

Effects of Abiotic Factors on the Distribution and Activity of the Invasive Argentine Ant (Hymenoptera: Formicidae)

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ABSTRACT The Argentine ant, *Linepithema humile* (Mayr), has spread worldwide, often decimating native ant populations and other arthropod species in invaded areas. It is not known what abiotic and biotic conditions limit its distribution. We investigated the distribution of the Argentine ant in the Jasper Ridge Biological Preserve in northern California, a nature preserve that has been partially invaded by these ants. Canonical correlation analysis showed that the Argentine ant is most likely to occur near the edges of the preserve, which are next to disturbed areas and in low-elevation areas. Native ant species are associated with higher-elevation areas farther from the preserve edge. Distance to surface water and insolation were less important in predicting Argentine ant distribution. This suggests that dispersal from disturbed areas strongly determines the spread of the invasion. We examined how the daily activity patterns of Argentine ants and several native ant species depend on soil temperature, air temperature, and relative humidity. There was considerable overlap in activity times, and there were no values of any of the abiotic factors measured in which native ant species were more likely to be active than Argentine ants. Because the Argentine ant is usually active at the same times as any native species, most native species in invaded areas are likely to encounter the invaders frequently. Diet overlap was high with most native ant species except for seed-eating species. Overlap in activity times may intensify both exploitative and interference competition between the Argentine and native ant species.

KEY WORDS *Linepithema humile*, colony activity, foraging, competition, invasion

STUDIES OF COMMUNITIES in flux, such as those subject to a biological invasion, can elucidate the roles of abiotic and biotic factors in structuring communities. The Argentine ant, *Linepithema humile* (Mayr), has invaded many areas of the world, displacing native ant species and other invertebrates where it invades (Foster 1908; Haskins and Haskins 1965, 1988; Crowell 1968; Erickson 1971; Tremper 1976; Ward 1987; De Kock 1990; Cole et al. 1992). It has been suggested that extremely successful biological invaders, such as the Argentine ant, generally have broad niches (Elton 1958; Baker and Stebbins 1965; Ehrlich 1986; Holdgate 1986; Porter and Savignano 1990). If broad environmental tolerance allows an invasive species to be active in the same range of abiotic conditions as a native one, competitive or predatory interactions may lead to the displacement of native species during an invasion (Elton 1958; Fausch and White 1981; Ward 1987; Banks and Williams 1989; Porter and Savignano 1990; D'Antonio and Vitousek 1992; Human and Gordon 1996, 1997).

Abiotic factors may affect the distribution of the Argentine ant. In the Central Valley of California, the range of the Argentine ant is probably limited by proximity to water (Ward 1987, Holway 1995). An ant species' activity patterns and range may depend in

part on its size and body color, which affect rates of heating and desiccation (Casey 1976, Tremper 1976). Behavioral strategies may affect tolerance of abiotic conditions (Marsh 1988), and the physical structure of nests may modulate temperature and humidity inside the nest (Andrews 1927, Brian 1973). Argentine ant workers are small, relative to those of many species of native ant, and may therefore be more vulnerable to desiccation (Tremper 1976).

The spread of the Argentine ant has been monitored since 1993 in the Jasper Ridge Biological Preserve in California, a reserve of 482 ha surrounded by residential and agricultural development. The invasion is proceeding at rates up to 300 m/yr, accompanied by a drastic decline in populations of native species and changes in the distributions of many other arthropods (Human and Gordon 1996, 1997). Both interference and exploitative competition seem to be important in the displacement of native ant species from invaded areas.

Here we relate the local distribution of the Argentine ant in the Jasper Ridge Biological Preserve to several abiotic factors. Ant species' ranges may be limited by elevation, proximity to water, or minimum annual temperature (Davidson 1977, Bernstein 1979, Cushman 1993). We consider the effects of distance to the nearest source of water; distance to the nearest edge of the preserve and thus to disturbed areas; elevation; and in-

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solation on Argentine ant distribution. We then compare the daily activity patterns and diets of the Argentine ant and several native ant species. The daily activity patterns of ant colonies may depend on abiotic factors such as soil temperature and relative humidity (Fielde 1904, Talbot 1943, Brian 1964, Marsh 1988, Vepsäläinen and Savolainen 1990, Dean 1992) and also on interactions with competitors, prey, or predators (Brian 1964, Lynch et al. 1980, Briese and Macauley 1980, Gordon 1988, Savolainen and Vepsäläinen 1988, Andersen 1992, Dean 1992, Andersen and Patel 1994). We relate activity patterns to 4 abiotic factors (time of day, soil temperature, air temperature, and relative humidity) and calculate the overlap in diet of Argentine ant and native ant species. Finally, we investigate whether abiotic conditions may limit the invasion of the Argentine ant and consider how temporal and resource overlap may lead to competition between the invasive and native ant species.

Materials and Methods

Study Site. This study was conducted at the 482-ha Jasper Ridge Biological Preserve in northern California (San Mateo County, 122° 13' W and 37° 24' N, 60–120 m in elevation). Vegetation types found at the preserve include serpentine grassland, annual grassland, redwood forests, chaparral, evergreen forest, oak woodland, wetland, and riparian systems (species listed in Sawyer and Keeler-Wolf 1995). Argentine ants have invaded ≈30% of the area of Jasper Ridge, primarily along the edge of the preserve. Jasper Ridge is surrounded by low-density residential areas and agricultural land, most of which has already been invaded by Argentine ants.

Ant Species Distributions. Between May 1993 and January 1996, we surveyed all of Jasper Ridge Biological Preserve for ants 3 times yearly. Surveys were conducted in May (following the end of the rainy season), September (at the end of the dry summer), and January (during the rainy season). For ant surveys, a map of the entire preserve was overlaid with a 100-m grid. By using survey points at the center of each hectare, we recorded the presence or absence of native ants and Argentine ants. For 5 min we searched visually for ants within a 20-m-radius circle of the survey point. If no ants were found, we left honey traps, consisting of 40-ml vials filled with 10 ml of honey, and collected them 24 h later. Details of the survey method and a test of its accuracy are described elsewhere (Human and Gordon 1996). In the September 1993, January 1994, and May 1994 surveys, native ant species were identified only as not Argentine ants, but thereafter they were identified to genus. In each time period, 296–318 ha were surveyed. A few survey points could not be reached during particular times of year because of flooding or poison oak (*Toxicodendron diversilobum* Jepson). Ant distribution data were entered into a geographical information system (ArcView GIS 1996).

For analysis, ant distribution data for each hectare were converted into a measure of incidence: the proportion of all surveys in which ants of a particular

genus were found. For example, if Argentine ants were detected in 7 of 9 surveys, Argentine ant incidence in that hectare was 0.78. Incidence was calculated for all ant species sampled in each hectare. Data from the 3 earliest surveys, in which native species were not identified, were not included in this calculation. This measure of incidence does not take into account temporal changes in the distribution of ants, but the distribution of the Argentine ant at Jasper Ridge changed very slowly, its front advancing at a rate of ≈300 m/y (Human and Gordon 1996).

By using spatial databases of the Jasper Ridge Preserve developed at the Center for Conservation Biology, Stanford University, we calculated the following for each survey point: distance to the nearest source of surface water (m), distance to the nearest edge of the preserve (m), mean elevation (m), mean summer solstice insolation ($\text{kJ}/\text{m}^2/\text{d}$), and slope (deg). Many streams in the preserve are present only briefly during the rainy season of especially wet years; to exclude these streams, only streams containing water for at least 4 mo out of the year were included in the calculation of distance to water. Physiographic variables were calculated from a digital elevation model with a horizontal resolution of 5 m, developed using the Arc/Info TOPOGRID function (Hutchinson 1989, 1993) from U.S. Geological Survey 1:24,000 digital hypsography (6.2-m contour intervals), spot elevations, and hydrology (Palo Alto Quad, USGS 1990). We calculated slope, the rate of change in elevation, by using the average maximum technique (Burrough 1986) applied in a 3 by 3 cell neighborhood over each cell in the raster data set. Potential clear sky insolation for June 21 was calculated using the Arc Macro Language program SOLARFLUX (Hetrick et al. 1993) with an atmospheric transmittance of 0.65. Mean values for each abiotic factor were calculated within a 20-m diameter circle around the survey point, the same area within which we searched for ants.

To examine the relationship of incidence of ant genera to abiotic factors, we used canonical correspondence analysis. Canonical correspondence analysis is an ordination technique that relates unimodal responses of distribution data, including abundance or incidence, to environmental variables (ter Braak 1987, 1988; Whittaker 1989; Palmer 1993). The technique takes into account relationships among independent variables. In canonical correspondence analysis, the linear combination of independent variables that best explains the differences in dependent variables is the 1st canonical axis, and additional axes are calculated to account for the remaining variation (ter Braak and Prentice 1988; Palmer 1993). Eigenvalues, which range from 0 to 1, are calculated for each axis to describe the fraction of variance that is accounted for by that axis.

Monte Carlo permutations were used to test statistically whether the incidence of ant genera was related to the abiotic variables by using CANOCO (ter Braak 1987). In each of 99 unrestricted Monte Carlo permutations, values of the abiotic variables and genera incidence were randomized, and new canonical

axes and eigenvalues were calculated. If 95% of the new eigenvalues calculated for axis I were lower than that eigenvalue in the fitted canonical correspondence analysis model, then axis I of the fitted model was considered to account for a significant proportion of the variance in dependent variables (ter Braak 1987). For a test of significance of the entire canonical correspondence analysis model, the eigenvalues of all axes were summed after each permutation, and those sums were compared with the sum of the original eigenvalues. Similar Monte Carlo permutations were used to test the significance of the contribution of each abiotic factor to the variance in ant distribution.

Distance to the preserve edge and elevation appeared to account for most of the differences in the distribution of all native ant genera (considered as 1 group) and the Argentine ant, and previous work suggested that the Argentine ant is limited to areas near permanently flowing water (Ward 1987, Holway 1995). To examine further the relationship of Argentine ant incidence and these 3 factors, hectares were classified by degree of Argentine ant establishment as follows: (1) firmly established (found in 75–100% of all surveys in 3 yr); (2) transitional (found in 14–74% of all surveys); and (3) absent (never found). To compare areas where Argentine ants were firmly established, transitional, and absent, we plotted the values of the abiotic variables with box plots. We performed no statistical analyses on these data because they were used in statistical analysis of the canonical correspondence analysis model, and because the 3 abiotic factors may not be independent of each other.

Activity Patterns. To compare the activity patterns of native ant species and Argentine ants, we observed colonies of Argentine ants and 4 native ant species: *Camponotus semitestaceus* Snelling, *Formica subpolita* Mayr, *Messor andrei* Mayr, and *Pheidole californica* Mayr. During each observation day, 6 colonies of each species of native ant and/or 12 Argentine ant nests were observed at 3-h intervals for 21 consecutive h. During each activity observation, we recorded the number of ants entering and exiting the colony within 2 min. The activity of all colonies was observed over 6 d; native ant colonies for 3 d in June 1994 and 3 d in July 1994, and Argentine ant colonies for 2 d in June 1994, 3 d in July 1994, and 1 d in August 1994. For 1 d in June, only colonies of native ants were observed, and for 1 d in August, only colonies of Argentine ants were observed. Data were collected in the summer months when activity is highest and most constant for all species (K.G.H., unpublished data). When activity counts were made, we also recorded the soil surface temperature with an infrared thermometer (Omega-scope model 0582), and relative humidity and air temperature 3 cm above the soil surface with an Omega temperature and relative humidity meter (model RH-21C, Omega Engineering Inc., Stamford, CT, USA).

Soil temperature, air temperature, relative humidity, and time of day are all related. To examine species differences in the relation of ant colony activity and the abiotic factors, we used canonical correspondence analysis, which accounts for relationships among in-

dependent variables. In this canonical correspondence analysis, colony activity (numbers of ants entering and exiting colonies) was considered the dependent variable, and soil temperature (°C), air temperature (°C), and relative humidity (%), were independent variables. Time of day was not included in the canonical correspondence analysis because the analysis cannot handle circular data. Monte Carlo simulations were used to test how well the canonical correspondence analysis model describes the relation of ant colony activity to the abiotic factors.

Diet Overlap and Forage Composition. To compare the diets of 4 native ant species and the Argentine ant, we intercepted foragers of each species returning to the colonies and their forage was identified. In July 1994 and April 1995, we collected forage from 9 colonies of Argentine ants, 12 colonies of *M. andrei*, 10 colonies of *F. subpolita*, 11 colonies of *P. californica*, and 9 colonies of *C. semitestaceus* in a chaparral-oak woodland at Jasper Ridge. The native ant species overlapped in range with each other but not with the Argentine ant; the area with the colonies of native species was 100–200 m from the invasion front of the Argentine ant. The forage of 100 ants returning to each colony during peak foraging hours was identified on site or collected and later identified in the laboratory. Forage was classified as follows: seeds, meat (dead or live insects), liquid food (indicated by distention of an ant's gaster), or other (twigs, bits of leaves, soil, rock, or unidentifiable matter). For ants of 1 native species, *F. subpolita*, we could not determine whether the gasters of workers were distended.

To compare the diet of the Argentine ant and each native ant species, we calculated overlap, O_{ij} , as

$$O_{ij} = \sum_{a=1}^n P_{ia}P_{ja} / \left(\sum P_{ia}^2 \sum P_{ja}^2 \right)^{1/2}$$

where P_{ia} and P_{ja} are the proportions of food category a in the diets of species i and j (Pianka 1973). The value approaches 1 as overlap increases.

Results

Ant Species Distributions. Argentine ants appear to have invaded Jasper Ridge Biological Preserve from the edge, and they appear to be most strongly established in areas near water (Fig. 1). Distance to edge, elevation, insolation and distance to water together explained a significant proportion of the variation in the distribution of ant genera. In the canonical correspondence analysis, eigenvalues of Axis I and Axis II were 0.46 and 0.02, respectively, indicating that the linear combination of environmental variables in Axis I described most of the variation in ant distribution explained by the model. The linear combinations were as follows:

$$\text{Axis I} = 0.75 e + 0.42 v - 0.04 s - 0.21 i + 0.18 w \quad [1]$$

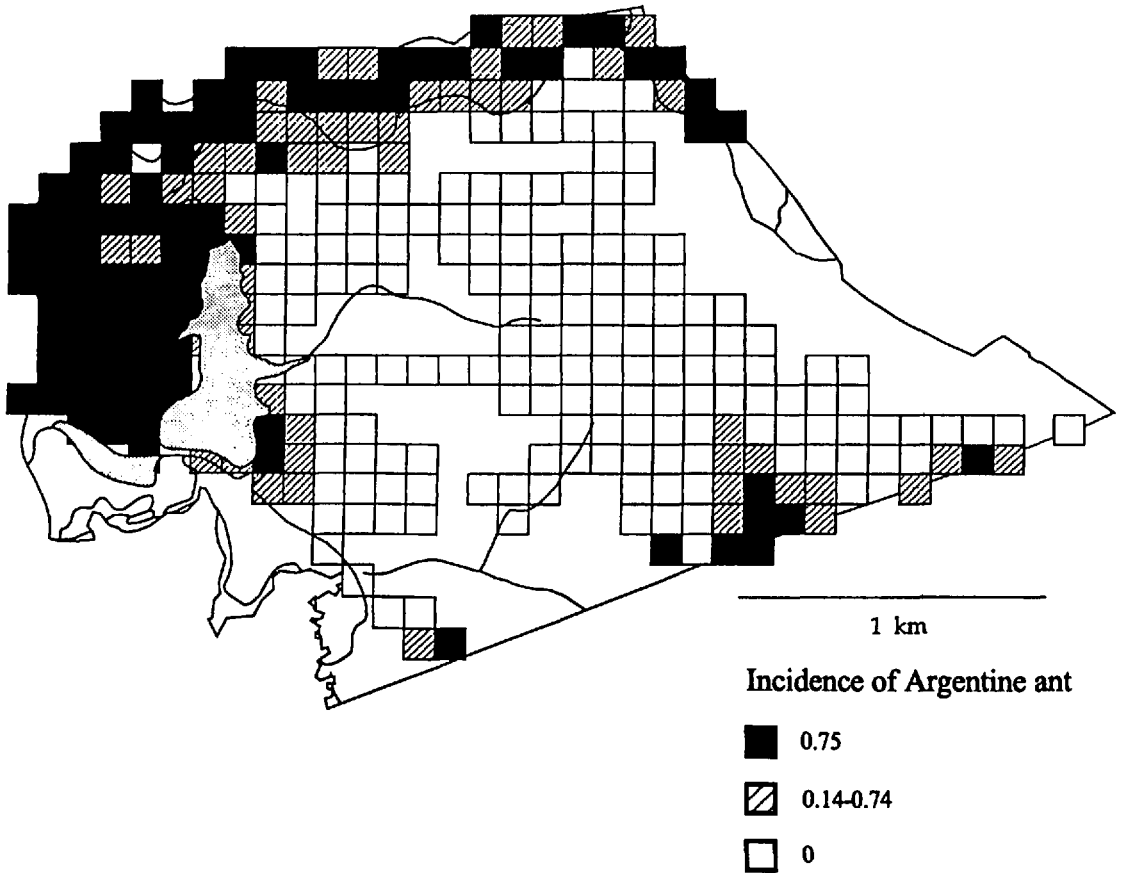


Fig. 1. Argentine ant incidence at Jasper Ridge Biological Preserve in 9 surveys over 3 yr. Each square represents 1 ha, and incidence was calculated for each ha as the proportion of 9 surveys in which the Argentine ant was found. The black line around the perimeter of the figure is the preserve boundary, black lines in the interior of the preserve represent streams, and a lake and a wetland area are shown in gray.

$$\text{Axis II} = -0.35 e + 0.9 v - 1.14 s - 0.75 i - 0.65 w, [2]$$

where e = distance to edge, v = elevation, s = slope, i = insolation, and w = distance to water. The coefficient of each describes the magnitude of its contribution to the axis. Monte Carlo simulations determined that both the 1st canonical axis alone and all axes combined contribute significantly to variation among genera in incidence ($P < 0.01$ for axis 1, $P < 0.01$ for the whole model). Axis II was not significant, so further axes were discounted.

In the ordination diagram (Fig. 2), abiotic variables are represented by arrows. Arrows point toward genera that tend to occur in areas with high values of the abiotic variable represented. The projection of each arrow on an axis indicates the magnitude of its contribution to that axis, and arrows are numbered by the value of the Axis I canonical coefficients of the abiotic factors they represent. For example, although arrow 5, representing the variable slope, is relatively long in the direction of Axis II, its projection on Axis I is small,

reflecting a small canonical coefficient in that axis (-0.04 , equation 1).

Distance to the preserve edge, weighted most heavily in Axis I, accounted for most of the variation among genera in distribution (canonical coefficient = 0.75 in axis I, $P = 0.01$, Monte Carlo permutations). The arrow for distance to the preserve edge (arrow 1) points generally to the right, indicating that ant genera that tend to occur far from the edge of the preserve fall on the right side of the ordination diagram (Fig. 2). *Crematogaster* spp., *Formica* spp., and *M. andrei* are generally found in areas far from the preserve edge, whereas Argentine ants and *Liometopum occidentale* Emery are generally found much closer to the edge. *Prenolepis imparis* Mayr and *Leptothorax* spp. were found in areas at intermediate distances from the edge. A dotted line drawn perpendicular to the arrow and through the origin ($1'$ in Fig. 2) separates the Argentine ant (LH) from most native ant genera.

Elevation contributed significantly to differences among ant genera in distribution ($P = 0.01$, Monte Carlo permutations). Ants found at highest elevations

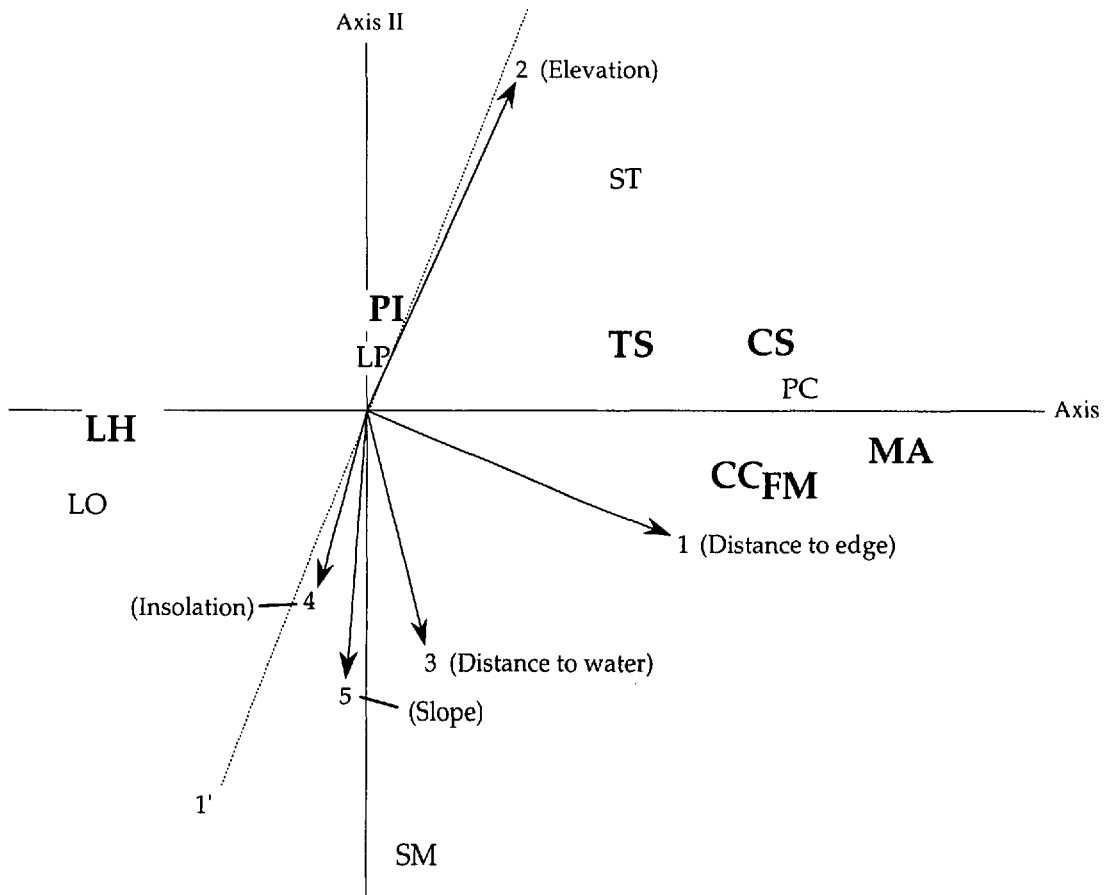


Fig. 2. Canonical correspondence ordination of ant incidence data during 9 surveys. Abiotic factors are represented by vectors as follows: 1, Distance to edge; 2, elevation; 3, distance to water; 4, insolation; 5, slope. To aid in the visual interpretation of the diagram, dotted line 1' is drawn perpendicular to vector 1. Ant genera that fall on opposite sides of this line occur, on average, in areas with different values of the abiotic factor represented, distance to edge. Axis II is plotted for convention only; its contribution to the variance in ant distribution is minimal. CC, *Crematogaster* spp.; CS, *C. semitestaceus*; FM, *Formica* spp.; LH, *L. humile*; LO, *L. occidentale*; LP, *Leptothorax* spp.; MA, *Missor andrei*; PC, *Pheidole californica*; PI, *Prenolepis imparis*; SM, *S. molesta*; and ST, *Stenamma* spp. LO, PC, ST, and SM (small letters) were rarely discovered in ant surveys; CC, CS, FM, LH, MA, PI, and TS (large letters) were discovered frequently.

included *Stenamma* spp. and *Camponotus* spp., and those found in lower elevations included *Solenopsis molesta* Mayr, *L. occidentale*, and the Argentine ant.

Insolation and distance to water explained small but significant amounts of variation among genera in distribution ($P = 0.01$ for insolation, $P = 0.02$ for distance to water). *S. molesta* and the Argentine ant were found in areas with the highest insolation and *P. imparis*, *Leptothorax* spp., and the Argentine ant were found closest to water. Slope did not explain any variation in distribution among ant genera ($P = 0.23$).

Of the 7 native ant species sampled frequently, shown in large letters in Fig. 2, *P. imparis* is most similar to the Argentine ant. *P. imparis* is the 1 species of native ant often seen foraging in the vicinity of Argentine ant nests. *P. imparis* colonies are active from November to June, during times when most native ant colonies are not active and when the Argentine ants are frequently inactive. *L. occidentale*, sampled rarely,

is also close to the Argentine ant on the ordination diagram. Like the Argentine ant, *L. occidentale* is a dolichoderine ant that makes long trails as it forages for the liquid exudate of insects (Wheeler and Wheeler 1986).

When the effects of distance to edge, elevation, and distance to water were each plotted separately, the results supported the patterns suggested by the canonical correspondence analysis. On average, the Argentine ant was most strongly established closer to the preserve edge, closer to water, and in areas at lower elevation (Fig. 3).

Activity Patterns. Soil temperature, relative humidity, and air temperature explained a significant proportion of the variation in the distribution of ant genera (Fig. 4). Eigenvalues of Axis I and II were 0.19 and 0.03, respectively, indicating that the linear combination of abiotic factors in Axis I accounted for most of

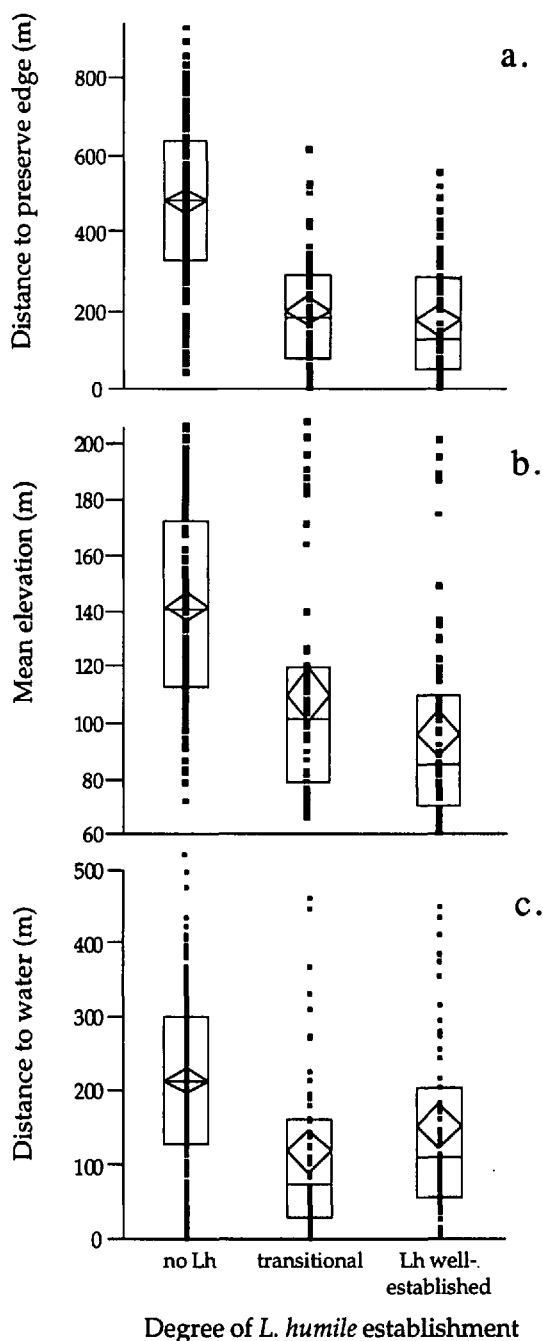


Fig. 3. Box plots of the relationship between degree of establishment by the Argentine ant and 3 environmental variables (a-c). Each dot represents 1 ha, and the box surrounds 50% of all observations. Horizontal lines in the centers of the boxes are medians, and diamonds show the mean values (center of the diamond) and standard error of the mean (height of the diamond). The right column in each graph represents hectares where Argentine ants are well established (found in 75–100% of all surveys over 3 yr). The middle column represents transitional hectares (Argentine ants found in 14–74% of all surveys) and the left column represents hectares in which Argentine ants were never observed.

the variance in colony activity explained by the model. The linear combinations were as follows:

$$\text{axis I} = 1.01 T_s + 0.94 R_h + 0.03 T_a \quad [3]$$

$$\text{axis II} = 0.81 T_s - 0.72 R_h - 0.49 T_a, \quad [4]$$

where T_s is soil temperature in degrees centigrade, R_h is relative humidity in percent, and T_a is air temperature in degrees centigrade. Monte Carlo simulations determined that both the 1st canonical axis alone, and all axes combined, contributed significantly to variation between species in activity ($P < 0.01$ for axis I, $P < 0.01$ for the whole model, 99 permutations). The low eigenvalue of axis I in this canonical correspondence analysis reveals that there is substantial overlap among ant species in abiotic conditions at which they are active. Axis II was not significant, so further axes were discounted.

All 3 of the abiotic factors contributed significantly to variation in colony activity ($P = 0.01$ for soil temperature, $P = 0.01$ for relative humidity, $P = 0.01$ for air temperature, Monte Carlo permutations). Soil temperature and relative humidity, represented most strongly in the 1st canonical axis, account for most of the differences among colonies in activity patterns. The outlying position of *F. subpolita* in the ordination diagram (Fig. 4) is probably partly a result of low overall activity of *F. subpolita* colonies relative to colonies of the other species tested.

The Argentine ant was somewhat more likely than the native ant species to be active in higher soil temperatures up to 70°C. Colonies of *P. californica* and *C. semitestaceus*, both of which are crepuscular and nocturnal, did not forage in temperatures >40°C. *F. subpolita* and *M. andrei* remained active up to ≈60°C (Fig. 5a). Air temperature measured with a thermocouple appeared to be highly correlated with infrared-derived soil temperature (Fig. 6c), so it is not surprising that for all species, the relations of colony activity to air and soil temperature were similar (Fig. 5a and b). Colonies of the Argentine ant were active in air temperatures up to 45°C, as were colonies of *M. andrei*, whereas other native ant species were more limited by air temperature (Fig. 5b).

Relative humidity may limit slightly the activity of all species (Fig. 5c); all ant species were more likely to be inactive when relative humidity was <40% (Fig. 5c). The Argentine ant was slightly more likely than native species to be active when relative humidity was high (Fig. 5c).

Time of day influenced colony activity. *C. semitestaceus*, *M. andrei*, and *P. californica* were usually inactive for some time in the middle of the day, though *M. andrei* only for a short period (Fig. 5c). The Argentine ants were often active throughout the day.

Overall, during the summer Argentine ants are active in a wider range of temperatures and relative humidities than colonies of *C. semitestaceus* and *F. subpolita*, and in a slightly wider range of temperatures, relative humidities, and times than *P. californica* (Fig. 5 a–d). Colonies of *M. andrei* are active under most of the same conditions as the Argentine ants,

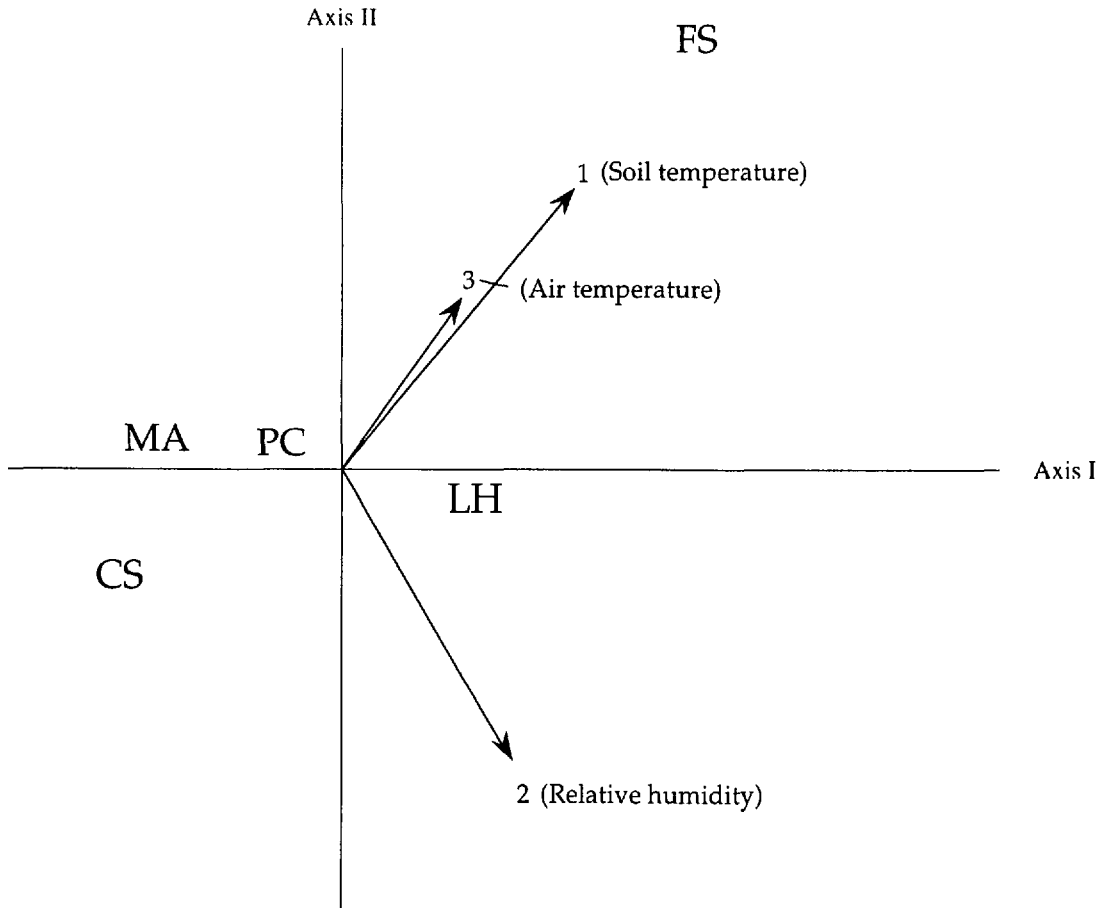


Fig. 4. CANOCO ordination of ant colony activity data. Abiotic factors are represented by vectors as follows: 1, soil temperature; 2, relative humidity; and 3, air temperature. Axis II is plotted for convention only; its contribution to the variance in ant distribution is minimal. CS, *Camponotus semitestaceus*; FS, *F. subpolita*; LH, *Linepithema humile*; MA, *Messor andrei*; PC, *Pheidole californica*.

with the exception of a short period of time in the middle of the day, characterized by high soil temperatures, when *M. andrei* colonies are usually inactive for a few hours but the Argentine ants are not (Fig. 5 a and d).

There are many sets of abiotic conditions in which colonies of native and Argentine ants are both active (Fig. 5). For example, whenever *P. californica* colonies are active during the day, so are the Argentine ants (Fig. 5d). There are no values of any of the abiotic factors measured in which the native ant species were more likely to be active than the Argentine ants.

Abiotic factors all depend upon each other. Relative humidity was high at low air temperatures (Fig. 6a), soil temperature increases from sunrise to midday before decreasing again (Fig. 6b), and air and soil temperatures are positively correlated (Fig. 6c). Canonical correspondence analysis takes the interaction of variables into account.

Diet Overlap. The 2 seed-eating ants tested, *M. andrei* and *P. californica*, overlapped only slightly in diet with the Argentine ant ($O = 0.011$ and 0.015 ,

respectively; Table 1). Most of the forage of *M. andrei* and *P. californica* was seeds, although like the Argentine ants, both the seed-eating species also brought some dead insects back to the colony (Table 1). *F. subpolita* and the Argentine ant overlap only in the collection of insects (Table 1), but insects made up a far larger fraction of the forage of *F. subpolita* (0.631) than of the Argentine ant (0.055). The diet of *C. semitestaceus* was similar to that of the Argentine ant: both species primarily collected liquid food.

Discussion

Distribution of Ants at Jasper Ridge. At Jasper Ridge, the Argentine ant is most likely to occur in areas that are close to the preserve edge and areas at low elevation, whereas native ant species are more abundant in the center of the preserve and at higher elevation.

The association of the Argentine ant with areas near the preserve edge may be due to its response to disturbance and to its mechanism of dispersal. Many

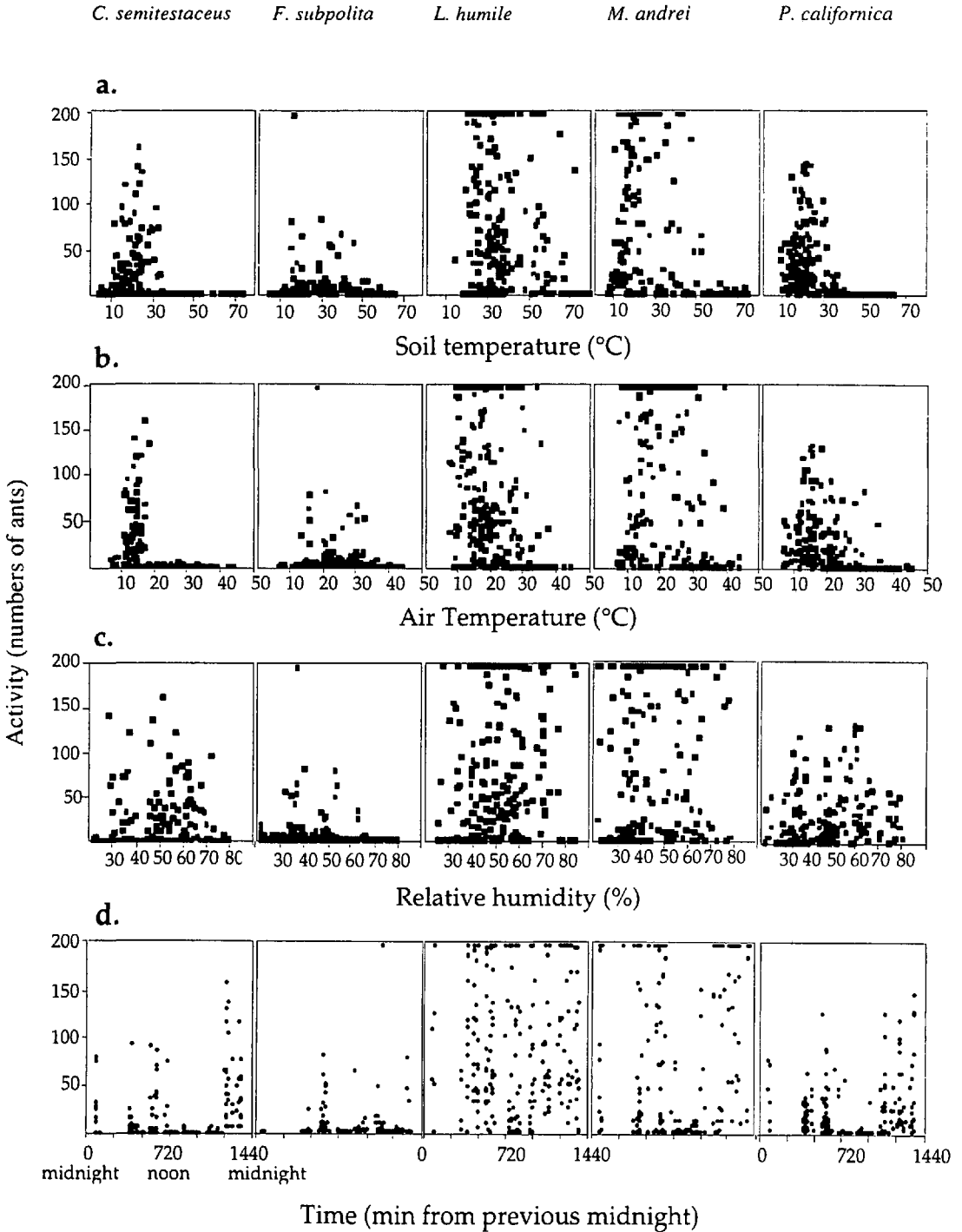


Fig. 5. The influence of the abiotic factors (a) soil temperature, (b) air temperature, (c) relative humidity, and (d) time on ant colony activity for 5 ant species. Ant colony activity was measured as the numbers of ants entering and exiting a colony within 2 min. Each dot on the figures represents 1 observation of 1 colony.

exotic species, including the Argentine ant, more easily invade areas that are disturbed by human activity (Ward 1987, Elton 1958, Simberloff 1981). This may be related both to increased opportunity for introduction

in areas with a great deal of human activity, and lack of competitors or predators, if native species are sensitive to disturbance and retreat. It is likely that the Argentine ant moved into the reserve from the de-

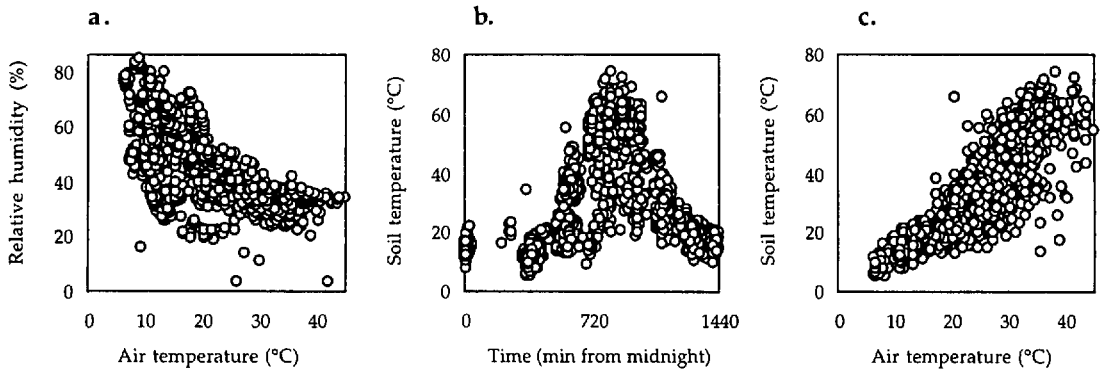


Fig. 6. Examples of the relationships among abiotic factors (a-c). Each dot represents 1 measurement of colony activity and the indicated abiotic factor.

veloped surrounding areas that have already been invaded.

The dispersal strategy of the Argentine ant may further explain why it tends to occur near the edges of the preserve. Mating flights have been observed only rarely in this species (Newell and Barber 1913, Skaife 1961). Occasional spot introductions of Argentine ants have been described in California's Central Valley (Holway 1995). This may have occurred through the accidental introduction of queens by humans, through queens or fragments of colonies rafting downstream in floods (Holway 1995), or through the founding of new colonies by winged queens. Over the last 3 yr, we have observed no spot introductions. In the Jasper Ridge Preserve, most areas along creek corridors are already invaded by Argentine ants, and there is little opportunity for the species to be introduced accidentally inside the preserve, because human activities within it are limited. Our results suggest that the Argentine ant occurs mostly at the preserve edges because it is expanding its range primarily by spreading along the ground through colony fission.

Table 1. Composition of forage and diet overlap between Argentine ants and 4 native ant species

	Ant species				
	LH	CS	FS	MA	PC
Proportion of food items					
Liquid food	0.916	0.825	0.000	0.000	0.000
Seeds	0.004	0.004	0.036	0.765	0.661
Insects	0.055	0.102	0.631	0.093	0.120
Other	0.025	0.069	0.333	0.141	0.219
Total number of food items					
	1,313	484	279	686	183
Proportion overlap with Argentine ant					
Low	—	0.997	0.060	0.011	0.015
High	—	0.998	0.066	0.016	0.023

In (C), values closest to 1 indicate the greatest degree of overlap. The low overlap value assumed that forage in the unidentified category (other) differed between species, and the high value assumed that forage in this category was identical. CS, *C. semitestaceus*; FS, *F. subpolita*; LH, *L. humile*; MA, *M. andrei*; PC, *P. californica*.

It seems unlikely that previous disturbance of the areas surrounding the preserve had already caused the native species to disappear from inside the preserve prior to invasion by Argentine ants. Within the preserve, native ant species and Argentine ants compete on the margin of the invasion, and native ant species disappear from invaded areas but persist elsewhere (Human and Gordon 1996, 1997). All of the 9 ha invaded by the Argentine ant between September 1993 and September 1995 were occupied in 1993 by native ant species.

Argentine ant incidence was high in low-elevation areas. However, elevation per se is unlikely to be the limiting factor, because the Argentine ant can be found in a few high-elevation areas of Jasper Ridge, and the species has been found up to 2,000 m in the Hawaiian islands (Zimmerman 1940, Cole et al. 1992). Elevation may be related to another environmental variable, such as soil moisture, that affects the Argentine ant directly. There may be a historical effect if the Argentine ant were introduced more frequently to low-elevation areas.

Studies in the Central Valley of California have suggested that Argentine ant encroachment into natural habitat is almost exclusively limited to areas with permanent sources of water and that the Argentine ant is more limited by proximity to water than are native ant species (Ward 1987). We found that several native taxa, including *Prenolepis imparis*, *Stenammina* spp., and *Leptothorax* spp. were as close to water, on average, as were Argentine ants. Many other taxa, including *Camponotus* spp., *P. californica*, and *Tapinoma sessile* Smith, were found only marginally farther from water than the Argentine ant (Fig. 2). Although Argentine ants tend to be more strongly established in areas closer to water (Fig. 1), there are many areas near water not yet invaded, and many areas far from water where Argentine ants are firmly established. The difference between the results of this study and previous ones may be due to climatic differences: the Central Valley is much drier and hotter, especially in the summer, than Jasper Ridge, which lies in the coastal foothills.

Colony Activity and Abiotic Conditions. It may be that the Argentine ant avoids temperature extremes by some behavioral means. A laboratory study that compared Argentine ants and other ant species native to central coastal California suggested that the Argentine ant has a low thermal tolerance, dying at temperatures close to 46°C (Tremper 1976). In the field, Argentine ant nests frequently experience soil temperatures >46°C, and they are active up to 70°C. It is possible that the Argentine ant copes behaviorally with heat more effectively than native species. In the laboratory, *M. andrei* workers died when exposed to temperatures >48.5°C (Tremper 1976). We found that *M. andrei* colonies were rarely active when soil temperatures exceeded 50°C. *M. andrei* are large black ants that are often found on trails and open areas where they may be unable to avoid temperature extremes.

Compared with most native ant species, Argentine ants are active in a wide range of abiotic conditions (Fig. 5). *M. andrei* and *P. californica* were active in a range of conditions similar to that of Argentine ants. By contrast, the activities of *C. semitestaceus* and *F. subpolita* were confined to a narrower range of times and temperatures. Because the Argentine ant is usually active whenever any native species is, most native species in invaded areas are likely to encounter the invaders frequently.

The diet of the Argentine ant overlaps with that of several species (Table 1). Argentine ant nests are active in a wider range of abiotic conditions than are *C. semitestaceus* or *F. subpolita*, the species with which it competes most for food. Diet overlap with *C. semitestaceus* is almost complete. Overlap with *F. subpolita* may be higher than measured in our study, because previous studies suggest that many *Formica* species, including *F. subpolita*, collect insect and plant exudate (Cook 1953, Dumpert 1981, Wheeler and Wheeler 1986, Cherix 1987), which makes up a significant proportion of the diet of Argentine ants. Diet overlap with *P. californica* and *M. andrei* was minimal. We measured the diets of native ant species and Argentine ant species in different areas, where resource availability may have varied, affecting food choice. Further work is needed at an invasion front to investigate effects of food availability on diet overlap.

The strong association of the Argentine ant with the edges of Jasper Ridge suggests that the most significant limits to its range expansion may be opportunity for introduction and its own mechanism of dispersal. Distance to water was less important than we expected, but a study that spans a wider range of conditions than ours might discover a stronger effect of moisture. Limiting human activity within nature preserves, and creating reserves with large area:perimeter ratios may prevent invasion of interior areas by Argentine ants and other invasive species that tend to track human disturbance. Elevation, or some parameter related to it, is also important to Argentine ant distribution, and further investigation of this might contribute to other management practices. The possibility of spatial autocorrelation should be kept in mind; sites near to each

other are likely to have similar environmental conditions and similar histories of Argentine ant establishment.

Abiotic factors explain much of the difference in distribution of Argentine and native ant species, which do not overlap on a scale of hectares, but little of the difference in activity patterns. At the edge of the invasion, on a scale of meters, Argentine and native ant species forage in the same areas, with substantial overlap in temporal patterns of foraging activity. These results suggest that whenever native ant colonies on the edge of the invasion are active, they are likely to interact with Argentine ants. Interactions between the invasive and native ant species may promote displacement of the native species. Frequent encounters may lead native species to retreat from food sources and possibly to emigrate. Where Argentine ants and native ants overlap substantially in diet, exploitation competition could reduce the foraging success of native ant colonies.

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