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Comparing mechanisms of competition among introduced and resident ants in China: from behavior to trophic position (Hymenoptera: Formicidae)

Lei NIE, Meihong NI, Dongdong NING, Hao RAN, Babar HASSAN & Yijuan XU

Abstract

Invasive ant species interact with both native and previously introduced ants in new environments. Their effects on resident species may vary warranting a careful examination of the possible mechanisms that govern these differences. We used individual and group aggression assays and an assay of walking speed to examine behavioral interactions between *Solenopsis invicta* BUREN, 1972 and one native and four previously introduced ant species in China. We also determined the toxicity of *S. invicta* venom to these resident ants and inferred differences in trophic position for all five ant species using stable isotope ($\delta^{15}\text{N}$) data. No differences in walking speed were observed between *S. invicta* and other species with the exception of the introduced *Anoplolepis gracilipes* (SMITH, 1857), which had a faster walking speed than *S. invicta*. Maximum aggression scores were observed between *S. invicta* and the introduced *Solenopsis geminata* (FABRICIUS, 1804) (2.83 ± 0.11) as well as the native *Pheidole yeensis* FOREL, 1902 (2.37 ± 0.15), followed by *A. gracilipes* (2.05 ± 0.15), in the individual aggression assay. In the group aggression assay, workers of *S. invicta* were very aggressive towards four resident ants and caused high mortality of *P. yeensis* (98%) and *S. geminata* (80%), followed by *Tapinoma melanocephalum* (FABRICIUS, 1793) (66%). However, one introduced ant, *A. gracilipes*, was more aggressive and caused high mortality in *S. invicta* (62%). The application of venom of *S. invicta* caused high mortality in *T. melanocephalum* ($61.68 \pm 8.62\%$) but did not differ from the mortality of *A. gracilipes* and *S. geminata*. In the trophic assay, *S. invicta* occupied a significantly higher trophic position than the native ant and two introduced species, but occupied a similar trophic position to the introduced species *S. geminata* and *Paratrechina longicornis*. These results suggest species differences in behavioral and trophic interactions between invasive and resident ants may promote co-existence for some species and that *S. geminata* is most likely to be replaced by *S. invicta*.

Key words: *Solenopsis invicta*, resident ants, aggressive behavior, venom toxicity, trophic position.

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Introduction

Invasive ant species have achieved ecological success in new environments, often with devastating effects on agriculture, public health and local biodiversity. Decreases in the diversity and abundance of arthropod communities, and especially of resident ants, have been observed after invasion by exotic ants (PORTER & SAVIGNANO 1990, ALLEN & al. 2004). Aggression and competition between invasive and resident ants for similar resources are fundamental factors affecting successful invasion and ecological change (PORTER & al. 1988). Colony size, the ability to locate and

monopolize resources quickly, and the degree of competition with and aggressive behavior towards non-nestmates have all been suggested as important components to competitive ability of ants (HOLWAY & al. 2002). In interspecific encounters, species with superior aggression scores are generally expected to have a competitive advantage (OBIN & VANDER MEER 1989). Moreover, fast running can help ants hunt, escape from predators and other threats, and in the construction of subterranean burrows and nests (WILSON 1976, ZOLLIKOFER 1994, GRAVISH & al. 2013,

RAMDYA & al. 2017). Therefore, differences in the walking speed of ant species can influence the outcome of competitive interactions.

The red imported fire ant, *Solenopsis invicta* BUREN, 1972, a highly aggressive ant native to South America, is a globally invasive pest and has been a challenging invasive species in China since 2003 (LEI & al. 2019). It has invaded most provinces of southern China and is expanding its range at a rate of 26.5 - 48.1 km / year (LU 2014). Its negative consequences include a reduction in the diversity and local distribution of resident arthropod communities, especially other ants (HUANG & al. 2012). For example, previous research suggests *S. invicta* can displace previously introduced ants (*Linepithema humile* (MAYR, 1868) and *Solenopsis richteri* FOREL, 1909) as well as dominant native congeners including *Solenopsis geminata* (FABRICIUS, 1804) and *Solenopsis xyloni* MCCOOK, 1880 (see PORTER & al. 1988).

Several studies have examined possible mechanisms for *Solenopsis invicta*'s invasion success (YANG & al. 2009, WILDER & al. 2011, CHEN & al. 2014, HU & al. 2018). High levels of aggression and competition between *S. invicta* and resident ants likely contribute significantly to their success in new environments (BHATKAR 1988, CALLAWAY & ASCHEHOUG 2000, MORRISON 2000, SHEN & al. 2007, FADAMIRO & al. 2009, LAI & al. 2015). The importance of these mechanisms likely varies by region as intra- and interspecific competition, predation, the structure of local arthropod communities, and the presence of other invasive ants can all respond to biotic and abiotic factors (BEGON & al. 1986, MEYERS 2002, LAI & al. 2015). Our study provides information on behavioral interactions between invasive and resident species by examining competition between resident ants and recently introduced *S. invicta* in China.

In this study, we examined competitive interactions between *Solenopsis invicta* and one native and four introduced ant species in China (hereafter all called resident ant species). We measured interspecific aggression in individual and group assays, and compared walking speed among species to assess possible behavioral mechanisms for competitive exclusion. To understand the role of trophic ecology and flexibility in the invasion success of *S. invicta*, we compared the trophic position of *S. invicta* with that of the resident ants by using stable isotopes ($\delta^{15}\text{N}$). Finally, detoxification of alkaloids by ants can lead to competitive asymmetries (LEBRUN & al. 2014); therefore we also examined the effect of fire ant venom on resident ants. By measuring these behavioral and ecological interactions among these common species in China, we hope to provide insight into mechanisms that may predict which ants may become dominant and have a greater impact on local biodiversity (KIRSCHENBAUM & GRACE 2008).

Material and methods

Insects: The fire ant (*Solenopsis invicta*) and five resident ants (i.e., *Pheidole yeensis* FOREL, 1902, *Solenopsis geminata*, *Anoplolepis gracilipes* (SMITH, 1857), *Tapinoma melanocephalum* (FABRICIUS, 1793), and *Paratrechina*

longicornis (LATREILLE, 1802)) were collected from different habitats in Guangdong and Guangxi Provinces, China (Tabs. S1 - 5). The species of ants were confirmed using a key (ZHOU 2001, ZENG & al. 2005). One species of these resident ants is considered native to China (*P. yeensis*), while four are introduced (*S. geminata*, *P. longicornis*, *T. melanocephalum* and *A. gracilipes*). Colonies were fed a 20% sugar : water (w / w) solution and frozen locusts (*Locusta migratoria* LINNAEUS, 1758) under laboratory conditions ($24 \pm 2^\circ\text{C}$, 75% relative humidity (RH), and 14 : 10 h L : D) for at least 1 week prior to the experiments.

Tests of walking speed: To compare walking speed between *Solenopsis invicta* and resident ant species, a medium-sized worker of each species was randomly selected and put into a long, open, cuboid pipe ($245 \times 2.5 \times 1.0 \text{ cm l} \times \text{w} \times \text{h}$). The inner walls of the pipe were covered in talc powder to prevent the ants from climbing (NING & al. 2019). Once the workers were introduced into the pipe, they always began to walk without being motivated. A Nikon D7000 (Thailand, Nikon Corporation) was used to record videos for more than 60 seconds. We started recording when an ant moved into the pipe, and we stopped shortly after the ant left the pipe. Videos were transferred to a laptop to calculate the speed (distance traveled divided by time) of the ants. Species-specific video clips of the last 60 seconds in which ants were traveling in a straight line were selected and analyzed to determine their mean speeds (centimeters / second). Videos of five workers (medium size) were randomly selected from each of five colonies (Tab. S1, as digital supplementary material to this article, at the journal's web pages) to estimate the walking speed of each ant species. Although there was the potential for ants to behave abnormally in the pipe, many studies of ant movement have been performed successfully by utilizing entirely artificial foraging arenas (e.g., BOVET & al. 1989, JONES & PHILLIPS 1990, DUROU & al. 2001, CHALLET & al. 2005, PEARCE-DUVET & al. 2011).

Aggressive behavior between *Solenopsis invicta* and resident ants: To examine the behavioral response of coexisting ants to *S. invicta* invasion, individuals were collected from colonies of each species in the *S. invicta*-invaded sites (Tab. S2). We quantified interspecific aggression between *S. invicta* and each of the resident ant species using a behavioral assay previously adopted by CARLIN & HÖLLDOBLER (1986). To test for interspecific individual aggression, one medium-sized *S. invicta* worker (length = 4 - 5 mm) and one medium-sized worker from each colony of each resident ant species were separately placed in a Fluon-coated Petri dish (diameter = 4.0 cm, height = 1.5 cm) using a brush. Interactions were scored using a scale from I to IV (RICE & SILVERMAN 2013): Ants exhibited no change in direction or posture upon encounter or turned and moved away (Level I), ants made antennal contact that lasted for more than one second (Level II), ants opened their mandibles or turned their gasters upwards or towards their heads (Level III), and both ants attacked each other and were twisted together or one ant

fiercely attacked the other with upper jaws grappling or stinging (Level IV). Interaction between two ants was recorded for five minutes, and the ants' attack scores were used to calculate an aggression index using the formula:

$$\frac{\sum_{i=1}^n \delta_i f_i}{T}$$

for each trial (RICE & SILVERMAN 2013), where δ_i and f_i are the interaction score and frequency of each act, respectively, and T is the total interaction frequency, which is defined as the sum of all contacts between ants. Five colonies were tested in ten trials per colony with different workers.

For group aggression experiments, ten medium-sized workers of *Solenopsis invicta* (body length = 4 - 5 mm) and ten workers of the other resident ants (medium size) from colonies of fire ant-invaded and non-invaded sites were placed in a Petri dish (diameter = 9 cm, height = 1.5 cm, sides coated with Fluon) using a brush. Mortality was recorded after 3 h. Five colonies were tested, and three trials for each colony with different workers were performed (Tab.S3). Ants that could not stand due to damage after the encounter were considered dead.

Venom toxicity test: The protocol adopted by Fox & al. (2019) was followed for the venom toxicity test. The toxicity of fire ant worker (body length = 4.01 ± 0.46 mm, body weight = 1.09 mg) venom to resident ants was bioassayed by direct application of venom droplets from excised gasters of living ants (Fox & al. 2019). Workers of the resident ants were exposed to one droplet (ca. 20 nl) of crude fire ant venom from workers of *Solenopsis invicta*. Ants of medium size of each species (body length: *S. geminata* = 3.58 ± 0.45 , *Paratrechina longicornis* = 2.84 ± 0.16 , *Pheidole yeensis* = 3.21 ± 0.37 , *Anoplolepis gracilipes* = 4.34 ± 0.19 , and *Tapinoma melanocephalum* = 2.4 ± 0.18 mm) were selected to test the venom. A living excised gaster extrudes a droplet of crude venom when gently pressed near the tip. Resident ants to be assayed were grouped ($n = 10$) inside 7-cm-wide acrylate Petri dishes containing 2 mL of water in an Eppendorf tube filled with a wet piece of cotton. After the application of venom, mortality was recorded at three time intervals: 1 h, 12 h and 24 h. Individuals failing to hang on to the substrate when the plates were tipped to the side were recorded as "knocked down" (when still moving) or "dead" (where clearly not moving). For negative controls, ants were only touched with a glass needle containing no chemicals. Ants from three colonies were tested (Tab.S4), and for each colony, ten workers were randomly selected for the test.

Analysis of trophic position: To investigate the relative trophic position of ants in *Solenopsis invicta*-invaded areas, we examined the stable isotope composition of workers of ant species collected from *S. invicta*-invaded areas. Workers of each species were collected from three invaded areas (Tab.S5) between September and October 2018. For each area, 200 ant workers were collected, pooled together and stored at -80°C . We removed the gasters from each worker to prevent the influence of recent

stomach contents on $\delta^{15}\text{N}$ values (FELDHAAR & al. 2010). We also collected a range of herbivorous insects (locusts, grasshoppers, mealy bugs, caterpillars, and phytophagous beetles) from each of the selected sites. The samples were dried (60°C) for 24 - 48 h and then ground with a mortar and pestle. One milligram of each sample was packed into a tin capsule.

An isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc., USA) was used to measure stable isotopes according to the manufacturer's instructions. The stable isotope abundance (δ) was calculated as follows:

$$\delta(\text{‰}) = \left[\left(\frac{R_{\text{Sa}}}{R_{\text{St}}} \right) - 1 \right] \times 1000$$

where R_{sa} is the detected value of the collected samples, and R_{st} is the detected value of the standard sample.

The isotope ratio of herbivores was used as a baseline to predict the trophic position of the ants (WILDER & al. 2011). The trophic position of ants was calculated as follows: Trophic position = $(\delta^{15}\text{aN} - \delta^{15}\text{hN}) / 3.4 + 2$, where $\delta^{15}\text{aN}$ is the value for ants, and $\delta^{15}\text{hN}$ is the value for herbivores. According to a previous review, the mean enrichment in δN for one consumer-trophic-level transfer was set at 3.4 (Post 2002).

Statistical analysis: Except as noted, all analyses were carried out using GraphPad Prism version 7.00 for Windows (GraphPad Software, La Jolla, California, USA). The normality of the data was assessed using the Shapiro Wilk test in SPSS software. A general linear model (GLM) was used to analyze the walking speed and individual aggression test data, followed by Tukey's multiple comparison test to determine the difference between the walking speed and scores of individual aggression in each colony of each species. Toxicity test data were analyzed using a Kaplan-Meier survival test followed by a log-rank (Mantel-Cox) test. The Kruskal-Wallis H test was also used to determine the difference in survival at each time interval in each colony. Student's t-test was used to analyze the group aggression mortality data and the trophic position data in Minitab 16 software. In all tests, the significance level (α) was 0.05. Correlation analysis was used where appropriate.

Results

Walking speed: Walking speed differed significantly between resident ants and *Solenopsis invicta* ($F_{5,120} = 56.59$; $p < 0.001$). Similarly, the walking speeds of ants belonging to different colonies differed significantly ($F_{4,120} = 3.90$; $p = 0.005$), and the interaction effect of colonies and ant species ($F_{20,120} = 214$; $p = 0.006$) was significant. The speed of *Anoplolepis gracilipes* (7.55 ± 0.49 cm / s) was significantly faster than that of all other resident ants and *S. invicta* (3.21 ± 0.12 cm / s). In contrast, walking speed did not differ between *S. invicta* and any of the four other resident ants (*Paratrechina longicornis*, *S. geminata*, *Pheidole yeensis* or *Tapinoma melanocephalum*) (Fig. 1).

Individual aggression: Individual aggression did not differ significantly among different colonies of the

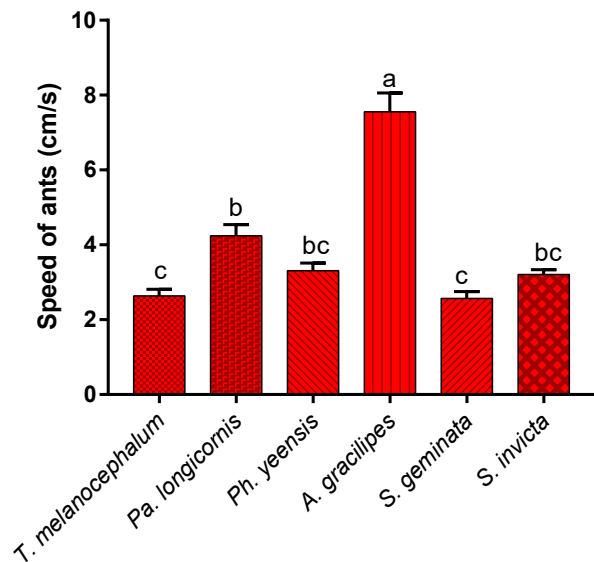


Fig. 1: Comparison of the walking speeds (mean \pm standard error) of *Solenopsis invicta* and five resident ants collected from different colonies. Bars with the same letter are not significantly different ($p > 0.05$, Tukey's test).

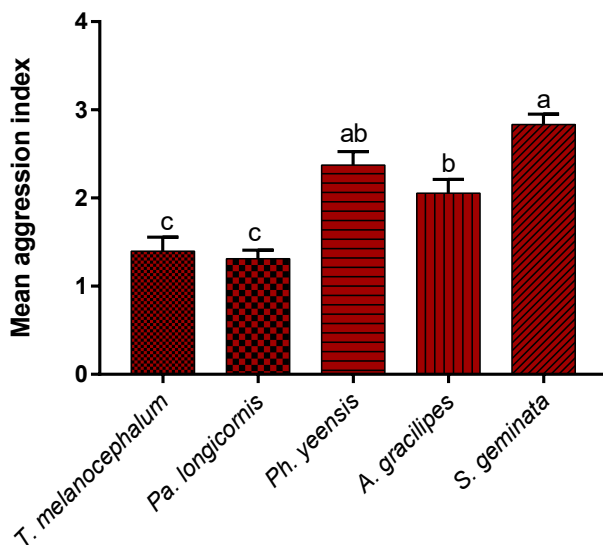


Fig. 2: Comparison of the aggression scores (mean \pm standard error) of resident ant colonies during individual aggression with *Solenopsis invicta*. Bars with the same letter are not significantly different ($p > 0.05$, Tukey's test).

same species ($F_{4, 225} = 0.55$; $p = 0.70$). However, aggression between *Solenopsis invicta* and other ant species varied significantly ($F_{4, 225} = 22.60$; $p < 0.001$), and there was a significant interaction between ant species and colony identity ($F_{16, 225} = 1.74$; $p = 0.04$). The highest aggression scores were observed between *S. invicta* and *S. geminata* (2.83 ± 0.11) and between *S. invicta* and *Pheidole yeensis* (2.37 ± 0.15), followed by *S. invicta* and *Anoplolepis gracilipes* (2.05 ± 0.15). Lower aggression scores were observed between *S. invicta* and *Paratrechina longicornis* (1.31 ± 0.09) and between *S. invicta* and *Tapinoma mel-*

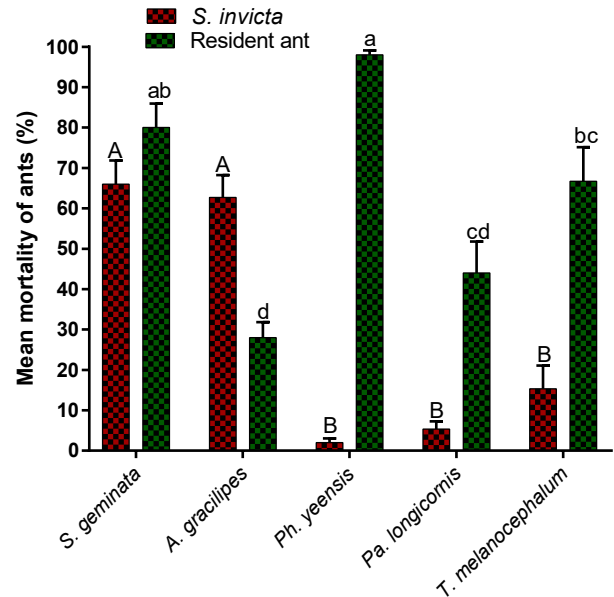


Fig. 3: Comparison of the mortalities (mean \pm standard error) of *Solenopsis invicta* and resident ants during group aggression. Bars with capital and small letters show the mortality of *S. invicta* and resident ants, respectively. Bars with the same letter are not significantly different ($p > 0.05$, Tukey's test).

anocephalum (1.39 ± 0.15). Aggression scores between *S. geminata* and *P. yeensis*, *A. gracilipes* and *P. yeensis*, and *P. longicornis* and *T. melanocephalum* did not differ significantly (Fig. 2). The relationship between walking speed and individual aggression was examined by calculating the correlation coefficient, and we observed no correlation between walking speed and individual aggression ($p > 0.05$).

Group aggression: In the group aggression assays, mortality varied among species pairs (Fig. 3). Workers of *Solenopsis invicta* were aggressive towards all four resident ant species, and higher mortality of *Paratrechina longicornis* ($t_4 = -2.89$; $p = 0.04$), *Tapinoma melanocephalum* ($t_4 = -2.66$; $p = 0.04$) and *Pheidole yeensis* ($t_4 = -77.01$; $p < 0.001$) than of *S. invicta* was observed in these pairs. However, the mortality of *S. geminata* and *S. invicta* did not differ significantly in this assay ($t_4 = -1.46$; $p = 0.21$). During group aggression with *Anoplolepis gracilipes* ($t_4 = 11.39$; $p < 0.001$), significantly higher mortality of *S. invicta* (62%) than of this resident ant (28%) was observed.

Venom toxicity test: Direct application of venom from gasters of *Solenopsis invicta* workers affect the resident ants differently ($H = 11.4$; $p = 0.02$). Overall mortality at the end of the trial (1 - 24h) was highest in *Tapinoma melanocephalum* ($61.68 \pm 8.62\%$), *Anoplolepis gracilipes* ($34.57 \pm 6.31\%$) and *S. geminata* ($32.58 \pm 8.56\%$), and these three species differed significantly from *Pheidole yeensis* (22.46%) and *Paratrechina longicornis* (21.85%) (Fig. 4 A). The survival time of *S. geminata* ($p = 0.02$), *P. longicornis* ($p = 0.02$) and *A. gracilipes* ($p = 0.003$) at each time interval was significantly different from that of *T. melanocephalum* ($p = 0.88$) and *P. yeensis* ($p = 0.41$) (Fig. 4B - F). The survival of *T. melanocephalum* differed

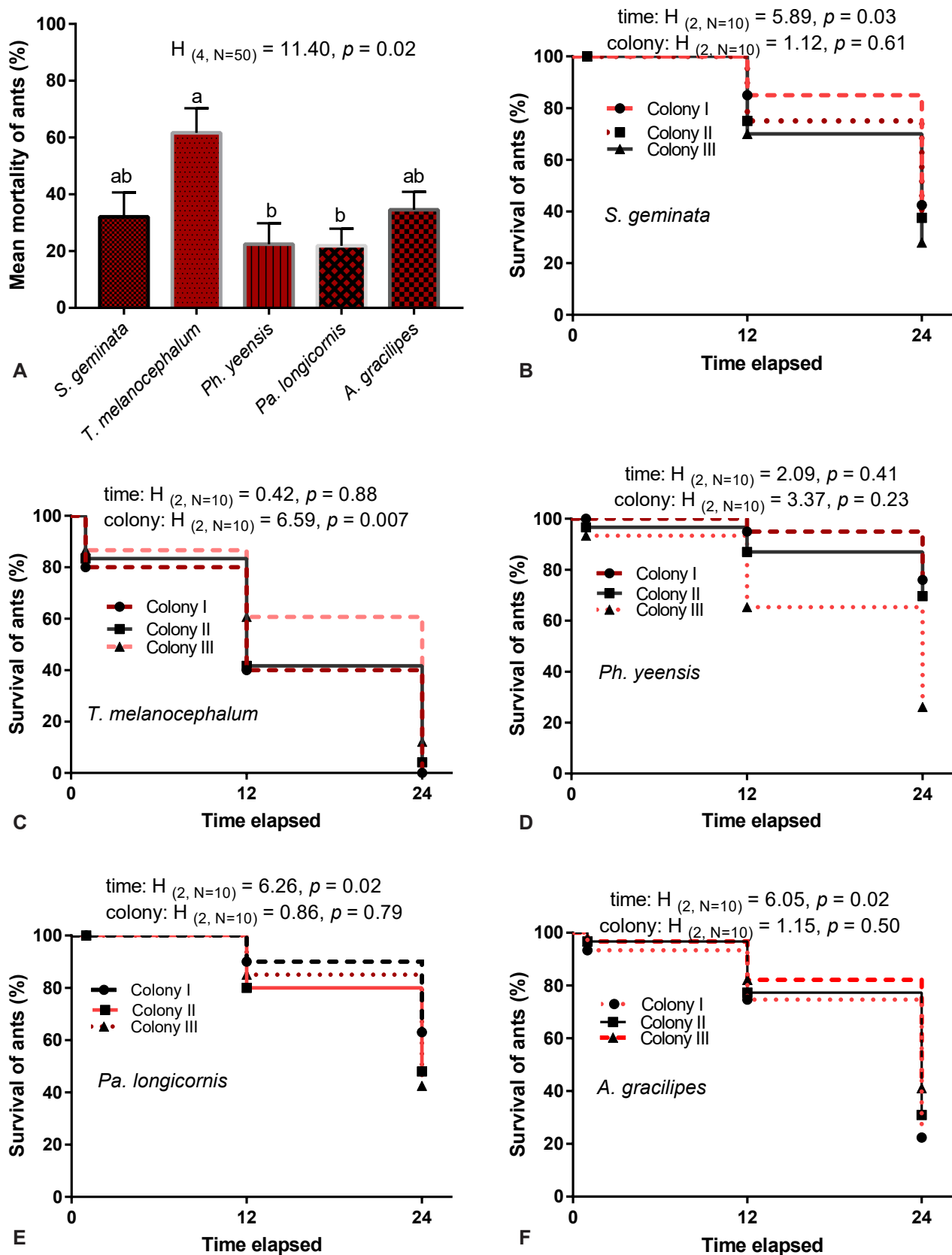


Fig. 4: Total mortality (mean \pm standard error, SE) of each resident ant at the end of the tested time (1 - 24h) after exposure to *Solenopsis invicta* venom (A). Survival (mean \pm SE) of five resident ants collected from three different colonies at three time intervals (1h, 12h, and 24h) after exposure to venom from *S. invicta* (B - F). Bars with the same letter are not significantly different ($p > 0.05$, Tukey's test).

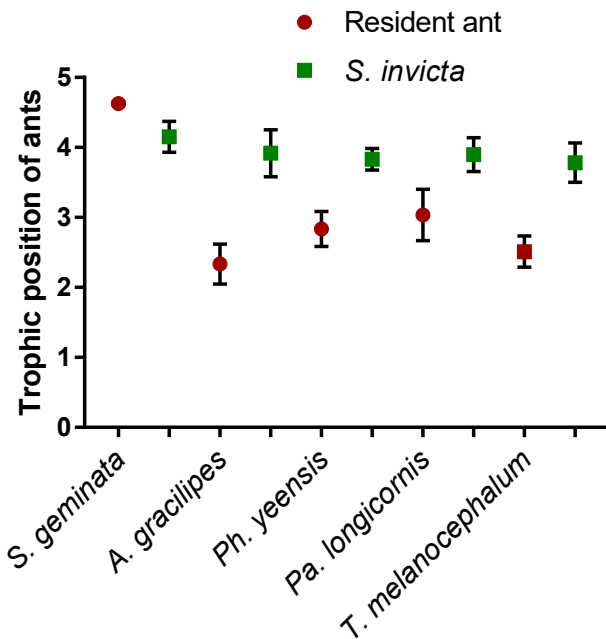


Fig. 5: The estimated trophic position (mean \pm standard error) of *Solenopsis invicta* and the resident ant species. Estimates of trophic position for each site incorporate $\delta^{15}\text{N}$ values of arthropods that are known herbivores as well as replicate colonies of *S. invicta* (as in POST 2002).

significantly among the three colonies ($p = 0.007$), while no significant differences in survival among the three colonies were observed for the other species.

Trophic position: *Solenopsis invicta* occupied a significantly higher trophic position than the resident ants *Pheidole yeensis* ($t_2 = -4.899$, $p = 0.04$), *Anoplolepis gracilipes* ($t_2 = -4.898$, $p = 0.04$), and *Tapinoma melanocephalum* ($t_2 = -5.02$, $p = 0.04$) but not *S. geminata* ($t_2 = 2.193$, $p = 0.16$) and *Paratrechina longicornis* ($t_2 = -1.472$, $p = 0.28$) (Fig. 5). Morphological characters such as the length of legs, which is indicative of walking speed, reflect trophic position or preferred microhabitat in ants. The relationship between the trophic position and walking speed of the ants was determined using Pearson correlation analysis. We observed no significant correlation between trophic position and walking speed in *S. invicta* ($r = 0.102$; $p = 0.62$), *S. geminata* ($r = 0.53$; $p = 0.80$), *A. gracilipes* ($r = -0.11$; $p = 0.58$), *P. yeensis* ($r = 0.062$; $p = 0.77$), *P. longicornis* ($r = -0.031$; $p = 0.88$) or *T. melanocephalum* ($r = -0.23$; $p = 0.25$).

Discussion

In battles involving social animals, the winning group often has superior numbers, but numerical advantage may be offset by the aggression, degree of preparedness and capability of fighting of the individual members of the group (TRANIELLO & BESHES 1991). Several factors contribute to the successful invasion of *Solenopsis invicta*, including the competitive ability and aggressive behavior of both individuals and entire colonies (CHEN & al. 2014, LAI & al. 2015). This study examined walking speed, interspecific

aggression, venom toxicity, and trophic position of *S. invicta* and five resident ant species in China. We found significant variation in each of these characteristics between *S. invicta* and the five resident ant species we examined.

Walking speed and pattern of movement are important factors in ecological interactions and may affect the competitive ability of ants during interspecific competition for food resources (PEARCE-DUVET & al. 2011). Rapid locomotion is essential for the transport of resources and information, response to threats, evacuation during flooding and in the construction of subterranean tunnels in ants (WILSON 1976, 1986). For example, *Solenopsis invicta* frequently contends with such events, and their proficiency in constructing nests within a wide range of soil conditions and ability to move fast within nests can facilitate successful establishment in new environments (TSCHINKEL 2006, GRAVISH & al. 2013). Foraging speed and pattern of movement in ants can create intense interspecific competition for food resources (PEARCE-DUVET & al. 2011). Faster-moving foragers have been hypothesized to be better discoverers of food, and they are associated with higher rates of carbohydrate intake (OSTER & WILSON 1979, DUSSUTOUR & SIMPSON 2009). A faster running speed during foraging also increases interspecific competition and aggressiveness in ants and other animals (PETREN & CASE 1996, GREVÉ & al. 2019). We found that the walking speed of *S. invicta* was significantly slower than that of the crazy ant *Anoplolepis gracilipes*, but not different from that of the other species. Differences in morphology can also affect speed; for example, longer legs allow faster movement (ZOLLIKOFER 1994, PEARCE-DUVET & al. 2011). Crazy ants have distinctly long legs (approximately 3.80 mm) compared to *S. invicta* (see ESPADALER & GÓMEZ 2001) which may account for their faster movement.

Previous studies showed that more aggressive individuals are generally bolder and more active (SEGEV & al. 2017), while slowly walking ants show low aggressiveness (COTE & al. 2010, RÉALE & al. 2010). However, the results of our study revealed no correlation between the individual aggression of ants and their walking speed. This may be due to differences in the natural habitats of these two ants. Fast-running ants with long legs prefer more open habitats than smaller ants with short legs, which prefer complex habitats (GIBB & PARR 2013, GIBB & al. 2015). Differences in habitat preference may therefore reduce interspecific competition.

During the individual aggression assay, maximum aggression scores were observed between *Solenopsis invicta* and *S. geminata* and *Pheidole yeensis*, followed by *Anoplolepis gracilipes*. In contrast, aggression between *S. invicta* and *Tapinoma melanocephalum* and *Paratrechina longicornis* was low, and workers of neither species participated in scrimmages, instead presenting only intimidating postures (GAO & al. 2011). The results of mortality in group aggression assays were similar in terms of species ranking. Previous studies showed that *S. geminata* and *T. melanocephalum* experience higher mortality in group and individual aggression assays with *S. invicta* (see WU & al. 2014,

LAI & al. 2015). *Solenopsis invicta* also suppresses nearby colonies of *P. yeensis* due to aggressive behavior (ZHOU & al. 2017). However, *A. gracilipes* was significantly more aggressive towards *S. invicta* and killed a larger number of *S. invicta* workers. *A. gracilipes* may be dominant to *S. invicta* due to its faster walking speed, larger body size, greater agility, higher physical aggression and use of chemical defensive compounds from a gland opening on the tip of its abdomen (ZHENG & al. 2007, DRESCHER & al. 2011, KRONAUER 2014). During individual aggression assays, *T. melanocephalum* and *S. invicta* did not act aggressively, but in group assays, the mortality of *T. melanocephalum* was greater than 65%. This may be due to their tendency to avoid confrontation during individual assays, while displaying different behaviors in group aggression assays (HUMAN & GORDON 1999, SAGATA & LESTER 2009).

Venom from *Solenopsis invicta* workers is composed of a complex mixture of alkaloids and is used for prey capture and colony defense. The venom was toxic to *Tapinoma melanocephalum*, *Anoplolepis gracilipes* and *S. geminata* and caused high mortality in these species. However, mortality of *Paratrechina longicornis* and *Pheidole yeensis* was lower, a finding in agreement with that of Fox & al. (2019) who observed that *P. longicornis* actively avoided application of fire ant gyne venom. Acidopore grooming, the ability to groom immediately after exposure to *S. invicta* venom, and increased survivorship were also observed in *P. longicornis* in previous studies (LEBRUN & al. 2015). Mortality of *P. yeensis* was high in the group aggression test while low in the venom toxicity test, suggesting that workers of *P. yeensis* are sensitive to physical attack but resistant to or able to detoxify the venom of fire ants. Several other studies also showed that *S. invicta* venom can cause mortality in *Linepithema humile*, *S. xyloni*, *Formica perpilosa* WHEELER, 1913 and *Spodoptera litura* (FABRICIUS, 1775) (see GREENBERG & al. 2008, LAI & al. 2010). Future studies will focus on evaluating venom from other tested species, such as *A. gracilipes*, which showed more aggression towards *S. invicta*.

Predicting the effects of an invasion on resident communities can be facilitated by understanding the trophic ecology of the species involved. Food availability and differences in trophic position between resident and introduced ants are important sources of variation that can enhance successful invasion. Species that excel at extracting nutrients from multiple trophic levels can reduce diversity by feeding at higher trophic levels, and maintain a higher abundance by feeding on lower trophic levels (TILLBERG & al. 2007). In our results, *Solenopsis invicta* occupied a higher trophic position than *Pheidole yeensis*, *Anoplolepis gracilipes* and *Tapinoma melanocephalum* but a similar trophic position to *Paratrechina longicornis* and *S. geminata*, indicating trophic similarity between these two ants (*P. longicornis* and *S. geminata*). Similar trophic positions can increase interspecific competition for food in these species, ultimately leading to trophic niche partitioning and / or competitive exclusion. The higher trophic position of introduced species, including *S. invicta*, than of native

ants might result in the depletion of important resources for resident species.

Based on our results and those of previous studies (e.g., PORTER & SAVIGNANO 1990), we suspect that *Solenopsis invicta* may displace *S. geminata* from these communities since the two species i) occupy the same trophic position; ii) have similar walking speeds and iii) are highly aggressive towards each other. Although *S. invicta* displayed high aggression towards or caused high mortality in four other resident species in our experiments, it may not displace them as readily because of different trophic positions. In addition, resident ants may display submissive behaviors to avoid attack by invasive ants (RICE & SILVERMAN 2013). Although the results of laboratory bioassays do not necessarily reflect the actual mechanisms of ant competition and aggression under field conditions, the results of our series of bioassays can provide insights into the interaction between local and invasive ants, and these insights will be useful for elucidating the competitive ability and dominance of *S. invicta* relative to resident ants in southern China. In addition, increasing numbers of exotic ants are invading new environments through development and economic globalization. The ecological and behavioral interactions among invasive ants are bound to reshape the local ant community and form a “novel community”. However, more complex interspecific relationships between invasive ants and local analogs, as well as other arthropods, may collectively determine the final outcome.

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Declarations

We confirm that this manuscript is original, has not been published elsewhere and is not under consideration by any other journal. All authors have contributed to the manuscript and approved its publication in this journal. All experiments were conducted according to the laws of the country where they were performed.

The authors confirm that there are no known conflicts of interest associated with this publication.

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