

GEOGRAPHIC VARIATION IN RESOURCE DOMINANCE–DISCOVERY
IN BRAZILIAN ANT COMMUNITIESDONALD H. FEENER, JR.,^{1,5} MATTHEW R. ORR,² KIRT M. WACKFORD,¹ JOSE M. LONGO,³
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Abstract. A predictive framework for the ecology of species invasions requires that we learn what limits successful invaders in their native range. The red imported fire ant (*Solenopsis invicta*) is invasive in the United States, Puerto Rico, Australia, New Zealand, and China. *Solenopsis invicta* appears to be a superior competitor in its introduced range, where it can cause the local extirpation of native species, but little is known about its competitive ability in its native range in South America. Here we examine the competitive ability of *S. invicta* for food resources in three widely separated Brazilian ant communities. Each of these communities contains 20–40 ant species, 8–10 of which were common and frequently interacted with *S. invicta*. *S. invicta* at all three sites was attacked by several species-specific phorid parasitoids, and at one site, two other species were attacked by their own specialized parasitoids. We examined interactions in these local communities for evidence that trade-offs among ant species between resource dominance and resource discovery, and between resource dominance and parasitoid vulnerability facilitate local coexistence. The trade-off between resource dominance and resource discovery was strong and significant only at Santa Genebra, where parasitoids had no effect on the outcome of confrontations at resources. At Bonito, parasitoids significantly reduced the ability of *S. invicta*, which was the top-ranked behavioral dominant, from defending and usurping food resources from subordinate species. In the Pantanal, *S. invicta* ranked behind three other ant species in a linear hierarchy of behavioral dominance, and lost the majority of its interactions with a fourth more subordinate species, *Paratrechina fulva*, another invasive species. Parasitoids of *S. invicta* were uncommon in the Pantanal, and did not affect its low position in the hierarchy relative to the other two sites. Parasitoids, however, did affect the ability of *Linepithema angulatum*, the top-ranked behavioral dominant in this community, from defending and usurping resources from behavioral subordinates. These results indicate that both interspecific competition and trait-mediated indirect effects of phorid parasitoids affect the ecological success of the red imported fire ant in its native range, but that the relative importance of these factors varies geographically.

Key words: Brazil; coexistence; competition; fire ant; Formicidae; invasive ants; native range; parasitoids; Phoridae; *Solenopsis invicta*; trade-offs.

INTRODUCTION

Invasive species are increasing the homogenization of the global biota through a variety of mechanisms (Lodge 1993, Lockwood and McKinney 2001, Keane and Crawley 2002, Shea and Chesson 2002, Olden and Poff 2003, 2004, Qian and Ricklefs 2006). Homogenization may increase as interactions between invasive and native species lead to the local extirpation of native species through competition, predation, or parasitism, or it may occur in the absence of such interactions simply because invasive species have broader environmental tolerances

and can thus spread more widely than native species. These various mechanisms are not mutually exclusive and may interact with one another. For example, relatively broader tolerances of invasive species in their introduced range could be due to escape from competitors, predators, or parasites in their native range, or new “niche opportunities” as a result of habitat modification in the introduced range (Keane and Crawley 2002, Shea and Chesson 2002). Gaining an understanding of these different mechanisms and their relative importance will require that we compare species interactions in both the introduced and native range of invasive species. For example, we cannot conclude that the success of an invader is the result of reduced competition in its introduced range without measuring the intensity of competition in its native range. However,

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such comparisons are still surprisingly rare (Ross et al. 1996, Callaway and Aschehoug 2000, Wolfe 2002, LeBrun et al. 2007).

Invasive ants are an increasing global problem and illustrate why comparative studies of mechanisms that regulate the distribution and abundance of these species in both their native and introduced ranges is essential to solving the species invasion problem. The red imported fire ant (*Solenopsis invicta*) and the Argentine ant (*Linepithema humile*) are two widespread, abundant, and ecological damaging invasive species. The densities of *S. invicta*, for example, are 4–10 times higher in its invasive range than in its native range (Porter et al. 1992, Porter et al. 1997), and it has reduced the abundance of many North American species (Hook and Porter 1990, Mann 1994, Allen et al. 1995, 2000, Kopachena et al. 2000). Numerous studies of these ants in their introduced ranges have attributed their invasion success to climatic favorability, adaptations to disturbed habitats, escape from natural enemies, competitive superiority, and genetic changes in colony structure during the invasion process (Tschinkel 1988, Ross et al. 1996, Porter et al. 1997, Tsutsui et al. 2000, Giraud et al. 2002, Holway et al. 2002, Tschinkel 2006). While these mechanisms are clearly not mutually exclusive, it is also likely that they are not equally important. Moreover, these mechanisms may interact with one another to enhance or diminish invasion success in unexpected ways. Proper evaluation of these mechanisms and their potential interactions require quantitative ecological studies from both the introduced and native ranges, yet quantitative studies in the native ranges of *S. invicta* and *L. humile* are rare (LeBrun et al. 2007).

Here we investigate species interactions in three widely separated local ant communities in Brazil in which *Solenopsis invicta* is a common and conspicuous member. Two of these local communities (Bonito and Pantanal) occur in the native range of *S. invicta*, whereas the third (Santa Genebra) occurs outside the eastern edge of the native range (Mescher et al. 2003). *Solenopsis invicta* may have invaded Santa Genebra and much of the rest of southeastern Brazil as a result of habitat modification due to deforestation. Natural enemies that may reduce the local population density of *S. invicta* in these local communities include competitively superior ant species and species-specific parasitoids in the dipteran family Phoridae. Each of these communities contained 20–40 ant species, 8–10 of which were common and frequently interacted with *S. invicta*. *Solenopsis invicta* at all three sites was attacked by 3–5 species of phorid parasitoids, and at one of the sites (Pantanal) two other ant species were attacked by their own specialized parasitoids.

We examined interactions in these local communities from the perspective of interspecific trade-off theory, which argues that local coexistence of interacting species requires the presence of interspecific trade-offs in the use of resources, vulnerability to natural enemies, and/or

sensitivity to environmental stresses (Chase et al. 2002, Chase and Leibold 2003, Kneitel and Chase 2004). In particular, we investigated these communities for the presence of a resource dominance–resource discovery trade-off and a resource dominance–parasitoid vulnerability trade-off (Feener 2000). These trade-offs are postulated to be common in local communities composed of omnivorous ground-foraging ant species (Feener 2000), and recent theoretical and empirical studies have demonstrated that they can indeed facilitate the local coexistence of competing ant species (Adler 1999, LeBrun and Feener 2002, 2007, LeBrun 2005, Adler et al. 2007). Moreover, empirical evidence suggests that introduced ant species that violate these interspecific trade-offs in a local community may become successful invaders and cause the subsequent extirpation of native species (Holway 1998, 1999).

Our study was designed to obtain answers to the following questions: (1) Are the local ant communities organized into linear dominance hierarchies at shared resources? (2) If linear dominance hierarchies do occur, what position does *S. invicta* occupy in the hierarchy? (3) Do the sites and species differ in the rates of resource discovery? (4) Is there a trade-off between resource discovery and resource dominance in these local communities? (5) How does the presence of species-specific phorid parasitoids affect the position of *S. invicta* and other host ant species in the dominance hierarchies and the expression of the dominance–discovery trade-off? Results of our study indicate that the answers to these questions vary geographically. In the *Discussion* we address the implications of this variation for understanding the invasion success of *S. invicta* in North America and other regions.

MATERIALS AND METHODS

Study sites

Our first study site was in the southern Pantanal in the state of Mato Grosso do Sul, near the town of Passo do Lontra (19°34' S, 57°01' W). The Pantanal (see Plate 1) is a large, seasonally inundated wetland that extends into parts of Paraguay, Bolivia, and Brazil and is considered the center of original native range of *Solenopsis invicta* (Mescher et al. 2003). We observed interactions among ant species during October and November 1997 in natural grassland bordered by *Tabebuia* savanna or by elevated patches of forest. These months marked the onset of the wet season before study sites were inundated. The Pantanal was the only site without a history of severe habitat alteration, although cattle graze at low densities in areas occupied by *S. invicta*. Our second site was also in the state of Mato Grosso do Sul, on a ranch outside the town of Bonito (21°08' S, 56°28' W). This site is well within the native range of *S. invicta*, although it is more upland and not subjected to seasonal flooding. *Solenopsis invicta* at this site occurs in deforested cattle pastures but not in the remaining fragments of the original forest cover. We

observed species interactions at this site between October and November 1998. Our third site was at Mata Santa Genebra (22°49' S, 47°06' W), a small (~250 ha) reserve in Sao Paulo State near the city of Campinas. The reserve is a remnant forest fragment, and the road around it, where *S. invicta* occurs, is an open transition into surrounding farmland. Santa Genebra is outside of *S. invicta*'s original native range (Trager 1991, Mescher et al. 2003), but *S. invicta* now occurs throughout southeastern Brazil and the population at Santa Genebra is well established and supports a full complement of phorid parasitoids. We selected this site because it was protected from human disturbance and differed in the ant and phorid faunas from the other two sites. We observed interactions among ant species on both sides of the dirt road that surrounds the reserve between April 1997 and February 1999.

Food resources and distribution

Food resources consisted of tuna canned in water that was compressed to uniform volume and density in a 0.5-cm³ plastic hypodermic syringe with its end cut off. Tuna resources were placed in the field based on *S. invicta*'s pattern of occurrence at a site. At Santa Genebra, where *S. invicta* colonies occurred primarily along the road ringing the reserve, we established four 2500-m roadside transects (hereafter "plots"). Stations for resources were located every 2.5 m along the road, and alternated on opposite sides of the road. We worked at this site in groups of 1–3, with each observer collecting data at up to three adjacent tuna resources located on the same side of the road. Each time that adjacent baits were placed in the field, their location was chosen at random, except that stations in direct sunlight were avoided during midday.

At Bonito and the Pantanal, *S. invicta* colonies were distributed throughout the habitat. Resource stations were established inside a 45 × 45 m quadrat (hereafter "plot") with horizontal and vertical lines every 5 m, and one station on every corner in the grid, for a total of 100 stations per plot. We used five plots in Bonito and six in the Pantanal. Plots were separated by 50 m to 4 km in Bonito and 50 m to 12 km in the Pantanal. Each station in a plot was used once, with the exception of six stations in the Pantanal, which were each used twice. At these sites, 2–6 observers monitored activity at three resources each simultaneously, while an extra person was responsible for collecting detailed observations at resources that attracted *S. invicta*. We observed 537 tuna resources at Santa Genebra, 500 at Bonito, and 606 in the Pantanal.

At Santa Genebra, tuna resources were left in the field for 3 h or until all of the resource was gone. At Bonito and the Pantanal, resources were left in the field for 3 h in the early morning or 2 h in the late afternoon, which helped to avoid the hottest midday temperatures, when most ant species were inactive.

Observations at resources

During the first 10 min after being put on the ground, resources were observed every 1–3 min. Thereafter resources were observed every 5–10 min, unless *S. invicta* appeared, in which case they were observed at least every 5 min and often were observed continuously. During each observation, we recorded temperature, humidity, the number and species of ants in contact with the resource, the number and species of ants in a 5 cm diameter circle around the resource, and the identity and number of phorid parasitoids present. For every resource we estimated the approximate percentage of the resource removed by each ant species that visited it.

Ants and phorid parasitoids not identified to species were identified to genus and then given a morphospecies number. All visually recognizable morphospecies were considered separate species, except a few very uncommon species of *Pheidole* and *Pseudomyrmex*, which were lumped. Morphospecies with the same number but from different sites were morphologically different. Specimens were deposited at the Museum of Zoology, University of São Paulo with their associated morphospecies identification code.

Outcomes at resources

Discovery time of a resource was quantified as the time elapsed between the time it was placed on the ground and the time that the first ant visited it. Resource discovery time of a focal ant species was measured as the time elapsed between the time the resource was placed on the ground and the time it was first visited by the focal species, regardless of when the focal species discovered the resource relative to other ant species (e.g., first, second, third, and so on). Mean discovery time for an ant species included only resources to which it was attracted and not resources which it never visited.

After discovery, an ant species won an encounter with another species at a tuna resource if any of the following conditions was met: (1) if it arrived first at a resource, remained at the resource in the presence of a second species, and the second species harvested less than one percent of the tuna; (2) if it was expelled temporarily from a resource, but returned to expel the species that initially displaced it; (3) if it arrived second at a resource, and the species that preceded it abandoned the resource in its presence; or (4) if it arrived second at a resource, and removed more than half of the resource even if the species that preceded it did not abandon the resource. Condition (4) was uncommon: it applied to a few interactions between *S. invicta* and large ants (mainly *Ectatomma*), where the large ant managed to carve and carry off a large portion of the resource while *S. invicta* remained upon the portion left behind. Interactions that did not fit any of these criteria were considered ties.

Small ants were considered to have abandoned a resource if the number of workers in contact with the tuna dropped to 0 and remained there. Large ants that did not recruit many nest mates, such as *Ectatomma*,

were considered to have abandoned a resource if they left the resource and did not harvest any more during the remainder of the observation period. At any one resource, we recorded more than one outcome between the same two species only if interactions between them were separated by a period during which a third species occupied the resource, with neither of the first two species present. This seldom occurred.

Statistical analysis

Resource discovery ability of ant species was estimated in two ways. First, we estimated median time to resource discovery using failure time analysis. In this analysis, median time to resource discovery was median time to first discovery in a right-censored Kaplan-Meier survival analysis with either site or ant species as the explanatory variables. We tested for significant differences in median discovery times among sites and among species within sites using the log-rank test and comparing confidence limits. Median discovery time is equivalent to the time it takes for 50% of the resources to be discovered at a site or by a species. Failure time analyses were conducted with the survival package available in R, version 2.3.1 (R Development Core Team 2006). Second, we estimated resource discovery ability of an ant species as the difference between the observed number of resources discovered first and the expected number of resources discovered first based on the total number of resources visited by each species:

$$D_i = O_i - T_i(F/T)$$

where D_i is the discovery ability of species i , O_i is the observed number of resources discovered first by species i , T_i is the total number of resources discovered by species i , F is the total number of resources discovered by all ants species, and T is the total number of times all resources were discovered by ant species. This measure of discovery ability was a modified version of the measure used by LeBrun and Feener (2007). The first estimate of discovery ability is an absolute estimate of discovery ability that does not account for differences in colony density, number of foragers, or forager behavior, whereas the second estimate is a relative measure of resource discovery that adjusts for species differences in colony density.

We defined resource or behavioral dominance as the ability of an ant species to gain or maintain control of a resource through superior fighting or recruitment abilities, whereas ecological dominance is the ability of an ant species to remove resources from the environment through a combination of resource dominance and resource discovery or numerical abundance (Davidson 1998). Resource dominance was estimated by constructing a set of matrices of dominance interactions for each community using the outcome of pairwise interactions at contested resources. We included only the most commonly observed species at a site (8 species for Bonito, 9 species for the Pantanal, and 10 species for Santa

Genebra) because adding additional species to a matrix left too many unresolved interactions to analyze the linearity of dominance hierarchies. We quantified behavioral dominance of each species in each matrix by calculating the proportion of total confrontations won and then adjusting it using Colley's bias-free method (Colley 2002). This method is used to rank college football teams and has an advantage over the unadjusted proportion of total confrontations won because it accounts for variation in the behavioral dominance of each species' competitors (Colley 2002, LeBrun and Feener 2007).

Linearity of the dominance hierarchy in each matrix was analyzed using the computer program MatMan Version 1.1 (de Vries et al. 1993, de Vries 1995, 1998, Noldus Information Technology 2002), which uses a randomization method to test the null hypothesis of matrix nonlinearity based on a modified version of Landau's h' statistic (de Vries et al. 1993, de Vries 1995, 1998). Landau's h' statistic ranges from 0 for perfectly circular dominance relationships to 1 for perfectly linear ones. We used 10 000 randomizations in our statistical tests. If the randomization test supported the hypothesis of a linear dominance hierarchy, we then used the program MatMan to rank the species by minimizing the number of intransitive interactions and ties and to identify pairwise interactions that were inconsistent with the rank order (de Vries et al. 1993, de Vries 1995, 1998). This method of ranking species was strongly correlated with the rankings provided by Colley's bias-free method.

Effect of the presence/absence of phorid parasitoids on the outcome of confrontations between focal host species and other host and non-host species was analyzed using 2×2 contingency tables in which the total number of wins and losses of the focal host species was compared in the presence and absence of phorid parasitoids. Because sample sizes were small for number of confrontations in the presence of parasitoids, we used the exact tests available in the program StatXact, version 7 (Cytel 2005), to calculate the significance of the phorids effects.

To determine whether *S. invicta*'s ability to defend a resource depended on the number of its workers present, we used a Mann-Whitney U test to compare the maximum number of *S. invicta* workers present at resources that it successfully defended with the maximum number present at resources it lost. Comparisons were made separately for *S. invicta*'s interactions with each of three common ant species: *Camponotus rufipes*, *E. brunneum*, and *P. fulva*. These three species were chosen because they won the majority of their encounters against *S. invicta*.

RESULTS

Resource discovery

Resource discovery times were significantly different among sites ($\chi^2 = 40.6$, $df = 2$, $P < 0.001$), with median discovery time faster at Santa Genebra (10 min, 95%

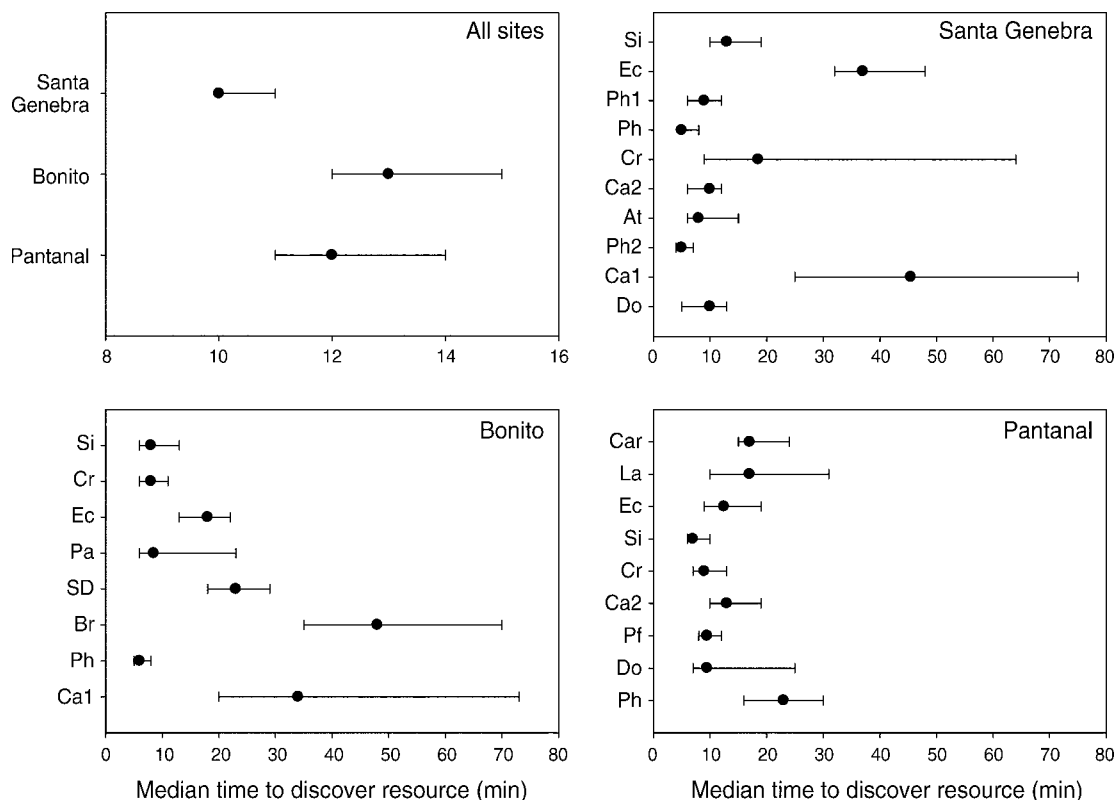


FIG. 1. Comparison of resource discovery times (min) among sites and among ant species within sites. Symbols are the median discovery time, and error bars show the lower and upper 95% confidence limits of the medians. Species are ordered by the proportion of confrontations won (with those winning the highest proportion at the top); see Fig. 3 for species names.

confidence interval [CI] = 10–11) than at either Bonito and the Pantanal (13 min, 95% CI = 12–15; 12 min, 95% CI = 11–14, respectively), which did not differ from one another (Fig. 1). Within each site, median time to resource discovery was significantly different among species (for Santa Genebra, $\chi^2 = 113.0$, $df = 9$, $P < 0.001$); for Bonito, $\chi^2 = 94.8$, $df = 7$, $P < 0.001$; for Pantanal, $\chi^2 = 27.0$, $df = 8$, $P < 0.001$), but discovery times were more uniform in the Pantanal (Fig. 1). The median rate of resource discovery for *Solenopsis invicta* was 7 min (95% CI = 6–10) in the Pantanal, 8 min (95% CI = 6–13) at Bonito, and 13 min (95% CI = 10–19) at Santa Genebra. Relative to other species at these sites, *S. invicta* had the faster rate of resource discovery in the Pantanal, the second fastest rate at Bonito, and only the seventh fastest rate at Santa Genebra (Fig. 1).

Our second measure of discovery ability adjusted for species differences in abundance by comparing the number of resources discovered first by a species against the number expected based on the total number of resources at which it was present at a site. This second measure of discovery ability was significantly correlated with our first measure at Bonito ($r = -0.75$, $P = 0.03$) and in the Pantanal ($r = -0.88$, $P = 0.002$), but not at Santa Genebra ($r = -0.09$, $P = 0.8$). All three sites deviated significantly from null expectation that ant

species discover resources in proportion to their presence at them ($\chi^2 = 414.56$, $df = 9$, $P < 0.0001$ for Santa Genebra; $\chi^2 = 45.39$, $df = 6$, $P < 0.0001$ for Bonito; and $\chi^2 = 34.74$, $df = 8$, $P < 0.0001$ for Pantanal). At Santa Genebra, *S. invicta*, *Ectatomma*, and species of *Pheidole* discovered a lower proportion of resources than expected ($\chi^2 = 37.19$, $df = 1$, $P < 0.0001$; $\chi^2 = 16.04$, $df = 1$, $P < 0.0001$; $\chi^2 = 65.06$, $df = 1$, $P = 0.0001$, respectively), whereas *Atta* and *Camponotus* sp. 2 discovered a much higher proportion than expected ($\chi^2 = 124.20$, $df = 1$, $P < 0.0001$; $\chi^2 = 164.91$, $df = 1$, $P < 0.0001$, respectively), and *Camponotus* sp. 1, *Crematogaster*, and *Dorymyrmex* discovered resources in the proportion expected. At Bonito, *S. invicta* and *Pheidole* discovered significantly more resources than expected ($\chi^2 = 14.97$, $df = 1$, $P = 0.0001$; $\chi^2 = 4.47$, $df = 1$, $P = 0.034$, respectively), while *Brachymyrmex*, *Camponotus*, and *Ectatomma* species discovered significantly fewer ($\chi^2 = 12.13$, $df = 1$, $P = 0.0005$; $\chi^2 = 7.58$, $df = 1$, $P = 0.006$; $\chi^2 = 4.45$, $df = 1$, $P = 0.035$, respectively) and *Crematogaster*, *Paratrechina*, and *Solenopsis* (*Diplophortum*) discovered resources at their expected proportions. In the Pantanal, only three species deviated significantly from expectation: *S. invicta* was better than expected ($\chi^2 = 8.68$, $df = 1$, $P = 0.003$), while *Camponotus rufipes* and *Pheidole* species were poorer discoverers than

TABLE 1. Proportion of confrontations won by host ant species against competing ant species in the presence and absence of phorid parasitoids at three sites in Brazil.

Site and host species	Competitors	Proportion won by host		<i>P</i>
		Parasitoid present	Parasitoid absent	
Santa Genebra <i>Solenopsis invicta</i>	all species	0.81 (31)	0.82 (279)	0.8
	<i>Ectatomma</i>	0.56 (9)	0.50 (32)	0.8
Bonito <i>Solenopsis invicta</i>	all species	0.27 (15)	0.93 (104)	0.0001
	<i>Ectatomma</i>	0.00 (5)	0.83 (24)	0.0001
	<i>Crematogaster</i>	0.25 (4)	0.93 (27)	0.0008
Pantanal <i>Solenopsis invicta</i>	all species	0.41 (12)	0.57 (182)	0.3
	<i>Linepithema angulatum</i>	0.20 (10)	0.88 (26)	0.0002
	<i>Paratrechina fulva</i>	0.33 (3)	0.22 (118)	0.6

Notes: The number in parenthesis is the total sample size. *P* values are based on exact tests of 2×2 contingency tables.

expected ($\chi^2 = 9.33$, $df = 1$, $P = 0.002$; $\chi^2 = 5.87$, $df = 1$, $P = 0.015$, respectively).

Resource dominance

We examined resource or behavioral dominance of the common ant species at our three study sites under four different conditions. First, we considered interactions among species that did not act as hosts for phorid parasitoids. Second, we considered interactions among host and non-host species in the *absence* of phorid parasitoids. This gave us an estimate of what dominance relationships among ant species would be if they were never affected by phorid parasitoids. Third, we considered interactions among host and non-host species in the *presence* of phorid parasitoids. This gave us an estimate of what dominance relationships among ant species would be if they were always affected by phorid parasitoids. Finally, we considered all observed interactions among host and non-host ant species. This gave a measure of the actual effect of phorid parasitoids on the dominance relationships among ant species.

At Santa Genebra, only *Solenopsis invicta* was attacked by phorid parasitoids. Phorid parasitoids observed at this site included *Pseudacteon* "mini" *obtusus*, *Pseudacteon solenopsidis*, and *Pseudacteon tricuspis*, with *P. solenopsidis* and *P. obtusus* the most common along recruitment trails (Orr et al. 1997, Seike 2002). One or more of these parasitoids were present during 31 out of 309 (0.10) interactions involving *S. invicta* that we observed at contested resources, and their presence had no significant effect on the outcome of confrontations between *S. invicta* and other ant species (Table 1).

The 10 most common species at Santa Genebra formed a significantly linear dominance hierarchy under all conditions. The nine non-host species formed a significant linear dominance hierarchy in the absence of *S. invicta* ($h' = 0.72$, $P = 0.005$), with *Ectatomma* and *Pheidole* sp. 1 taking the top two ranks (Table 2). When interactions involving host and non-host species in the absence of parasitoids were considered, *S. invicta* emerged as the dominant species in a statistically

significant linear hierarchy ($h' = 0.78$, $P < 0.001$), although *Ectatomma* had a slightly higher Colley ranking (Table 2). When only parasitoid-mediated interactions involving non-host species and parasitoid-mediated interactions involving *S. invicta* were included, *S. invicta* was still ranked first in a significantly linear hierarchy ($h' = 0.72$, $P = 0.013$). Not surprisingly, the dominance hierarchy was significantly linear when all interactions were included ($h' = 0.79$, $P < 0.001$) and *S. invicta* remained the top-ranked species (Table 2). Thus, at Santa Genebra, the presence of phorid parasitoids had no effect on the outcome of confrontations among ant species and no effect on the dominance relationships among them.

At Bonito, *S. invicta* was again the only ant species that was attacked by phorid parasitoids, which were present at 15 of 119 (0.13) interactions involving this species. Phorid parasitoids observed at this site included *Pseudacteon curvatus*, *Pseudacteon dentiger*, *Pseudacteon litoralis*, *Pseudacteon nudicornis*, and *Pseudacteon tricuspis*, with *P. nudicornis* and *P. dentiger* most common along recruitment trails (Seike 2002). In contrast to Santa Genebra, however, the presence of parasitoids (mostly *P. nudicornis*) at contested resources had a significant effect on the outcome of confrontations between *S. invicta* and other species (Table 1). In the presence of parasitoids, *S. invicta* won only 0.27 of its confrontations with other species, while in their absence it won 0.93 of its confrontations. This parasitoid-induced asymmetry in the outcome of confrontations was also significant for interactions involving *Ectatomma* and *Crematogaster*, two of the strongest competitors of *S. invicta* (Table 1).

In contrast to Santa Genebra, we found no evidence for significant linear dominance hierarchy at Bonito (Table 3). The seven non-host species did not form a statistically significant linear dominance hierarchy in the absence of *S. invicta*, with *Crematogaster* and *Paratrechina fulva* taking the top two ranks in behavioral dominance (Table 2). When interactions involving non-host species and *S. invicta* in the absence of parasitoids were considered, the linearity of the dominance hierar-

TABLE 2. Statistics for dominance relationships among the most common ant species at Santa Genebra, Bonito, and Pantanal study sites in Brazil.

Site and species	Non-host species		Parasitoids absent		Parasitoids present		All interactions	
	Rank	Colley	Rank	Colley	Rank	Colley	Rank	Colley
Santa Genebra								
<i>Solenopsis invicta</i>			1	0.77	1	0.80	1	0.78
<i>Ectatomma</i> sp.	1	0.84	2	0.81	2	0.80	2	0.81
<i>Pheidole</i> sp. 1	2	0.69	3	0.65	3	0.65	3	0.65
<i>Pheidole</i> spp.	3	0.55	4	0.52	4	0.51	4	0.51
<i>Crematogaster</i> sp.	4	0.61	5	0.58	5	0.58	5	0.58
<i>Camponotus</i> sp. 1	5	0.44	6	0.38	6	0.42	6	0.38
<i>Atta</i> sp.	6	0.40	7	0.35	7	0.37	7	0.35
<i>Pheidole</i> sp. 2	7	0.49	8	0.45	8	0.46	8	0.45
<i>Camponotus</i> sp. 2	8	0.23	9	0.22	9	0.19	9	0.22
<i>Dorymyrmex</i> sp.	9	0.25	10	0.26	10	0.22	10	0.26
Bonito								
<i>Solenopsis invicta</i>			NA	0.90	NA	0.33	1	0.83
<i>Crematogaster</i> sp.	NA	0.74	NA	0.60	NA	0.74	2	0.61
<i>Ectatomma</i> sp.	NA	0.62	NA	0.55	NA	0.65	3	0.58
<i>Paratrechina fulva</i>	NA	0.67	NA	0.57	NA	0.68	4	0.56
<i>Solenopsis</i> (<i>Diplorhoptrum</i>)	NA	0.57	NA	0.47	NA	0.59	5	0.46
<i>Brachymyrmex</i> spp.	NA	0.46	NA	0.43	NA	0.44	6	0.43
<i>Pheidole</i> spp.	NA	0.28	NA	0.25	NA	0.31	7	0.26
<i>Camponotus</i> sp.	NA	0.18	NA	0.22	NA	0.24	8	0.27
Pantanal								
<i>Linepithema angulatum</i>			1	0.73	NA	0.28	2	0.60
<i>Camponotus rufipes</i>	NA	0.69	2	0.78	NA	0.71	1	0.78
<i>Solenopsis invicta</i>			3	0.62	NA	0.48	4	0.61
<i>Ectatomma</i> sp.	NA	0.77	4	0.71	NA	0.83	3	0.73
<i>Crematogaster</i> sp.	NA	0.59	5	0.59	NA	0.65	5	0.61
<i>Camponotus</i> sp.	NA	0.34	6	0.27	NA	0.41	6	0.29
<i>Paratrechnia fulva</i>			7	0.36	NA	0.42	7	0.37
<i>Dorymyrmex</i> sp.	NA	0.29	8	0.19	NA	0.34	8	0.21
<i>Pheidole</i> spp.	NA	0.32	9	0.26	NA	0.38	9	0.29

Notes: Dominance was measured from interaction matrices constructed for non-host ant species, host and non-host species in the absence of phorid parasitoids, host and non-host species in the presence of parasitoids, and the sum of all interactions. Linearity of dominance hierarchies was tested using a randomization test based on a modified version of Landau's h' statistic. "Rank" is the dominance rank of a species in a statistically significant linear dominance hierarchy in which intransitivities were minimized. Ranks in nonsignificantly linear hierarchies are indicated as "NA," or not applicable. "Colley" is the Colley ranking of a species, which is an unbiased measure of the proportion of confrontations won.

chy was nearly significant ($h' = 0.57$, $P = 0.13$), with *S. invicta* scoring higher in behavioral dominance than any other species (Table 2). When interactions among non-host species and those involving *S. invicta* that were mediated by parasitoids were considered, linearity of the dominance hierarchy was not statistically significant (Table 3), but now *S. invicta*'s score of behavioral dominance was lower than five of the seven other species (Table 2). When all observed interactions were included in the dominance analysis, *S. invicta* emerged as the top-ranked dominant in a nearly significant linear dominance hierarchy (Table 2). Although, parasitoids strongly affected the dominance score of *S. invicta* when present, their overall effect on dominance interactions among ant species at Bonito was limited, due to their low prevalence.

In the Pantanal, three of the nine most common ant species, *S. invicta*, *Linepithema angulatum*, and *Paratrechina fulva*, were attacked by their own species-specific phorid parasitoids. Parasitoids associated with *S. invicta* at this site included *P. curvatus*, *P. dentiger*, *P. litoralis*, *P. nudicornis*, and *P. tricupis*, with *P. nudicornis* the most

common species along recruitment trails (Seike 2002). *Linepithema angulatum* was attacked by *Pseudacteon lontrae* (Mattos and Orr 2002, Orr et al. 2003; *L. angulatum* was previously identified as *L. piliferum* [Orr et al. 2003]) and *P. fulva* by an unidentified species of *Pseudacteon*. Parasitoids were present at 12 of 194 (0.06) confrontations involving *S. invicta*, 10 of 36 (0.28) confrontations involving *L. angulatum*, and three of 121 (0.02) confrontations involving *P. fulva*. Outcomes of confrontation between *S. invicta* and other species and between *P. fulva* and other species were unaffected by the presence of parasitoids (Table 1), but parasitoids had a significant negative effect on the proportion of confrontations won by *L. angulatum* (Table 1). *L. angulatum* won 0.88 of its confrontations in the absence of parasitoids but only 0.20 in their presence.

Although there was no statistically significant linear dominance hierarchy among non-host species (Table 3), a statistically significant dominance hierarchy did emerge from interactions among all nine species in the absence of phorids ($h' = 0.68$, $P = 0.02$), with the four top ranks going to *L. angulatum*, *C. rufipes*, *S. invicta*,

TABLE 3. Significance tests for linearity of the dominance hierarchies at Santa Genebra, Bonito, and Pantanal study sites.

Site	Non-host species		Parasitoids absent		Parasitoids present		All interactions	
	h'	P	h'	P	h'	P	h'	P
Santa Genebra	0.72	0.005	0.78	<0.001	0.63	0.01	0.79	<0.001
Bonito	0.50	0.35	0.57	0.13	0.45	0.27	0.67	0.06
Pantanal	0.71	0.17	0.68	0.02	0.48	0.16	0.69	0.02

Notes: We report h' , the modified Landau's h statistic, which corrects for unknown relationships (see deVries 1995). P values were determined from a randomization test available in the computer program MatMan Version 1.1 (Noldus Information Technology 2002; see *Materials and methods: Statistical analysis* for more details).

and *Ectatomma* (Table 2). When parasitoid-mediated interactions were included in the interaction matrix, linearity of the dominance hierarchy was no longer significant (Table 3). In the presence of parasitoids, *S. invicta* had the fourth highest score of behavioral dominance, while *L. angulatum* had the lowest. Interestingly, parasitoids also affected the relative behavioral dominance of the non-host species *Ectatomma* and *C. rufipes* as measured by their Colley scores. In the absence of parasitoids, *C. rufipes*' Colley score was higher than *Ectatomma* (0.78 vs. 0.71), whereas in the presence of parasitoids it was lower (0.71 vs. 0.83; Table 2). When all observed interactions were included, there again was a significant linear dominance hierarchy among species ($h' = 0.69$, $P = 0.02$), in which the first four ranks were occupied by *C. rufipes*, *L. angulatum*, *Ectatomma*, and *S. invicta*. Thus, in the complete absence of parasitoids, *S. invicta* and *L. angulatum* ranked slightly higher in behavioral dominance (one level in each case) compared to their rankings with parasitoids (Table 2).

A persistent inconsistency in species ranking in this local community involved the interaction between *S. invicta* and *P. fulva*. *P. fulva* was ranked seventh in the dominance hierarchy because it generally had low success against most species in the community, but it nevertheless won a majority of its confrontations against *S. invicta*, which was ranked fourth in the community. This inconsistency appears to be the result of a specialized attack behavior that *P. fulva* uses against *S. invicta* during confrontations at resources (see *Results: Interactions of Solenopsis invicta with competitive dominants*).

Amount of resource retrieved by a species is a measure of its ecological dominance. At Santa Genebra, the top three behavioral dominant species (*S. invicta*, *Ectatomma*, and *Pheidole* sp. 1) retrieved 60–70% of each resource they discovered, whereas less dominant species retrieved a maximum of 30%. At Bonito, the behavioral dominance of *S. invicta* at resources was reflected in its ecological dominance. It retrieved between 50–60% of each resource it discovered, whereas the rest of the species retrieved in the range of 2–15% (Fig. 2). In the Pantanal, however, the positive relationship between behavioral and ecological dominance was less clear. Here, the third- and fourth-ranked behavioral dominants, *Ectatomma* and *S. invicta*, were

closely matched ecological dominants, each harvesting 40% of the resources they visited. The top-most behavioral dominant, *C. rufipes*, was the third-ranked ecological dominant, retrieving 30% of each resource discovered. The second-ranked behavioral dominant, *L. angulatum*, was a distant fourth-ranked ecological dominant retrieving only 10% of the resources it discovered, reflecting the significant impact phorid parasitoids had on its resource retrieval (Fig. 2).

Dominance–discovery trade-off

We tested for the presence of a trade-off between resource dominance and resource discovery in the three local ant communities by looking for a negative correlation between the behavioral dominance (Colley

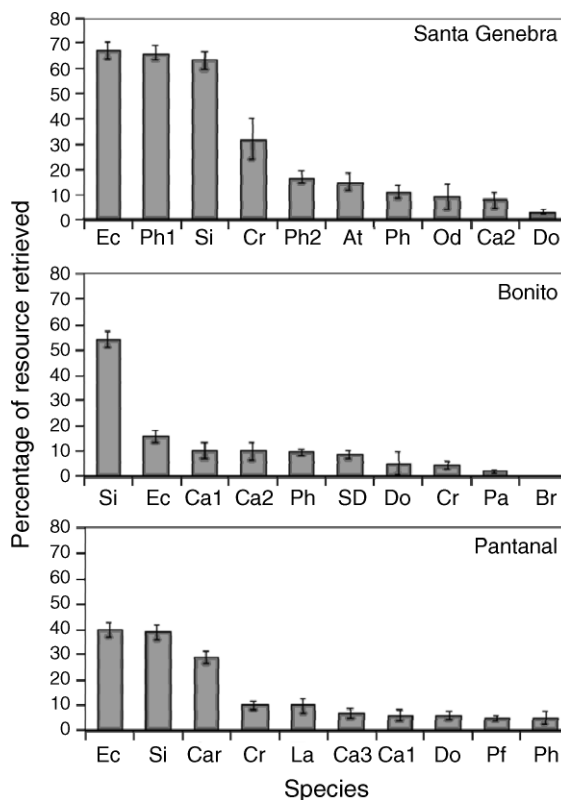


FIG. 2. Percentage (mean \pm SE) of each resource located by an ant species that it retrieved, by study site. The 10 ant species that harvested the highest percentages in each community are shown. See Fig. 3 for species names.

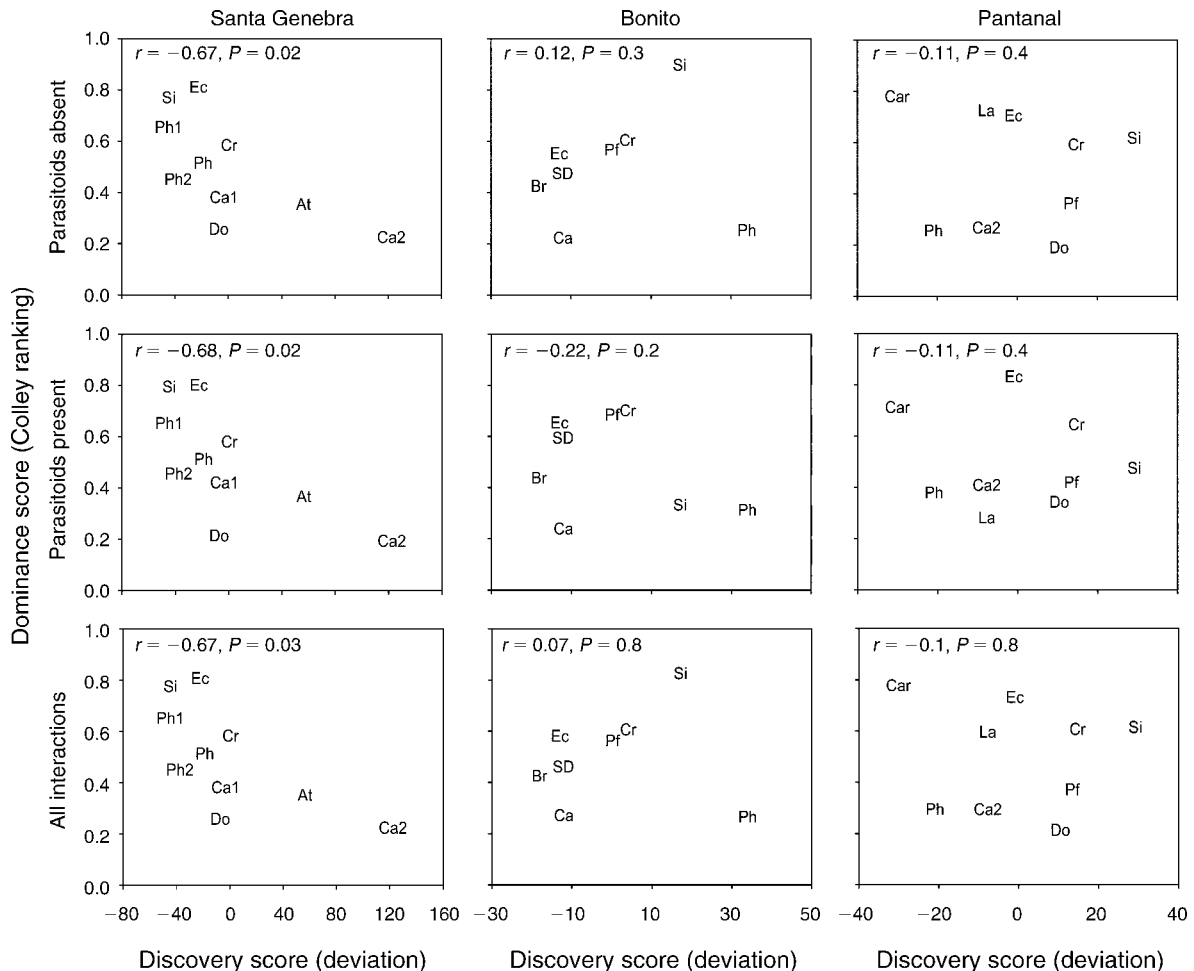


FIG. 3. Resource dominance–discovery trade-offs at the three study sites under the conditions of host and non-host species in the absence of phorid parasitoids, host and non-host species in the presence of parasitoids, and the sum of all interactions. The host species at Santa Genebra and Bonito included only *Solenopsis invicta*, whereas in the Pantanal host species included *S. invicta*, *Linepithema angulatum*, and *Paratrechina fulva*. r is the Pearson product-moment correlation coefficient, and P is its associated significance value derived from a one-tailed test. Species codes are as follows: At, *Atta* sp.; Br, *Brachymyrmex* sp.; Car, *Camponotus rufipes*; Ca, *Camponotus* sp.; Ca1, *Camponotus* sp. 1; Ca2, *Camponotus* sp. 2; Cr, *Crematogaster* sp.; Do, *Dorymyrmex* sp.; Ec, *Ectatomma*; Pf, *Paratrechina fulva*; Ph1, *Pheidole* sp. 1; Ph2, *Pheidole* sp. 2; Ph, *Pheidole* spp.; La, *Linepithema angulatum*; SD, *Solenopsis (Diplorhoptrum)* spp.; Si, *Solenopsis invicta*.

score) of a species and the deviation from expectation in the number of resources discovered by a species (our second measure of resource discovery). At Santa Genebra there was a significant negative correlation between our measure of resource dominance and our measure of resource discovery among the non-host ant species and in the presence and absence of phorid parasitoids when *Solenopsis invicta* was included (Fig. 3). There was no significant negative relationship between resource dominance and discovery at Bonito under any conditions (Fig. 3). It is worth noting that *S. invicta* was far more dominant for its level of resource discovery in the absence of parasitoids compared to the other species, but this was not so in the presence of parasitoids (Fig. 3). By reducing the dominance of *S. invicta*, parasitoids caused the relationship between

dominance and discovery to become negative, although not significantly so. There was no significant negative relationship between resource dominance and discovery in the Pantanal either, although the relationship tended toward negative values under all conditions (Fig. 3). The presence or absence of phorids had no apparent effect on the sign or strength of this relationship.

Interactions of Solenopsis invicta with competitive dominants

Solenopsis invicta may have been reluctant to recruit to resources already occupied by ants dominant to it in the Pantanal, as evidenced by its far greater tendency to appear first at a resource than second in pairwise encounters with these species. It was observed first at a resource in 52 of 69 (75%) of its interactions with *C.*

rufipes, 17 of 19 (89%) of its interactions with *Ectatomma*, and 27 of 31 (87%) of its interactions with *P. fulva*. When *S. invicta* arrived first, its success defending a resource against *C. rufipes* depended on the number of *S. invicta* present (Mann-Whitney *U* Test, $P < 0.001$), but against *P. fulva* and *Ectatomma*, recruitment was not related to resource defense (Mann-Whitney *U* Test, $P > 0.05$). Instances when *S. invicta* arrived second at baits occupied by *E. brunneum* and *P. fulva* occurred too infrequently for analysis, but against *C. rufipes*, *S. invicta* arrived second 17 times, and each time it failed to displace *C. rufipes*.

Solenopsis invicta's lack of dominance against *P. fulva* was particularly curious, given the low success of *P. fulva* in confrontations with most other species. Observations of confrontations of these species in the field suggest that *P. fulva* employed a species-specific attack strategy against *S. invicta*. When these two species met at a resource, *P. fulva* workers would rush at *S. invicta* workers, climb on their backs and appear to throttle them with their mandibles. *S. invicta* workers responded to these attacks by quickly retreating from contested resources.

DISCUSSION

Evidence from numerous studies suggests that competition in local ant communities often results in linear dominance hierarchies, in which competitively dominant species regularly displace subordinate species at food or nest sites (Vepsäläinen and Pisarski 1982, Fellers 1987, Hölldobler and Wilson 1990, Morrison 1996, Cerdá et al. 1997, Morrison et al. 2000, Retana and Cerdá 2000, Holway et al. 2002, LeBrun and Feener 2002, 2007, LeBrun 2005, LeBrun et al. 2007). In the absence of any compensatory mechanisms, the inevitable outcome of linear dominance hierarchies is competitive exclusion of all but the most dominant species. This appears to occur in the introduced range of successful invasive species such as the Argentine ant *Linepithema humile* (Holway 1998) and the red imported fire ant *Solenopsis invicta* (Porter and Savignano 1990; but see Morrison 2002), but single-species ant communities are typically rare in nature, and this is particularly true in the native ranges of invasive species. These observations suggest that compensatory mechanisms that counter the effects of linear dominance hierarchies are usually present in local ant communities, promoting the local coexistence of species. Moreover these observations suggest that invasive ants often violate these compensatory mechanisms in their introduced range but not in their native range. Interspecific trade-offs in resource use, vulnerability to natural enemies, and sensitivity to environmental stress are one general class of compensatory mechanisms that may promote species coexistence in local ant communities (Cerdá et al. 1997, Adler 1999, Feener 2000, LeBrun and Feener 2002, 2007, LeBrun 2005, Adler et al. 2007).

Our study provides support for the presence of linear competitive dominance hierarchies and compensatory interspecific trade-offs in three local ant communities found in the Brazilian range of the red imported fire ant, *Solenopsis invicta*. At Santa Genebra, there was a strong, statistically significant linear dominance hierarchy among the 10 most common species (Table 2). This linear dominance hierarchy was countered by an equally strong, statistically significant trade-off in the ability of species to dominate resources and discover them (Fig. 3). Although *S. invicta*, the top-ranked species in the dominance hierarchy, was attacked by several species of phorid parasitoids, their presence had no significant effect on the ability of *S. invicta* to win confrontations at resources (Table 1). Thus, of the factors we examined, a dominance-discovery trade-off appeared to promote coexistence in this community, in which ecological dominance was shared by *S. invicta*, *Ectatomma*, and *Pheidole* sp. 1.

At Bonito, the eight most common species formed a nearly statistically significant linear dominance hierarchy in the absence of parasitoids, but this trend toward linearity disappeared entirely in their presence (Table 2). In contrast to the situation at Santa Genebra, the presence of parasitoids greatly reduced the ability of *S. invicta* to win confrontations with other species and its rank in the proportion of confrontations won dropped from first to seventh place in their presence (Tables 1 and 2). We found no evidence for a resource dominance-discovery trade-off in this community (Fig. 3). In fact, *S. invicta*, the most dominant species in the absence of parasitoids, had the second-highest resource discovery rate in the community and discovered significantly more resources first than expected from its abundance (Fig. 2). It was a distinct outlier in a plot of resource dominance vs. resource discovery in the absence of parasitoids, but in their presence the dominance of *S. invicta* dropped into a range commensurate with its discovery ability (Fig. 3). Thus, by indirectly reducing the behavioral dominance of *S. invicta*, the presence of parasitoids appears capable of countering the possible extirpative effects of the linear dominance hierarchy at Bonito. However, at the time of our study, parasitoids were present at only 13% of interactions involving their host and had little observed effect on the ecological dominance of *S. invicta*.

In the Pantanal, the nine most common species formed a significant linear dominance hierarchy. *S. invicta* was clearly less behaviorally dominant in Pantanal than it was at the other two sites. Not only did it only rank fourth in behavioral dominance in this community, *P. fulva*, a species that ranked below it in behavioral dominance, bested *S. invicta* in a majority of their confrontations. In the Pantanal, *S. invicta* had a higher rate of resource discovery than any of the other eight common species and discovered a higher proportion of resources first than expected from its abundance (Fig. 2). *S. invicta*'s disadvantage in behavioral domi-



PLATE 1. Natural grassland habitat of the red imported fire ant (*Solenopsis invicta*) in the Brazilian Pantanal near Passo do Lontra. This area is seasonally flooded between December and May. Trees in the photograph are a flood-resistant *Tabebuia* species, which often forms a monodominant canopy in areas of the Pantanal. Photo credit: D. H. Feener, Jr.

nance against competitors such as *Camponotus rufipes* and *Ectatomma* was offset by its superior ability at resource discovery. This relative advantage at resource discovery allowed *S. invicta* to share ecological dominance with *Ectatomma* and *C. rufipes*.

We found no evidence for a significant dominance–discovery trade-off in the Pantanal (although the trend was negative), but as in Bonito, the ability of the top-ranked behavioral dominant to win interspecific confrontations at resources was strongly affected by the presence of parasitoids (Fig. 3). Here the top-ranked dominant was *Linepithema angulatum*, whose ranking dropped to eighth place in the presence of parasitoids (Tables 1 and 2). When all interactions in both the presence and absence of phorids were considered, *L. angulatum* ranked second in overall behavioral dominance, behind *C. rufipes*. Significantly, *L. angulatum* was not an ecological dominant in the Pantanal due to the effect of phorid parasitoids. Interactions in the Pantanal appeared to be controlled by the vulnerability of a behaviorally dominant species (*L. angulatum*) to the indirect effects of parasitoids and the ability of a behaviorally subordinate species (*S. invicta*) to discover resources faster than behaviorally dominant species.

What accounts for the differences in the relative importance of trade-off mechanisms operating in these three communities? We suspect that variation in the local community of phorid parasitoids is certainly one factor (Seike 2002). At Santa Genebra, during our study the most common species of phorid parasitoid along

recruitment trails of *S. invicta* was *Pseudacteon solenopsidis*. This species tends to herd individual workers away from their recruitment trail without disturbing the trail and typically does not change the ability of *S. invicta* to defend or usurp food resources from other species (Orr et al. 1997). At the other two sites, the most common species of phorid parasitoids at *S. invicta* recruitment trails were *Pseudacteon nudicornis* and *Pseudacteon dentiger* (Seike 2002), two species that do interfere with the ability of *S. invicta* to defend and usurp resources. Other factors might include the differences in the composition of the local ant communities and their relative abilities of resource dominance and discovery. For example, tempo of resource discovery was faster in Santa Genebra than it was at the other two sites (Fig. 1). Thus, while *S. invicta* discovered resources faster than any other species in the Pantanal and was second fastest at Bonito, it was at a competitive disadvantage in resource discovery at Santa Genebra, where it ranked seventh out of 10 species. The high ranking in behavioral dominance of *S. invicta* at Santa Genebra and Bonito and its lower ranking in the Pantanal, on the other hand, suggest that *S. invicta* was at a competitive disadvantage in behavioral dominance in the Pantanal compared to the other two sites.

Other uninvestigated factors may also contribute to shifts in the relative importance of various trade-offs in local communities. Our study plots in the Pantanal are seasonally inundated between February and June, during which time *S. invicta* retreats to high-ground

refugia, while other ant species either permanently or seasonally nest in vegetation (e.g., *Camponotus rufipes*, *Crematogaster*). Seasonal inundation may regularly disrupt the process of competitive exclusion, phorid populations, and/or alter the balance of trade-offs in the local community (Folgarait et al. 2004). Our sites also varied in relative exposure to extreme temperature, which suggests that a trade-off between resource dominance and thermal vulnerability may affect our local communities as they do in other open habitats (Cerdá et al. 1997, 1998a, b, Bestelmeyer 2000).

Results of our study suggest that the application of interspecific trade-off theory can greatly enhance our understanding of ecological interactions involving invasive ant species. Furthermore, we would argue that its continued application may lead to a more predictive framework for invasion ecology. Our study supports the idea that the red imported fire ant faces intense interspecific competition in its native range (LeBrun et al. 2007) and that this competition in some localities may be mediated by the indirect effects of phorid parasitoids. These interactions may help explain why fire ant population densities are 4–10 times lower in South America compared to North America (Porter et al. 1997). Indeed, in the absence of phorids, South American fire ants may occur at densities comparable to those seen in their exotic range (Folgarait et al. 2004). Our results also suggest that a comprehensive understanding of the success of an invasive species will require comparisons at multiple sites within its native range, as well as comparisons between the native and introduced ranges.

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