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Introduced fire ants can exclude native ants from critical mutualist-provided resources

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Abstract Animals frequently experience resource imbalances in nature. For ants, one resource that may be particularly valuable for both introduced and native species is high-carbohydrate honeydew from hemipteran mutualists. We conducted field and laboratory experiments: (1) to test if red imported fire ants (*Solenopsis invicta*) competed with native ants for access to mutualisms with aphids, and (2) to quantify the effects of aphid honeydew presence or absence on colony growth of native ants. We focused on native dolichoderine ants (Formicidae, Dolichoderinae) because they are abundant ants that have omnivorous diets that frequently include mutualist-provided carbohydrates. At two sites in the southeastern US, native dolichoderine ants were far less frequent, and fire ants more frequent, at carbohydrate baits than would be expected based on their frequency in pitfall traps. A field experiment confirmed that a native ant species, *Dorymyrmex bureni*, was only found tending aphids when populations of *S. invicta* were suppressed. In the laboratory, colonies of native dolichoderine ants with access to both honeydew and insect prey had twice as many workers and over twice as much brood compared to colonies fed only ad libitum insect prey. Our results provide the first experimental evidence that introduced ants compete for access to mutualist-provided carbohydrates with native ants and that these carbohydrates represent critical resources for both introduced and native ants. These results challenge traditional paradigms of arthropod and ant nutrition and contribute to growing evidence of the importance of nutrition in mediating ecological interactions.

Keywords *Solenopsis invicta* · Dolichoderinae · Mutualism · Invasive species · Honeydew

Introduction

Resource imbalances are commonly experienced by animals in nature. The relative amount of nutrients found in food items often does not match the balance of nutrients required by animals to achieve maximum fitness (Sterner and Elser 2002; Simpson and Raubenheimer 2012). As a consequence, animals often need to balance their diets between multiple different but complementary resources (Simpson and Raubenheimer 2012). For example, facultatively mutualistic ants must balance their diet between

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high-carbohydrate honeydew or nectar and high-protein insect prey (Pontin 1978; Way 1963; Davidson 1997; Stadler and Dixon 2005). When given free choice of carbohydrates and protein, ants will regulate their intake of each nutrient to specific levels depending upon the number of workers and brood in the nest (Dussutour and Simpson 2008, 2009). However, in nature, animals often do not have free choice of resources. Particular resources may be spatially or temporally variable due to seasonality or competition and animals may need to adjust their diet, if possible, to compensate for dietary deficiencies (Simpson et al. 2004; Fanson et al. 2012; Simpson and Raubenheimer 2012).

Mutualisms and mutualist-provided resources appear particularly important for diet regulation and colony growth of invasive ants (Lach et al. 2010). Carbohydrate rewards from mutualists can increase the success of introduced ants and exacerbate their effects on native arthropods (Macom and Porter 1995; Eubanks 2001; Grover et al. 2007; Savage et al. 2009, 2011; Wilder et al. 2011a, b). Introduced ants often engage in mutualisms with honeydew-producing hemipterans and plants with extrafloral nectaries in their introduced ranges (Beggs 2001; Helms and Vinson 2002; Holway et al. 2002; Wilder et al. 2011a). However, it remains unclear how the exploitation of mutualisms by invasive ant species impacts native ants that may rely on these same mutualisms for colony growth and survival. For example, no study has experimentally tested whether introduced ants compete with native ants for access to mutualisms. Furthermore, even if there is competition for these specific resources, the potential consequences of the loss of mutualist-provided carbohydrates for native ants are hypothesized to be relatively unimportant because, as long as insect prey are available, energy from carbohydrates is thought to be easily substituted by energy from insect prey, including energy-dense lipid and catabolism of protein for energy (Slansky and Rodriguez 1987; Wilder and Eubanks 2010).

More generally, honeydew and other sources of liquid carbohydrates (e.g., nectar and extrafloral nectar) from mutualist hemipteran and plant partners have long been hypothesized to be important energy resources for ants and other arthropods (Stadler and Dixon 2005; Wäckers et al. 2005). The benefits to ants of consuming liquid carbohydrates have been investigated in many studies. Yet, nearly all of these studies have focused on how consumption of carbohydrates affects the behavior of worker ants, including activity, aggression, and foraging for other food sources (Davidson 1997; Stadler and Dixon 2005; Grover et al. 2007; Kay et al. 2010). Few studies have examined other potential fitness benefits such as increased worker or brood production (Grover et al. 2007; Helms and Vinson 2008; Wilder et al. 2011b). This focus was based on the hypothesis that carbohydrates are primarily used as fuel for activity and that protein is the primary nutrient limiting the growth of brood (Davidson 1997). However, studies of two invasive ant species have shown that, even when insect prey are available ad libitum, the addition of honeydew (Helms and Vinson 2008; Wilder et al. 2011b) or liquid carbohydrates (Grover et al. 2007) results in substantial increases in both worker and brood number in colonies. It is unclear if the non-substitutability of honeydew and nutrients in insect prey (i.e., lipid and protein) for ant colony growth is specific to these two invasive ants or occurs in a wider range of species. Demonstrating that honeydew, specifically, increases colony growth, even when other nutrients (i.e., lipid and protein in insect tissues) are available ad libitum for other ant species, would more generally challenge the longstanding paradigms that protein is the primary nutrient limiting brood production and that dietary nutrients are easily substitutable.

We examined competition for mutualist-provided resources between introduced red imported fire ants (*Solenopsis invicta*) and native ants and the potential consequences of this competition for the colony growth of native ants. The first goal of this study was to test if native and introduced ants compete over access to mutualist-provided carbohydrate resources. While numerous studies have examined competition between introduced ants and native ants, no study has tested if introduced ants compete with or exclude native ants from mutualist-provided resources. The second goal of the study was to test if the presence of mutualist-provided carbohydrates would affect colony growth of native ants when insect prey are provided ad libitum. Presumably, the nutrients found in insect prey, especially lipid, should be able to compensate for any loss of energy from carbohydrates. Native ants from the subfamily Dolichoderinae (*Dorymyrmex bureni*, *Forelius mccooki* and *F. pruinosus*) were chosen for this research because they are dominant members of many ant communities and exhibit omnivorous diets (Andersen 1997; Blüthgen et al. 2003; Davidson et al. 2003). Moreover, unlike some other native ants, dolichoderine ant nests are rarely raided by red imported fire ants and often exist in close proximity to fire ant nests in the field (Calixto et al. 2007a, b). Yet, the abundances of dolichoderine ants are lower in areas with fire ants and these ants increase in abundance when fire ants are removed (Calixto et al. 2007a, b). Competition for mutualist-provided carbohydrate resources is a potential explanation for this pattern because both native dolichoderine ants and introduced populations of fire ants frequently consume liquid carbohydrates in nature (Holway et al. 2002; Calixto et al. 2007b).

Materials and methods

Recruitment to carbohydrate baits in the field

At two widely separated sites, we conducted surveys to compare the frequency with which *S. invicta* and several common native ant species were found at carbohydrate baits and in pitfall traps. The null expectation was that ants should be found at comparable frequencies at baits and in pitfall traps, which provide a relative estimate of ant activity. This study was conducted in Lick Creek Park in College Station, Texas, USA, in May 2008 and Tuskegee National Forest near Auburn, Alabama, USA, in June 2008.

At each site, we placed a transect of pitfall trap stations (Texas, $n = 50$; Alabama, $n = 40$). At each station we placed three pitfall traps (vials with a 2.5 cm diameter) in a triangle with each trap located 1.5 m from the center of the triangle. We opened traps 12 h after pitfall installation to minimize any effects of soil disturbance on pitfall trap captures and added propylene glycol to a depth of 3 cm inside each trap. We collected vials after 24 h and then combined the contents of the three traps at each station into one sample.

Two hours after collecting pitfall traps, we placed a transect of carbohydrate baits (Texas, $n = 25$; Alabama, $n = 19$) haphazardly within 10 m of the pitfall transect. Each bait consisted of half a 15-mL centrifuge tube filled with 10–20 % sucrose solution by volume and plugged with cotton. Baits were placed on the ground between 0800 and 1000 hours. We identified the ants foraging at each bait after 1 h (morning), 6 h (afternoon), and 24 h (next morning).

We used Chi-square goodness of fit tests to compare the frequency of occurrence of *S. invicta* and common native ants from the subfamily Dolichoderinae (Texas: *D. bureni* and *F. pruinosus*; Alabama: *F. mccooki*) in pitfall traps and at carbohydrate baits. Ants frequently co-occurred in pitfall traps but never co-occurred at carbohydrate baits. To calculate the expected frequency of ants at baits using data from pitfall captures, we added the total number of pitfall traps in which each species was found and divided this by the number of species captured in that transect. For the expected frequencies, we only used data on occurrences of *S. invicta* and the dolichoderine ants of interest. For example, if there were two species of ants and both species were found in all of the pitfall traps, then we would expect each species to be found at 50 % of the baits. We calculated the observed frequency for the Chi-square test as the proportion of baits at which each species was present. All statistical analyses were conducted in SAS 9.2 (SAS Institute, Cary, NC, USA).

Effects of *S. invicta* suppression on aphid tending

This experiment was conducted at Tuskegee National Forest near Auburn, Alabama. We established six plots measuring 6 × 6 m that were separated by a minimum of 100 m. In each corner of each plot, we placed one cotton plant with aphids and another cotton plant without cotton aphids (*Aphis gossypii*) 1 m apart. Cotton plants without aphids were included as a control to ensure that the presence of ants on plants was specifically due to the presence of aphids and not some other aspect of the plants such as exploration of a new area, foraging for insect prey, or use of a more shaded microhabitat. Cotton plants (*Gossypium hirsutum*) were grown from seed in a greenhouse and selected for the experiments when they were ca. 1 m tall. Plants were randomly assigned to one of two treatments: aphids present or aphids absent. Plants with aphids present were inoculated with ca. 300 cotton aphids, a density commonly encountered in the field (Eubanks 2001). Aphids were selected from a greenhouse colony and allowed to acclimate to plants for 48 h before being transported to the field. In the field plots, plastic pots containing cotton plants were placed in holes such that the rim of the pot was level with the soil and the spaces surrounding each pot were filled with soil. For the following 2 days, the upper and lower leaves were visually searched for ants at 0800, 0930, and 1100 hours and the numbers of *S. invicta* and *D. bureni* workers present were recorded. We used these count data to calculate an average number of workers of each ant species on each plant.

We randomly selected three of the six plots for *S. invicta* suppression. We suppressed *S. invicta* by killing colonies with boiling water (Tschinkel 2006; LeBrun et al. 2007). Colonies of *S. invicta* were removed from within the 6 × 6 m plots and also from within a 24-m wide buffer zone around each plot. We then placed two new cotton plants in each corner of each plot (one with aphids and another without aphids) and counted the number of workers of *S. invicta* and *D. bureni* present at 0800, 0930, and 1100 hours for 2 days. We then calculated the average number of ants on each plant. New cotton plants were used so that we could control the number of aphids on plants and to avoid any effect of residual chemical cues from ant foraging trails. To summarize, for the control plots ($n = 3$), we had data on average ant abundance on plants at time 1 and time 2, and for the *S. invicta* suppression plots ($n = 3$), we had data on average ant abundance at time 1 (before suppression) and time 2 (after suppression).

A two-factor, split-plot, repeated-measures analysis of variance (ANOVA) was used to test the effects of time, plot treatment (*S. invicta* suppression or control), and plant treatment (aphids or no aphids) on the total number of ants on cotton plants. Separate repeated-measures ANOVAs were conducted on the abundance of *S. invicta* and *D. bureni*.

Effects of aphid honeydew on colony growth

Colonies of *F. pruinosus, D. bureni* and polygyne *S. invicta* were excavated from the campus of Texas A&M University (College Station, Brazos County, Texas, USA) in the summer of 2009. We were able to collect sufficient numbers of queen-right colonies of *S. invicta* and of *F. pruinosus*. However, while *D. bureni* colonies were abundant in the field, queens were rarely found in excavated colonies of this species; this limitation resulted in small sample sizes for this species.

Ants were separated from the soil and used to make standardized experimental colonies (*S. invicta*: 1–20 queens, 50 brood and 1 g wet mass of workers; *F. pruinosus*: 1 queen, 50 brood and 0.5 g wet mass of workers; *D. bureni*: 1 queen, 50 brood and 0.25 g wet mass of workers). While queen number is unrelated to *S. invicta* colony growth in the laboratory (Wilder et al. 2011b), we varied the number of queens present in *S. invicta* colonies in the laboratory because queen number varies widely for polygyne colonies in nature (Tschinkel 2006). The mass of workers added to laboratory colonies of each species was related to their relative colony sizes in the field (*S. invicta* > *F. pruinosus* > *D. bureni*). Each colony from the field was used to make an experimental colony that represented a single replicate. Colonies were housed in containers (56 cm length × 40 cm width × 14 cm height) lined with fluon to prevent ants from escaping. Each container housed two pots, each of which was filled with potting soil and held two cotton plants with 4–6 true leaves. Pots were watered twice a week and cotton plants were replaced when they exceeded 45 cm in height. For the aphid treatment (*S. invicta* $n = 27$, *F. pruinosus* $n = 13$, *D. bureni* $n = 5$), we added cotton aphids, *Aphis gossypii*, onto plants and allowed aggregations to become established. For the control group (*S. invicta* $n = 24$, *F. pruinosus* $n = 13$, *D. bureni* $n = 3$), we kept plants free of aphids by searching them twice a week and manually killing any aphids found. Each colony was provided with two freshly-killed crickets (*Acheta domesticus*) three times per week; this level of feeding was ad libitum prey for colonies used in these experiments. The colony room was maintained on a 12:12 h light:dark photoperiod with 40–70 % humidity and a daily temperature cycle that included 8 h during daylight at 32 °C and 16 h at 24 °C. Colonies were maintained in the laboratory for 60 days after which time they were frozen. We then separated and counted the final number of workers and brood present in each colony. We used a two-factor multivariate analysis of variance (MANOVA) to compare the effects of ant species and aphid treatment on final colony size (multivariate responses: final number of workers and brood in ant colonies). We then conducted *t* tests to examine the effect of aphid presence on each response (final worker and brood) for each species to clarify the nature of significant multivariate effects.

Results

Recruitment to carbohydrate baits in the field

In Tuskegee National Forest, both *F. mccooki* and *S. invicta* were captured in nearly all the pitfall traps. After 1 h, the frequency of ants at baits was not significantly different from the pattern in pitfall traps ($\chi^2_1 = 2.81$, $p = 0.09$). However, in the afternoon and following morning, fire ants dominated a majority of carbohydrate baits, and relatively few baits were controlled by *F. mccooki* (afternoon: $\chi^2_1 = 4.31$, $p = 0.04$; morning after 24 h: $\chi^2_1 = 7.55$, $p = 0.006$; Fig. 1a). After 24 h, 79 % of baits were controlled by *S. invicta* while only 11 % of baits were controlled by *F. mccooki* (Fig. 1a).

A qualitatively similar pattern was observed in College Station. There was no significant difference between the frequency of ants in pitfalls and at baits after 1 h ($\chi^2_1 = 2.15$, $p = 0.34$) or 6 h ($\chi^2_1 = 2.85$, $p = 0.24$). However, after 24 h, *S. invicta* dominated 100 % of carbohydrate baits, which was a significantly higher frequency than expected based on the relative prevalence of fire ants and dolichoderine ants in pitfall traps ($\chi^2_1 = 6.65$, $p = 0.04$; Fig. 1b).

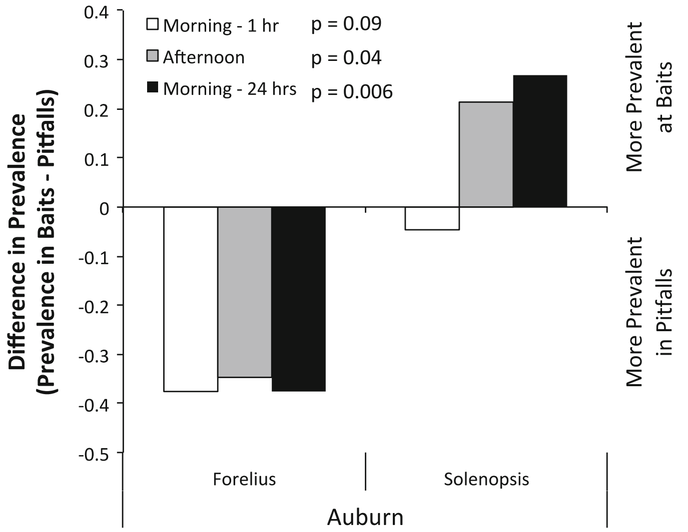
Effects of *S. invicta* suppression on aphid tending

The repeated-measures analysis indicated that the patterns of *S. invicta* abundance on plants in control and suppression plots changed before and after *S. invicta* suppression (Fig. 2; time × suppression × aphids; $F_{1,42} = 4.64$, $p = 0.037$). Before the suppression treatment, there were significantly more *S. invicta* on plants with aphids ($F_{1,42} = 3.98$, $p = 0.05$), but no overall differences between control and suppression plots in the numbers of *S. invicta* ($F_{1,2} = 0.60$, $p = 0.52$). After the suppression of *S. invicta* in the suppression plots, there were virtually no *S. invicta* in these plots, but there were still significant numbers of ants on plants with aphids in the control plots, in which *S. invicta* had not been suppressed (suppression × aphids: $F_{1,42} = 17.1$, $p < 0.001$).

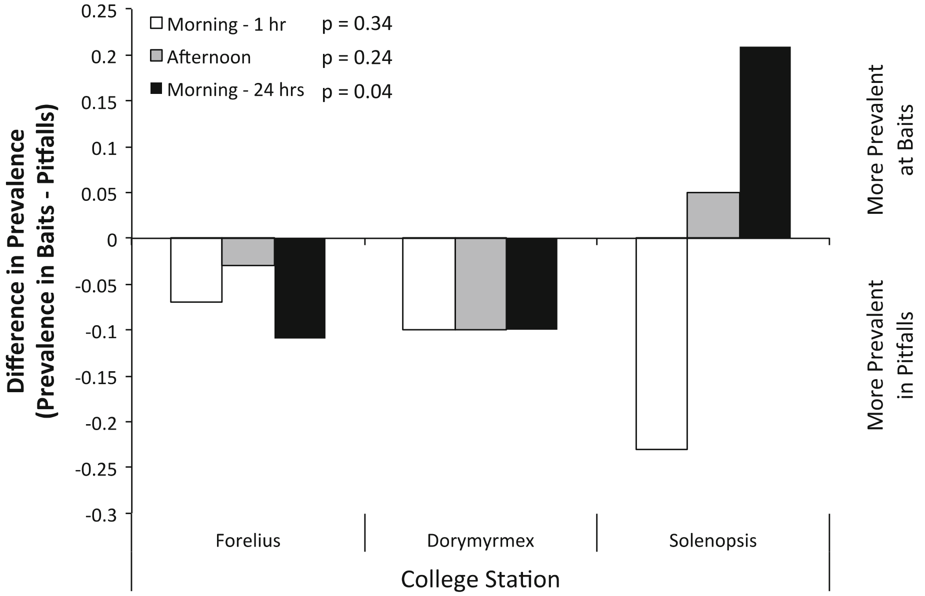
In the repeated-measures analysis of *D. bureni* abundance, there was also a significant time by suppression by aphid interaction ($F_{1,42} = 13.9$, $p < 0.001$). However, the nature of the interaction was quite different. Prior to *S.*

Fig. 1 Difference in prevalence of ants at baits and pitfalls (prevalence at baits–prevalence in pitfalls) at two study sites in the southern USA: **a** Auburn, Alabama and **b** College Station, Texas. Data are presented for *Solenopsis invicta* and three native ant species: *Dorymyrmex bureni*, *Forelius mccooki* and *Forelius pruinosus*. *Positive values* indicate that ants are more prevalent at baits than in pitfalls, while *negative values* indicate that ants were more prevalent in pitfalls than at baits

(A) Auburn



(B) College Station



invicta suppression, there were almost no *D. bureni* on plants. In contrast, after *S. invicta* suppression, the abundance of *D. bureni* on plants with aphids increased 5-fold in the *S. invicta* suppression plots although there were still almost no *D. bureni* present on plants in the control plots (suppression × aphids: $F_{1,42} = 21.3$, $p < 0.001$).

Effects of aphid honeydew on colony growth

After 60 days, experimental colonies of ants provided with honeydew and insects were significantly larger compared to colonies provided with only ad libitum insect prey in an overall analysis (MANOVA: treatment: Wilks' Lambda = 0.89, $F_{2,77} = 4.9$, $p = 0.01$). No significant differences were evident among ant species with respect to their response to aphid honeydew (MANOVA: species × treatment: Wilk's Lambda = 0.95, $F_{4,154} = 1.06$, $p = 0.38$), and colonies fed honeydew and insect prey had 35–126 % more workers and 96–367 % more brood compared to colonies that were only provided with ad libitum insect prey (Fig. 3). The number of brood in colonies of the dolichoderine ants provided with access to honeydew was also 2–3 times higher than that added at the start of the experiment.

Further analyses revealed that for both *F. pruinosus* (workers: $t_{24} = 3.25$, $p = 0.003$; brood: $t_{23} = 2.60$, $p = 0.02$) and *S. invicta* (workers: $t_{55} = 3.11$, $p = 0.003$; brood: $t_{49} = 2.25$, $p = 0.03$), there were significantly more

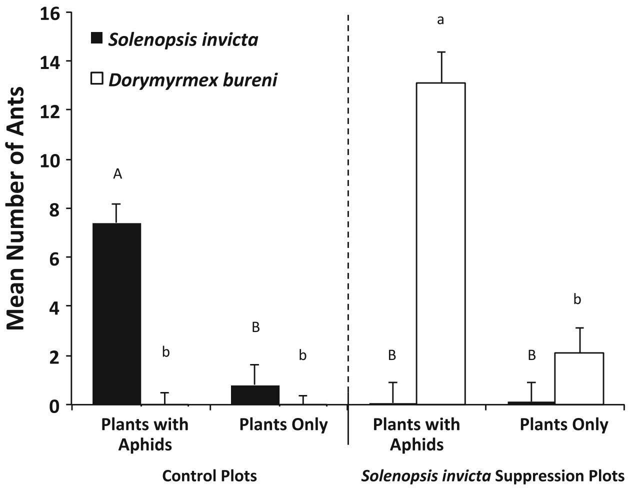
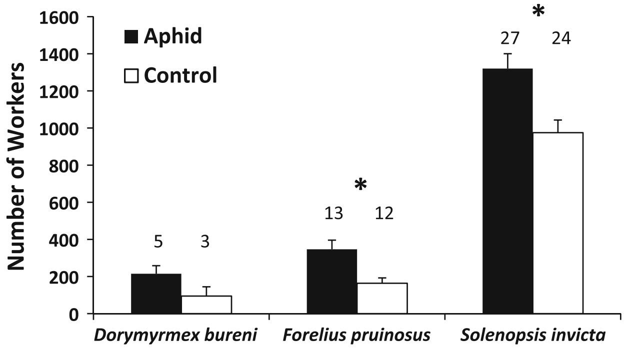


Fig. 2 Comparisons of the mean number (+1SE) of *Solenopsis invicta* and *Dorymyrmex bureni* present on cotton plants either with aphids (*plants with aphids*) or without aphids (*plants only*) in experimental plots with natural densities of fire ants (*control*) or in which fire ant colonies had been experimentally removed (*Solenopsis invicta* suppression). Data are from the final time period after suppression had been conducted on the suppression plots. Separate analyses were conducted for *S. invicta* (*uppercase letters*) and *D. bureni* (*lowercase letters*)

(A) Number of Workers



(B) Number of Brood

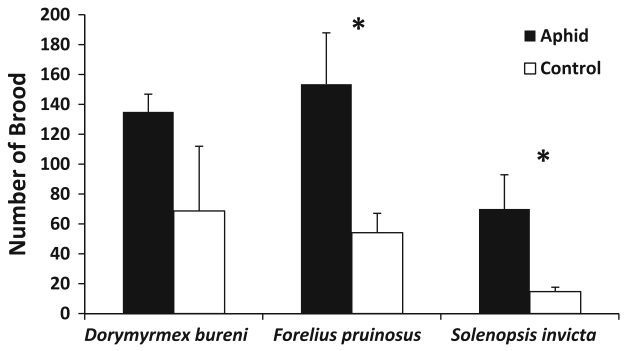


Fig. 3 Comparisons of the mean number (+1SE) of **a** workers and **b** brood present in colonies of *Solenopsis invicta, Dorymyrmex bureni* and *Forelius pruinosus* maintained with ad libitum insect prey plus a cotton plant either with aphids (*aphid*) or without aphids (*control*). *Numbers above the bars* in **a** indicate the number of colonies and are the same for **a** and **b**. *$p < 0.05$

workers and brood in colonies provided with both honeydew and insect prey compared to colonies with only ad libitum insect prey (Fig. 3). The effect of aphid honeydew on colony growth was not significant for *D. bureni* (workers: $t_6 = 1.76$, $p = 0.13$; brood: $t_6 = 1.88$, $p = 0.11$), but this was the species with the smallest sample sizes.

Discussion

Mutualist-provided carbohydrates are important resources for many ants (Pontin 1978; Way 1963; Davidson 1997; Stadler and Dixon 2005). Recently, studies have shown that engaging in mutualisms with honeydew-producing hemipterans can aid the success of introduced ants. However, the effects of changing resource availability (e.g., mutualist-provided resources) for native ants that interact with introduced ants have remained unknown. Our results provide the first experimental evidence that introduced ants compete for access to mutualist-provided carbohydrates with native ants and exclude native ant species from this critical resource. Typically, competition for one specific source of energy would be relatively inconsequential if other sources of energy are readily available. Yet, we also show that the loss of mutualist-provided resources contributes to decreases in the colony growth of native ants even when other sources of energy and nutrients (i.e., insect prey) are available ad libitum. There is growing evidence that the availability of key nutrients can have an important influence on the structure and function of ecological communities (Sterner and Elser 2002; Hawlena and Schmitz 2010; Simpson and Raubenheimer 2012). Yet, our results provide some of the first evidence that the availability of key nutrients can also mediate the effects of introduced species on native species.

Liquid carbohydrates represented a critical energy resource for experimental ant colonies in this study even though other sources of energy (e.g., lipid and protein) were present ad libitum in insect prey (Porter 1989; Macom and Porter 1995). The importance of liquid carbohydrates, in particular, as a source of energy for ants is likely related to differences in the digestive capabilities of ant larvae versus adult workers. Adult *S. invicta* workers, for example, have a much reduced digestive system compared to larvae and must carry all solid food sources to larvae for digestion (Vinson 1983; Tschinkel 2006). Hence, when only insect prey are available, larvae may divert resources away from their own growth to digest food to provide energy to worker ants. This dynamic could impinge upon larval growth and limit energy available to workers because of the balance that larvae must make between nourishing themselves versus feeding workers. In contrast to solid food, liquid carbohydrates are easily digested by worker ants and allow them to fully satisfy their own energetic needs without diverting resources away from the provisioning of brood. The importance of carbohydrates for ant colonies explains why this macronutrient is tightly regulated by ant colonies and why mutualisms between ants and plants or hemipterans that produce high-carbohydrate food resources have repeatedly evolved and are widespread in nature (Hölldobler and Wilson 1990; Stadler and Dixon 2005; Dussutour and Simpson 2009; Cook et al. 2010).

Fire ants kill and consume a wide range of invertebrates and vertebrates, and predation is an important mechanism through which fire ants negatively affect native species and communities (Hook and Porter 1990; Porter and Savignano 1990; Vinson 1994; Eubanks 2001). However, predation by *S. invicta* fails to explain declines in some native species. For example, colonies of some native ants, including species of *Dorymyrmex* spp. and *Forelius* spp., are rarely attacked by *S. invicta* and are often located adjacent to *S. invicta* colonies (Calixto et al. 2007a, b). Yet, these native species often decline in abundance in areas with fire ants and increase in abundance when fire ant populations are suppressed (Porter and Savignano 1990; Calixto et al. 2007a, b). Our results suggest that competition for a specific resource, mutualist-provided carbohydrates, coupled with the non-substitutability of this resource, may contribute to declines of these dolichoderine ants in areas invaded by *S. invicta*. In addition to dominating access to mutualisms with hemipterans on small herbaceous plants like those in our experiment, previous work has shown that *S. invicta* is nearly the only species of ant found tending hemipterans on shrubs and trees throughout the southeastern USA (Wilder et al. 2011a). *Solenopsis invicta* are also able to dominate access to mutualisms even during the hottest part of the day by using underground foraging tunnels to move between their nests and the shade of the plants where hemipterans are located (Tschinkel 2006).

There has been significant debate in the literature about whether or not introduced populations of *S. invicta* negatively affect native ant communities (Porter and Savignano 1990; Morrison 2002; King and Tschinkel 2006; Calixto et al. 2007a, b; King and Tschinkel 2008; LeBrun et al. 2012). Differences in the response of native ant communities to *S. invicta* could, in part, be related to the prevalence of native species that rely on mutualist-provided resources. For example, the frequency of ant species that regularly engage in mutualisms with honeydew-producing hemipterans, especially dolichoderines, appeared to be higher in two studies that report a negative impact of *S. invicta* on native ants (Porter and Savignano 1990; Calixto et al. 2007a, b) compared to two studies that did not (King and Tschinkel 2006, 2008). Communities with native species that rely on mutualist-provided carbohydrates may be more negatively affected by *S. invicta* because *S. invicta* is able to monopolize mutualist carbohydrates (i.e., non-substitutable resources important for colony growth). Further work is needed to test if the community composition of native ants, especially the prevalence of native ants that rely on mutualist-provided carbohydrates, can explain variation in the response of native ants to *S. invicta* and other invasive ants generally.

Our results have important implications for ant nutritional ecology. We provide evidence for multiple species of ants that high-carbohydrate honeydew from mutualists represents a critical resource that cannot be substituted by energy and nutrients in insect prey. Nearly all studies of the benefit of mutualist-provided carbohydrates for ants has assumed that they are used as fuel for worker activity, aggression, or foraging, and only recently has it been realized that these resources may also be critical for colony growth, including the production of workers and brood (Davidson 1997; Grover et al. 2007; Helms and Vinson 2008; Dussutour and Simpson 2009; Kay et al. 2010; Wilder et al. 2011a, b). The growth of ants and other arthropods has long been hypothesized to be limited by protein, but growing evidence suggests that energy is also needed for growth, especially in metamorphosing insects (Fagan et al. 2002; Dussutour and Simpson 2009; Raubenheimer et al. 2009; Wilder and Eubanks 2010; Simpson and Raubenheimer 2012). These results suggest that traditional paradigms of ant nutrition, including that (1) colony growth is limited primarily by protein, and (2) sources of energy such are carbohydrates and lipid are interchangeable may need to be reevaluated. Ants require specific concentrations of nutrients and sometimes specific sources of nutrition, such as carbohydrates, to maximize colony growth, worker activity and worker survival (Dussutour and Simpson 2009; 2012). Finally, our results show that nutritional ecology can have important implications for understanding the impact of introduced species on native species. Introduced species can competitively exclude native species from accessing specific nutritional resources and, in turn, could negatively affect the growth of native ants.

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Conflict of interest The authors declare that they have no conflict of interest.

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