

AN EXPERIMENTAL STUDY OF COMPETITION BETWEEN FIRE ANTS AND ARGENTINE ANTS IN THEIR NATIVE RANGE

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Abstract. An understanding of why introduced species achieve ecological success in novel environments often requires information about the factors that limit the abundance of these taxa in their native ranges. Although numerous recent studies have evaluated the importance of natural enemies in this context, relatively few have examined how ecological success may result from differences in the magnitude of interference competition between communities in the native and introduced ranges of nonnative species. Here we examine how native-range competitive environments may relate to invasion success for two important invasive species, the red imported fire ant (*Solenopsis invicta*) and the Argentine ant (*Linepithema humile*), in a region of native-range sympatry. At two study sites in northern Argentina, we used stable-isotope analysis, a variety of observational approaches, and two different reciprocal removal experiments to test (1) whether *S. invicta* competes asymmetrically with *L. humile* (as suggested by the 20th century pattern of replacement in the southeastern United States) and (2) the extent to which these two species achieve behavioral and numerical dominance. Stable-isotope analysis and activity surveys indicated that *S. invicta* and *L. humile* are both omnivores and forage during broadly overlapping portions of the diel cycle. Short-term removal experiments at baits revealed no competitive asymmetry between *S. invicta* and *L. humile*. Longer-term colony removal experiments illustrated that *S. invicta* and *L. humile* experience an approximately equal competitive release upon removal of the other. Our results indicate that neither *S. invicta* nor *L. humile* achieves the same degree of behavioral or ecological dominance where they co-occur in native populations as they do in areas where either is common in their introduced range. These results strongly suggest that interspecific competition is an important limiting factor for both *S. invicta* and *L. humile* in South America.

Key words: Argentina; Argentine ant; competition; fire ant; invasion; *Linepithema humile*; removal experiment; *Solenopsis invicta*.

INTRODUCTION

Although research on biological invasions has grown enormously since Elton's (1958) seminal synthesis, most work in this field remains exclusively focused on introduced populations. This introduced-range bias may limit an understanding of the general causes of invasion success. Research on populations of invasive species in their native ranges, for example, can reveal important differences between native and introduced populations (e.g., in the prevalence of polygyny [Ross et al. 1996], in the relative genetic diversities of populations and the prevalence of intraspecific aggression [Tsutsui et al. 2000], or in the resistance of competitors to allelopathic chemicals [Callaway and Aschehoug

2000]). These differences can provide surprising insights into the success of introductions (Wolfe 2002).

The ecological and evolutionary histories of introduced species influence their ability to spread into new environments in numerous ways. Ecological success, for example, may result from nonnative species escaping their predators, parasites, or pathogens (Mitchell and Power 2003, Torchin et al. 2003). The importance of enemies in this context is underscored by their key role in biological control (De Bach 1974). Interspecific competition, by comparison, has received less attention with respect to invasion success, especially for animal introductions. Disparities in the magnitude of interspecific competition between communities in the native and the introduced ranges of nonnative species may nonetheless contribute importantly to ecological success in new environments (Vermeij 1991, Tilman 1999, Callaway and Aschehoug 2000). If the competitive environments of donor communities are more intense than those of recipient communities, for example, then an invader's competitive ability should more closely resemble species

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from its native range than species from its introduced range (Tilman 1999).

In this study we examine how native-range competitive environments may relate to invasion success for two widespread, abundant, and ecologically damaging invasive species: the Argentine ant (*Linepithema humile*) and the red imported fire ant (*Solenopsis invicta*). Our focus is novel in that we address the nature of interspecific competition between two invasive species in a region of extensive native-range sympatry. Although it is recognized that *S. invicta* and *L. humile* originate from the same general region of South America, our recent surveys reveal that these two ants frequently co-occur in floodplain woodlands along the major rivers of northern Argentina. *Solenopsis invicta* occurs from the vicinity of Rosario, Argentina, north along the Río Paraná to its confluence with the Río Paraguay and from there north in the drainage of the Río Paraguay into Paraguay and southern Brazil (Buren et al. 1974, Ross and Trager 1990, Mescher et al. 2003). The native range of *L. humile* overlaps the southern portion of the red imported fire ant's range and is centered on the Río Paraguay and the lower Río Paraná drainages of northern Argentina and surrounding regions (Tsutsui et al. 2001, Wild 2004) (see Appendix A).

Despite the large number of published studies on *S. invicta* and *L. humile*, remarkably little information exists concerning interactions between the two species. Several decades after *L. humile* was first recorded in the United States (in 1891), it had spread throughout the Southeast (Suarez et al. 2001). Introductions of *S. invicta* (and *S. richteri*) followed the arrival of *L. humile* in this region, and these fire ants (especially *S. invicta*) spread quickly and apparently at the expense of the Argentine ant. Although imported fire ants appear to have displaced Argentine ants from the southeastern United States, supportive evidence is largely anecdotal. In roadside surveys conducted near Mobile, Alabama, for example, Glancey et al. (1976) found *S. invicta* common in areas that were previously dominated by *L. humile*. Likewise, Buren et al. (1974) state that *S. invicta* replaced *L. humile* in New Orleans, Louisiana, a location where Argentine ants were considered a pest in the early 1900s. Wilson (1951) speculated that *L. humile* might hold its own in urban areas but lose ground to *Solenopsis* in more open environments. The currently patchy and largely urban distribution of *L. humile* in the southeast (e.g., Buczkowski et al. 2004) fits Wilson's conjecture.

Unlike the situation in North America, in South America, *S. invicta* and *L. humile* occur in species-rich communities of ants (Allen et al. 1974, Suarez et al. 1999) and often coexist. The presumed intensity of interspecific competition in these communities may contribute to the success of *L. humile* and *S. invicta* introductions (Feener 2000). Consistent with this hypothesis are studies documenting that introduced

populations of *S. invicta* and *L. humile* exceed native ants in how quickly they discover food and in how effectively they usurp food from competitors (Porter and Savignano 1990, Human and Gordon 1996, Holway 1999, Morrison 2000). Little is known about the competitive rankings of *S. invicta* and *L. humile* in South American ant communities, however.

Here we examine the dynamics of interspecific competition in omnivorous ant communities from South America that include both *S. invicta* and *L. humile*. We use stable-isotope analysis, a variety of observational approaches, and two types of reciprocal removal experiments to test the following hypotheses. First, given the historical pattern of displacement in the southeastern United States, we predict that, in South America, *S. invicta* competes with *L. humile* in an asymmetrical manner, with fire ants acting as the behavioral dominant. Second, as a result of presumed differences in the competitive environments of North and South America, we predict that neither *S. invicta* nor *L. humile* achieve the extreme levels of behavioral or numerical dominance observed in their introduced ranges. Given the unique focus of this study, our results provide a novel and informative measure of the manner in which geographical disparities in competitive environments may contribute to success of animal invasions. Moreover, an improved understanding of the manner in which *S. invicta* and *L. humile* interact with one another seems warranted given the prominence of these species as invaders and the likelihood that the extent of their introduced range sympatry will increase over time as a result of the unfortunate, but perhaps inevitable, range expansions anticipated for both species (Morrison et al. 2004, Roura-Pascual et al. 2004).

METHODS

Study sites

We conducted research at two sites in northern Argentina: (1) Ocampo (28°29' S, 59°16' W), 6 km east of the town of Villa Ocampo (Santa Fe Province) in the floodplain of the Río Paraná, and (2) Herradura (26°31' S, 58°17' W), 5 km east of the town of Herradura (Formosa Province) and along Río Paraguay. Fieldwork took place during November–December 2003 and November–December 2004. The two sites, separated by ~300 km, are in the Chaqueña phytogeographical province.

Ocampo receives an average of 124 cm of rain a year (data from Reconquista, Argentina [80 km to the south of Villa Ocampo]). We worked in open savanna habitats that had scattered *Acacia* trees and small stands of dense subtropical forest (see Plate 1). Herradura receives an average of 139 cm of rain per year (data from Formosa, Argentina [40 km to the north of Herradura]). We worked in and adjacent to a riverside park maintained for camping and fishing. Subtropical forest and wetlands surround this site. Although a modified habitat, this site supports a diverse ground-foraging ant community with

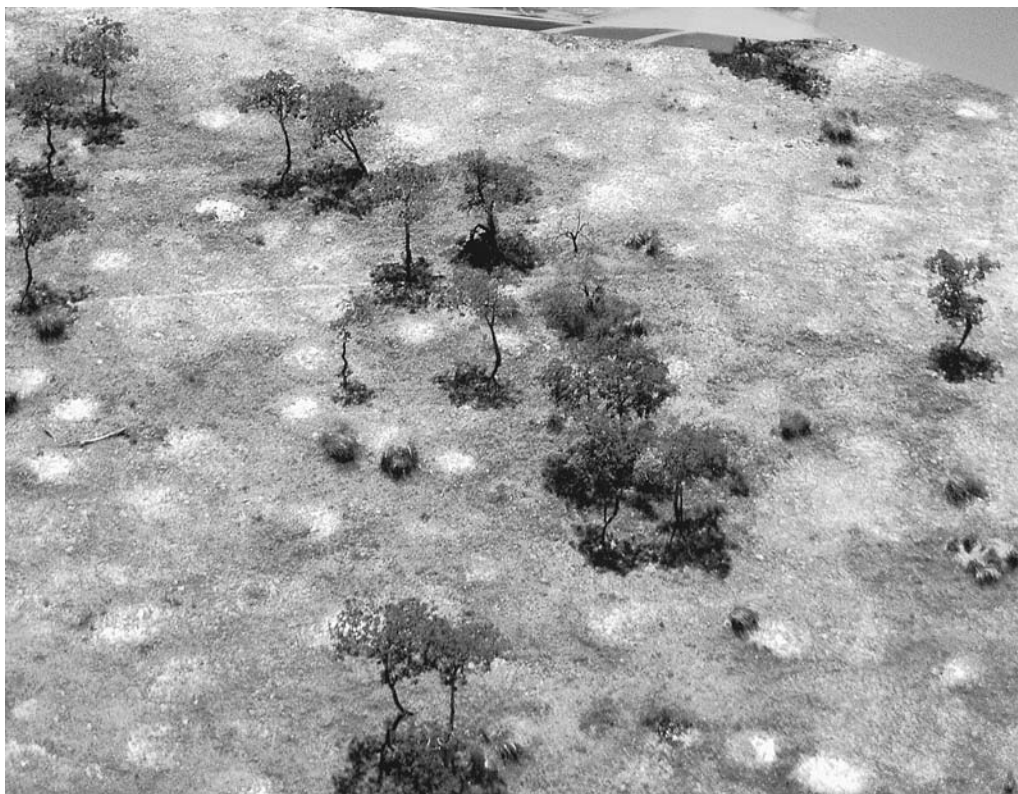


PLATE 1. An aerial photo of the field site near Villa Ocampo, Argentina. The white circles of bare soil, ~1 meter in diameter, are adjacent to active and abandoned ant nest mounds constructed primarily by *Solenopsis invicta* with a lesser number constructed by *Camponotus punctulatus*. The mounds are often secondarily occupied by *Linepithema humile* and *S. (Diplorhoptrum)* sp. This area was the site of one of the plots in the colony removal experiment. Photo credit: C. R. Smith.

high densities of *S. invicta* and *L. humile*. Both Ocampo and Herradura can become extensively flooded during the wet season. We replicated all work at both sites except for the colony removal experiment (performed only at Ocampo).

Species

Both of the study sites fall within the native ranges of *L. humile* and *S. invicta* (Pitts 2002, Wild 2004) (see Appendix A). No other species of *Linepithema* is common in this part of Argentina (Wild 2004). The only other member of the *Solenopsis saevissima* species group that occurs in this area (*S. macdonaghi*) is easily differentiated from *S. invicta* based on morphology (Pitts 2002) and did not occur at either study site. Our sites are near areas known to contain polygyne *S. invicta* (Mescher et al. 2003). However, populations of *S. invicta* at both sites were apparently comprised of monogyne colonies. Extensive nest excavations never revealed more than one queen per colony.

At both sites we define the community of competitors that interact with *S. invicta* and *L. humile* as those ant species observed foraging at baits in the morning and evening, the periods when *S. invicta* and *L. humile* are most active in the austral spring. Voucher specimens are

deposited at the Bohart Museum of Entomology, University of California at Davis (UCDC), the University of Illinois, and the Natural History Museum Bernardino Rivadavia in Buenos Aires.

Stable-isotope analysis

To infer the relative trophic positions of *L. humile* and *S. invicta*, we analyzed stable isotopes of carbon and nitrogen from field-collected workers. Nitrogen isotopes can clarify the relative trophic positions of species in food webs. Over a broad range of taxa, for example, 2–3‰ enrichment in nitrogen isotopes typically separates trophic levels (Deniro and Epstein 1981, Post 2002, McCutchan et al. 2003, Vanderklift and Ponsard 2003). Carbon isotopic values of consumers reflect the photosynthetic pathway (C_3 or C_4) by which the carbon was fixed in plant forage (Lajtha and Michener 1994).

At each site, we collected workers from at least 10 colonies of both *L. humile* and *S. invicta* and from 1–5 colonies of other common ant species. Samples were frozen within 1 h of collection, dried in an oven at 60°C for two days, and stored with desiccant until processing. Each sample consisted of the head, thorax, and legs (after Tillberg et al. 2006) of 10–15 workers from one colony such that the sample mass summed to ~1500 µg.

Samples were analyzed at the University of California Davis Stable Isotope Facility. The standard for carbon analysis was PeeDee Belemnite carbonate; atmospheric air was the standard for nitrogen analysis.

At each site, we compared $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between *L. humile* and *S. invicta* using a MANOVA to test for an overall difference, followed by two one-way ANOVAs to detect the source of the difference ($\delta^{15}\text{N}$ or $\delta^{13}\text{C}$), if one was present. To control family-wide error rate, the *P* values for the one-way ANOVAs were adjusted according to the sequential Bonferroni procedure. The relative trophic position of other ant species was categorized based on their foraging ecology. High-trophic-position ants include army ants in the genera *Labidus* and *Neivamyrmex*, the ponerimorph genera *Ectatomma*, and *Pachycondyla*, and the genus *Forelius*. Low-trophic-position ants included species that rely heavily on plant material, honeydew, extrafloral nectar, or fungus (genera *Acromyrmex*, *Cephalotes*, *Cyphomyrmex*, *Nesomyrmex*, and *Myrmelachista*). Ants with omnivorous diets and intermediate $\delta^{15}\text{N}$ values were from a wide variety of genera including *Azteca*, *Brachymyrmex*, *Crematogaster*, *Dorymyrmex*, *Paratrechina*, *Pogonomyrmex*, *Pseudomyrmex*, and *Solenopsis* (subgenus *Diplorhoptrum*).

Activity profiles

To quantify temporal patterns of foraging activity for *S. invicta* and *L. humile*, we established 10 1-m² plots at each site in areas where we observed *L. humile* and *S. invicta* on the ground within 0.5 m of one another. We sampled plots every 4 h over 24 h by collecting all ants detected within each plot during 5-min sampling periods. Plots were separated by at least 50 m.

Short-term removal experiment

In 2003 and 2004, we conducted competitor removal experiments to test the degree to which *L. humile* and *S. invicta* differ in competitive dominance. These experiments compare the ability of the two species to capture food in each other's presence (control) with their ability to capture food when their main competitor (i.e., *L. humile* or *S. invicta*) is excluded (treatment). At each study site, we established bait stations (Ocampo, *N* = 23; Herradura, *N* = 16) that were at least 25 m apart and were situated in areas where *L. humile* and *S. invicta* foraged within ~0.5 m of one another. At each station we placed 2 g of tuna in oil at the center of circular laminated cards (24 cm in diameter). Tuna baits are often used in studies of omnivorous ant communities to simulate large persistent food items. This type of bait represents a particularly relevant resource at our study sites because ants often scavenge stranded aquatic organisms (e.g., fish, snails). Control and treatment trials were conducted at the same time of day over three consecutive days. We performed controls on the first day to prevent treatment manipulations from influencing the outcome of controls, but the order of removal trials was

always randomized. In the treatments we aspirated all *L. humile* or *S. invicta* workers that approached the bait station and then released them >1 m away from the station. At each station, we monitored all ants until 60 min after a species had recruited at least 10 workers. Stations at which multiple species contested baits at the end of 60 min were monitored until only one species remained. We recorded the identity and number of all ants present and, at the end of each trial, vouchered all species observed. In 2004, upon completion of the final removal trial, we set four pitfall traps at 90° angles, 2 m from each bait station. Traps provide a measure of local forager density. Pitfall traps were installed using a pipe to remove a soil plug exactly the size of the trap. This method minimizes soil disturbance. Prior to all sampling, we left pitfall traps, 50-mL centrifuge tubes with a 3 cm diameter opening, closed for 48 h to eliminate any digging-in effects. Traps were charged with a solution of water, odorless detergent, and salt and remained open for 48 h.

We analyzed data for the short-term removal experiments as follows. We used chi-square goodness-of-fit tests to evaluate whether reciprocal removal of *L. humile* or *S. invicta* enhanced the ability of the unremoved focal species to monopolize resources. In this analysis the outcomes of control trials were used as the expected values. To test for any competitive asymmetry between *L. humile* and *S. invicta*, we evaluated the significance of the three-way interaction term from a log-linear model describing the interaction of species identity (*L. humile* or *S. invicta*) by treatment (competitor present or absent) by outcome (bait won or lost). A significant interaction indicates the existence of a competitive asymmetry. We also used log-linear analysis to test for between-site differences in the responses of *L. humile* and *S. invicta*. We used logistic regression to determine whether the outcome of control trials resulted from differences in relative local worker density between *L. humile* and *S. invicta*. Relative local worker density was estimated by subtracting the mean number of *S. invicta* workers in pitfall traps from that location (i.e., bait station) from the mean number of *L. humile* workers in those same traps. We evaluated the significance of worker density by comparing the fit of the full model to the fit of the model that excluded the predictor variable term. For sample sizes <50, this approach behaves more reliably compared to explicit tests of the parameter estimate (Quinn and Keough 2002).

Colony removal experiment

Because the removal experiments described above capture short-term and small-scale aspects of competition between *L. humile* and *S. invicta*, we also performed a longer-term and larger-scale reciprocal colony removal experiment to test whether the two species undergo different levels of ecological release upon removal of competing colonies. We performed this experiment at Ocampo where we established 22 plots (10 × 10 m) in

open savanna habitat in 2004. Plots were separated by at least 50 m, and the complete array spanned 20 ha. We selected plot locations by searching for areas where *L. humile* and *S. invicta* foraged together within 1 m of one another. The center of each plot was then set at the midpoint between the *S. invicta* mound nearest the location where we observed the two species together and the nearest large *L. humile* nest. In each plot we established a square grid of 16 equally spaced bait stations and installed pitfall traps at the plot center and at each corner. Trapping methods were the same as in the short-term removal experiment. Each plot was assigned to one of three experimental groups: control ($N=9$), *L. humile* removal ($N=6$), or *S. invicta* removal ($N=7$). We assigned treatments to plots in order to maximize the degree of spatial interspersal among experimental groups.

To remove colonies of *S. invicta* and *L. humile*, we used boiling water and localized soil excavation. Although more labor-intensive than using pesticides, this approach minimizes nontarget effects. Superficial *L. humile* nests, those at the base of trees or in grass tussocks, were treated with boiling water alone. We attempted to remove all nests of the focal species inside each treatment plot and within a surrounding 10-m buffer zone. This buffer size is sufficient to prevent the foraging territories of adjacent fire ant colonies from overlapping the plot (Tschinkel et al. 1995). In order to assure that *L. humile* removal plots would not be recolonized by this somewhat nomadic species, concentrations of *L. humile* workers were removed from an additional 5-m buffer area. *Solenopsis invicta* removals required the elimination of 1.9 ± 1.2 (mean \pm SD) colonies inside the plot and an additional 4.6 ± 3.2 in the buffer zone, while *L. humile* removals required the removal of 2.8 ± 2.1 ground nests in the plot and an additional 4.7 ± 4.5 ground nests in the buffer zone. Additional nests of *L. humile* removed from trees and grass tussocks required no soil disturbance. To mimic soil disturbances inherent in colony removals, we sham-treated control plots by excavating and pouring boiling water onto 5–9 randomly chosen locations (each 0.5×0.5 m) within these plots or their buffer zones that did not contain obvious ant nests. We matched the number of sham disturbances in controls to the amount of soil disturbance required to remove focal competitors from adjacent removal plots.

We sampled all plots prior to colony removals and then 12–18 days after treatment. Sampling consisted of baiting and pitfall trapping. To bait each plot, we placed tuna baits on 7×7 cm laminated cards at each of the 16 stations in the plot. At 30 and 90 min after bait placement (at 07:30), we identified and counted all ants at the stations. Species that were in sole control of baits at 90 min were considered winners. Baits were removed, and a minimum of 4 h after baiting, during the early afternoon when ground temperatures were too hot to

allow any of the species active in the morning to forage, we returned and opened the pitfall traps.

We quantified spatial overlap in the foraging ranges of *L. humile* and *S. invicta* using the corner pitfall traps from the pre-manipulation sample of the colony removal plots. The presence/absence data from these traps were analyzed using the co-occurrence platform in EcoSim (Gotelli and Entsminger 2004). For this analysis, *S. invicta* or *L. humile* were scored as “present” only if traps contained a median number of workers or more for that species. Thus the analysis evaluated whether *S. invicta* and *L. humile* were positively, negatively, or randomly associated at locations where their workers were common. Row totals in the random matrices were fixed, but column totals were free to vary. The program uses the *c*-score statistic to compare the observed level of co-occurrence with the distribution of random matrices to determine the probability of observing that level of co-occurrence by chance (Stone and Roberts 1990, Gotelli 2000).

We quantified the degree of competitive release exhibited by *L. humile* and *S. invicta* as follows. For each plot, we calculated the fraction of bait stations controlled by either *L. humile* or *S. invicta* in the final sampling period that were controlled by the opposite competitor in the initial sampling period. For *L. humile* and *S. invicta* separately, we then used two-sample *t* tests to compare these proportions between control and treatment plots. In order to improve normality, these proportions were arcsine square-root transformed prior to analysis (Sokal and Rohlf 2000). In one control plot, a colony of the behaviorally dominant *Crematogaster quadricornis* was inactive during the initial sampling period but captured a majority of the baits in the final sampling period. Because this did not occur in any removal plot, we eliminated this plot from the analysis. Another control plot was identified by its studentized residual as an outlier (Quinn and Keough 2002) and was similarly excluded. In this plot *S. invicta* captured a single bait station in the initial sampling period, but *L. humile* captured this station in the final sampling period.

We used pre-removal baiting data from our 22 experimental plots to generate a behavioral dominance hierarchy for the Ocampo ant community. To assemble this hierarchy, we collated 84 observations of turnovers (cases in which one species displaced another from a bait) for the eight most common species at baits on our plots. Turnover data for rare species were too scarce (≤ 4 interactions per species) to resolve their relative behavioral dominance. We considered a species to be in control of a bait when it had recruited 10 or more workers and when no other species had more than three workers present. To construct this dominance hierarchy, we first entered the total number of wins and losses observed for every possible species pair into a two-dimensional matrix. A species won an interaction if it replaced a species that had previously controlled the resource. Species were arranged so as to minimize the

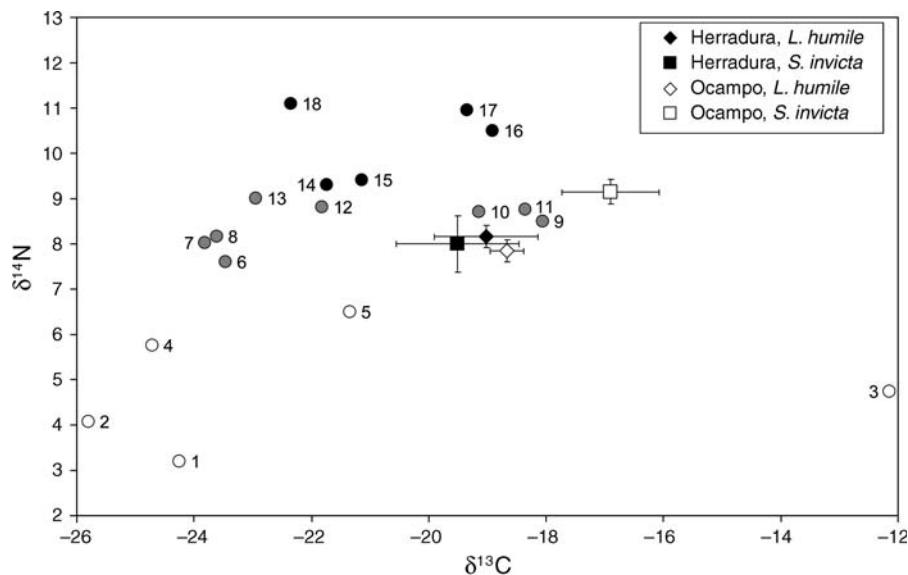


FIG. 1. Stable isotope values (means \pm SE) for carbon and nitrogen for *Solenopsis invicta* and *Linepithema humile* at Ocampo and Herradura in northern Argentina within the context of the entire ant community. Numbered circles represent mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for ants with plant-based (honeydew, nectar, extrafloral nectar; white symbols), omnivorous (gray symbols), and predatory (black symbols) diets from the following ant genera: 1, *Myrmelachista*; 2, *Nesomyrmex*; 3, *Cyphomyrmex*; 4, *Cephalotes*; 5, *Acromyrmex*; 6, *Pseudomyrmex*; 7, *Crematogaster*; 8, *Brachymyrmex*; 9, *Dorymyrmex*; 10, *Paratrechina*; 11, *Pogonomyrmex*; 12, *Azteca*; 13, *Solenopsis (Diplorhoptrum)*; 14, *Pachycondyla*; 15, *Labidus*; 16, *Forelius*; 17, *Neivamyrmex*; 18, *Ectatomma*.

number of intransitivities. For linear hierarchies, this arrangement will cause the majority of wins between species pairs to cluster in the upper right triangle of the matrix (Cerdá et al. 1997, Morrison et al. 2000). To assess matrix linearity, we used the statistical package MatMan version 1.0 (MatMan 1998), which compares the observed matrix with a set of randomized matrices to test whether the observed linearity represents a significant departure from chance (de Vries 1998, LeBrun 2005). In addition to behavioral dominance, we estimated ecological dominance by calculating the fraction of baits captured by each species in the pre-removal sampling period for all stations in which the species was also present in that station's pitfall trap. Ecological dominance thus considers a species' foraging success relative to its abundance (Andersen 1992, LeBrun 2005).

RESULTS

Stable-isotope analysis

Stable-isotope analysis indicated that *L. humile* and *S. invicta* have largely overlapping trophic positions at our two study sites (Fig. 1). At Ocampo, multivariate analysis revealed that the combined isotopic signature of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differed between *L. humile* and *S. invicta* (Wilks' lambda, 0.551, $F_{2,26} = 10.593$, $P < 0.01$). Subsequent univariate analyses showed no difference in these species' carbon signatures. However, the mean $\delta^{15}\text{N}$ value was slightly higher for *S. invicta* (by 1‰) compared to *L. humile* (one-way ANOVA, $F_{1,27} = 9.736$,

$P < 0.02$). At Herradura, there was no difference in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ between *S. invicta* and *L. humile*. As would be expected, stable isotope values for both *L. humile* and *S. invicta* fell within the range of values obtained from the other omnivorous ants in the system (Fig. 1; C. V. Tillberg and A. V. Suarez, unpublished data).

Activity profiles

At both Herradura and Ocampo, *S. invicta* and *L. humile* exhibited similar activity patterns over the course of the diel cycle (Fig. 2). At Ocampo, the less mesic site, foraging activity for both species peaked in the early morning and late evening. At Herradura, *S. invicta* exhibited a more constant level of activity, while the foraging activity of *L. humile* peaked in late evening and to a lesser degree in early morning.

Characteristics of the ant communities

Diverse communities of ground-foraging ants (>40 species) occur at both sites. With respect to species that were attracted to at least 10% of the bait stations, we observed 11 species at Ocampo and 10 species at Herradura (Table 1). Moreover, four out of the five most common ant species were shared across sites: *L. humile*, *S. invicta*, *Dorymyrmex thorasicus*, and *Pheidole* cf. *obscurithorax*. This latter species was a common competitor of *S. invicta* and *L. humile*. *Pheidole* cf. *obscurithorax* exhibits morphological characteristics intermediate between *P. obscurithorax* and *P. jelskii* (S. P. Cover, personal communication). Like *S. invicta*

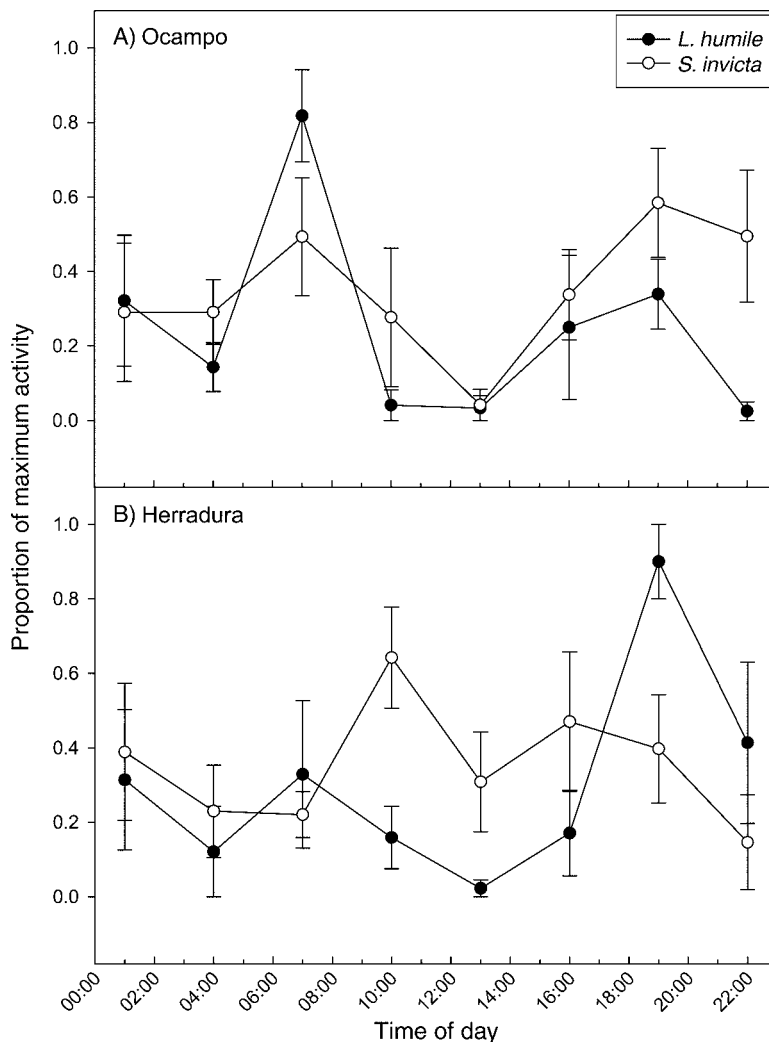


FIG. 2. Activity patterns of *Solenopsis invicta* and *Linepithema humile* at (A) Ocampo and (B) Herradura. For each time interval, counts for a plot were transformed into the fraction of the maximum number of workers active in that plot over all sampling periods to yield a proportion of maximum activity measure. The graph shows the means (\pm SE) across all plots of the proportion of maximum activity.

and *L. humile*, *P. obscurithorax* is native to northern Argentina and Paraguay and has invaded other continents (Storz and Tschinkel 2004). *Pheidole* cf. *obscurithorax* differs from *S. invicta* and *L. humile* in that it employs groups of workers to cooperatively carry large, intact prey items back to its nest.

Analysis of the eight most common competitors at Ocampo revealed a marginally significant, linear hierarchy (Landau's improved linearity index, $h' = 0.61$, $P = 0.06$; Table 2). *Solenopsis invicta* and *L. humile* were not the most behaviorally dominant species in this assemblage. Two species, *Camponotus blandus* and *Camponotus punctulatus*, proved dominant to both *S. invicta* and *L. humile*, and *Crematogaster quadriformis* was dominant to *L. humile*. Because only one interaction was observed between *Crematogaster quadriformis* and *S. invicta*, their relative behavioral dominance remains

uncertain. *Solenopsis invicta* succeeded in taking roughly the same number of baits from *L. humile* (five baits) as *L. humile* took from *S. invicta* (four baits).

Short-term removal experiment

The same four species discovered baits most rapidly at our two study sites: *L. humile*, *S. invicta*, *P. cf. obscurithorax*, and *D. thorasicus*. At both sites *L. humile* discovered food resources before *S. invicta* did (Ocampo, likelihood ratio $\chi^2 = 7.1$, $df = 2$, $N = 33$, $P < 0.03$; Herradura, likelihood ratio $\chi^2 = 11.1$, $df = 2$, $N = 24$, $P < 0.004$). Resource discovery was uniformly rapid. Average discovery time by any ant was 1.8 ± 3.1 min at Ocampo (mean \pm SD) and 1.1 ± 1.7 min at Herradura. These rapid dynamics mean that interspecific differences in mean discovery times were small; *L. humile* discovered resources, on average, 4.1 min faster compared to *S.*

TABLE 1. Ant species at the Herradura and Ocampo field sites in northern Argentina that were observed at a minimum of 10% of bait stations employed in the short-term removal experiment.

| Species | Prevalence at baits |
|--|---------------------|
| Ocampo | |
| <i>Camponotus blandus</i> | 0.22 |
| <i>Camponotus punctulatus</i> | 0.15 |
| <i>Crematogaster quadriformis</i> | 0.11 |
| <i>Dorymyrmex thorasicus</i> | 0.55 |
| <i>Linepithema humile</i> | 0.96 |
| <i>Paratrechina</i> cf. <i>fulva</i> | 0.19 |
| <i>Pheidole</i> sp. A | 0.11 |
| <i>Pheidole</i> cf. <i>obscurithorax</i> | 0.52 |
| <i>Solenopsis invicta</i> | 0.74 |
| <i>Solenopsis substituta</i> | 0.26 |
| <i>Wasmannia auropunctata</i> | 0.11 |
| Herradura | |
| <i>Crematogaster quadriformis</i> | 0.41 |
| <i>Dorymyrmex thorasicus</i> | 0.26 |
| <i>Ectatomma edentatum</i> | 0.19 |
| <i>Linepithema humile</i> | 0.81 |
| <i>Pheidole</i> sp. A | 0.11 |
| <i>Pheidole</i> cf. <i>obscurithorax</i> | 1.00 |
| <i>Pheidole</i> sp. B | 0.22 |
| <i>Pseudomyrmex denticollis</i> | 0.26 |
| <i>Solenopsis invicta</i> | 0.78 |
| <i>Solenopsis</i> (<i>Diplorhoptrum</i>) sp. A | 0.19 |

Note: Prevalence equals the fraction of bait stations at which each species was observed foraging.

invicta at Ocampo and 2.5 min more quickly at Herradura. There were insufficient observations to test *P. cf. obscurithorax* and *D. thorasicus* independently. However, discovery order did not differ between *L. humile* and *P. cf. obscurithorax* + *D. thorasicus* (Ocampo, likelihood ratio $\chi^2 = 2.8$, $df = 2$, $N = 34$, $P = 0.24$; Herradura, likelihood ratio $\chi^2 = 0.29$, $df = 2$, $N = 36$, $P = 0.87$).

Relative densities of *S. invicta* and *L. humile* workers strongly influenced the outcome of competition in control trials. Logistic regression revealed that the difference between the number of *L. humile* and *S. invicta* captured in pitfall traps significantly predicts the outcome of competition (Ocampo, $N = 11$, odds ratio = 1.6, $G^2 = 4.6$, $P < 0.03$; Herradura, $N = 9$, odds ratio = 1.8, $G^2 = 7.5$, $P < 0.006$). This relationship is also evident when the relative numbers of workers captured in pitfall traps at plot corners in the colony removal experiment are compared to the outcome of the pre-removal baiting sample at those same locations (logistic regression, $N = 64$, odds ratio = 1.2, $G^2 = 28.5$, $P < 0.0001$; Fig. 3). There was no significant difference between sites in the abundance of either *L. humile* or *S. invicta* in pitfall traps (Kruskal-Wallis test, *L. humile*, $N = 20$, $Z = 1.5$, $P = 0.13$; *S. invicta*, $N = 20$, $Z = 0.0$, $P = 1.0$).

At both Herradura and Ocampo, exclusion of *L. humile* from baits enhanced the ability of *S. invicta* to capture baits (Ocampo, goodness-of-fit $\chi^2 = 4.66$, $df = 1$, $N = 23$, one-tailed $P < 0.03$; Herradura, goodness-of-fit $\chi^2 = 4.42$, $df = 1$, $N = 16$, one-tailed $P < 0.03$), while exclusion of *S. invicta* did not increase the likelihood of bait capture by *L. humile* (Ocampo, goodness-of-fit $\chi^2 = 0.708$, $df = 1$, one-tailed $P = 0.25$; Herradura, goodness-of-fit $\chi^2 = 2.618$, $df = 1$, one-tailed $P = 0.88$; Fig. 4). Log-linear analysis, however, revealed no difference in the strength of competitive release exhibited by *S. invicta* and *L. humile* (Ocampo, likelihood ratio $\chi^2 = 0.03$, $df = 1$, $P = 0.87$; Herradura, likelihood ratio $\chi^2 = 3.17$, $df = 1$, $P = 0.08$; Fig. 4). There was also no difference between sites in the degree to which either *S. invicta* or *L. humile* was competitively released by the removal of the other (log-linear analysis, *S. invicta*, likelihood ratio $\chi^2 = 0.02$, $df = 1$, $P = 0.88$; *L. humile*, likelihood ratio $\chi^2 = 1.49$, $df = 1$, $P = 0.22$).

TABLE 2. Behavioral dominance matrix for the ant community at Ocampo.

| Species | <i>C. bla.</i> | <i>C. pun.</i> | <i>S. inv.</i> | <i>Cr. qu.</i> | <i>L. hum.</i> | <i>P. obs.</i> | <i>D. tho.</i> | <i>S. sub.</i> | Total | Behavioral dominance | Relative abundance | Ecological dominance |
|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|-------|----------------------|--------------------|----------------------|
| <i>C. bla.</i> | ... | | 1 | | | 2 | 3 | 1 | 7 | 1 | 0.02 | na |
| <i>C. pun.</i> | | ... | 4 | | 3 | 2 | 2 | | 11 | 1 | 0.17 | 0.25 |
| <i>S. inv.</i> | 0 | 0 | ... | 1 | 5 | 8 | 13 | 2 | 29 | 0.74 | 0.98 | 0.26 |
| <i>Cr. qu.</i> | | | 0 | ... | 4 | 2 | 1 | | 7 | 0.88 | 0.05 | 0.20 |
| <i>L. hum.</i> | | 0 | 4 | 0 | ... | 7 | 10 | 2 | 23 | 0.66 | 0.98 | 0.55 |
| <i>P. obs.</i> | 0 | 0 | 1 | 0 | 0 | ... | 2 | | 3 | 0.13 | 0.45 | 0 |
| <i>D. tho.</i> | 0 | 0 | 0 | 0 | 0 | 0 | ... | 3 | 3 | 0.09 | 0.48 | 0.05 |
| <i>S. sub.</i> | 0 | 0 | 0 | | 0 | | 1 | ... | 1 | 0.11 | 0.35 | 0 |
| Total | 0 | 0 | 10 | 1 | 12 | 21 | 32 | 8 | 84 | $P = 0.06$ | | |

Notes: Cell entries show the outcome of competitive interactions at baits. Rows list the number of interactions won; columns list interactions lost. Boldface type indicates the cell containing the majority of wins for that interaction. Empty cells are species combinations for which no interactions were observed. The focal species, *Linepithema humile* and *Solenopsis invicta*, and their interactions with one another are underlined. Behavioral dominance is the proportion of interactions won; the P value reported at the bottom of that column provides a measure of whether the observed matrix is more linear than would be expected by chance. Relative abundance is the proportion of pitfall traps that captured each species. Ecological dominance was estimated as the fraction of baits that a species controlled for all stations at which it was captured in pitfall traps. Species not sufficiently common in pitfall traps to calculate an ecological dominance score are indicated with "na." Abbreviations are: *S. inv.*, *S. invicta*; *C. bla.*, *Camponotus blandus*; *C. pun.*, *Camponotus punctulatus*; *Cr. qu.*, *Crematogaster quadriformis*; *L. hum.*, *L. humile*; *P. obs.*, *Pheidole obscurithorax*; *D. tho.*, *Dorymyrmex thorasicus*; *S. sub.*, *Solenopsis substituta*.

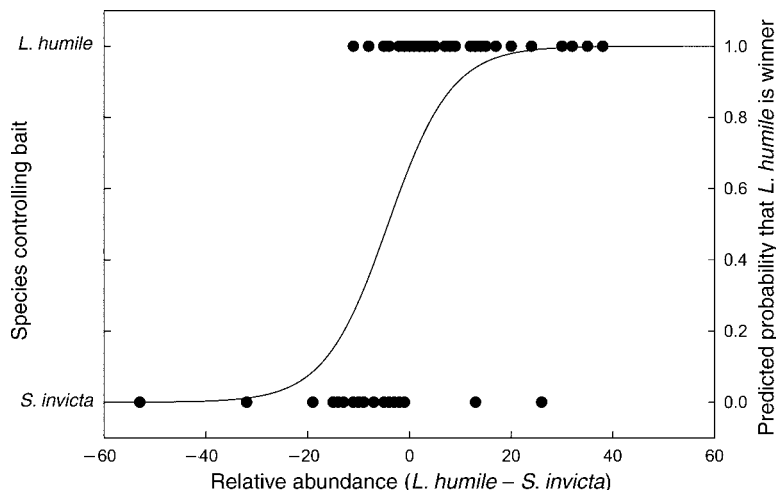


FIG. 3. Outcome of competition between *Linepithema humile* and *Solenopsis invicta* for pre-manipulation baiting from the colony removal experiment: logistic regression of the species that captured the corner baits vs. its relative abundance.

Colony removal experiment

Prior to colony removals, treatment plots did not differ with respect to the mean number of *S. invicta* and *L. humile* captured in pitfall traps (two-sample *t* test, $t = 1.1$, $df = 12$, $P = 0.25$) or in the proportion of traps that captured these two species (out of 108 traps, 70 captured *S. invicta* and 72 captured *L. humile*). Within plots, however, *S. invicta* and *L. humile* tended to control mutually exclusive areas. By considering traps that contained a median number of *S. invicta* or *L. humile* workers, we found that these species co-occurred at or above median densities substantially less often than would be expected by chance (EcoSim null model analysis, observed *C* score = 483, expected *C* score = 160, $P < 0.0001$). This segregation is evident in the nonoverlapping pattern of bait capture in the pre-manipulation sample (see Appendix B).

While colony removal treatments greatly reduced the abundance of *S. invicta* and *L. humile*, neither species was entirely eliminated. In post-removal sampling, for example, *S. invicta* succeeded in capturing $26\% \pm 9\%$ (means \pm SE) of the bait stations that it captured in the pre-removal sampling, while *L. humile* captured $38\% \pm 10\%$ of the bait stations it captured in the pre-removal sampling. Measured in this way, the effectiveness of the treatments did not differ between the two species (two-sample *t* test, $t = 0.79$, $df = 11$, $P = 0.44$).

Reciprocal colony removal of *S. invicta* and *L. humile* released the unremoved focal species from competition (Fig. 5). The degree of this release was fairly symmetric. *Linepithema humile* captured 32% more bait stations previously held by *S. invicta* in removal plots compared to control plots (two-sample *t* test, $t = -3.3$, $df = 9$, one-tailed $P < 0.005$), whereas *S. invicta* captured 20% more bait stations previously held by *L. humile* in removal plots compared to control plots (two-sample *t* test, $t = -2.3$, df

$= 11$, one-tailed $P < 0.02$; Fig. 5). Combining all baits taken by species aside from the focal competitors, other ant species exhibited a significant release from competition in the *L. humile* removal plots (two-sample *t* test, $t = -4.0$, $df = 6$, one-tailed $P < 0.004$) but not in the *S. invicta*

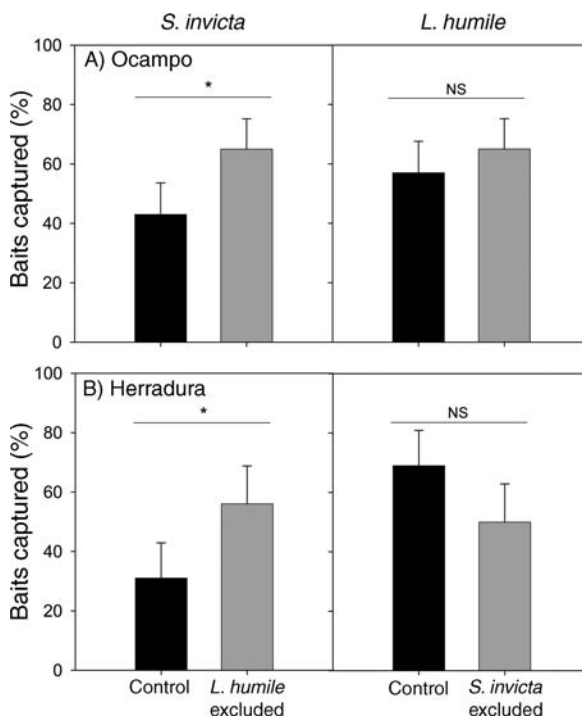


FIG. 4. Tests of competitive release from the short-term removal experiment conducted at (A) Ocampo and (B) Herradura showing the percentage of all baits captured (mean \pm SE) by *Solenopsis invicta* and *Linepithema humile* in the presence and absence of one another. Asterisks indicate significant differences ($P < 0.05$).

removal plots (two-sample t test, $t = -1.0$, $df = 11$, one-tailed $P = 0.17$). However, the absolute magnitude of the response of other ant species to the removal of the focal competitors was roughly similar (Fig. 5).

DISCUSSION

Activity surveys and stable-isotope analyses demonstrate the potential for interspecific competition between *S. invicta* and *L. humile*. At multiple locations in Ocampo and Herradura, fire ants and Argentine ants exhibited broadly overlapping foraging activity periods (Fig. 2). Temporal overlap was greatest at Ocampo. In addition to foraging at the same times, stable isotope signatures indicate that these species occupy similar trophic positions (Fig. 1). At both study sites, *S. invicta* and *L. humile* belong to diverse assemblages of omnivorous ants and have diets intermediate between highly predaceous species, such as army ants, and species that mostly consume plant exudates, honeydew, or seeds (Tillberg et al. 2006) (Fig. 1). Nitrogen isotope signatures for *L. humile* and *S. invicta* did not significantly differ at Herradura but did diverge slightly at Ocampo, with *S. invicta* having a 1‰ more enriched signal. The magnitude of this difference, however, is insufficient to place *L. humile* and *S. invicta* on different trophic levels. Cabana and Rasmussen (1994), for example, found that consumers from different trophic levels tend to be enriched by $\sim 3\%$ per trophic level. The difference in nitrogen isotope signatures between *L. humile* and *S. invicta* from Ocampo may reflect interspecific differences in predatory behavior or honeydew consumption. These data on temporal and trophic overlap combined with the observation of frequent, intense conflicts over both artificial and natural food items indicate that these two species compete strongly.

Although literature accounts suggest that *S. invicta* may be a superior competitor to *L. humile*, at least in the southeastern United States, we found little evidence for such a competitive asymmetry at our study sites in Argentina. In unmanipulated trials *S. invicta* and *L. humile* exhibited comparable abilities to take over baits from one another (Table 2). Control of this type of resource depended upon disparities in the local density of each species (Fig. 3). Interestingly, the inflection point for the logistic curve illustrated in Fig. 3 falls close to zero, which is the expectation for symmetric competition. The outcome of our short-term removal experiments again revealed evidence inconsistent with the notion that *S. invicta* is superior to *L. humile* in competitive ability. Our results, in fact, suggest the opposite. *Solenopsis invicta* captured more baits in the absence of *L. humile* than when *L. humile* was present, but we observed no such competitive release for *L. humile* when we removed *S. invicta*. Lastly, and perhaps most convincingly, our colony removal experiments provide little evidence for a competitive asymmetry between *S. invicta* and *L. humile*. Local worker densities

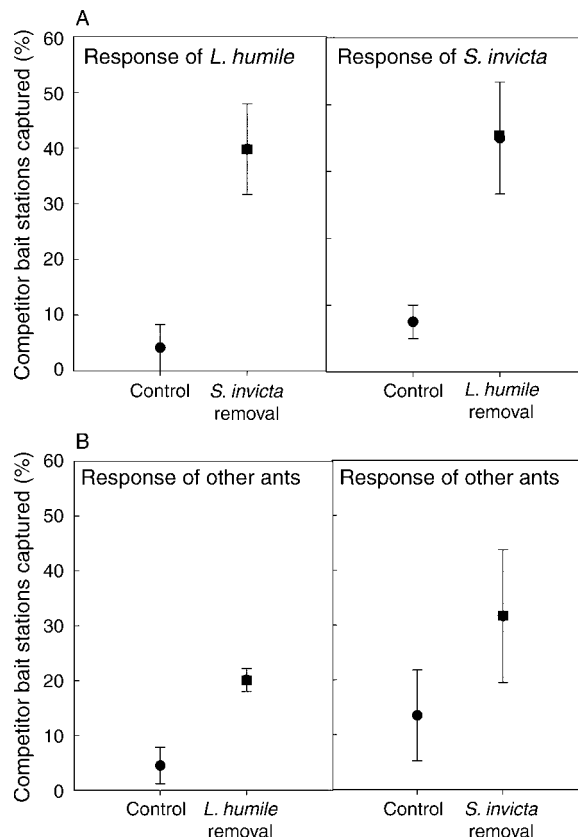


FIG. 5. Results of the colony removal experiment (mean \pm SE). (A) Response of *Linepithema humile* and *Solenopsis invicta* to the removal of one another's colonies. Competitive release was measured as the percentage of the bait stations captured by the competitor species in the pre-manipulation sample that the focal species captured in the final sample. (B) Response of species of ants other than *L. humile* and *S. invicta* to the removal of these two focal competitors.

of these two species are negatively associated, which in combination with the strong influence of worker densities on the outcome of competition (Fig. 3), results in areas in which resources are exclusively controlled by one or the other species (see Appendix B). When we removed colonies at the scale of 10×10 m plots, both species displayed a substantial, and approximately equal, release from interspecific competition.

What do these results tell us about ecological coexistence between these two dominant and outwardly similar competitors? Both *S. invicta* and *L. humile* are omnivorous scavenging species that rely on rapid, mass recruitment to capture food items. Moreover, our reciprocal removal experiments point to strong and roughly symmetric competition between *S. invicta* and *L. humile*. The inverse relationship between the local densities of these competitors in places where they co-occur (Fig. 3) and the frequency of habitat patches that contain only one or the other species, but not both, suggests an unstable, condition-dependent coexistence.

The competitive symmetry and apparently unstable coexistence observed in floodplain habitats in Argentina suggests that local displacement of one species by the other is likely when these species come into contact outside of their native range. However, the displacement of *L. humile* by *S. invicta* from all but limited refugia, as occurred in the southeastern United States, may not be the rule. Differences in habitat, social form (Porter et al. 1991, Mescher et al. 2003), degree of uniclonality (Tsutsui et al. 2000, Buczkowski et al. 2004, Holway and Suarez 2004), and prevalence of natural enemies (Porter et al. 1992) between the introduced and native ranges of these species, as well as between distinct parts of their introduced ranges, make specific predictions about the conditions favoring one species over another difficult. However, our finding of highly symmetric competitive abilities in Argentina indicates the potential for dynamic change in these species' competitive balance. Special attention should be paid to these species' interactions in new areas of secondary contact, such as California and Australia, as well as in old areas of secondary contact, such as the southeastern United States, where *S. invicta* is reacquiring its load of natural enemies (Williams et al. 1998, Morrison and Porter 2005, Porter and Gilbert 2005).

Based on our understanding of this system, flooding events might be a key factor in promoting coexistence between *S. invicta* and *L. humile*. The river floodplain woodlands and savannas are subject annually to floods of variable duration and magnitude. There were no obvious habitat differences between areas containing high densities of *L. humile* and those with high densities of *S. invicta*. However, these species exhibit unique strategies to cope with inundation. Argentine ants retreat temporarily into trees and other emergent vegetation, housing brood and queens inside dead limbs, under loose bark, or in dense clumps of leaves. *Solenopsis invicta*, in contrast, occupies the apical portions of its nest mounds and will float en masse to higher ground if mounds become completely submerged. At our study sites, it seems likely that flooding events restrict *S. invicta* and *L. humile* to species-specific microhabitats that provide suitable refuges from flooding. The ability of these species to respond rapidly to disturbances, such as flooding events, may predispose them for success in the human-modified environments of their introduced ranges.

An additional goal of this study was to examine whether or not *S. invicta* and *L. humile* achieve the extreme levels of behavioral or ecological dominance documented for introduced populations of both species. Both *S. invicta* and (especially) *L. humile* discovered food resources quickly. However, in contrast to studies from the introduced range (Porter and Savignano 1990, Holway 1999), neither species stood out as being an exceptionally fast discoverer of food resources relative to other species in the assemblage. Moreover, the bait turnover data in Table 2 indicate

that neither *S. invicta* nor *L. humile* is the most behaviorally dominant species in these communities. This situation differs from the results of studies from the United States that typically show *S. invicta* and *L. humile* to be the most behaviorally dominant taxon in areas where either of these two species is common (Porter and Savignano 1990, Holway 1999). For reasons that remain unclear, ants that were behaviorally dominant to *S. invicta* and *L. humile* were relatively rare in the habitats sampled.

Solenopsis invicta and especially *L. humile* were among the most ecologically dominant species in the assemblage as measured by their ability to monopolize large, persistent food resources (Table 2). The apparently higher ecological dominance of *L. humile* relative to *S. invicta* may arise because *S. invicta* colonies were less often actively foraging (E. G. LeBrun, C. V. Tillberg, and D. A. Holway, *personal observations*). Reflecting the difference in ecological dominance, other omnivorous ant species captured more baits with the removal of *L. humile* colonies, but the response of these other ant species to the removal of *S. invicta* colonies, although of similar magnitude, was too variable to be significant (Fig. 5). Multiple species achieve ecological dominance in the presence of both red imported fire ants and Argentine ants (Table 2). The ecological dominance of these species in areas with both *S. invicta* and *L. humile* again contrasts sharply with invaded communities in North America (Porter and Savignano 1990, Holway 1999). The use of large resources, although justified in this system, may underestimate the competitive ability of larger bodied species and species such as *P. cf. obscurithorax*, which excel at the retrieval of smaller food items. Limited observations of insect baits, for example, indicated that *P. cf. obscurithorax* is highly proficient at capturing these smaller resources.

An unresolved question in invasion biology is the degree to which populations of introduced species, especially animals, are limited in their native ranges by interspecific competitors. We found that in the native ranges of two important invasive species, *L. humile* and *S. invicta* restrict each other's ability to forage and to capture food resources. These effects likely translate into reduced colony growth, reduced reproductive output, and ultimately smaller population sizes. Moreover, a number of ant species in these systems exhibit competitive abilities that appear equal to or greater than those of *L. humile* and *S. invicta*. While not diminishing the potential importance of escape from coevolved enemies (Porter et al. 1997) or behavioral changes that occurred following introduction into new environments (Ross et al. 1996, Tsutsui et al. 2000), these findings strongly suggest that release from interspecific competition contributes importantly to the success of *L. humile* and *S. invicta* when these species are introduced into new environments. This effect may be heightened by strong biogeographical

disparities in the importance of interspecific competition between ant communities in North and South America. The floodplains of central South America have the remarkable distinction of being the native range for a number of invasive ants including *S. invicta*, *S. richteri*, *L. humile*, *P. obscurithorax*, *Wasmannia auropunctata*, *Pseudomyrmex gracilis*, and *Paratrechina fulva*. The dual pressures of intense interspecific competition and frequent flooding may have selected for species-level traits that make these ants inherently proficient invaders. Moreover, the proximity of this region to major port cities (e.g., Buenos Aires, Rosario, Asunción) make it particularly important as a source of both current and potential invasive species.

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APPENDIX A

A map of northern Argentina showing the location of the study sites and the region of native-range overlap for *S. invicta* and *L. humile* (*Ecological Archives* E088-004-A1).

APPENDIX B

A diagram illustrating the nonoverlapping pattern of bait capture in the colony removal plots before manipulation (*Ecological Archives* E088-004-A2).