Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasions

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Mutualisms play key roles in the functioning of ecosystems. However, reciprocally beneficial interactions that involve introduced species also can enhance invasion success and in doing so compromise ecosystem integrity. For example, the growth and competitive ability of introduced plant species can increase when fungal or microbial associates provide limiting nutrients. Mutualisms also may aid animal invasions, but how such systems may promote invasion success has received relatively little attention. Here we examine how access to food-for-protection mutualisms involving the red imported fire ant (*Solenopsis invicta*) aids the success of this prominent invader. Intense interspecific competition in its native Argentina constrained the ability of *S. invicta* to benefit from honeydew-producing Hemiptera (and other accessible sources of carbohydrates), whereas *S. invicta* dominated these resources in its introduced range in the United States. Consistent with this strong pattern, nitrogen isotopic data revealed that fire ants from populations in the United States occupy a lower trophic position than fire ants from Argentina. Laboratory and field experiments demonstrated that honeydew elevated colony growth, a crucial determinant of competitive performance, even when insect prey were not limiting. Carbohydrates, obtained largely through mutualistic partnerships with other organisms, thus represent critical resources that may aid the success of this widespread invasive species. These results illustrate the potential for mutualistic interactions to play a fundamental role in the establishment and spread of animal invasions.

extrafloral nectar | stable isotopes | community ecology | cotton aphid | *Aphis gossypii*

Mutualisms, interspecific interactions in which individual participants jointly benefit, influence the composition and function of ecological systems (1–9). Reciprocally positive interactions, for example, can enable species to expand their realized niches (1) and to inhabit otherwise intolerable environmental conditions (2). Mutualisms may provide resources that are necessary for the persistence and reproduction of some community members or that act as critical supplements that increase the fitness of others (1, 2, 5, 6). Although the importance of mutualisms is best known from natural or closely coevolved systems, growing evidence suggests that mutualisms also may aid the establishment, spread and ecological impact of introduced species (1–9).

Mutualisms involving the transfer of limiting resources and nutrients may be especially important in contributing to invasion success. The success of plant introductions, for example, can be enhanced when mutualistic organisms, such as nitrogen-fixing bacteria and mycorrhizal fungi, provide key nutrients to invading plants (7, 8). Mutualisms also may aid the success of animal introductions (1, 9), but, unlike the situation for plants, much less is known about how specific resources obtained from mutualisms enhance the ecological success or spread of introduced animals. Moreover, little to nothing is known concerning linkages between the high population densities often attained by introduced animals and disparities in the use or availability of mutualist-derived resources between native and introduced populations (e.g., through competitive release).

Here we test the hypothesis that greater access to food-for-protection mutualisms contributes to the ecological success of the red imported fire ant (*Solenopsis invicta*) in its introduced range. *S. invicta* ranks as one of the world's most destructive introduced species because of its ability to disrupt natural and agricultural systems (10–12) and to impact human health (13). Accordingly, control efforts in the United States alone annually exceed 1 billion dollars (12), and the worldwide economic and environmental toll will continue to increase as the red imported fire ant spreads around the world (14). In its introduced range *S. invicta* often controls sources of plant-based carbohydrates, especially honeydew-producing Hemiptera (15, 16) and floral and extrafloral nectar (EFN) (17, 18). Assimilation of carbohydrates, especially those made available through access to mutualisms, can increase worker survival and colony growth rates of fire ants (16, 19). Hence, monopolization of honeydew and other carbohydrate-rich resources seems likely to contribute to the success of *S. invicta* invasions (15). However, next to nothing is known about resource use of *S. invicta* in native populations in South America, which on average are less dense (20) and experience greater interspecific competition (20, 21) than introduced populations. In this study we combined field surveys, manipulative experiments, and stable isotope analyses to quantify (*i*) the degree to which introduced populations of *S. invicta* have access to mutualisms and their associated high-carbohydrate resources, compared with the degree of access experienced by native populations, and (*ii*) how access to mutualist-provided carbohydrates contributes to colony performance under both field and laboratory conditions.

Results and Discussion

In intercontinental comparisons, we found that *S. invicta* foraged on trees more frequently in the United States (~ 40% of trees, on average, per site) than its native Argentina (~ 5% of trees, on average, per site (Table S1 and Fig. 1*A*). This disparity was considerable, especially given that we carefully chose sites to ensure that comparisons were not confounded by fire ant density, which encompassed a wide range of densities and did not differ, on average, between our study sites in the United States and in Argentina (Fig. 1*A*). The higher prevalence of *S. invicta* on above-ground vegetation in its introduced range should allow greater utilization of concentrated sources of plant-based carbo-

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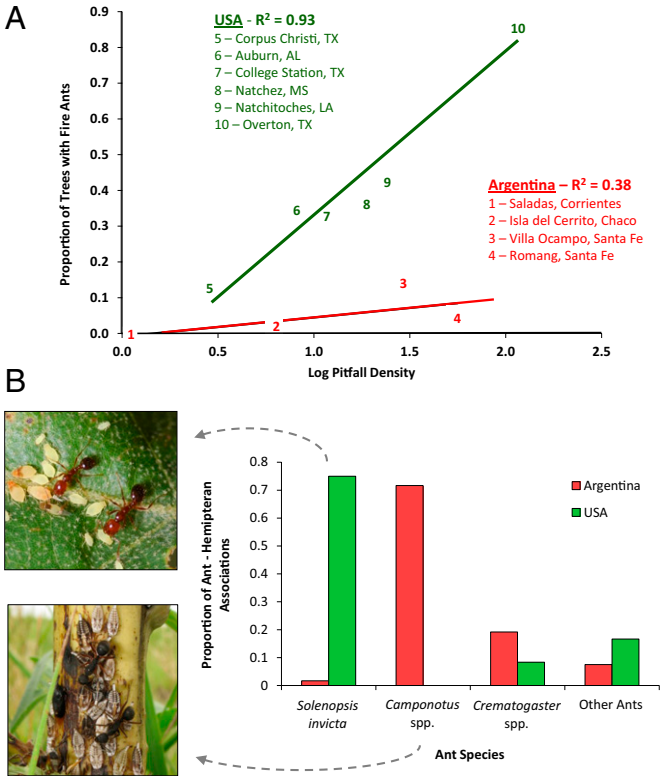

Fig. 1. *S. invicta* more frequently foraged on trees ($F_{1,7} = 45.2$, $P < 0.001$) (*A*) and tended aggregations of honeydew-producing Hemiptera ($\chi^2_3 = 6103$, $P < 0.0001$) (*B*) in the United States (introduced range) than in Argentina (native range), even though the average density of fire ants at our study sites did not differ between the two regions [United States: 30.3 ± 17.3 fire ants per pitfall trap (mean ±1 SE); Argentina: 23 ± 12.6 fire ants per pitfall trap; $t_8 = 0.31$, $P = 0.76$]. In *A* the numbers represent study sites (Table S1).

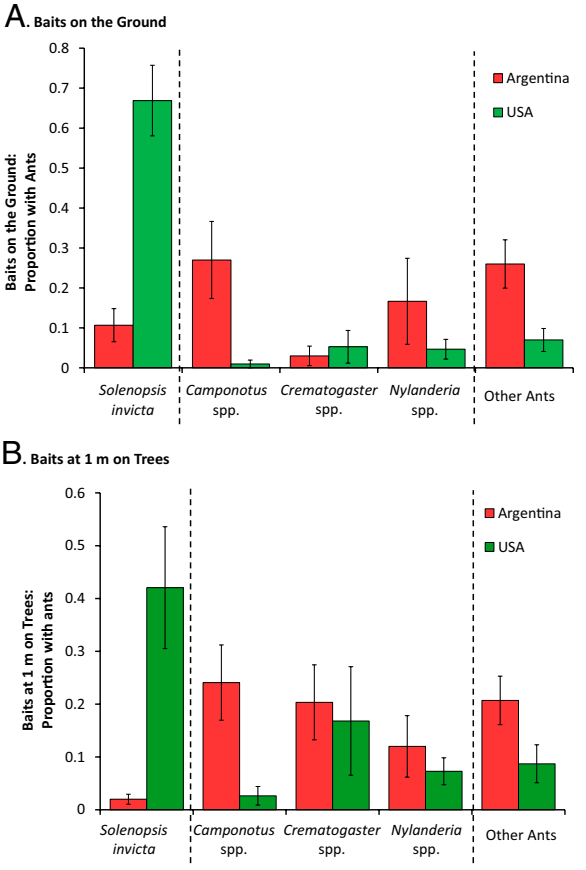

Fig. 2. Despite qualitative similarities in the common ant genera present, the identity of ants in control of carbohydrate baits differed strongly between the United States and Argentina: (*A*) Ground baits and (*B*) tree baits (multivariate analysis of variance: Wilks' λ: $F_{5,12} = 9.46$, $P < 0.001$). In the United States *S. invicta* controlled carbohydrate baits ($F_{1,15} = 23.2$, $P < 0.001$) more frequently than did interspecific competitors (summed), whereas in Argentina this pattern was reversed ($F_{1,16} = 8.33$, $P = 0.01$). Bars represent mean ±1 SE. Species names of ants from both regions are listed in Table S2.

hydrates, such as EFN and honeydew. To test this idea, we identified ants tending arboreal aggregations of honeydew-producing Hemiptera at our study sites. Fire ants in Argentina dominated only 2% of hemipteran aggregations; the overwhelming majority was controlled by ants in other genera: *Camponotus* (72%); *Crematogaster* (19%); and *Azteca, Cephalotes, Nylanderia*, and all other genera (8%) (Fig. 1*B*, and Table S2). In contrast, in the United States *S. invicta* dominated 75% of hemipteran aggregations, with other ants controlling the minority (*Camponotus* spp., 0%; *Crematogaster* spp., 8%; other genera, 16%) (Fig. 1*B* and Table S2). In addition, although the EFN-bearing *Acacia caven* dominated three study sites in Argentina, fire ants rarely occupied trees at these sites (3%). In contrast, in the United States fire ants occurred frequently on EFN-bearing plants, such as *Chamaecrista fasciculata* (41%).

To complement the hemipteran and EFN-bearing plant surveys, we quantified monopolization of sucrose baits, which mimic natural sources of plant-based carbohydrates. As in the hemipteran survey, the assemblage composition of ants in control of sucrose baits strongly differed between the United States and Argentina. Although *S. invicta* controlled a minority of ground and tree baits in its native range (2% on trees and 11% on the ground), it monopolized 42% (on trees) to 67% (on the ground) of baits in its introduced range (Fig. 2). There also was a strong negative relationship between the proportion of arboreal baits controlled by *S. invicta* and aggressive species of *Camponotus* and *Crematogaster*, but there was no relationship between the proportion of arboreal baits controlled by *S. invicta* and all other ants (Fig. 3). These results also show that, even in the United States, arboreally foraging competitors can exclude *S. invicta* from mutualist-derived resources (Fig. 3*A*), although they do so less frequently because they occur at lower densities than in Argentina (Fig. 2 and Table S2). Hence, our results support the hypothesis that interspecific competition prevents *S. invicta* from monopolizing mutualist-provided carbohydrates in its native range, whereas a lack of strong competitors in the United States allows *S. invicta* greater access to these critical resources (20, 21).

If intercontinental disparities in the control of honeydew and other high-carbohydrate resources reflect quantitative differences in resources assimilated by fire ants, then this variation should be detectable from stable isotope analysis (22–25). We estimated the trophic position of *S. invicta* by comparing the enrichment of δN^{15} in workers with that in herbivorous and carnivorous arthropods from each of our sites (22–25). These estimates revealed the relative contribution of mutualist-provided carbohydrates versus animal-based resources assimilated by fire ants at each of our study sites. Fire ants in the United States occupied a significantly lower trophic position compared with those from Argentina, as would be expected if *S. invicta* assimilated a greater proportion of mutualist-provided carbohydrates in its introduced range (Fig. 4). Our estimates of trophic position suggest that in Argentina *S. invicta* is intermediate between primary and secondary carnivores. In contrast, across introduced populations in the United States, this species typically

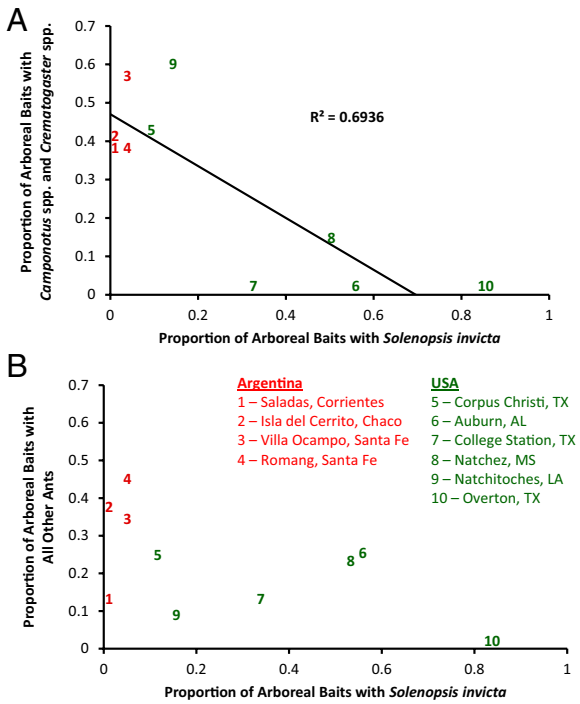

Fig. 3. (*A*) There was a strong negative relationship ($F_{1,8} = 15.6$, $P = 0.004$) between the proportion of arboreal carbohydrate baits (i.e., baits placed at a height of 1 m on trees) controlled by *S. invicta* and the proportion of baits controlled by the aggressive arboreally foraging species of *Camponotus* and *Crematogaster*. (*B*) No significant relationship ($F_{1,8} = 4.2$, $P = 0.08$) existed between the proportion of arboreal baits controlled by *S. invicta* and those controlled by all other ants excluding *Camponotus* spp. and *Crematogaster* spp.

resides in a position lower than a primary carnivore (Fig. 4). This difference appears even more striking given the low nitrogen content of honeydew and EFN [usually <1% amino acids (26)] compared with that of insects [*ca*. 50% amino acids (27)]. Mutualist-provided resources would need to be consumed in relatively large amounts to shift δN^{15} values to the extent observed. Estimates of trophic position also exhibited more variation in ants in Argentina than in the United States (Fig. 4), possibly reflecting the stabilizing effects of honeydew or nectar (which derive from a basal trophic position) relative to animal-derived resources (which likely originate from multiple trophic levels).

Finally, we examined how consumption of mutualist-provided carbohydrates affected colony growth by rearing fire ants with and without honeydew-producing aphids (*Aphis gossypii*) in the laboratory and in the field. After 7 wk, laboratory colonies of *S. invicta* with access to aphids on plants were 20% larger than those grown with cotton plants but no aphids (Fig. 5*A*), even though we provisioned all colonies with ad libitum insect prey. We extended this experimental approach into a field setting that involved free-living *S. invicta* colonies around which we planted cotton and either added or manually removed cotton aphids. After 7 wk, pitfall captures of *S. invicta* in the aphid-present treatment exceeded those in the aphid-absent treatment (Fig. 5*B*). Fire ants were nearly twice as abundant in field plots with honeydew-producing aphids, likely because of the positive effects of aphid honeydew on fire ant colony growth as observed in the laboratory. Although immigration also may have increased densities in field plots, this possibility seems unlikely, given that we removed all nonexperimental colonies from a 30-m buffer zone around each plot before the start of the experiment. These experimental results corroborate recent studies that demonstrate the key role of plant-based carbohydrates for colony growth of *S. invicta* [honeydew from mealybugs (16) and EFN (19)] (Fig. 5*C*). As a result, mutualist-provided carbohydrates may aid the spread of fire ants by increasing the density and propagule production of established populations. However, whether the presence or abundance of mutualisms in an area predisposes it to be invaded remains unknown.

Our findings support the hypothesis that the remarkably high densities of *S. invicta* in the United States (20) result, at least in part, from its differential ability to control mutualist-provided, high-carbohydrate resources in the United States compared to its

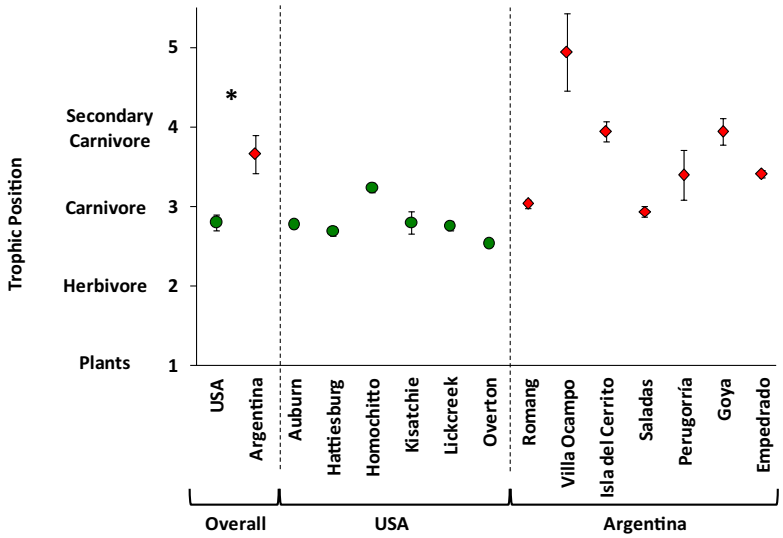

Fig. 4. The estimated mean ± 1 SE trophic position of *S. invicta* was significantly lower in the United States (introduced range) than in Argentina (native range) ($t_{11} = 2.33$, $P = 0.04$), as would be expected if fire ants in the United States have a greater proportion of honeydew and EFN in their diet. Estimates of trophic position from the United States also exhibited less variation than did estimates from Argentina (Levine's test: $F_{6,5} = 9.18$, $P = 0.03$). Such a disparity is expected given that all mutualist-provided resources derive from primary production, whereas animal-based resources originate from multiple trophic levels. Estimates of trophic position for each site incorporate δN^{15} values of arthropods that are known predators and herbivores as well as replicate colonies of *S. invicta* (as in ref. 26). *$P < 0.05$.

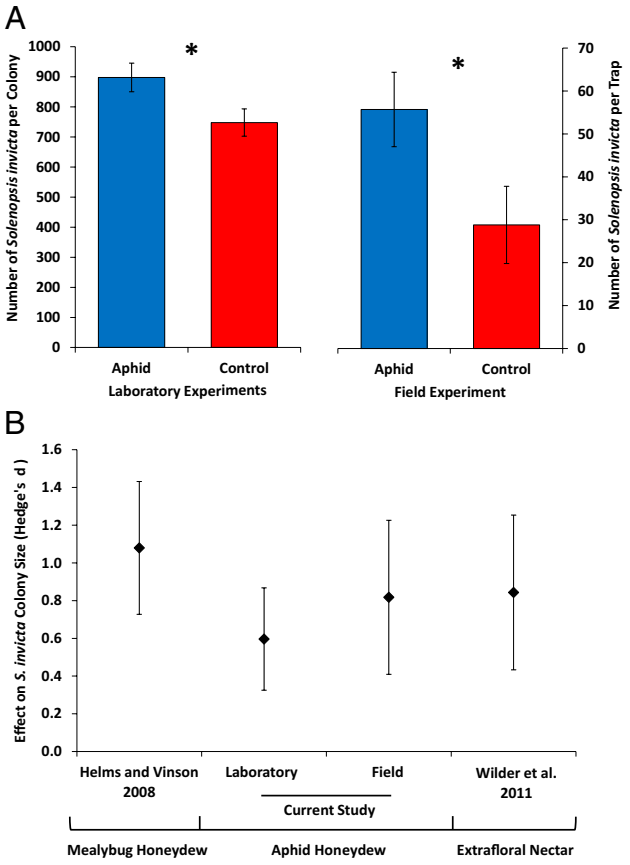

Fig. 5. (*A*) Laboratory colonies of *S. invicta* with access to honeydew from cotton aphids grew significantly larger than colonies deprived of honeydew ($F_{1,54}$ = 5.27, P = 0.03), even though all colonies had access to ad libitum insect prey. In a field manipulation, pitfall captures of *S. invicta* were higher in plots where colonies had access to honeydew-producing cotton aphids than in plots where cotton aphids were experimentally removed ($F_{1,21}$ = 4.61, P = 0.04). In this manipulation we planted cotton around focal *S. invicta* colonies in open fields, removed surrounding colonies, and used pitfalls to trap ants in focal plots after 7 wk. (*B*) Our manipulations of aphids affected fire ant colony growth to a degree comparable to that reported in other recent studies that tested the effects of different mutualist-provided foods on the growth of *S. invicta* colonies. *P < 0.05.

native Argentina. Although *S. invicta* feeds directly on plant tissues in some circumstances (28), honeydew and EFN—resources obtained from mutualisms with insects and plants—represent the primary sources of plant-based carbohydrates available to this species (18). Reduced levels of interspecific competition in the United States (10) compared with Argentina (20, 21) appear to grant fire ants nearly unrestricted access to carbohydrate-rich resources in their introduced range; assimilation of these resources in turn stimulates colony growth and enhances competitive performance. This dynamic likely gives rise to positive feedback whereby the ecological dominance of this species is consolidated further through increasing control of carbohydrate-rich resources.

Mutualisms have been documented to aid the invasion of a wide range of plants (7, 8). Here we demonstrate differential access to mutualist-provided resources and its associated effects on the trophic ecology of an invasive animal. The positive effects of mutualisms on the success and spread of introduced species likely are not restricted to fire ants. Introduced populations of yellowjacket wasps and all the most widespread and damaging species of ants (i.e., at least six species) often are found in association with mutualists that provide carbohydrates (24, 29–34).

Introduced species represent ubiquitous participants in a wide variety of mutualistic interactions. Such mutualisms encourage invasion success to a degree that currently is underappreciated and may well alter how ecologists view the relationship between biotic interactions and invasion success (1, 7, 9). Our results further underscore the importance of mutualisms in this context and hint at an explanation for invasion success that involves biogeographic disparities in the relative importance of competition and mutualism. Moreover, although mutualisms and mutualistic networks help generate and maintain biodiversity (6), introduced species can infiltrate these networks and divert resources for their own success with potentially cascading effects on community structure (35).

Materials and Methods

Study Sites. Fieldwork was conducted at seven sites in the United States and seven sites in northern Argentina (Table S1 and Fig. S1). We selected study sites carefully so they were similar in habitat type (Fig. S2). The *S. invicta* reaches peak abundance in open grassland and savannah habitat. Hence, our study sites in the United States and Argentina were in comparable savannah habitats (i.e., grassland interspersed with trees) (Fig. S2). The density of *S. invicta* in its introduced range (the United States) exceeds that in its native Argentina (20). If we had sampled sites that were indicative of average values in each region, we would have been unable to rule out the higher density of fire ants in the United States as an explanation for their greater use of honeydew and other natural sources of carbohydrates. Hence, we chose study sites representing a wide range of *S. invicta* densities in both the United States and Argentina; mean densities at our sites did not differ between the two regions (United States: 30.3 ± 17.3 fire ants per pitfall trap, Argentina: 23 ± 12.6; t_8 = 0.31, P = 0.76) (Fig. 1). In addition to removing the potentially confounding effects of density, our choice of sites ensured that our results apply to a wide range of colony densities in both the native and introduced ranges. Sampling and experiments were conducted from May through September of 2008 and 2009 in the United States and during January 2008, 2009, and 2010 in Argentina.

Ant–Hemipteran Interactions. To quantify the ability of *S. invicta* to control honeydew-producing Hemiptera, we carefully searched vegetation at each site for ant-tended aphids, mealybugs, scales, planthoppers, treehoppers, and other potential mutualist partners (including whiteflies and lepidopteran larvae). Whenever we located honeydew-producing insects, we collected several individuals along with individuals of the ant species found tending them; honeydew producers later were identified as to family (Fig. S3 and Table S2). Data were collected for each taxonomic group of honeydew-producing insect separately (Table S2), but we lumped all such groups together to facilitate analysis (i.e., each hemipteran aggregation represents a datum). We then used a χ^2 test to test if the frequency with which different ants (*S. invicta*, *Camponotus* spp., and *Crematogaster* spp.) tended honeydew-producing insects differed between the native and introduced ranges of *S. invicta*.

Carbohydrate Resources on Plants. To complement the hemipteran surveys, we also quantified the degree of tree foraging and the monopolization of sucrose baits, which mimic natural sources of plant-produced carbohydrates. Comparisons centered on the relative ability of *S. invicta* to control carbohydrate resources in its native range (n = 4 sites in Argentina) and in its introduced range (n = 6 sites in the United States). We first surveyed 30–50 trees at each study site to examine how frequently fire ants foraged in trees. Because important sources of carbohydrates (e.g., flowers, extrafloral nectaries, and honeydew-producing hemipterans) are present on the aboveground portions of trees, these data provide a measure of how frequently fire ants locate and control such resources in their native and introduced ranges. We used a one-factor analysis of covariance (ANCOVA) to test for intercontinental differences in the frequency with which fire ants foraged on trees; in this analysis we treated region as the categorical variable and fire ant density in pitfall traps as the covariate.

To assess monopolization of sucrose baits, we placed carbohydrate baits either on the ground 1 m from the base of a tree or at a height of 1 m on the trunk of a tree. Each bait consisted of half of a 15-mL centrifuge tube filled with sugar water (10–25% sugar by weight) and plugged with cotton. Initially, we monitored carbohydrate baits for 24 h; however, it soon became clear that the species of ant that controlled the bait (i.e., ants seen feeding at the bait and defending it from other ants) after 1 h almost always was the

species controlling the bait after 24 h. Hence, we revised our procedure to collect the ant species controlling baits 1 h after they first were made available. All baits were placed in the field in the morning between 8:00 and 9:30 AM, when temperatures were relatively moderate and ant activity was high. To test for differences in the frequency with which *S. invicta* controlled carbohydrate baits, we used a two-factor ANCOVA with bait location (ground versus tree trunk) and region (the United States or Argentina) as the categorical variables and fire ant density in pitfall traps as the covariate.

We used pitfall traps to estimate the ground activity of ants. At each site, we installed pitfall trap stations 5–10 m from the trees that we sampled in the bait surveys. Pitfall trap sampling was run 1 or 2 d before the bait trials to ensure that captures were representative of the abundance and activity of ants close to the sampling period but would not be affected by potential changes in activity level of ants caused by the baits. In addition, activity at carbohydrate baits was unlikely to have affected pitfall trap captures because of the distance between baits and traps and because of the brief duration of bait sampling. At each pitfall trap station, we placed three traps in a triangular arrangement with ~2 m separating each trap (a 50-mL centrifuge vial with a 2.5-cm diameter opening). Holes for pitfall traps were drilled 12–18 h before we charged traps to reduce potential effects of soil disturbance on captures. To charge traps, we placed the vials so that the opening was level with the soil and added 25 mL of either ethylene glycol or water mixed with liquid soap. We collected traps after 24 h and combined the three vials at each station so that there was one sample for each station at each site (n = 18–50 samples per site). Ant species captured in pitfall traps are listed in Table S3. For fire ants and for a few other key groups (e.g., *Camponotus, Nylanderia,* and *Crematogaster*), we estimated density as the average number of individuals captured in pitfall traps at each site. Although the density of fire ants did not differ between regions (Fig. S4), captures of other key groups were higher in Argentina than in the United States. Perhaps most notably, the combined abundance of *Camponotus* and *Crematogaster* in Argentina exceeded that in the United States (t_8 = 2.71, P = 0.03).

Stable Isotopes and Trophic Position. We estimated the trophic position of *S. invicta* by comparing the enrichment of δN^{15} in workers with that of herbivorous and carnivorous arthropods from each of our sites (n = 6 sites in the United States; n = 7 sites in Argentina). At each study site, we located 10–15 *S. invicta* colonies that were at least 50 m away from the locations of sucrose-baiting trials. We disturbed each colony and collected 10–50 fire ant workers. We also collected a range of herbivorous (e.g., mealybugs, planthoppers, grasshoppers, and phytophagous beetles) and carnivorous (e.g., spiders, praying mantids, odonates) arthropods from each of our sites. All arthropods were killed immediately either by storing them on ice or by placing them in 95% ethanol; both methods are suitable means of storage for δN^{15} samples (22). We later dried all samples at 60 °C for 24–48 h. To prepare samples for isotopic analysis, arthropods were ground with a mortar and pestle, and 0.8–1.3 mg of each sample was packed into a tin capsule. For fire ants, we first removed the abdomens from each worker and then placed 0.8–1.3 mg of workers without abdomens (two to six individual ants) into a tin capsule. Abdomens were removed from ants to prevent recent stomach contents from influencing δN^{15} values; this approach provides more relevant information about long-term assimilation and incorporation of nutrients from foods into tissues (22).

One potential problem in comparing stable isotope measures among sites is that the value of δN^{15} for animals feeding at the same trophic level can exhibit spatial heterogeneity (23). Hence, comparisons of stable isotopes among sites need to be placed in a frame of reference. Accordingly, we used the approach developed by Post (23) to estimate the trophic position of *S. invicta* relative to that of known herbivores and carnivores from the same site. We then used a t test to compare the mean trophic position of *S. invicta* between the United States and Argentina; data points in this analysis are the mean trophic position values of *S. invicta* from each site.

Carbohydrates and Fire Ant Performance in the Laboratory and Field. We combined the results of two separate laboratory experiments (19) that tested the effect of aphid honeydew on the growth of *S. invicta* colonies. In both experiments, fire ant colonies were collected from the field and reduced to standard sizes (*ca*. 1,200 workers, 50 brood, and one to three queens) and placed in plastic containers with cotton (*Gossypium hirsutum*) plants. We manipulated the presence of the cotton aphid (*Aphis gossypii*) by adding or removing aphids from cotton plants weekly.

We also conducted a manipulative experiment to examine how access to honeydew affects fire ant colonies in the field. This experiment was conducted on the campus of Texas A&M University in College Station, TX, in a recently mown field. In this field, we located 26 *S. invicta* colonies with mounds <30 cm in diameter. All other fire ant colonies within 30 m of focal colonies were dug up and removed from the study area to prevent immigration. In early June, we planted four rows of cotton around each focal colony; each row was 2 m long with 0.5 m between each row. The aboveground biomass of cotton in each plot was measured at the end of the experiment. Each experimental plot was watered once every 5–7 d. We assigned alternate plots to control and aphid treatments. When most cotton plants had four true leaves (June 30), we manually removed aphids from cotton plants in control plots and inspected plants for aphids in aphid plots once per week throughout the experiment.

We used pitfall traps to measure the activity of fire ants in each plot (Fig. S4). Four pitfall traps, each 2.5 cm in diameter, were placed in each plot within 0.5 m of each corner of the plot. Pitfall traps were installed initially on June 27 and were capped when not in use. Pitfall traps were charged with 25 mL of ethylene glycol and opened for three 48-h sampling periods: June 28–29, July 19–20, and August 15–16. This scheme allowed us to measure fire ant activity in plots pretreatment, 3 wk posttreatment, and 7 wk posttreatment. The number of fire ants captured in pitfall traps could reflect changes in the density of ants in the plot (e.g., resulting from increased colony size) and also changes in ant activity level (resulting from higher levels of recruitment). Fire ants form underground foraging tunnels between the nest and persistent resource finds (e.g., plants with aphids) (12). This behavior suggests that greater recruitment to plants with aphids in the aphid treatment is unlikely to have biased pitfall captures. In addition, high-carbohydrate supplements can decrease the foraging activity of ants (36) and of fire ants in particular (37, 38). High carbohydrate resources potentially could increase the activity level and aggression of ants toward competitors (39). However, it is unclear whether such responses would affect capture levels, because nearby colonies of fire ants were removed, polygynous colonies of fire ants (most colonies in our study are polygynous) show little intraspecific aggression in the United States, and potential interspecific competitors were rare (i.e., <5% of ants in pitfall traps). To test for the effects of aphid treatment on the pitfall captures of fire ants, we used an ANCOVA with pretreatment *S. invicta* captures and the aboveground biomass of cotton as covariates and the experimental group as the categorical variable.

Finally, we used Hedge's d effect size to compare the effects of plant-based resources on the performance of fire ant colonies from several experiments that reared colonies in the presence or absence of mealybug honeydew (16), aphid honeydew in the laboratory and field (this study), and EFN (19).

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