Solenopsis invicta Suppress Native Ant by Excluding Mutual Exploitation from the Invasive Mealybug, *Phenacoccus solenopsis*

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ABSTRACT

Mutualistic interaction between invasive ants and honeydew-producing hemipterans has been extensively examined in many studies. Laboratory experiments showed that invasive ant *Solenopsis invicta* (Hymenoptera: Formicidae) suppress ghost ants *Tapinoma melanocephalum* (Hymenoptera: Formicidae) through interference competition. However, relatively less testing have been done to evaluate the competition for mutual exploitation between the two ant species in the field. Here, we investigated the interference of the fire ant *S. invicta* on the interactions between the ghost ant *T. melanocephalum* and the invasive mealybug *Phenacoccus solenopsis* (Hemiptera: Pseudococcidae) in the field. The results showed that fire ant invasion significantly suppressed honeydew exploitation by ghost ant. Fire ant suppression markedly increased the ghost ant foraging activity both on plants and the ground. Ant diversity in fire ant-infested plots was significantly reduced compared with in fire ant-free plots. Compared with in the no-ant plots, the colony growth rate of mealybug significantly increased, and the parasitism of mealybug was obviously decreased, both in fire ant-infested plots and in fire ant-free plots. Colony growth rate of mealybug in fire ant-infested plots was greater than fire ant-free plots. These results suggest that *S. invicta* suppresses the exploitation of honeydew-producing hemipterans by ghost ant and occupies most of the honeydew resource.

INTRODUCTION

Beneficial interactions between ants and hemipterans occur extensively in many ecosystems (Helms and Vinson, 2002; Holway *et al.*, 2002; Simberloff, 2006; Brightwell and Silverman, 2010). In such a relationship, ants frequently protect hemipterans against their predators and parasitoids (Bishop and Bristow, 2001; Renault *et al.*, 2005; Daane *et al.*, 2007; Powell and Silverman, 2010). Ants also stimulate the feeding potential of hemipterans and help them reach favorable parts of host plants (Way, 1963; Wu *et al.*, 2013). In return, ants obtain large amounts of honeydew produced by hemipterans (Stachowicz, 2001; Davidson *et al.*, 2004; Stadler and Dixon, 2005). Previous studies indicated that mutualisms between ants and hemipterans have a profound effect on the composition and function of ecological systems (Bruno *et al.*, 2003; Schmitt and Holbrook, 2003). For example, mutualistic interaction between invasive ant and aphid plays a fundamental role in the establishment and spread of ant invasion (Wilder *et al.*, 2011a).

However, how such interaction system facilitated invasion success received relatively little attention.

The monopoly of resources by invasive species is one of the most critical threat to ecosystem because it can significantly influence native communities (Moller, 1996; Holway *et al.*, 2002). Resource competition and mutualism exploited by invasive species can play a role in the disintegration of original ecosystems (Traveset and Richardson, 2006). The availability of important nutrients can also profoundly affect the structure and function of ecological communities (Hawlena and Schmitz, 2010; Simpson and Raubenheimer, 2012). For example, high-carbohydrate honeydew produced by hemipterans is a valuable food resource for invasive ants and native species. As a product of mutualistic relationships, essential resources enhance the ecological success or spread of invasive ants. As an important food resource, honeydew can also facilitate the invasion of *Solenopsis invicta* (Wilder *et al.*, 2011a). Honeydew produced by aphids is important in the diet of the invasive ant species *S. invicta* (Helms and Vinson, 2002). The colony growth and worker survival of *S. invicta* are significantly enhanced when these ants provided honeydew produced by hemipterans (Zhou *et al.*, 2012a). Furthermore, the colonies of the native ant

Dorymyrmex bureni (Hymenoptera: Formicidae) with access to honeydew and insect prey support twice as many workers and twice as much brood under laboratory conditions compared with ants feeding on insect prey only (Wilder *et al.*, 2013). Therefore, honeydew produced by hemipterans plays a critical role in these mutualistic interactions (Way, 1963; Baylis and Pierce, 1992).

Previous studies showed that fire ants invasion has negative effects on native communities (Vinson, 1994; Eubanks, 2001; Savage *et al.*, 2011; Wilder *et al.*, 2011a, b; Wang *et al.*, 2013). The extraordinary densities and increased feeding efficiency of invasive ants at introduced locations are important for their success. Invasive ants compete with and prey on different vertebrates; mutual interactions with numerous plants and other insects are also disrupted (Helms and Vinson, 2002; Holway *et al.*, 2002). Predation is an important mechanism by which fire ants negatively affect native species communities. Numerous invertebrates and vertebrates are negatively affected and killed by fire ants (Vinson, 1994; Eubanks, 2001). Monopolization and competition for important resources by fire ants are other reasons for colony disintegration and declines in native species populations in fire ant-infested areas. For instance, native ant populations are significantly suppressed, and mutualism with aphids is almost monopolized by *S. invicta* (Wilder *et al.*, 2013). A similar study reported that Argentine ants interfered with the foraging of native ant species and prevented the establishment of new colonies of native ant species (Human and Gordon, 1996). Although many studies have determined the effects of invasive ants on native communities, the effects of invasive ants on subdominant and subordinate ant species in the recipient biota may be mediated through a diversity of competitive mechanisms (Morrison, 2000).

Red imported fire ant, *S. invicta,* and mealybug, *P. solenopsis,* are two important invasive species in South China. Abundant populations of these two invasive species are present in ecosystems. Both have caused serious damage to agriculture and forestry production (Zeng *et al.*, 2005; Lu *et al.*, 2008). Furthermore, *S. invicta* and *Phenacoccus solenopsis* frequently form mutual relationships. Both species substantially benefit from this relationship, which is mainly reflected in the improvement of population growth and fitness (Zhou *et al.*, 2012a, b, 2013). Mutualism between *S. invicta* and *P. solenopsis* is extensively present. In addition to *S. invicta*, ghost ant, *Tapinoma melanocephalum* (Hymenoptera: Formicidae), have also established interactions with *P. solenopsis* (Zhou *et al.*, 2012a, 2014a). *T. melanocephalum* is an invader whose native range remains unknown. Nevertheless, studies have suggested that this species

originates from Africa or Asia (Wheeler, 1910). Ghost ant workers frequently tend honeydew-producing insects and scavenge for dead insects in the fields (Smith, 1965). *T. melanocephalum* has thrived for a long time in southern China, where it is fully established as a resident species. We focused on the *T. melanocephalum* because this species is abundant in south China and requires omnivorous diets that frequently include mutualist-provided honeydew. Previous results suggested that *T. melanocephalum* was one of the dominant species in the areas infected by *S. invicta* (Lu *et al.*, 2014). Numerous studies have examined competition between fire ants and native ants (Porter and Savignano, 1990; Holway, 1998; King and Tschinkel, 2006; King and Porter, 2007; Wilder *et al.*, 2013; Zhou *et al.*, 2014b). However, relatively little research has tested if invasive ants compete with or exclude native ants from mutualist-provided resources. Studies demonstrating the mechanism by which invasive ant influence the mutual exploitation of another ant is also insufficient. Direct studies on the competition between ant species could provide more accurate information for better understanding the mechanism of interspecific competition. Here, we conducted a series of field experiments to test whether *S. invicta* suppress native ant by excluding mutual exploitation from the invasive mealybug *P. solenopsis*.

MATERIALS AND METHODS

Plants and insects

Hibiscus rosa-sinensis (Malvales: Malvaceae) plants were cultivated in plastic flowerpots (18 cm × 14 cm × 17 cm) in the greenhouse. Each plant was approximately 25 cm in height and had 20 true leaves. The ovisacs of *P. solenopsis* were collected from the campus of South China Agricultural University and placed on the *H. rosa-sinensis* plants. The 1st instar mealybug nymphs were inoculated on the *H. rosa-sinensis* plants and raised for several generations. The mealybug colonies was reared in the laboratory at maintained temperature 27±2 ℃ with relative humidity 60–70%.

Field investigation

Our investigation was conducted in an experimental field of South China Agricultural University (23° 09′ 40.44″ N, 113° 21′ 41.09″ E), in the suburbs of Guangzhou, China. The experimental fields are located in a fireweed ecosystem and uniformly covered with scrub plants and grass (mainly *Zoysia tenuifolia*) (Poales : Poaceae). According to our continuous investigation, *S. invicta* colonies are polygynic and have been established for 3 years. *H. rosa-sinensis* was grown naturally and present as major vegetation. All the *H. rosa-sinensis* plant were 100-150 cm in height (stems

and leaves were completely developed, flowers not opened during the whole experimental stage). We established plots measuring 5 × 5 m. Adjacent plots were separated by a minimum of 150 m. The experimental plots included three treatments: (1) Plots with an infestation of *S. invicta* colonies (n=12). (2) Plots remaining free of *S. invicta* colonies (n=10). *S. invicta* colonies were suppressed by treating with boiling water (Lebrun *et al.*, 2007). Fire ant workers were not completely excluded from the plots, while the number was quite small (no more than four workers in pitfall trap). The *S. invicta* colonies were eliminated within the 5 × 5 m plots and also from within a 35-m wide buffer zone around each plot. (3) Plots with *S. invicta* infestations in which the bases of the main stems of the plants were covered with paraffin. Paraffin was used as barrier to keep plants ants-free in the plots (n=15). *H. rosa-sinensis* plants in each plot was evenly distributed. One *H. rosa-sinensis* plant was haphazardly selected in each plot. We conducted our experiment at the end of February 2012. The average temperature was approximately 26 °C during the day. On sunny days, the first instar of mealybug transferred to each selected plant separately by using small plastic tubes with cotton plugs before this mealybug was introduced to the study site. During this transfer, four tubes, each containing 100 individuals, were placed on the top branches of each *H. rosa-sinensis* plant. After the plug was removed, the nymphs crawled out from the tubes and started move to the tender plant leaves. We started investigation for foraging activity of *S. invicta* and *T. melanocephalum*, and other native ants on each *H. rosa-sinensis* plant and the surrounding ground on March 2, 2012. The investigation was conducted fortnightly. Ants foraging activity on the plants was determined by counting the number of foraging ants moving up and down the plant trunk for 3 min. Pitfall traps were used to determine the foraging activity on the ground surface. A circle with its center point located at the selected *H. rosa-sinensis* plant, with a radius of approximately 40 cm was drawn. Four pitfall traps (*i.e.*, a 50 ml centrifuge tube with 25 ml of 75% alcohol) were placed inside the circle at an angle of 90° from each other. Each centrifuge tube was embedded

in the ground. The mouth of the centrifuge tube was placed parallel to the ground surface. We collected pitfall traps after 24 h and then combined the contents of the four tubes at each plot into one sample. All ant species occurring on plants and captured in pitfall traps were recorded. At the end of our investigations, the surviving mealybug and mummified mealybug was counted. We defined the colony growth rate of mealybug as the final population divided by the initial population density.

Statistical analysis

All data were tested for a normal distribution with the Shapiro-Wilk test. A one-way analysis of variance (ANOVA), using Type III sum of squares or independent sample t-test, was performed to compare the means among all measured variables when the data were normally distributed and had similar variances. For the data that were not normally distributed, the nonparametric Kruskal-Wallis test was applied for comparing the median. The Mann-Whitney test for multiple comparisons among the different groups was used if the results of the Kruskal-Wallis test showed significant differences at the 0.05 level. We used the general linear model (GLM) to analyze the mixed effects of fire ant invasion and location (on ground/on plant) on ant diversity. All statistical analyses were conducted with SPSS version 14.0 (SPSS Inc., Chicago, IL).

RESULTS

Effects of S. invicta *invasion on foraging activity of* T. melanocephalum

The results showed that *S. invicta* was not present on plant in the fire ant-free plots. The suppression of *S. invicta* significantly decreased the foraging activity of *S. invicta* on plants with time sequence (Fig. 1A, Table I, Fire ants: Time × Fire ants). *S. invicta* suppression markedly increased the ghost ant foraging activity on plants (Fig. 1B, Table I, Ghost ants: Fire ants). This effect on ghost ants increased with time sequence (Table I, Ghost ants: Time × Fire ants). In fire ant-free plots, foraging worker numbers of *S. invicta* on the ground significantly decreased

Table I.- Analysis of variance of ants foraging activity on plants in fire ants-infested plots.

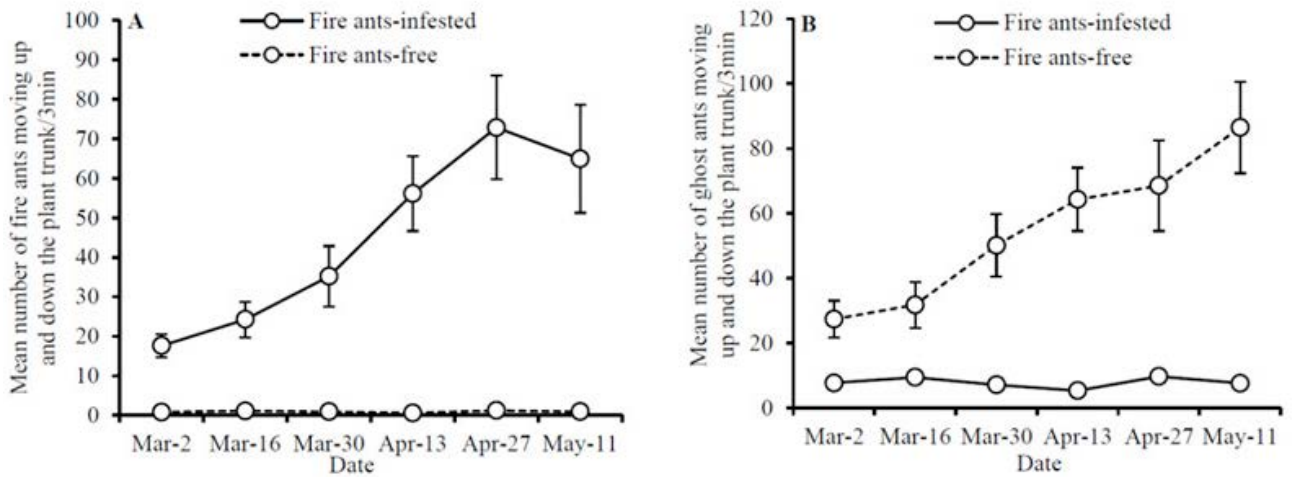| Source of variation	Fire ants				Ghost ants			
	SS	df	F	P	SS	df	F	P
Time	14,075.220	5	4.783	0.001	13,798.420	5	5.337	0.000
Fire ants	64,001.616	1	108.753	0.000	72,064.002	1	139.354	0.000
Time × Fire ants	13,996.614	5	4.757	0.001	14,557.148	5	5.630	0.000
Error	70,620.633	120			62,055.350	120		

Fig. 1. Dynamics of ant foraging activity on plants in fire ant-infested plots and fire ant-free plots. **A**, Fire ants; **B**, Ghost ants.

Table II.- Analysis of variance of ants foraging activity on ground in fire ants-infested plots.

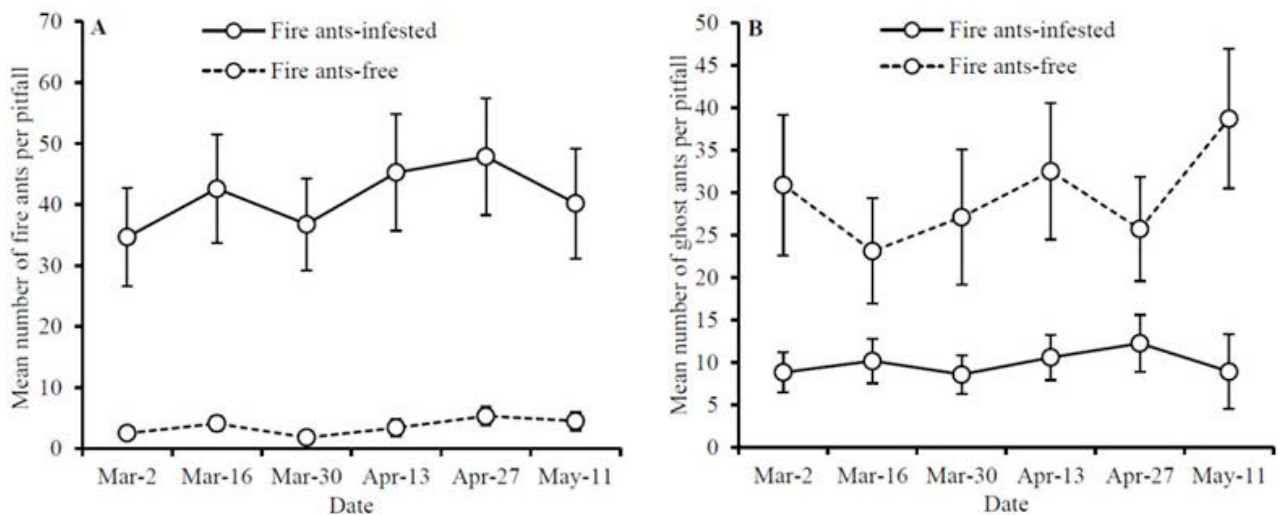| Source of variation	Fire ants				Ghost ants			
	SS	df	F	P	SS	df	F	P
Time	1,009.972	5	0.389	0.855	734.075	5	0.465	0.802
Fire ants	46,289.020	1	89.224	0.000	12,801.616	1	40.535	0.000
Time × Fire ants	455.245	5	0.176	0.971	1,082.196	5	0.685	0.635
Error	62,255.417	120			37,897.733	120		

Fig. 2. Dynamics of ant foraging activity on ground in fire ant-infested plots and fire ant-free plots. **A**, Fire ants; **B**, Ghost ants.

(Fig. 2A, Table II, Fire ants: Fire ants). *S. invicta* suppression positively affected the foraging activity of ghost antson the ground (Fig. 2B, Table II, Ghost ants: Fire ants). However, this positive effect on ghost ant declined with our investigative time sequence (Table II, Ghost: Time × Fire ants).
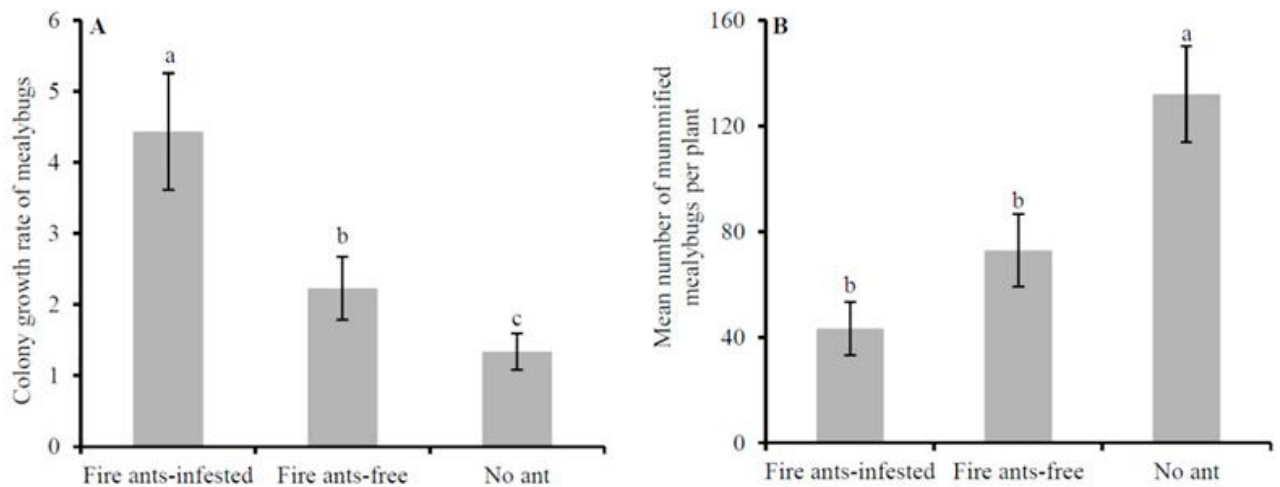
Fig. 3. Effects of ants' tending on mealybug colony growth (**A**, mean growth rate; **B**, mean number of mummified mealybugs). Different letters above bars indicate statistically significant differences between the treatment and the control. **A**, Mann-Whitney test, *P* = 0.05; **B**, LSD test, *P* = 0.05.

Effects of S. invicta *invasion on ant diversity*

The results showed that the number of ant species both on the plants and the ground in fire ant-infested plots were less as compared to fire ant-free plots (Table III). Ant diversity in fire ant-infested plots was significantly reduced compared with in ant-free plots (Table IV, Ants). Ant diversity on ground was significantly more than on plants (Table IV, Locations). In addition, significant effects on the ant diversity were found for the interactions between ant and location treatments (Table IV, Locations × Ants). We found that the native ant *Diacamma rugosum* (Hymenoptera: Formicidae) occasionally appeared on the plants in fire ant-free plots, but the numbers were quite small. All of the collected ant species belonged to four subfamilies with ten genera and twelve species (Table III).

Effects of ant tending on mealybug colony growth

The results showed that ant tending significantly affected the colony growth rate of mealybugs (Fig. 3A, χ^2=16.693, *df*=2, *P*<0.001, Kruskal-Wallis test). The mean colony growth rate in fire ant-infested plots was significantly greater than that in fire ant-free plots (Fig. 3A, *U*=27.000, *P*=0.03, Mann-Whitney *U* test). The mealybug colony growth rate in fire ant-free plots was significantly greater as compared to plots with no ants (Fig. 3A, *U*=29.500, *P*=0.01, Mann-Whitney *U* test). Parasitism was significantly different across the three types of plots (*F*=9.409, *df*=2, *P*=0.001, One-way ANOVA). The number of mummified mealybugs in no-ant plots was greater than that in fire ant-infested and fire ant-free plots (*P*<0.001, *P*=0.011, respectively, LSD test).

DISCUSSION

Invasive ants are generally recognized by their extreme aggression and broad omnivory. For instance, *S. invicta* invasion has negatively affected the structure and function of ecosystems (Nattrass and Vanderwoude, 2001; Wojcik *et al*., 2001; Eubanks *et al*., 2002; Cook, 2003; Epperson and Allen, 2010). Native communities can be displaced by invasive species in the invaded areas (Holway *et al*., 2002). The native species *S. geminata* (Hymenoptera: Formicidae) and *S. xyloni* (Hymenoptera: Formicidae) have been extensively displaced since *S. invicta* invaded the area (Trager, 1991; Tschinkel, 1988). *S. invicta* also compete with native dolichoderine ants *D. bureni* for access to mutualistic relationships with aphids (Wilder *et al*., 2013). The results showed that foraging activity of ghost ant species *T. melanocephalum* was significantly suppressed by fire ant invasion. This is consistent with previous studies that the abundance of dolichoderine ants was lower in areas with fire ants and that these ants increased in abundance when fire ants were removed (Calixto *et al*., 2007a, b).

As a competitor, *S. invicta* gained access to food resources and reached high population densities by reducing the populations of native species (Wilder *et al*., 2013). *S. invicta* eventually dominated in most of the foraging arenas against *S. geminata* and *S. xyloni* (Morrison, 2000). *S. invicta* is a greedy predator, its invasion of cotton fields results in 38% and 50% decreases in the survival of *Chrysopa perla* (Neuroptera: Chrysopidae) larvae and lady beetles, respectively (Eubanks *et al*., 2002). In an

Table III.- Ant species on ground surface and on plant in fire ant-infested plots and fire ant-free plots.

Ant species	Surface		Plant	
	Fire ant- infested plots	Fire ant-free plots	Fire ant- infested plots	Fire ant-free plots
Ponerinae				
Odontoponera Mayr				
*Odontoponera transvers*a (Smith)	×	√	×	×
*Leptogen*ys Roger				
Leptogenys chinensis (Mayr)	×	√	×	×
Pachycondyla Smith				
Pachycondyla luteipes (Mayr)	×	√	×	×
Diacamma Mayr				
Diacamma rugosum (Le Guillou)	√	√	×	√
Myrmicinae				
Solenopsis Westwood				
Solenopsis invicta Buren	√	√	√	√
Pheidole Westwood				
Pheidole pieli Santschi	×	√	×	×
Pheidole yeensis Forel	×	√	×	×
Pheidologeton Mayr				
Pheidologeton diversus (Jerdon)	√	√	×	×
Monomorium Mayr				
Monomorium pharaonis (L.)	×	√	×	×
*Monomorium oriental*e (Mayr)	×	√	×	×
Dolichoderinae				
Tapinoma Foerster				
Tapinoma melanocephalum (Fabricius)	√	√	√	√
Formicinae				
Plagiolepis Mayr				
Plagiolepis rothneyi (Forel)	×	√	×	×
Total species number	4	12	2	3

√, the ant species is present; ×, the ant species is absent.

Table IV.- Analysis of variance of ant diversity in plots.

Source of variation	SS	df	F	P
Location	77.042	1	99.409	0.000
Ants	63.375	1	81.774	0.000
Location × Ants	57.042	1	73.602	0.000
Error	15.500	20		

Location, the position of ant appeared (on ground surface or on plant); **Ants**, the different treatments of the experiments (fire ant- infested plots or fire ant-free plots).

S. invicta-invaded area, species richness and populations of the native ant community decrease by 70% and 90%, respectively (Porter and Savignano, 1990). *S. invicta* monopolizes the mutualistic relationships with hemipterans on plants. The ant *D. bureni* found tending aphids only when *S. invicta* was removed (Wilder *et al.*, 2013). *S. invicta* is the dominant ant species found tending aphids on shrubs and trees in the southeastern parts of the United States (Wilder *et al.*, 2011b). To dominate access to mutualisms, *S. invicta* even transferred their nests to places near plants where hemipterans were located (Tschinkel,

2006). In this study, *S. invicta* invasion disturbed the interaction between *P. solenopsis* and the ghost ant *T. melanocephalum*. Foraging activity of ghost ants was significantly decreased and the abundance of ant diversity was largely restrained in fire ant-infested plots. Zhou *et al*. (2012a) also showed that the foraging frequency of *T. melanocephalum* is restrained by interference from *S. invicta* when the two ant species are foraging on the same plant under laboratory condition. Only one native ant species was observed foraging on plants in fire ant-infested plots. This result is consistent with findings that *S. invicta* adversely affects the relationship between native ants and bean aphids by reducing the population density of native ants (Huang *et al*., 2010). *T. melanocephalum* appeared more frequently on *H. rosa-sinensis* plants than *D. rugosum* in this study. This result may suggest that *T. melanocephalum* could resist the attack of other native species. *T. melanocephalum* workers effectively utilize their pygidial gland secretions as an alarm-defense system during aggressive encounters with other invaders (Tomalski *et al*., 1987). Previous studies have also shown that some ant species can withstand interspecific competition by invasive ants. For example, *Monomorium minimum* (Hymenoptera: Formicidae) can coexist with *S. invicta* in the southeastern United States (Porter and Savignano, 1990). *Monomorium ergatogyna* (Hymenoptera: Formicidae) was the only native ant that resisted the displacement caused by Argentine ants by releasing potent chemical defensive compounds (Adams and Traniello, 1981; Holway, 1999). *Dorymyrmex* spp. and *Forelius* spp., were often located adjacent to *S. invicta* colonies and rarely attacked by *S. invicta* (Calixto *et al*., 2007a, b). The results also showed that ant diversity on plants were significantly higher than that on ground. This may suggest that honeydew produced by *P. solenopsis* has exacerbated the competition between *S. invicta* and native ants. Wilder *et al*. (2011) also reported that honeydew produced by aphids elevate colony growth of *S. invicta* and aid the competitive ability of this invasive species.

Tending by ants can facilitate the colony growth of hemipterans (Buckley, 1987; Way, 1963). Aphid populations and predation affecting sentinel bollworm eggs were greater in the presence of *S. invicta* than in its absence (Kaplan and Eubanks, 2002a; Diaz *et al*., 2004; Coppler *et al*., 2007). The colony growth of mealybug was facilitated by Argentine ants (Phillips and Sherk, 1991; Daane *et al*., 2006, 2007). *P. solenopsis* population was greater in fire ant-infested plots than in fire ant-free plots (Zhou *et al*., 2012a). This study confirmed that the colony growth rate of mealybugs was greater in fire ant-infested plots than in fire ant-free plots. We also found that the mealybug growth rate exhibited a greater increase in fire

ant-free plots as compared with the no-ant plots. This result was consistent with our previous study, which showed that *T. melanocephalum* protects mealybugs from natural enemies and contributes to mealybug colony growth, both ladybeetles and parasitoids showed a strong avoidance response to *T. melanocephalum* (Zhou *et al*., 2014a). Although the native ant *D. rugosum* was also observed on plants in fire ant-free plants, it was less frequent compared with the occurrence of *T. melanocephalum*, which suggest that most honeydew produced by mealybug was occupied by *T. melanocephalum* on fire ant-free plots. The result was that mummified mealybug numbers in fire ant-free plots were significantly lower than those in no-ant plots, which confirmed our hypothesis. The result also enhances the evidence that *S. invicta* suppresses the exploitation of honeydew-producing hemipterans by ghost ants in the field.

CONCLUSION

Our results demonstrate that both fire ant *S. invicta* and ghost ant *T. melanocephalum* can facilitate colony growth of mealybug by repulse parasitoids. However, honeydew exploitation by ghost ant significantly declined when fire ant were introduced, ghost ant foraging was increased when fire ants were excluded. Ant diversity was significantly reduced when fire ants were included. These results suggest that *S. invicta* suppresses the exploitation of honeydew producing hemipterans by ghost ant and occupies most of the honeydew resource.

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Conflict of interest statement
We declare that we have no conflict of interest.

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