C, a single 1.5-ml micro centrifuge vial filled with cotton that was saturated with a 10% sucrose solution was placed 5 cm away from each nest entrance in a random direction. After 1 h vials were collected and the species inside were recorded. We predict that if RIFA is competitively suppressing native species, it will occupy baits both near their own nests and near the nests of the co-occurring native species. However, by restricting RIFA foraging with exclosures, we posit that native ants will forage on the provided resource given the opportunity.

We used carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) stable isotope analyses for 10 colonies per species to determine if the competing species were consuming similar dietary resources. Individuals were collected directly from nests before any bait studies were performed, and then frozen at −20 °C. The petiole, post-petiole and gaster were removed to eliminate any residual food particles that could alter the isotopic signature (Tillberg *et al.*, 2006). Each replicate consisted of five homogenized workers with the same head width to attain the minimum weight required for analysis. As RIFA has a polymorphic worker caste, we used individuals that had 0.7 mm head widths to reduce isotopic variation from body size (Roeder & Kaspari, 2017). Delta values (δ) were calculated as:

$$\delta = \left(\left(\frac{R_{\text{sample}}}{R_{\text{standard}}}\right) - 1\right) * 1000$$

where δ, reported in per mil notation (‰), represents the ratio of heavy to light isotopes within a sample (R_{sample}) relative to the ratio in an international standard (R_{standard}). Ants were dried to constant mass at 60 °C for 48 h and weighed to the nearest 0.001 mg on a Cahn microbalance (Cahn Instruments). All stable isotope analyses were performed at the University of California Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, U.K.).

Statistical analysis.

All analyses were run in R, ve3.3.0. A GLMM with colony identity as a random factor was used to compare differences in the biomass of ants foraging across different time periods. Beta regression was used to compare ant activity, as a continuous proportion, to surface temperature. A GLMM with colony identity as a random factor was also used to compare $CT_{\max}$ and body size values, with Tukey post-hoc comparisons used to test for differences among species. Standard ellipse areas corrected for small sample size (SEA_c) were calculated to determine if species overlapped in trait space in the R package 'SIBER' (Jackson *et al.*, 2011). GLMs with binomial distributions were used to compare occupation (i.e. presence/absence) of baits near colonies with and without exclosures. MANOVA was used to calculate isotopic differences between the two competing species, and SEA_cs were calculated to determine the extent of overlap in $\delta^{13}C$–$\delta^{15}N$ bi-plot space.

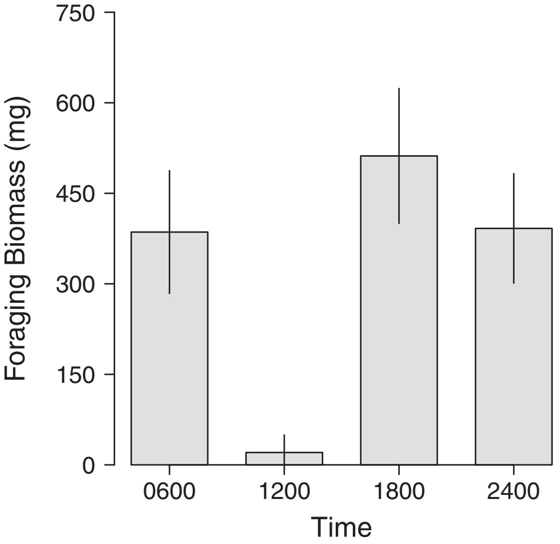

Fig. 1. Temporal differences in mean foraging biomass (±SE) of 20 red imported fire ant colonies (*Solenopsis invicta*; RIFA) across four different times of day on the University of Oklahoma Biological Station lawn.

Results

Foraging biomass of fire ant colonies

Temperature at different times of day regulated the foraging biomass of RIFA (GLMM: $F = 40.77$, d.f. = 3, $P < 0.001$; Fig. 1) with random effects suggesting individual colonies vary up to 160.1 mg (=1SD) higher or lower than the group average around 68% of the time. At the coolest temperatures – 24.10 °C (06:00) and 27.37 °C (24:00) – colonies on average allocated 391.84 and 385.74 mg of biomass, respectively, towards baits. This investment level increased by *c.* 32% (511.92 mg) at 18:00 hours when temperatures increased to 44.05 °C. At 12:00 hours, however, high surface temperatures (48.43 °C) were associated with a significantly lower foraging biomass per colony ($\bar{x} = 20.52$ mg).

Temperature as a structuring mechanism of ant assemblages

Over a normal summer day at the UOBS, surface temperature ranged from 20.2 to 61.0 °C (Fig. 2a). Total ant activity declined with increasing temperature (beta regression: estimate = −0.117, pseudo $r^2 = 0.77$, $P < 0.001$), but this result

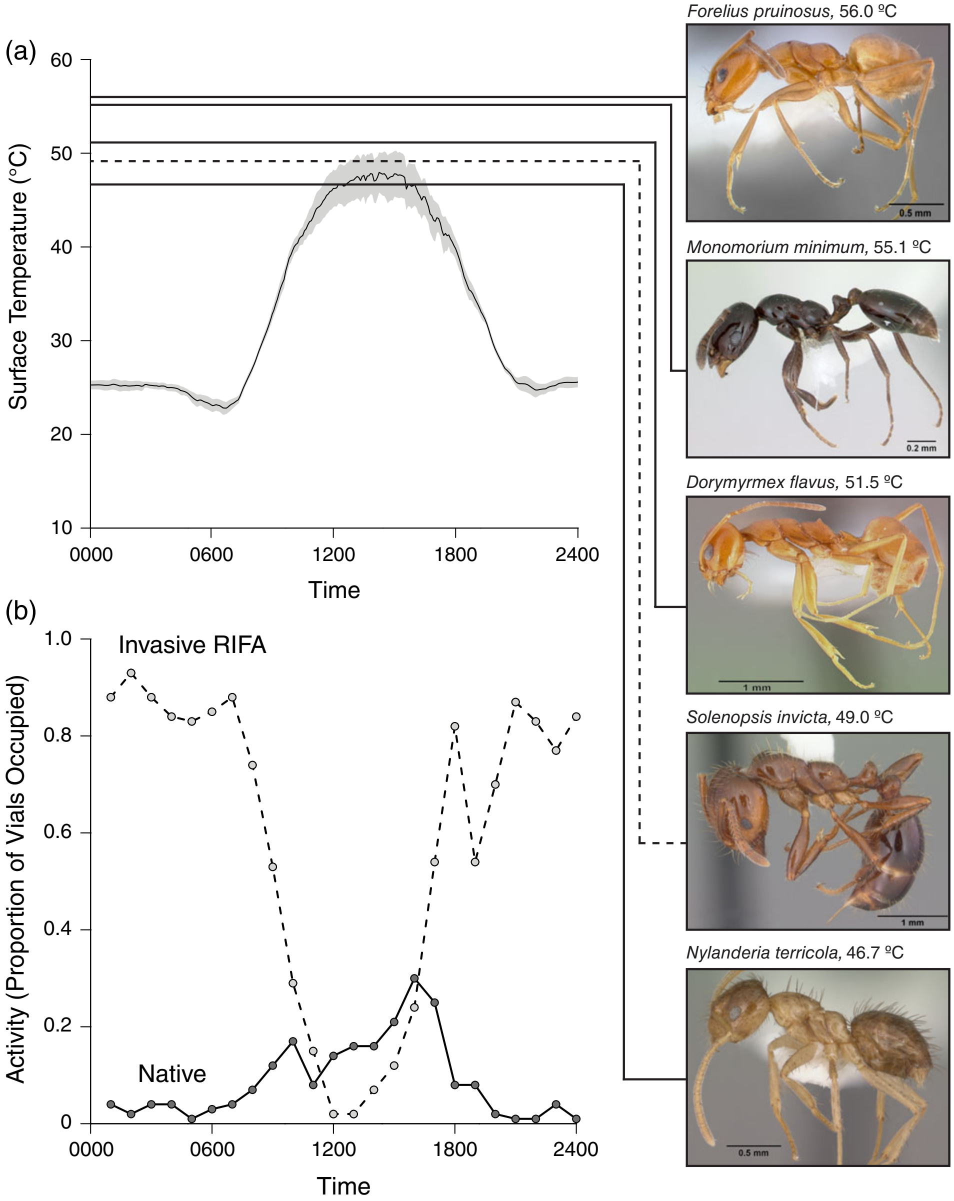

Fig. 2. Temperature, thermal tolerance and activity of ant species during a daily cycle on the University of Oklahoma Biological Station lawn. Panel (a) represents the average surface temperature and 95% confidence interval (black line with grey polygon, respectively) recorded from 20 days in July and August. Horizontal lines represent the critical thermal maximum for each species collected at the location. Panel (b) shows the proportion of 10% sucrose baits occupied by either invasive red imported fire ants (*Solenopsis invicta*; RIFA) or native ants across time. Native species are represented by dark grey (–) lines, whereas invasive RIFA are represented by light grey (---) lines. Ant images were taken by April Noble and Jen Fogarty from www.AntWeb.org. [Colour figure can be viewed at wileyonlinelibrary.com].

was driven by a reduction in the foraging activity of the invasive and abundant RIFA (beta regression: estimate = −0.158, pseudo $r^2 = 0.84$, $P < 0.001$; Fig. 2b). In contrast, activity of native ant species increased with temperature (beta regression: estimate = 0.085, pseudo $r^2 = 0.74$, $P < 0.001$; Fig. 2b) due to the presence of three thermophilic species: *Dorymyrmex flavus*, *Forelius pruinosus* and *Monomorium minimum*. The lone outlier, *Nylanderia terricola,* was collected in <1% of vials, generally at night or early morning and never at temperatures above 30 °C.

Ants in this assemblage differed in thermal tolerance and body size

Of the five ant species found on the lawn of the UOBS, most had different $CT_{\max}$ values (GLMM: $F = 146.24$, d.f. = 4, $P < 0.001$; Fig. 2a) and three of the four native species had higher $CT_{\max}$ values than RIFA (Table 1). Only two species, *F. pruinosus* and *M. minimum,* had similar thermal tolerance values (Table 1). These ants also differed by up to an order

Table 1. Traits of workers and colonies for the five ant species found on the lawn of the University of Oklahoma Biological Station.

Species	$CT_{\max}$ (°C)	Worker mass (mg)	Estimated workers per colony	Estimated biomass per colony (mg)	Colony size reference
Solenopsis invicta	49.0 ± 0.4c	0.237 ± 0.020a	~220 000	52140	Tschinkel (1988)
Forelius pruinosus	56.0 ± 0.3a	0.099 ± 0.004b	~100 000	9900	Kaspari & Valone (2002)
Monomorium minimum	55.1 ± 0.2a	0.047 ± 0.002c	~3000	141	Van Pelt (1958)
Dorymyrmex flavus	51.5 ± 0.5b	0.216 ± 0.012a	~1000	216	Kaspari & Valone (2002)
Nylanderia terricola	46.7 ± 0.2d	0.078 ± 0.004bc	~300	23	Smith (1965)

Worker mass and critical thermal maximum, $CT_{\max}$, are reported as means ± SE with letters indicating significant differences between species from Tukey post-hoc tests ($P < 0.05$). Colony sizes are estimated from the listed reference. Biomass is calculated by multiplying the mean worker mass by the estimated number of workers per colony.

of magnitude in body size from the low 0.047 ± 0.002 mg of *M. minimum* to 0.237 ± 0.020 mg of RIFA (GLMM: $F = 64.70$, d.f. = 4, $P < 0.001$; Table 1).

Competitive interactions between invasive and native ant species

When the $CT_{\max}$ of each individual was plotted against that ant's dry mass, only 10.6% of all ellipse area overlapped in trait space (Fig. S1). This overlap occurred between two species, RIFA and *D. flavus*. Therefore, we examined these two species for competitive interactions by testing bait occupation near nests, with and without exclosures. Exclosures did not reduce RIFA foraging near their own nests (GLM: $\chi^2 = 0.37$, df = 1, $P = 0.545$; Fig. 3a), and RIFA occupied both a similar number of baits and the majority of baits near their nests (95%) and near *D. flavus* nests (80%) when exclosures were not present (GLM: $\chi^2 = 2.18$, df = 1, $P = 0.139$). When *D. flavus* nests were enclosed, their occupation rate of baits increased from 20% to 85% (GLM: $\chi^2 = 18.43$, df = 1, $P < 0.001$; Fig. 3a), and the number of baits occupied by RIFA decreased from 80% to 5% (GLM: $\chi^2 = 26.59$, df = 1, $P < 0.001$).

Stable isotope values revealed dietary differences between RIFA and *D. flavus* (MANOVA: Pillai's Trace = 0.392, $F_{2,17} = 5.48$, $P = 0.015$; Fig. 3b), with only 5.93% standard ellipse overlap despite both species occupying a similar amount of total area in $\delta^{13}C$–$\delta^{15}N$ bi-plot space (SEA$_c$: RIFA = 3.99‰^{2}; *D. flavus* = 3.42‰^{2}; Fig. 3b). For carbon, both species spanned the continuum of C_3 to C_4 plants ($\delta^{13}C_{\text{RIFA}} = -26.2‰$ to $-18.0‰$; $\delta^{13}C_{D.\ flavus} = -22.4‰$ to $-15.8‰$) and did not differ (ANOVA: $F_{1,18} = 4.32$, $P = 0.052$), although $\delta^{15}N$ values between the species did vary (ANOVA: $F_{1,18} = 11.57$, $P = 0.003$) and ranged from 7.93‰ to 9.91‰ in RIFA and 9.28‰ to 10.94‰ in *D. flavus*.

Discussion

Here we show how the abiotic environment and biotic interactions regulate coexistence of species in an invaded urban ant assemblage. Traits such as thermal tolerance and body size combine to shape a species' niche which, in turn, affects the activity patterns of invasive and native ants over a wide range of conditions. RIFA used its immense workforce to competitively suppress the native species, *D. flavus*, whose thermal tolerance and body size were most similar on baits. However, stable isotope analysis suggests that *D. flavus*' persistence is likely due to dietary differences. Combined, we suggest that using multiple components of species' niches – including morphology, physiology, behaviour and nutrition – will provide a more complete picture of how native and invasive species are able to coexist in similar environments.

Temperature as a structuring mechanism

Throughout large portions of the southern United States, the five species we observed at the UOBS commonly occur and overlap in their distribution (Guénard *et al.*, 2017). Most of these species excel in disturbed landscapes and are opportunistic, perhaps allowing them to monopolize an increasingly common habitat – lawns. Urban areas continue to expand, and in doing so create heat islands which present novel thermal environments to both native and invasive species (Oke, 1982; Angilletta Jr *et al.*, 2007). As urban temperatures may reach levels higher than the thermal limits of species, this turnover in habitat may result in a lower diversity of taxa (McKinney, 2006). For example, a summer daily cycle on the lawn of the UOBS occurs over a 41 °C range – a range that is likely problematic for some tiny ground-dwelling ectotherms, and opportunistic for others. Yet in a forest patch a mere 200 m to the west of the UOBS lawn, tall elms and oaks shade an environment that not only peaks at 11 °C lower than the lawn, but also harbours almost three times the number of ant species in a similar-sized area (Table S1).

Competition and coexistence

We originally predicted that species in this urban locale should have little overlap in traits such as thermal tolerance to reduce biotic interactions during a daily cycle. Our data suggest that when compared to RIFA, this is the case for three of the four native ant species (Table 1). However, the one native species that had similar traits, *D. flavus*, was dominated at sucrose baits both near and far away from their nest. One way in which RIFA could accomplish this feat was their immense workforce, as colonies were able to mobilize an incredible amount of biomass; an amount that on average was larger than the estimated colony biomass for three of the four native species on the lawn (Table 1).

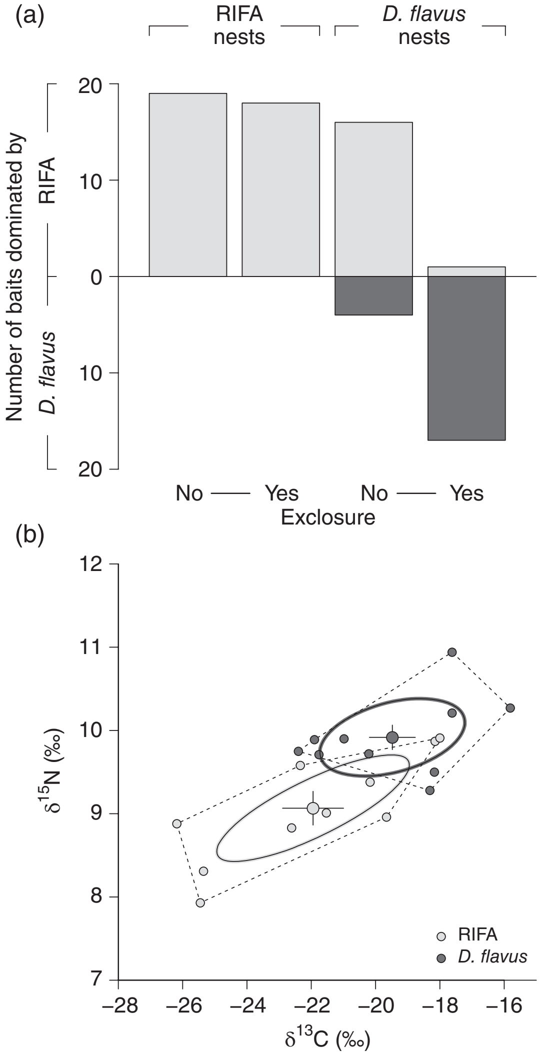

Fig. 3. Competitive interactions and dietary differences between invasive red imported fire ants (*Solenopsis invicta*; RIFA; light grey) and the native *Dorymyrmex flavus* (dark grey). Panel (a) shows the number of 10% sucrose baits, out of 20, occupied by either species (above the midline = RIFA, below = *D. flavus*) near nests with or without exclosures. Panel (b) shows the mean ± SE and spread of nitrogen and carbon stable isotope values from 10 colonies of each species. Convex hulls connect the outermost points and are denoted by --- lines, whereas maximum-likelihood standard ellipses are denoted by – lines and contain approximately 40% of the points.

Yet for RIFA this level of investment is miniscule, an amount equal to less than 1% of an average colony's mass and likely an underestimate of a colony's foraging workforce. Despite these competitive outcomes, *D. flavus* persists in this environment, perhaps due to a third niche axis – nutrition.

A nutritional way forward with niches

In homogeneous environments such as lawns, nutrients may be controlled by dominant species or individuals. It has been hypothesized that carbohydrate resources in particular are important for fuelling activity and producing workers, especially for the large colonies that invasive ant species typically maintain (Lach, 2005; Tillberg *et al.*, 2007; Wilder *et al.*, 2011; Wills *et al.*, 2015). Moreover, carbohydrate-rich honeydew from fluid-feeding hemipteran is a prime resource over which ant colonies often compete (Blüthgen *et al.*, 2004; Wilder *et al.*, 2013) and is only slightly enriched in δ^{15}N compared to the plant from which it was produced (Sagers & Goggin, 2007). When dominant ants monopolize such resources, as we hypothesize colonies of RIFA do at our study site, isotopically they appear as cryptic herbivores (Davidson *et al.*, 2003; Roeder & Kaspari, 2017). In contrast, less dominant ants such as *D. flavus* are often competitively displaced from these carbohydrate resources (Wilder *et al.*, 2013).

Despite displacement, energy can be obtained by catabolizing protein or consuming the lipids of insect prey (Slansky & Rodriguez, 1987). Thus, increased consumption of nitrogen-rich arthropods, either through predation or scavenging, may lead to enriched δ^{15}N values – a result we observed in the *D. flavus* at the UOBS. Dietary divergence, revealed through natural variation in stable isotope values, may not only reveal the outcome of past competitive interactions between species, but also may be important for understanding how species that are similar morphologically or physiologically are able to coexist.

Conclusions

Numerous studies have quantified (i) how the abiotic environment affects ant species (Porter & Tschinkel, 1987; Kaspari, 1993; Cerdá *et al.*, 1998; Bestelmeyer, 2000; Holway *et al.*, 2002; Vogt *et al.*, 2003; Lessard *et al.*, 2009; Wittman *et al.*, 2010; Stuble *et al.*, 2013), or (ii) the biotic interactions between invasive and native ant species (Porter & Savignano, 1990; Human & Gordon 1996; Suarez *et al.*, 1998; Holway, 1999; Sanders *et al.*, 2003; LeBrun *et al.*, 2012; Resasco *et al.*, 2014). Our work builds on this body of knowledge by focusing on trait-based niche differences towards a better understanding of how species coexist in a shared habitat. Given that urbanization and habitat modification continue to create environments on which invasive species excel (Shochat *et al.*, 2010), our findings suggest future outcomes for areas currently under development. Furthermore, if nutrition is the missing link for trait-based studies, then simply quantifying differences is not enough. Instead, focus should be placed on the biological mechanisms underlying those nutritional sources that are facilitating the persistence of invasive species such as RIFA in novel environments.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of ant species from a 30 × 30 m plot in lawn and forest habitat of the University of Oklahoma Biological Station. Individuals were collected off cricket baits ($n = 16$) spaced 10 m apart, and by hand-collecting in each habitat for 90 min. x indicates presence and – indicates absence.

Figure S1. Critical thermal maximum and body size (i.e. dry mass) differences across the five ant species on the lawn of the University of Oklahoma Biological Station. For each species, convex hulls connect the outermost points and are denoted by --- lines, whereas maximum-likelihood standard ellipses are denoted by – lines and contain approximately 40% of the points.

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