The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant (*Linepithema humile*)

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Abstract

The Argentine ant is a common pest of mediterranean-type ecosystems worldwide, causing widespread extirpation of many native ant species. This study examines spatial and temporal patterns of invasion at a local scale, investigates the effects of this invader on native ant communities and assesses causal mechanisms for these spatial, temporal and numerical patterns, particularly in relation to local climate. Argentine ant workers were more active in the drier months of summer and fall, and abundance was correlated with cumulative precipitation the previous winter. Argentine ant worker abundance greatly increased in conjunction with El Niño events. No similar relationship existed for native ants. This invasive ant affected native ant abundances differently by species: some species were able to tolerate its presence temporarily. Overall, this study provides a framework of factors to consider when devising control strategies for the invasive Argentine ant.

Introduction

Invasive exotic species, including exotic ants, cause extirpation of native plants and animals (Erickson 1971; Holmes and Cowling 1997; Way et al. 1997), alter relationships among them (Mooney and Drake 1986; Williamson 1996) and interrupt ecosystem processes (Vitousek 1986; Richardson 1998). Identifying and describing patterns of invasion of non-native species can be crucial to efforts at stopping and eradicating these species (Bergelson et al. 1993; D'Antonio 1993). For example, identifying the role of disturbance in exotic species' establishment and spread will inform management strategies, while revealing relationships of the invader with the abiotic environment and with biotic communities may aid in setting containment and eradication goals. Since invasive species can have cascading trophic effects throughout communities (Allen et al. 1994; Suarez et al. 2000; Christian 2001), predicting areas of potential spread by invaders and understanding the possible effects should help mitigate their consequences.

Argentine ants (*Linepithema humile*) have become major pests on nearly all continents (Williams 1994; Suarez et al. 2001), primarily in mediterranean-type communities around the world (Majer et al. 1994; Passera 1994). They first appeared in California in 1907 (Woodworth 1908), spread rapidly through agricultural and urban development (Suarez et al. 2001), and were often associated with human disturbance (Erickson 1971; Knight and Rust 1990; Suarez et al. 1998). Increasingly, Argentine ants are invading natural communities (Cole et al. 1992; Holway 1995; Human and Gordon 1996), spreading in two main ways: through colony

budding (Holldobler and Wilson 1990) and over larger distances through jump dispersal, usually aided by human transport (Suarez et al. 2001). More rarely, they naturally disperse long distances along rivers and floodplains (Ward 1987; Holway 1998). Unlike many other ant species, introduced Argentine ant queens usually do not have a nuptial flight (Markin 1970), and local spread is often a diffusive process.

The success of an invader depends on its own characteristics (Newsome and Noble 1986) and on the community being invaded (Crawley 1987). Factors governing success include an organism's ability to tolerate abiotic conditions (Human et al. 1998; Holway et al. 2002b), outcompete native species (Holway 1999), or occupy an uninhabited niche (Sidorovich et al. 1999). On the other hand, community properties such as disturbance (Crawley 1987) or facilitation by resident species (Brown and Carter 1998) may also influence an invading species' success. It is often quite difficult to determine the exact cause of an organism's success (Moulton and Pimm 1986; Crawley 1987). However, understanding the conditions under which an invader can thrive, and the spatial and temporal patterns of the invasion, may enhance the ability to predict potential new sites of invasion and the times and conditions those sites are most vulnerable to invasion; this may improve our chances of stopping the invasion pre-emptively.

Abiotic factors may shape species distributions, especially in harsh environments (Argnott and Vanni 1993), while biotic factors may play a relatively greater role in shaping species distributions in more benign environments (Connell 1961). In California, the Argentine ant's superior competitive ability is well documented (Human and Gordon 1996; Holway 1999). However, the ultimate distribution of this species in California is determined by abiotic factors: it cannot tolerate extremes in temperatures (Human et al. 1998; Holway et al. 2002b), while water limitation may play a larger role in their spread than interactions with native species (Holway et al. 2002a). Local movement may also reflect these same abiotic factors (Ward 1987; Holway 1998; Human et al. 1998). Near human habitation, activities such as watering lawns may facilitate invasion, while in natural areas weather patterns such as rainfall and fog drip influence it. In California, rainfall (and

therefore water availability) varies greatly among years and seasons, with potential impacts on the ability of the Argentine ants to invade new areas. Uncovering how patterns of behavior of this species are linked to large-scale or local weather patterns will help to determine times when this ant is more likely to spread, and therefore will help set priorities for managing this species, especially at a local scale which is primarily the scale at which land management decisions are made.

Our study investigates local patterns of spread and possible causes of those patterns of the invasive exotic Argentine ant. We have three main goals: (1) to understand spatial and temporal patterns of invasion at a local scale (the scale of a Reserve situated in an urban/natural interface (a few kilometers)); (2) to investigate the effects of this invader on native ant communities; and (3) to assess causal mechanisms for these spatial, temporal and numerical patterns in relation to local climate. We examine how small-scale invasion patterns may be caused by large-scale weather phenomena.

Materials and methods

Site description

The study was conducted at the UC Natural Reserve at Fort Ord, Monterey County, California (37°16′ N, 121°49′ W, 6.5 km N of Monterey), along an urban/natural interface. This 242 hectare reserve is 2 km inland of the Monterey Bay, and has coastal grasslands, maritime chaparral and oak woodland communities. The western edge of the Reserve borders residential and commercial development; the northern and eastern edges border abandoned grazing land. The southern edge is bordered by commercial development and a busy four-lane road. The Reserve includes a toxic cleanup area in its northeastern portion, where groundwater has been pumped through a filter and then into the soil year round since 1988 as part of an ongoing cleanup process.

Data collection

We used transects of pitfall traps to estimate ant distribution and relative abundance. We placed

six transects throughout the Reserve, extending from the Reserve boundary towards the interior of the Reserve: two transects on the southern edge, one on the eastern, two on the northern boundary and one in the pump cleanup area. The two transects on the northern edge are in an uninvaded part of the Reserve. We avoided the western edge because of large areas of poison oak .

We placed transects so that they would be perpendicular to the invasion front and therefore both invaded and uninvaded sites would be sampled with each transect. We extended transects each year relative to the invasion front to ensure that the exact location of the invasion front was measured. Most transects contained a minimum of 11 traps placed 10 m apart. However, on the eastern boundary, the Argentine ants extended into the Reserve so far that we placed the pitfalls every 50 m for the first 200 m, while pitfalls on the uninvaded northern boundary were every 5 m. The southern, eastern and pump transects were in maritime chaparral habitat. The eastern transect also ran through mixed oak woodland/maritime chaparral habitat. The two northern transects ran through primarily oak woodland habitat.

Pitfall traps are effective for sampling epigaeic (ground foraging) ant communities, and provide an unbiased method for comparing their activity within an area over time (Andersen 1991). Neither arboreal species or hypogaeic ants (underground or leaf litter foragers) are usually captured. Species with different colony densities and size can also distort results (Andersen 1991). Each pitfall trap had a 30 ml glass test tube filled with 10 ml ethylene glycol that was left in the ground for 7 days. A 15×1.9 cm PVC pipe served as a permanent placeholder for the tubes. We identified and counted individuals from each ant species. We conducted surveys in invaded areas every 3 months between September 1998 and September 2001, except for winter 1999, and in uninvaded areas every 3 months between September 1998 and September 1999.

Rainfall data were from the Castroville CA, Monterey county, station of the UC Integrated Pest Management California Weather Database (approximately 10 km north of Fort Ord; http://www.cimis.water.ca.gov/), which correlate well with weather data taken near Fort Ord (Fox unpublished). We used data daily collected and then summed over calendar months and seasons or averaged over time between survey dates for analysis.

Temporal fluctuations

To investigate seasonal and yearly variation in *L. humile* activity, we compared ant occurrences at the first five pitfalls from the edge of the Reserve along transects in invaded areas. Since these traps were consistently occupied by *L. humile*, variation in numbers was due to weather and season, although, since *L. humile* is highly nomadic, some of the seasonal and annual variation could have been due to localized nest movement. We compared the surveys by season: spring – March through May; summer – June through August; autumn – September through November; and winter – December through February. To determine seasonal patterns of activity for native ants, we compared ant occurrences in the last five pitfalls on the same transects, where *L. humile* never appeared. To compare yearly variation, we used data from the autumn surveys, since this is the season when *L. humile* was most abundant. We analyzed all temporal comparisons with a repeated measure ANOVA (Proc Mixed, SAS Version 8.2).

Numerical effects of L. humile *on native ants*

To assess the effects of *L. humile* on the abundance of native ants, we tested for a relationship between the number of *L. humile* and the number of native ants in samples obtained in non-winter months, when both groups were most active. Hypogaeic ants may be less sensitive to *L. humile* invasions than epigaeic ants because of the difference in their foraging patterns (Ward 1987). Therefore, we analyzed each of these groups separately. For this analysis, we considered three groups of native ant species: (1) a winter active epigaeic ant (*Prenolepis imparis*); (2) non-winter active hypogaeic ants; and (3) non-winter active epigaeic ants. We transformed abundance ($-1/(x+1)$) for linearity and analyzed the data using Spearman rank correlations (Proc Corr, SAS Version 8.2).

Most pitfall traps had < 20 ants, but approximately 1% of traps had > 300 ants, where it appeared that entire nests were captured. We counted all traps with > 300 ants as having 300. Pitfall traps with no ants were excluded from the analyses of numerical effects. We used data from all transects in the correlation analysis.

Spatial distribution of L. humile

We define the invasion front as the edge of the *L. humile* distribution at any given time. Rarely, stray foragers would fall into pitfall traps at distances from concentrated abundances of *L. humile*. Because these foragers were probably scouts and did not truly represent *L. humile* distribution, we did not count pitfalls with *L. humile* workers if the previous two pitfall traps (closer to the edge of the Reserve) had no *L. humile*. To compare movements across seasons, we standardized the front relative to the winter, 1999 survey, since this is the first survey where we were able to detect the front for the southern and pump transects. The fronts for these transects measured in subsequent surveys are all relative to winter 1999.

Climatic influences

The central California coast is characterized by rainy, cool winters and dry summers. These features of weather vary annually (from 1997 to 2000, precipitation ranged from 322 to 742 mm/year), and are often driven by macroweather patterns such as El Niño. In central California, El Niño winters tend to be relatively wet and warm. In order to determine effects of precipitation on ant abundance, we regressed *L. humile* abundance in the autumn, which is the season when *L. humile* abundances are highest, on cumulative precipitation in the previous winter. Ant densities were taken from the transects in the invaded areas: *L. humile* densities were determined from the first five pitfall traps on each survey; native ants densities were from the last five pitfall traps. Since *P. imparis* primarily forages during the cold wet months, we did not include this species with the other native ants. To determine the effect of cumulative winter precipitation on native ants, we regressed abundance of native ant species in the autumn against cumulative precipitation in the previous winter.

To determine the time of year when changes in the spatial distribution of *L. humile* are greatest, we regressed distribution change (measured as changes in the edge of the front) against precipitation, averaged over the 3 months prior to the survey, which corresponds to the time between survey dates. The distribution data are from the transects in invaded areas.

Results

The UC Reserve at Fort Ord has a diverse array of ant species: aside from Argentine ants, there are 21 species of native ants (Table 1). While most species were epigaeic, we occasionally captured four hypogaeic species in pitfall traps. Voucher specimens have been deposited at the Bohart Museum of Entomology, UC Davis, and the UC Santa Cruz Natural History Museum.

Temporal fluctuations

Abundance of both *L. humile* and native ants differed among transects ($F_{3,29} = 14.95$; $P < 0.0001$). Since the eastern transect was significantly different than the two southern and pump transects, we analyzed the eastern transect separately. The eastern transect sustained densities of *L. humile* ∼6 times greater than densities on the other transects and here *L. humile* invaded furthest into the Reserve. The eastern boundary may be different from the other edges because it is bounded by an abandoned, grazed field, which probably supplies invading propagules to the Reserve, while the south side is bounded by buildings near a busy road. Ant densities varied both seasonally and over years. For the southern and pump area transects, relative densities of *L. humile*, which reflect activity, were significantly higher in the dry months of summer and autumn than in the wetter months of spring and winter ($F_{3,40} = 6.44$; $P = 0.0012$; Figure 1a). Annually, *L. humile* activity in the autumn varied 10-fold ($F_{3,35} = 10.81$; $P < 0.001$; Figure 1b), from approximately 7 per transect in 2001 to more than 70 per transect in 1998. Abundance in 1998

Table 1. Ants of Fort Ord, Monterey County, USA.

Subfamily, species	Foraging habits	Nesting habits	Feeding habits
Ecitoninae			
Neivamyrmex opacithorax	Hypogaeic	Ground	Predator
Myrmicinae			
Crematogaster marioni	Epigaeic	Arboreal	Omnivore
Crematogaster mormonum	Epigaeic	Ground	Omnivore
Leptothorax andrei	Hypogaeic	Ground	Omnivore
Messor andrei	Epigaeic	Ground	Seed harvester/ omnivore
Monomorium ergatogyna	Epigaeic	Ground	Omnivore
Myrmecocystus testaceus	Epigaeic	Ground	Omnivore
Myrmica species	Epigaeic	Ground	Omnivore
Pogonomyrmex subdentatus	Epigaeic	Ground	Seed-harvester/ omnivore
Solenopsis molesta	Hypogaeic	Ground	Omnivore
Stenamma diecki	Hypogaeic	Ground	Predator
Stenamma species	Hypogaeic	Ground	Predator
Formicinae			
Camponotus semitestaceus	Epigaeic	Ground	Omnivore
Camponotus vicinus	Epigaeic	Ground	Omnivore
Formica lasiodes	Epigaeic	Ground	Omnivore
Formica moki	Epigaeic	Ground	Omnivore
Formica subpolita	Epigaeic	Ground	Omnivore
Prenolepis imparis	Epigaeic	Ground	Omnivore
Dolichoderinae			
Dorymyrmex bicolor	Epigaeic	Ground	Omnivore
Dorymyrmex insanus	Epigaeic	Ground	Omnivore
Linepithema humile	Epigaeic	Ground	Omnivore
Tapinoma sessile	Epigaeic	Ground	Omnivore

This list includes only ants that fell into pitfall traps, thereby excluding some arboreal or litter-dwelling ants. Epigaeic ants forage above-ground; hypogaeic forage in the leaf litter or below ground. All ants are native except *L. humile*.
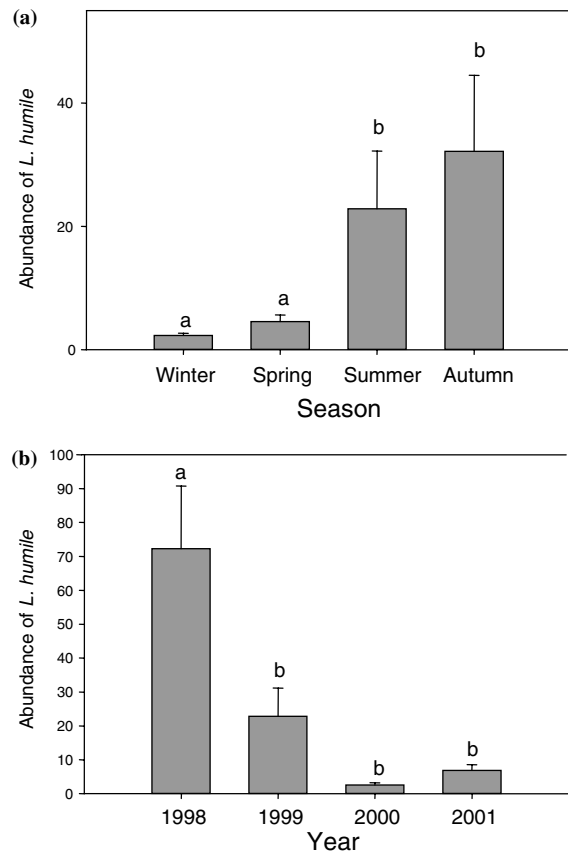

Figure 1. Comparison of seasonal (a) and yearly (b) differences in abundance of *L. humile* per transect (mean + 1 se) in southern and pump transects. For Figure 1a, averages are over all years and different letters correspond to significant differences ($P < 0.05$). In Figure 1b, abundance is for autumn season only. Different letters indicate significant differences among years ($P < 0.01$).

was significantly greater than in all other years ($t_{35} = 7.42$; $P < 0.0001$), but there were no significant differences among the three other years. On the eastern boundary, abundances of *L. humile* were highest in the autumn and lowest in the winter ($F_{3,21} = 7.76$; $P = 0.001$), and annual abundances in 1998 were greater than in any other year ($t_{13} = 9.68$; $P < 0.0001$). Annual abundances on the eastern transect were ~9 times greater than on the southern and pump transects, and there was greater variation in abundance.

Native ants had a very different activity pattern than *L. humile* (Figure 2) in the southern and pump transects. For all native ants combined, there was no significant effect of season or year ($F_{3,50} = 0.99$; $P = 0.40$ for season; $F_{3,19} = 0.63$; $P = 0.61$ for year), although there was some indication of greater activity in spring. However, there were seasonal differences in ant species composition: in winter, the ant community was dominated by one species, *P. imparis*.

Over time, *L. humile* was more abundant and/ or more active than native species in autumn ($F_{1,31} = 4.77$; $P = 0.037$) and summer ($F_{1,30} = 14.13$; $P = 0.0007$). In contrast, more native ants, especially *P. imparis*, were active in
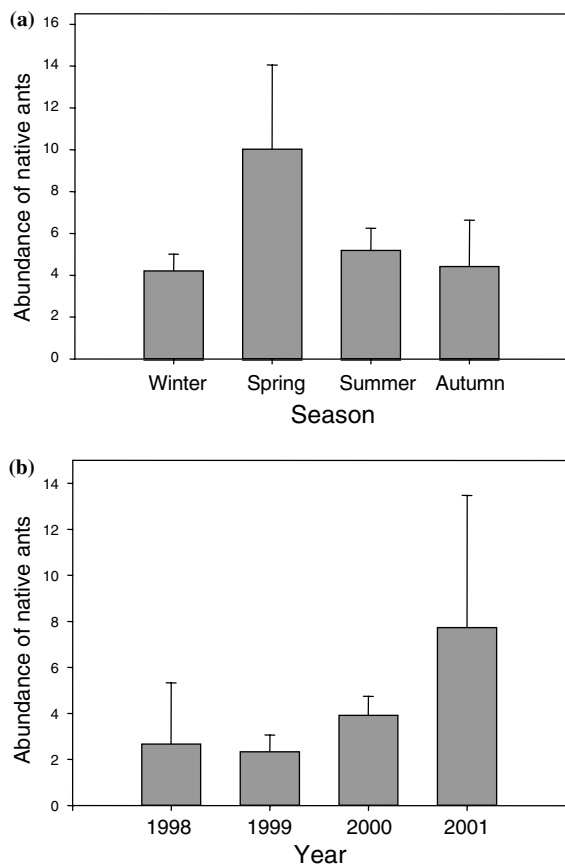
Figure 2. Yearly differences in abundance per transect of all native ant species combined (mean +1 se). (a) Represents average abundance by season. (b) Abundance is for autumn season only.

winter ($F_{1,31} = 4.09$; $P = 0.05$). Spring densities of the native and introduced ants were similar. More *L. humile* than all native ants species combined were active in the autumn season of 1998 ($F_{1,42} = 4.70$; $P = 0.036$) and 1999 ($F_{1,85} = 8.46$; $P = 0.0046$). There were no significant differences in abundances of native ants and *L. humile* for autumn 2000 and autumn 2001.

Numerical effects of L. humile *on native ants*

Both native ant species abundance ($R^2 = -0.68$; $P < 0.0001$) and diversity ($R^2 = -0.68$; $P < 0.0001$) were greatly reduced in the presence of *L. humile*. Most traps had foragers of either *L. humile* or native ants. However, when introduced and native ants co-occurred in traps (12%

of all traps), the native ants tended to be either *Dorymyrmex insanus* (42%), *Monomorium ergatogyna* (53%), or *P. imparis* (19%), and to be in areas where abundance of *L. humile* was increasing and native ant abundances were decreasing.

Ants with different foraging strategies may respond differently to *L. humile* invasions. At Fort Ord, abundances of both epigaeic ($R^2 = -0.71$; $P < 0.0001$) and hypogaeic ($R^2 = -0.30$; $P < 0.0001$) ant species decline in the presence of *L. humile*. However, these results should be viewed with some caution, since pitfall traps are not the optimal method for sampling abundance of hypogaeic ants.

Spatial distribution of L. humile

There was little net change in *L. humile* distribution into the Reserve on the southern and pump boundaries during 1998–2001 (Figure 3a). However, *L. humile* spread rapidly into the Reserve on the eastern boundary (Figure 3b). We could not positively identify the front on the eastern side until 1999 because *L. humile* spread was so rapid, even though we increased the length of this transect by over 50 m at each survey date. Overall, *L. humile* distribution possibly increased by over 150 m in this time period.

In drier seasons (summer, autumn), *L. humile* distribution shifted towards the interior of the Reserve, while in wetter seasons, their distribution shrank towards the edges of the Reserve. By the end of this study, net distribution of *L. humile* on the different transects varied from −10 m (a retreat of 10 m) to a positive incursion into the Reserve of 80 m. Annual rates depended on which season was compared on an annual basis. Autumn to autumn rates varied from a retreat of 50 m/year to an advance of 10 m/year.

Based on the relative densities of all the ants, we identified three zones of *L. humile* activity (Figure 4). We examined residence of *L. humile* across all seasons and considered the eastern front separately. The zone of permanent residence, where *L. humile* was active throughout the year, was near the edge of the Reserve: *L. humile* abundance peaked nearest the edge of the Reserve, and was higher in this zone than any other, for all transects (Figure 4). The abundance
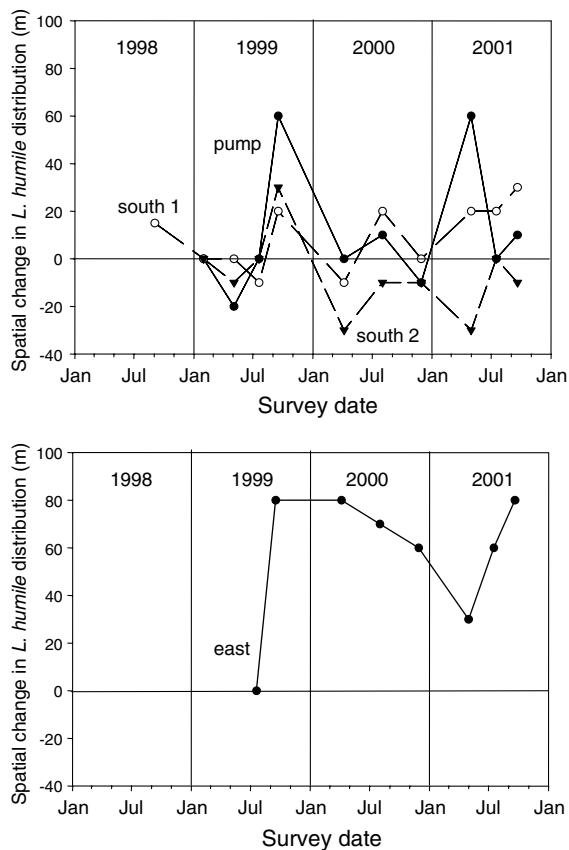
Figure 3. Seasonal change in *L. humile* distribution relative to where *L. humile* was first detected. The 0 line is the original position. Positive values are movement of *L. humile* distribution from the edge into the Reserve: negative values are a retreat from the interior of the Reserve toward the edge. The top graph shows the two south transects and the pump transect. The lower graph shows only the eastern transect.

Figure 4. Spatial distributions of *L. humile* and all native ants for the southern and pump transects (top graph) and eastern transect (bottom graph). Distance is from the edge of the Reserve (0 m) into the interior of the Reserve (note that this 0 m is different from the 0 m on Figure 3). Each point is the mean (±1 se) of each pitfall over all years, seasons. Zones are explained in the text.

of *L. humile* in the permanent residence zone was up to four times greater on the eastern transect than in the others. In the zone of Temporary Residence, *L. humile* fell into pitfall traps between 60% and 95% of the time; this is the zone with the most variable seasonal occurrence of *L. humile*. In the non-resident zone, the few *L. humile* that fell into pitfall traps (< 1 ant per pitfall < 20% of the time) were probably scouts and did not represent nest movement into the area.

Overall, the distribution and abundance of native ant species on the Reserve was strongly, and negatively, correlated with Argentine ant presence. On a finer scale, native ant abundance differed by species according to zone. Native ants
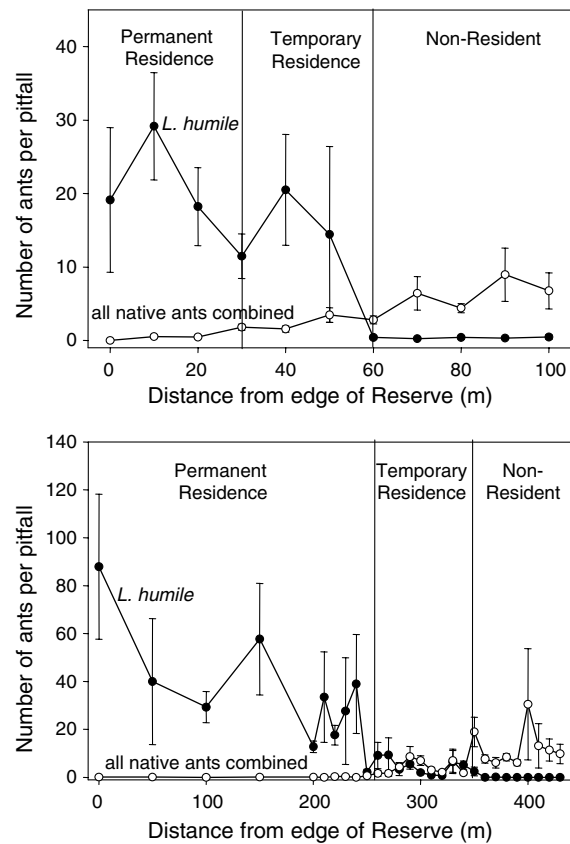
were mostly absent from the permanent residence zone, but three native species maintained populations in the zone of temporary residence (Figure 4). Abundance of native ants increased in the non-resident zone, where *L. humile* was largely absent.

Three species, *P. imparis*, *D. insanus*, and *M. ergatogyna*, maintained workers in the temporary residence zone, probably due to their behavioral characteristics. On all transects, both the abundance and variation in abundance of *M. ergatogyna* workers was highest in the areas with no *L. humile*. Both *D. insanus* and *P. imparis* maintained low worker densities in areas of temporary *L. humile* residence, although they

dropped out almost entirely in the permanent residence zone. There was little overlap in foraging times of *L. humile* and *P. imparis* ($R^2 = 0.55$; $P < 0.0001$), which may explain why they can coexist temporarily. However, *D. insanus* and *M. ergatogyna* were active during the same time of year as *L. humile*; the ability of these workers to coexist with *L. humile*, at least temporarily, may lie in other behaviors of these ants. At Fort Ord, even *P. imparis*, *D. insanus* and *M. ergatogyna* are nearly absent in areas that have been invaded for longer periods of time, but workers can temporarily co-exist with *L. humile* in areas of more recent invasion.

Climatic influence on L. humile

For the southern and pump transects, variation in *L. humile* abundance in the autumn, when they were most active, was largely explained by the cumulative precipitation the previous winter ($R^2 = 0.54$; $P = 0.004$; Figure 5a). Native ant abundance on the same transects in the autumn, however, did not reflect precipitation in the previous winter ($P = 0.45$; Figure 5b). Spatial distribution of *L. humile* on the southern and pump transects was only marginally negatively related to precipitation in the period prior to sampling ($R^2 = 0.07$; $P = 0.08$; Figure 6): *L. humile*'s distribution tended to spread into the interior of the Reserve during the drier months of summer and autumn.

Discussion

L. humile is successfully invading natural areas in mediterranean-type communities, causing widespread local extinctions of native species. The numerical domination of this one species could have cascading effects throughout the community. For example, *L. humile* is omnivorous, eating nectar, insects, carrion and liquid (honeydew of Homopterans) (Woodworth 1908; Flanders 1943), but primarily they eat liquid food (either plant nectar or honeydew) (Human et al. 1998; DiGirolamo 2004). Replacing native ants as a group can indirectly alter plant and insect communities. For example, the higher densities of *L. humile* may support larger populations of
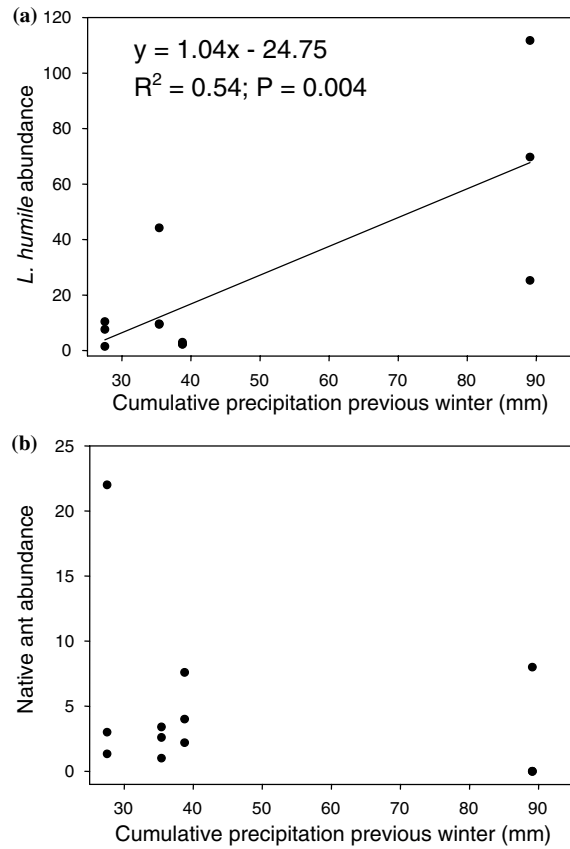
(a)

$y = 1.04x - 24.75$
$R^2 = 0.54; P = 0.004$

(b)

Figure 5. Comparison of mean *L. humile* (a) and native ant (b) abundance in autumn with cumulative precipitation the previous winter. Abundances for *L. humile* and native ants are for autumn only. Each point represents one transect on a survey date.
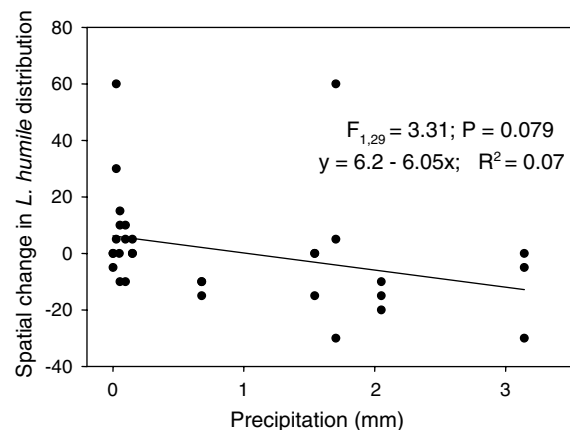
$F_{1,29} = 3.31; P = 0.079$
$y = 6.2 - 6.05x; R^2 = 0.07$

Figure 6. Relationship between spatial limits of *L. humile* distribution and mean precipitation. Precipitation is averaged over the 3 months prior to the survey date.

Homopterans through their tending, indirectly harming some plants, while extirpating Army ants (*Neivamyrmex* spp.) and harvester ants (*Messor* spp. and *Pogonomyrmex* spp.), which are among the most sensitive of the natives to Argentine ant invasions (Suarez et al. 1998). The latter effects are particularly troubling, considering the important roles these ants play in communities as major predators of insects and seeds (Holldobler and Wilson 1990), respectively.

Seasonal variation in *L. humile* abundance is probably linked to their diet, as well as to their reproductive cycle. *L. humile* forages primarily during the dry seasons (summer and autumn). Since plant liquid food sources (and thus Homopteran honeydew) diminish after the rain stops in mid- to late spring (Bristow 1991), the increased activity in the dry season may be due in part to higher worker ant allocation to foraging for scarcer food and less to nest maintenance. But, since new worker production begins in March and peaks in October (Markin 1970), this increased activity probably reflects an actual increase in worker number. Because of these seasonal shifts, it is critical to survey for *L. humile* during the autumn, when their abundance is highest, to grasp the full extent of their invasion. Annual variation in abundance of *L. humile*, on the other hand, is largely affected by winter precipitation. This finding supports the idea that Argentine ant invasions are linked to water availability, since Argentine ants are also found near permanent sources of water (Ward 1987; Holway 1995; Human et al. 1998).

The mediterranean climate along the central California coast drives the seasonal and annual patterns in *L. humile* abundance. El Niño winters may be the time *L. humile* expands its range or, on a local scale, at least gains a foothold in newly invaded territory. Interestingly, at Fort Ord, while abundance and spatial distribution of *L. humile* were tied to precipitation, the pump transect, where there was continual water available, did not differ in relative abundance patterns from those transects in drier habitat. This seemingly counter-intuitive result may be related to unexamined site factors, such as its historic use as a hydrocarbon dispersal area or its disturbance history, or to an intrinsic reproductive cycle of *L. humile*.

Native ant abundance was strongly and negatively correlated with *L. humile* abundance. At Fort Ord, most or all epigaeic species succumb to *L. humile*, which is consistent with other studies (Holway et al. 2002a). In areas of permanent *L. humile* residence, practically all epigaeic species were locally extinct. Elsewhere, hypogaeic species are found in Argentine ant invaded areas, and are thought to be less sensitive to *L. humile* invasions than epigaeic species because of their different foraging patterns (Ward 1987). At Fort Ord, however, *L. humile* significantly affected four hypogaeic species. The sensitivity of hypogaeic species is surprising, since they forage so differently from *L. humile*, and one would expect that would shield them from direct interactions with the invader. At Fort Ord, the local extinction of native ants is nearly complete in areas of *L. humile* permanent residence. Only the hypogaeic thief ant *Solenopsis molesta*, which can live inside nests of *L. humile*, survived in invaded areas at Fort Ord (personal observation), consistent with data from southern California (Suarez et al. 1998). Too few *S. molesta* fell into pitfall traps at Fort Ord to analyze them separately.

Native species are extirpated by *L. humile* at various rates, probably due to different intensities of competitive and aggressive interactions (Human and Gordon 1996; Holway 1999). The primarily winter foraging ant *P. imparis* survived temporarily in areas that *L. humile* inhabits at Fort Ord that are probably newly inhabited patches, where *L. humile* has not completely invaded (and therefore occupies at lower densities). However, in areas of permanent *L. humile* residence, abundance of *P. imparis* severely declined. This pattern at Fort Ord differs from those found in other parts of California, where *L. humile* and *P. imparis* can co-occur (Human and Gordon 1996; Suarez et al. 1998). *D. insanus* and *M. ergatogyna* persisted with *L. humile* longer than most other native ants, even though their generalist diet greatly overlaps with *L. humile* (Wheeler and Wheeler 1986). When paired at baits, *M. ergatogyna* outcompetes *L. humile* through the use of chemical defense (Holway 1999). On the other hand, *D. insanus* is a poor direct competitor of *L. humile* (Holway 1999), though it is able to quickly recruit to baits

(Holway 1999). *P. imparis* and *D. insanus* are broadly distributed across the United States, and *M. ergatogyna* is locally one of the most abundant species on the Reserve. The properties that make these species geographically successful may be the same things that make them temporarily able to fend off extirpation. Because, not all species are extirpated at the same rate, and especially because the most abundant ants remain for some time after the initial invasion, the full impacts of *L. humile* on native communities may be masked for several years.

Ants, in general, perform many important functions in communities. In most terrestrial environments they are the major predators of insects and small invertebrates (Holldobler and Wilson 1990). They move large amounts of soil (Lyford 1963), and at small scales, they create mosaics of nutrient concentrations and patchy plant distributions, especially during the early stages of succession because they bring dead animals and plants back to their nests (Petal 1978). Unfortunately, the ecological roles of many of the species on the Reserve are not known. At Fort Ord, densities of Argentine ants in invaded areas are greater than that of all native ants combined, and corresponds to a reduction in the ecological complexity of the ant community. Various behaviors of over 21 species of native ants are replaced with just one type of feeding and nesting behavior. Thus, *L. humile* should have large, cascading indirect effects on the surrounding community.

This study provides a framework of factors to consider when devising control strategies for invasive species. Specifically, knowledge of the patterns of population cycling and the causes of these patterns will help identify times when the species are most vulnerable to control. For example, baiting may be more advantageous if done in the drier months when workers are foraging for scarcer resources. Or, spraying may be better done in the winter months when there are lower abundances of worker ants. Awareness of dispersal patterns of both native and invasive species should help predict future changes in spatial distribution of the invader, and areas that are priorities for control can be determined. When monitoring invasions, short-term studies may over- or under-estimate invasion rates, particu-

larly for the species that are responsive to abiotic factors in variable environments such as coastal California. Observations of native species persisting with an invader may represent the process of displacement and not the final outcome. Finally, the invader may impact species not in direct competition with itself, and cause local extinctions of species that would have been hard to have predicted beforehand, with extensive and probably unexpected ecological implications.

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