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Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species

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Abstract Interactions between the invasive Argentine ant, *Linepithema humile*, and native ant species were studied in a 450-ha biological reserve in northern California. Along the edges of the invasion, the presence of Argentine ants significantly reduced the foraging success of native ant species, and vice versa. Argentine ants were consistently better than native ants at exploiting food sources: Argentine ants found and recruited to bait more consistently and in higher numbers than native ant species, and they foraged for longer periods throughout the day. Native ants and Argentine ants frequently fought when they recruited to the same bait, and native ant species were displaced from bait during 60% of these encounters. In introduction experiments, Argentine ants interfered with the foraging of native ant species, and prevented the establishment of new colonies of native ant species by preying upon winged native ant queens. The Argentine ants' range within the preserve expanded by 12 ha between May 1993 and May 1994, and 13 between September 1993 and September 1994, with a corresponding reduction of the range of native ant species. Although some native ants persist locally at the edges of the invasion of Argentine ants, most eventually disappear from invaded areas. Both interference and exploitation competition appear to be important in the displacement of native ant species from areas invaded by Argentine ants.

Key words Exploitation · Interference · Competition · Argentine ant · Invasion

Introduction

Invasive species can have devastating effects on native species and communities, but the dynamics of invasion processes are often unknown, and it is frequently not clear how invasive species displace local ones (Elton 1958; Lawton and Brown 1986; Simberloff 1981, 1986; Vitousek 1986; Hegenveld 1988; Porter and Savignano 1990). Scientists have repeatedly sought to identify common characteristics of successful invaders and invaded communities (Simberloff 1981; Lawton and Brown 1986; Mooney and Drake 1986; Holdgate 1986; Drake et al. 1989). These investigations conclude that, although some generalizations about invasive species make intuitive sense, most are not yet supported by data or are not useful in predicting the success of introduced species. Lodge (1993) argues that only detailed studied of particular invasions of particular communities can help us understand how species colonize new areas.

The Argentine ant has become an increasingly important global invader, particularly in Mediterranean-type climates. Argentine ant colony structure resembles that of other aggressively invasive ants including *Wasmannia auropunctata* and the polygynous form of *Solenopsis invicta*, the fire ant. Areas invaded by Argentine ants, like those invaded by *W. auropunctata* and *S. invicta*, support impoverished native arthropod communities (Foster 1908; Haskins and Haskins 1965, 1988; Crowell 1968; Erickson 1971; Tremper 1976; Clark et al. 1982; Lubin 1984; Medeiros et al. 1986; Ward 1987; Porter et al. 1988; De Kock 1990; Porter and Savignano 1990; Cole et al. 1992; Holway 1995). Although several researchers have documented the disappearance of native ant species from areas invaded by Argentine ants, we know little about the mechanisms of displacement. Here we ask how competition between an invasive ant and a native ant species may eventually result in replacement of the native ant fauna by Argentine ants.

The role of competition in structuring communities has been controversial (Roughgarden 1983; Schoener 1982, 1983; Connell 1983; Simberloff 1983), but there is considerable evidence that interspecific competition contributes to patterns of distribution and abundance in ant communities (Lynch et al. 1980; Davidson 1985; Rosengren 1986; Savolainen and Vepsäläinen 1988; Andersen and Patel 1994). These papers either investigate the differences between communities with and without a partic-

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ular ant species, or compare foraging strategies among species to make conclusions about competition.

Communities experience rapid flux during the displacement of native species by invasive species, and native species frequently compete with invasive ones (Elton 1958; Porter et al. 1988; D'Antonio and Vitousek 1992). Because invasions may proceed quickly, they represent opportunities for ecologists to investigate the process as well as the results of competition: That is, we can investigate interactions between individuals that lead to displacement.

In this study, we ask (1) whether Argentine ants affect the foraging success of native ant species, (2) what sorts of interactions lead to this effect, and (3) how competition between native ant species and Argentine ants influences ant distribution and abundance.

Methods

The study was conducted from May 1993 to November 1994 at Jasper Ridge Biological Preserve, a 450-ha reserve in northern California (San Mateo County 122° 15′ to 122° 12′ 30″ W and 37° 25′ 24″ to 37° 25′ N, 75- to 100-m elevation). Vegetation types found at Jasper Ridge include serpentine grassland, annual grassland, redwood forests, chaparral, evergreen forest, oak woodland, and riparian systems. The preserve is surrounded by low-density residential areas and agricultural land, most of which has already been invaded by Argentine ants. Argentine ants appear to be moving into the preserve from surrounding areas. Their range within the preserve has expanded 0–300 m/year at various sites along the boundary (unpublished data).

Baiting experiments

To observe encounters between the Argentine ants and native ants, and to examine differences in ability to compete for food, we conducted baiting experiments. In June 1993, we chose three grassland sites, measuring approximately 30 m by 90 m that crossed the border of the invasion of *Linepithema humile*. Each site was divided into 24–27 10 m×10 m squares that we designated as bait stations. At each of the 75 bait stations, we conducted baiting sessions ten times between 1 June and 29 August 1993. During each baiting session, 1-cm^3 piles of bait were set on soil or litter. We observed baits at 20-min intervals for 3 h, and recorded the species and number of ants within 5 cm of the bait. Bait was set out between 5:00–6:00 a.m. or 6:00–7:00 p.m., so it attracted both diurnal and nocturnal species. At each site there were equal numbers of baiting sessions in mornings and evenings. For each baiting session and for each ant species (Table 1), we calculated the duration of time spent at bait and the maximum number of ants that recruited to bait.

Between September 1993 and November 1994, baiting experiments were carried out twice a month. Baits were set out 4 h before dark and observed 1.5, 3.5, and 5 h later.

Preliminary bait choice experiments with cookie, tuna, and crickets indicated that all four ant species tested, *Camponotus semitestaceus, Messor andrei, L. humile*, and *Pheidole californica*, either preferred cookie crumbs (Pecan Sandies) or were equally attracted to all baits. Cookie crumbs were used in baiting experiments during the summer of 1993. Then, baits combining tuna, cookie, and honey were used in baiting experiments from September 1993 to November 1994.

To determine whether the presence of Argentine ants influences the foraging success of native ant species, we compared the foraging behavior of native ant species in the presence and absence of Argentine ants. Bait stations were divided into three categories: (1) bait stations that attracted native ant species only; (2) bait stations that attracted Argentine ants only; and (3) those that attracted both invasive and native ant species. In several cases, bait stations changed category between 1993 and 1994. The two time periods were treated as two different bait stations, and thus, data were analyzed for more than 75 bait stations. We compared the foraging of native ant species in bait station types 1 and 3, and the foraging of Argentine ants in bait station types 2 and 3. For this comparison, all native ant species were grouped, and the probability with which they found baits was calculated by dividing the number of times ants recruited to bait by the total number of times bait was set out in each station. In this analysis, we included only the eight native ant species that recruited to baits more than five times (Table 1).

Table 1 Ant species found at Jasper Ridge using three survey methods: pitfall traps, honey traps, and visual searching

Ant species	Abbreviation used in text, tables, figures
Crematogaster coarctata[a]	Cc
Crematogaster sp.	
Camponotus semitestaceus[a]	Cs
Camponotus cf. vicinus[a]	Cv
Formica moki[a]	Fm
Formica subpolita	
Leptothorax sp.	
Linepithema humile[a]	Lh
Messor andrei[a]	Ma
Neivamyrmex california	
Pheidole californica[a]	Pc
Prenolepis imparis	
Solenopsis molesta[a]	Sm
Stenamma sp.	
Tapinoma sessile[a]	Ts

[a] A species that recruited to baiting stations at least five times between June and September 1993

The baiting experiments were designed to measure the outcome of competition between Argentine ants and native ant species in regions where their foraging ranges overlapped. We included only those bait stations where foragers of a native ant species were seen at least once during the baiting sessions.

Although there was very little overlap between the Argentine ants and native ants at the 100-m scale (see results of ant distribution survey), there was considerable overlap at the 10-m scale of these baiting experiments. For example, a *Crematogaster coarctata* nest was located in a bait station in which both Argentine ants and native ants were found foraging. The eight bait stations immediately surrounding this station included two in which only Argentine ants foraged, four in which only native ants foraged, and two others in which both Argentine ants and native ants foraged. Seven of the eight ant species observed here forage at distances greater than the 10 m separating bait stations. Only *Solenopsis molesta* may not forage across distances up to 10 m.

During many baiting sessions in the summer of 1993, both Argentine ants and native ant species recruited to the same baits. In this case, we classified a native ant species as "displaced" if it recruited to the bait, but left after Argentine ants arrived. When Argentine ants and native ants recruited to the same bait, ants sometimes fought. "Fighting" includes biting legs, antennae or the petiole; quick movement, with open mandibles, toward other ants; and upward tilting of the gaster with subsequent retreat of a facing ant (the latter was observed only in *C. coarctata, L. humile, Tapinoma sessile*, and *S. molesta*). We took notes on the occurrence of fighting during approximately half of the sessions when Argentine ants and native ants recruited to the same bait.

Colony activity observations

To determine how much foraging time is available to native ant species and Argentine ants, we recorded daily foraging patterns of five ant species: *C. semitestaceus, Formica subpolita, L. humile, M. andrei,* and *P. california.* At 3-h intervals, for 21 h, we recorded numbers of ants going into and coming out of the nest entrance. We observed 6 colonies of each species of native ant and 12 nests of *L. humile* on 3 days in June 1994, 3 days in July 1994, and 1 day in August 1994.

Argentine ant introduction experiments

To investigate how native ant foragers respond during encounters with Argentine ants, we set up semi-artificial introduction experiments in the field, where workers from Argentine ant colonies were allowed to interact with workers from native ant colonies. Introduction experiments were conducted in areas not infested with Argentine ants.

Seven Argentine ant colonies were collected from the Stanford University campus, 10 km from the study site, at least 1 month prior to introduction experiments. Colonies were housed in boxes that allowed workers but not queens to leave their box through a tube. Each colony contained 500–1500 workers and 1 to 6 queens, with brood of all stages.

Bait was placed near the nest opening or foraging trail of a native ant colony: *C. semitestaceus* (canned tuna and cookie crumbs), *P. californica* (cookie crumbs) and *M. andrei* (cookie crumbs). In 1993, we tested three colonies of each species three times each, and we allowed native ants to forage briefly at the bait before giving Argentine ant workers access. In 1994, we allowed the Argentine ants to forage first at experimental baits, and compared native ant recruitment to these baits and to baits without Argentine ants. In both years, at least six ants of the first species were foraging at baits when the second species was allowed access to it. Experiments were conducted when the native ant colony was foraging (e.g., early morning or late afternoon for *M. andrei*, at night for *C. semitestaceus* and at dawn or dusk for *P. californica*).

In 1993, when native ant foragers had remained at the bait for 15 min, we allowed Argentine ants to exit their box and forage at the bait. Numbers of both species at the bait were recorded at 5-min intervals. An experiment ended when one species left the bait and remained away for at least 15 min. In one case, both species remained at bait for longer than 2 h and the experiment was terminated. At the end of an experiment, the box of the Argentine ant colony was closed and Argentine ant foragers were collected by aspirator and placed back in their box. The ant species that remained at the bait at the end of the experiment was counted as "persistent". Data were analyzed by tabulating the frequency with which native ants persisted at baits after the arrival of the Argentine ant foragers.

In 1994, we performed introduction experiments with the same three species, in the same general area as in 1993. To compare native ant activity in the presence and absence of Argentine ants, we placed two piles of bait at equal distances from the nest openings or foraging trails of colonies. Argentine ants were allowed to forage at one bait (the experimental bait), immediately after it was set on the ground. We counted the numbers of ants at each bait (experimental and control) every 2 min. Experiments ended when one species was absent from the experimental bait for 15 min. Two colonies of *P. californica* and two of *M. andrei*, were tested three times each, and two colonies of *C. semitestaceus* were tested twice each. Data were analyzed in two ways: (1) we compared native ant recruitment to experimental and control baits with a paired Wilcoxon signed rank test (Sokal and Rohlf 1981) using the total number of ants counted during all observations; and (2) as in 1993, we tabulated the frequency with which native ants persisted at baits despite the presence of the Argentine ant foragers.

Queen introduction experiments

To test for the effect of Argentine ants on the establishment of new native ant colonies, we introduced native ant queens to areas with and areas without Argentine ants. In July 1994 we caught winged queens of *M. andrei* as they emerged from their colonies. We glued one end of a 1- to 2-m monofilament line to each queen's thorax, and tied the other end to a stake. The tethered queens were placed in the field at (1) the site from which they were collected, a grassland area with no Argentine ants, or (2) an adjacent grassland site, approximately 200 m away, infested with Argentine ants. Twenty queens were placed in each area between 6:00 a.m. and 8:00 a.m., when both Argentine ants and *M. andrei* were active. We observed queens at 30-min intervals for 2–3 h, recording the species and number of ants that touched or behaved aggressively toward the queen.

Ant distribution surveys

We monitored changes in ant distribution by surveying all of Jasper Ridge Biological Preserve for ants in May and September 1993, and January, May, and September 1994. Survey points were 10- to 25-m^2 areas at the center of each square hectare of the Preserve. Some survey points were inaccessible owing to poison oak or water: we were able to survey 289 ha out of the possible 450. Each point was searched for ants for 5 min: we searched by scanning vegetation and soil, turning over rocks and dead wood, and sifting through litter. If no ants were found within 5 min, we set two honey traps on the ground. Honey traps consisted of 40-ml vials filled with 10 ml of honey, and we checked the honey traps for live and dead ants after 24 h.

To check this survey method, we conducted a second survey using pitfall traps. We chose 20 sites in areas where Argentine ants had been detected either visually or by honey traps, and 20 sites in areas where Argentine ants had not been detected. Sites were separated by at least 50 m. At each site, we set four pitfall traps: 40-ml vials filled with 30 ml of a 1:1 mixture of water and ethylene glycol. Soil corers were used to remove a plug of soil with little disturbance to surrounding soil or litter, and traps were set flush with the soil surface. We smeared tuna oil around the edges of two pitfall traps at each site. At each site, we also visually searched for ants for 5 min, and we set out two honey traps. Pitfall and honey traps were collected after 48 h.

Results

Baiting experiments

The presence of Argentine ants reduced the probability that native ant species found or recruited to baits, and vice versa (Fig. 1). Native ant species were more likely to find and recruit to baits in areas without than areas with the Argentine ants (Fig. 1, probability of recruitment in area 1 vs area 3, Wilcoxon signed rank test, $P < 0.001$). Conversely, Argentine ants were more likely to find and recruit to baits in areas without native ant species than in areas with native species (Fig. 1, probability of recruitment in area 2 vs area 3, Wilcoxon, $P < 0.001$). Thus, the foraging success of native ant species was negatively affected by the presence of the Argentine ants, and Argentine ants foraged less successfully in the presence of native ant species.

Argentine ants were significantly more likely than native ant species to recruit to baits. We compared the proportion of trials when native ant species came to baits in all areas in which they foraged with the proportion of trials when Argentine ants came to baits in all areas in which the Argentine ants foraged. In individual comparisons, Argentine ants were far more likely than each na-

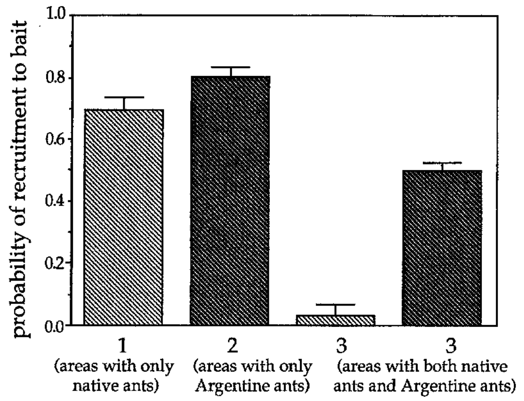

Fig. 1 Native ant species are less likely to recruit to baits than Argentine ants, and they forage less effectively in areas with Argentine ants than in areas without. *Bars* indicate the likelihood of recruitment to baits placed in each of three types of areas: *1* Areas with native ants only, 2 areas with Argentine ants only, and *3* areas with both native and Argentine ants. *Dark-shaded bars* represent Argentine ants, *light-shaded bars* represent native ant species. Probability of recruitment was calculated by dividing the number of times ants recruited to bait in a bait station by the total number of times bait was placed in that bait station. Error bars show standard errors of the means

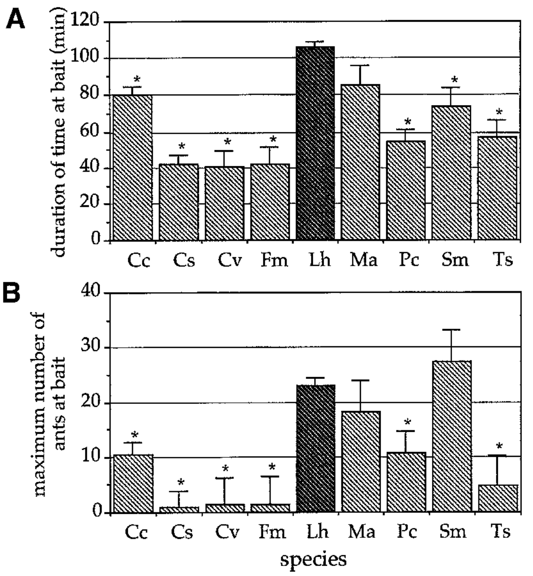

Fig. 2A, B Argentine ants spent more time at baits and recruited in higher numbers than native ant species. Argentine ants, *Lh*, are represeved by *dark-shaded bars*, and native ants by *light-shaded bars*. See Table 1 for abbreviations. *Asterisks* mark a significant difference between Argentine ants and the indicated native ant species (Wilcoxon, duration of time at bait: all $P<0.0001$ except for Ma, $P=0.06$; maximum number of ants at bait, Wilcoxon, all $P<0.0001$ except for Ma, $P=0.05$ and Sm, $P=0.06$)

tive ant species to find and recruit to baits (Wilcoxon, all 8 comparisons had $P < 0.0001$). Even when all native ant species were grouped, Argentine ants were more likely to find baits than native ant species (Fig. 1, probability of recruitment, native ant species vs Argentine ants, Wilcoxon, $P < 0.05$).

Table 2 Frequency of displacement of native species and frequency of fighting, during baiting sessions when both Argentine ants and the indicated native ant species recruited to the same pile of bait. *n* indicates the number of baiting sessions with both Argentine ants and the indicated native ant species. Native ant species were displaced from baits by the Argentine ants more frequently than not, and fights between native ants and Argentine ants were frequent. Abbreviations for native ant species are in Table 1

Ant species	*n*	Frequency of native ant displacement (proportion of *n*)	Frequency of fighting
Cc	15	0.40	0.60
Cs	39	0.59	0.64
Cv	9	0.67	0.80
Fm	7	0.57	0.67
Ma	4	0.50	1.00
Pc	8	0.75	0.50
Sm	5	0.60	1.00
Ts	10	0.90	0.00

Argentine ants spent more time at baits and recruited in higher numbers than most species of native ant (Fig. 2). Argentine ants spent significantly more time at baits than all native ant species except *M. andrei* (Fig. 2A), and recruited in significantly higher numbers than all species except *M. andrei* and *S. molesta* (Fig. 2B).

When both Argentine ants and a native ant species recruited to the same pile of bait, they frequently fought, and native ant species were frequently displaced (Table 2). Some native ant species, such as *C. coarctata*, are less frequently displaced from baits than others, such as *T. sessile*, and some species, such as *M. andrei* and *S. molesta*, are more likely to fight than others, such as *T. sessile*.

Colony activity observations

Throughout the 3 months, Argentine ants foraged for longer than any of the native ant species tested (Fig. 3). They also foraged in higher numbers than most of the native ant species (Fig. 3). *Messor andrei* colonies frequently had as many foragers as Argentine ant colonies, but *M. andrei* rarely foraged during the middle of the day, while Argentine ants did so frequently.

Argentine ant introduction experiments

During introduction experiments, the three native ant species tested varied in their response to the Argentine ants. In 26 of 27 experiments in 1993, one species clearly displaced the other from the bait. In the remaining experiment, both *C. semitestaceus* and Argentine ants remained at the bait for over 2 h. Argentine ants displaced *P. california* from bait in all nine experiments. *Messor andrei* generally excluded Argentine ants from bait (eight of nine experiments), and *C. semitestaceus* was sometimes displaced from bait by the introduced Argentine ants (four of nine experiments). The outcome of the

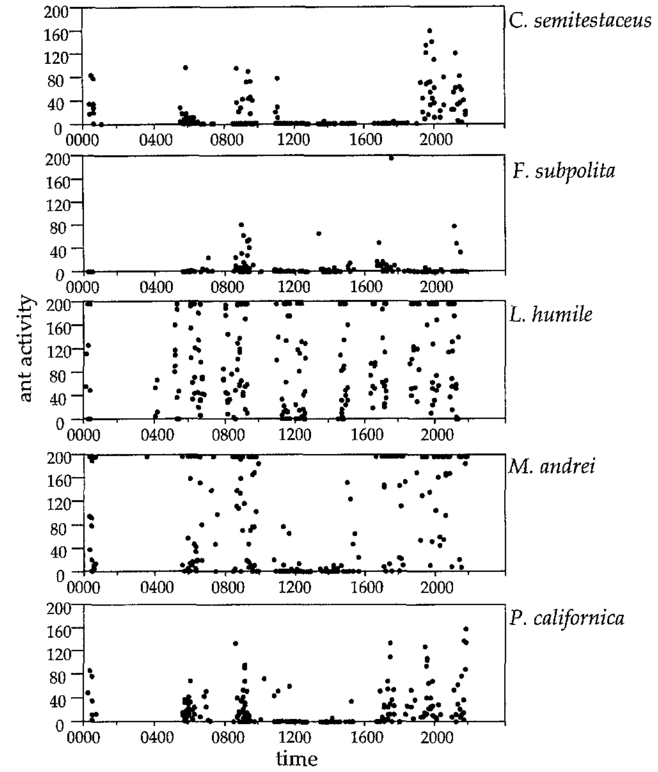

Fig. 3 Argentine ant colonies foraged in higher numbers, and were active for longer during the day, than four native ant species. Each *point* shows ant activity, the sum of ants entering and exiting the colony, in one observation. During the summer of 1994, six colonies of each species were observed for 7 days each. *Messor andrei* most closely resembled the Argentine ants, except midday when *M. andrei* colonies were usually inactive

Table 3 Native ant species' recruitment to baits where *L. humile* was introduced (experimental baits), and baits without *L. humile* (controls). Abbreviations as in Table 1. For each experimental and control bait, we calculated the sum of all ants observed at baits. Native ant species recruited in significantly higher numbers to control baits than to baits with *L. humile* (paired Wilcoxon test, Sokal and Rohlf 1981, *P* indicated in the last column)

Native ant species	Mean sum of ants that recruited to baits		*P*
	Experimental (with *L. humile*)	Control (no *L. humile*)	
Cs	208	393	0.047
Ma	363	712.2	0.031
Pc	30.2	80.5	0.016

experiment did not depend upon the number of native ants that recruited to the piles of bait before Argentine ants were introduced (linear regression, P=0.57 for *C. semitestaceus*, P=0.91 for *M. andrei*, displacement in nine of nine experiments for *P. californica*).

In 1994, when Argentine ants were allowed to forage at baits first, *P. californica* was always excluded from experimental baits with Argentine ants (six out of six experiments). In 1994, *M. andrei* was more likely to be excluded from baits than in 1993: Argentine ants excluded *M. andrei* from baits in half the experiments (three out of six). *Camponotus semitestaceus* always displaced Argentine ants (four out of four experiments) in 1994.

Although native ants often persisted at experimental baits, each native ant species always recruited in lower numbers to experimental baits (with the Argentine ants) than to control baits (Table 3, paired Wilcoxon, P=0.047, 0.031, 0.016 for *C. semitestaceus, M. andrei,* and *P. californica*, respectively).

Native ants and Argentine ants almost invariably fought during these experiments. In both 1993 and 1994, Argentine ants and *C. semitestaceus* fought during all experiments (13 out of 13), and *C. semitestaceus* ants killed Argentine ants in at least 6 of 13 experiments. Argentine ants and *P. californica* also fought during all experiments (15 out of 15), with some mortality of both species (*P. californica* during at least 3 experiments, Argentine ants during at least 2). *Messor andrei* and Argentine ants usually fought (12 out of 15 experiments), and *M. andrei* ants killed Argentine ants in 5 out of 15 experiments.

Queen introduction experiments

Argentine ants quickly swarmed over the *M. andrei* queens that were tethered in their area. Very few *M. andrei* ants, and no ants of other species, interacted with queens placed in the serpentine grassland area. After 2.5 to 3 h, many more ants had found the queens placed in Argentine ant-invaded areas (average 16.4 Argentine ants per queen) than found queens in non-invaded areas (average 0.64 *M. andrei* per queen, Mann-Whitney U-test, z=–2.887, P=0.004). The Argentine ants were very aggressive toward the tethered queens, biting the queens' antennae, legs, wing-stubs, and petioles in 14 of 14 cases where Argentine ants found the queens. *Messor andrei* fought with tethered queens much more rarely – in only 4 of 11 cases where they found the queens (G-test for independence, G=6.69, P<0.01).

Ant distribution surveys

Native ant species were much more abundant where Argentine ants were absent. Our 40-site survey, which combined visual searching, honey traps, and pitfall traps, indicated that there were many more native ant species in areas not invaded by Argentine ants than in areas with Argentine ants (average number of species: 3.65 vs 0.05, Wilcoxon signed rank test, S=609, P<0.0001). Only *Prenolepis imparis* was found in areas with Argentine ants, and only at one site. Using all survey methods, we found 15 species of ant, listed in Table 1. In our seasonal surveys of the preserve, Argentine ants and a native ant species occurred together in only 2.5% of all survey points, all of which were along the edges of the Argentine ant invasion. Note that although Argentine ants and native ant species appear to occupy separate regions at

Table 4 Numbers indicate the number of hectares. The last column records the advance of the Argentine ants, in hectares, over the given time period. The last two rows summarize the expansion of the Argentine ant range over two different 12-month periods

Time interval	Argentine ants		
	Moved into	Moved out of	Advanced
May to Sept 93	14	9	5
Sept 93 to Jan 94	6	18	–12
Jan to May 94	28	9	19
May to Sept 94	10	5	5
May 93 to May 94	18	6	12
Sept 93 to Sept 94	20	7	13

the 100-m scale of the distribution survey, there was significant overlap at the 10-m scale of baiting experiments.

Pitfall trap results verified the effectiveness of visual surveys and honey traps. In each of the 20 sites where Argentine ants were found in pitfall traps, we also discovered them visually and found them in honey traps. In areas without Argentine ants, the mean number of native ant species found in visual surveys and honey traps did not differ from the mean number found in pitfall traps (Student's *t*-test, *df*=38, *t*=1.355, *P*=0.1835).

During the 17 months of the five surveys, Argentine ants moved into 21 new ha and moved out of 34 ha where they had been previously seen. Over two different 12-month periods (May 1993 to May 1994 and September 1993 to September 1994), the Argentine ants expanded their territory by 18 and 20 ha. From May 1993 to May 1994, the Argentine ants disappeared from 6 ha in which they had been previously sampled, and from September 1993 to September 1994, they disappeared from 7 ha. In all hectares newly occupied by Argentine ants, native ant species had been sampled in at least one, and sometimes all, of the previous surveys. Argentine ants did not move into new areas at a uniform rate. Over 12 months, the invasion front moved as much as 300 m (3 ha) in some areas, and 0 m in some. Because we sampled only one survey point per hectare, the margin of error is 100 m.

The range expansion of Argentine ants varied seasonally, with most expansion occurring in spring and summer (Table 4). Between May and September 1993, Argentine ants moved into more new areas than they left. However, between September 1993 and January 1994, Argentine ants lost ground. In January, there were either no ants or only *P. imparis* at many points where Argentine ants had been found in September. From January to May 1994, and May to September 1994, Argentine ants moved back into lost ground and into new areas.

Discussion

Along the edges of areas invaded by Argentine ants, ant communities include both native ant species and the Argentine ants. Over the 17 months of our work, many of these communities reduced to a single species: Argentine ants. What happens along the edges of the distribution of Argentine ants that leads, eventually, to the emigration or death of native ant colonies? In the ephemeral mixed communities studied along the edges of the distribution of Argentine ants, Argentine ants behave similarly to strongly competitive ants described elsewhere (Rosengren 1986; Fellers 1987; Andersen and Patel 1994): their presence reduces the foraging success of other ant species. Aggressive interactions with the Argentine ants and reduced foraging success can contribute to the disappearance of native ant species from areas invaded by Argentine ants. Several native ant species sometimes emigrate: we have observed this in *M. andrei, P.californica* and *C. coarctata*. In *M. andrei* and *C. coarctata*, emigration occurred immediately following a series of aggressive interactions with Argentine ants.

In baiting experiments and in introduction experiments, the presence of Argentine ants depressed the foraging success of native ant species at artificial baits (Fig. 1 and Table 3). This may result from interference or exploitation or both. Significantly decreased foraging success may cause native ant colonies to leave areas invaded by Argentine ants. The differences between our introduction experiments in 1993 and 1994 are intriguing and merit further exploration.

Invasive Argentine ants directly interfere with the foraging activity of native ant species. Argentine ants fought with native ant species 62% of the times two species were observed together at baits (Table 2). It is likely that aggression between Argentine ants and native ant species is not limited to interactions at food. The reaction of Argentine ants to *M. andrei* queens shows that Argentine ants clearly can interfere with the establishment of new colonies of native ant species. Fighting could be a significant cost to native ant species both in mortality and in foraging success, since native ants were frequently displaced from baits.

Argentine ants can exploit resources that would otherwise be used by native ant species, and this may reduce the foraging success of native ant colonies. Argentine ants are more likely than native ants to find baits (Fig. 1), indicating that Argentine ant nests are more effective than native ant colonies at covering space. This may be due either to larger numbers of ants per nest, or to more effective searching behavior, or both (Gordon 1995). Argentine ants forage longer than all species of native ant tested (Fig. 3). Once they find food, Argentine ants also persist at the bait for a longer time than native ant species (Fig. 2A), and recruit in higher numbers (Fig. 2B).

Both colony size and foraging behavior may contribute to the Argentine ant's success as an invader. Jones and Phillips (1990) compared, in the laboratory, the foraging strategies of *S. invicta* and native ant species, and found that native ants were more efficient foragers, by several measures, than *S. invicta*. They concluded that *S. invicta's* effectiveness as a competitor is due to its large colony size. Here we have not compared the foraging efficiency of individual ants of different species, but our results demonstrate that Argentine ant nests are more effective at foraging, by several measures, than those of the native ant species they encounter at Jasper Ridge. Large nest size may be only one of the factors that contribute to the competitive ability of Argentine ants. The high nest density of the Argentine ants may also be important, as may be the foraging efficiency of individual ants and the tendency of ants to persist despite interference (Fig. 2). Interestingly, Argentine ant foraging activity was depressed in areas where they come into contact with native ant species (Fig. 1). Native ants may interfere with the foraging of Argentine ants, and Argentine ant colonies may also be smaller in these areas.

Although competition affects the foraging success of Argentine ants as well as native species, it is the native ant species that eventually disappear. We found minimal overlap between the distributions of native ant species and Argentine ants when sampled by hectare, and we found that Argentine ants moved into areas previously occupied by native ant species. In some areas surveyed, Argentine ants spread as quickly as 300 m in 17 months. Argentine ants move 50–150 m per year in riparian areas in California's Central Valley (Holway 1995). Erickson (1971) described a similar rate of spread of Argentine ants across a field in San Luis Rey, San Diego County, California. It is intriguing that the Argentine ants disappeared from several spots in which they had previously been sampled. It is possible that earlier samples were from small satellite colonies that never established, or that differences in rainfall and temperature regimes between years meant that a previously suitable microclimate became unsuitable for the Argentine ants. We plan to address this in future research.

This work raises several interesting questions. Many factors may influence foraging success, and foraging success may be only one factor that determines colony survival. It would be interesting to know how proximity to Argentine ant colonies affects the frequency of interactions between native ants and Argentine ants; how much foraging time native ant colonies can lose to such interactions; and how much of the potential food of native ant species is removed by the invasive ants.

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