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Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California

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Abstract Invasive species, where successful, can devastate native communities. We studied the dynamics of the invasive Argentine ant, *Linepithema humile*, for 7 years in Jasper Ridge, a biological preserve in northern California. We monitored the distributions at the hectare scale of native ant taxa and *L. humile* in the spring and fall from 1993 to 1999. We also studied the invasion dynamics at a finer resolution by searching for ants in 1-m² plots. Our results are similar at both scales. The distributions of several native species are not random with regard to *L. humile*; the distributions of several epigeic species with similar habitat affinities overlap much less frequently than expected with the distribution of *L. humile*. We found that season had a significant influence on the distributions of *L. humile* and several native taxa. Over the 7-year period, *L. humile* has increased its range size in Jasper Ridge largely at the expense of native taxa, but there is seasonal and yearly variation in this rate of increase. Studies of invasions in progress which sample across seasons and years may help to predict the spread and effects of invasive species.

Keywords Biological invasions · Invasive species · Species distributions · *Linepithema humile*

Introduction

Biological invasions can severely disrupt native ecosystems, and have therefore received considerable attention (Mooney and Drake 1986; Drake et al. 1989; Vitousek et al. 1996; Williamson 1996; Simberloff et al. 1997). Empirical studies of invasions seek to determine the rate of

spread of the invader and its effects on the native community. It is often difficult to measure rate of spread because the advance of a species along a transect might not reflect its true rate of spread. For example, a species may diffuse from one location into many, as did the European starling, *Sturnus vulgaris*, from New York to the rest of the continental United States. The effects of invasive species on native communities are difficult to measure because such effects are species-dependent and may vary temporally. Further, the dynamics of an invasion can change from year to year or season to season. To predict accurately the spread of any invasive species, long-term studies of invasions in progress are likely to be necessary.

The invasive Argentine ant, *Linepithema humile*, is an important pest species which devastates many ant and other arthropod populations where it is introduced (Haskins and Haskins 1965; Crowell 1968; Bond and Slingsby 1984; Ward 1987; Cole et al. 1992; Human and Gordon 1997; Suarez et al. 1998). The Argentine ant has increased its range in California since its introduction in the early 1900s (Ward 1987; Holway 1995; Human and Gordon 1996). This may be due to its ability to locate and use resources efficiently (Gordon 1995; Human and Gordon 1996; Holway 1999) and its ability to interfere with other native ant species (Human and Gordon 1996, 1999; Holway 1999).

Argentine ant colonies, unlike colonies of many other species, disperse by nest emigration and budding rather than aerial dispersal. Several researchers have examined the rate at which *L. humile* is increasing its range in California and its effects on native ant taxa. Holway (1998) examined the rate at which *L. humile* diffused along 20 approximately 120-m transects in a riparian habitat in northern California. Sampling at about the same time each summer, he found that the mean yearly increment in spread along the transects was approximately 10 m year⁻¹, and this rate depended upon the proximity of the transect to a permanent stream (Holway 1998). Other studies in California have reported rates of spread of about 100 m year⁻¹ (Erickson 1971; Holway 1995) to

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0–300 m year⁻¹ (Human and Gordon 1996). The discrepancies among studies suggest that the season in which distributions are measured, and whether measures are 1- or 2-dimensional, may both affect conclusions about rate of spread. For example, measures of spread in one habitat type in one dimension in one season may not reflect variation in rate of spread.

Many native epigeic (above-ground foraging) ant species in California fail to persist with *L. humile* when it invades (Tremper 1976; Ward 1987; Human and Gordon 1997; Holway 1998; Suarez et al. 1998). Yet some species are apparently able to coexist with *L. humile*, most notably *Prenolepis imparis*. This may be because *P. imparis* is generally active in the cooler, wetter months when interactions with *L. humile* are less likely (Tschinkel 1987; Ward 1987; Suarez et al. 1998). Suarez et al. (1998) sampled ants in southern California over the course of 1 year and found that several taxa, including *P. imparis*, coexisted with *L. humile* and did not seem to be affected by abiotic conditions associated with habitat fragmentation. Holway (1999) and Ward (1987) also found that *P. imparis* did not seem to be affected by *L. humile*.

To examine the dynamics of an invasion in progress, we sampled the ant fauna of Jasper Ridge Biological Preserve (JRBP) in northern California each spring and fall from May 1993 to September 1999, using samples 100 m apart. To our knowledge, this is among the most complete long-term data sets on a biological invasion in progress. We call these samples at the hectare scale “overview samples.” We also conducted thorough searches of 1-m² plots at a finer resolution in the spring and fall of 1998 to determine how well our overview sampling techniques detected the ant fauna at JRBP. We call these “1-m² samples.” Our data set allows us to investigate variation in the rate of spread of the invasive Argentine ant and variation in its effects on the distributions of native taxa. Here, we ask:

1. Are the patterns we observe in our overview samples verified by our 1-m² samples?
2. Do the distributions of particular native ant species overlap with *L. humile* more or less frequently than expected?
3. Are there seasonal and year-to-year changes in the distributions of native taxa and *L. humile*?
4. What is the rate of invasion at the hectare scale in two dimensions, and does this rate vary?

Materials and methods

Study site

We measured the distributions of ants at JRBP, a 481-ha reserve in northern California (San Mateo County 122°15′–122°12′30″ W and 37°25′24″–37°25′N, 66–207 m elevation). Vegetation types at JRBP include serpentine grassland, annual sandstone grassland, chaparral, oak woodland, riparian woodland, redwood forest, and evergreen forest. JRBP is surrounded by developed and agricultural

Table 1 Ant species detected from 1993 to 1999 at Jasper Ridge Biological Preserve (JRBP). Species in the same genus are lumped under that genus name in the text, figures, and tables

Ant species
<i>Neivamyrmex californicus</i>
<i>Aphaenogaster occidentalis</i>
<i>Crematogaster coarctata</i>
<i>Leptothorax andrei</i>
<i>L. rudis</i>
<i>L. nevadensis</i>
<i>Messor andrei</i>
<i>Pheidole californica</i>
<i>Stenammina diecki</i>
<i>Stenammina</i> sp. A
<i>Solenopsis molesta</i>
<i>Camponotus semitestaceus</i>
<i>Camponotus cf. vicinus</i>
<i>Formica moki</i>
<i>F. subpolita</i>
<i>Prenolepis imparis</i>
<i>Linepithema humile</i>
<i>Liometopum occidentale</i>
<i>Tapinoma sessile</i>
<i>Hypoconerops opacior</i>

al areas which have been invaded by *L. humile*. We have detected 20 ant species in our surveys at JRBP (Table 1).

Sampling ant distributions

Overview samples

Each May and September from 1993 to 1999, we monitored the distributions of native ants and *L. humile* at JRBP. The preserve was divided into 1-ha quadrants using an aerial photograph. A sample plot was a circle of 20-m radius at the center of each 1-ha quadrant. Some sample plots were not accessible because of the presence of poison oak (*Toxicodendron diversilobum*), flooding, or dense vegetation. At each sample plot (the 20-m circle), we recorded the species of live ants seen during 5 person-minutes spent using general collecting techniques: searching under rocks and dead logs, briefly sifting through leaf litter, and scanning tree trunks and vegetation (Wheeler 1910; Hölldobler and Wilson 1990). Though these sampling methods often overlook cryptic species, they provide a good estimate of the conspicuous species present (Andersen 1991).

We also recorded the species found dead in the midden piles of ant nests (especially those of the harvester ant, *Messor andrei*). All species of ants found as carcasses were considered to be active in that sample plot. *M. andrei* foragers never go farther than approximately 17 m from the nest and 80% of a colony's foraging area is within 10 m of the nest (Brown and Gordon 2000). Ants in the midden piles of *M. andrei* thus reflect the presence of species within our sampling plots separated by a distance of 100 m.

Between 1993 and 1996, if no ants were found in the 5-min searching periods, we left two 40-ml vials partially filled with honey as traps and collected them 24 h later to identify the ants in the vial. We left two vials to provide an opportunity for subordinate species to find the bait despite interference interactions with dominant species such as *L. humile*. This honey-trap method used between 1993 and 1996 may bias our results toward finding more species by attracting ants that we would not otherwise detect.

To test the effectiveness of our sampling and honey-trap methods, a previous study at JRBP by Human and Gordon (1996) compared the distributions measured with these methods with data collected from pitfall traps. It found that the overview sampling methods used here detected the same number of species as pitfall trapping. Our sampling methods detect the species present and active at a sampling point. Like any sampling method that depends on species being active to be detected, our method is slightly biased toward detecting only active species.

1-m² samples

Because our overview sampling method might be biased toward discovering abundant, conspicuous species, we examined the distributions of native taxa and *L. humile* at a finer resolution by making intensive searches at the 1-m² scale. We selected a 12-ha region of oak woodland, bordered by both serpentine and non-serpentine grasslands, and divided by an intermittent stream. Most of the oaks were coast live oaks, *Quercus agrifolia*, and ground cover was non-serpentine grassland. Within this section, we chose 20 1-m² plots at random from an aerial photograph. We searched each of the 1-m² plots for 5 person-minutes on 12 occasions in the spring and 11 occasions in the fall of 1998. We searched under rocks and fallen logs, sifted through leaf litter and tufts of bunch grass, and scanned vegetation. We recorded the species identity of all ants seen in each 1-m² plot.

In the spring and fall of 1998, we searched each of the 20 1-m² plots three times in each of the following time intervals: 0900–1200, 1200–1600, 1600–1800, and 1800–2100 hours. In addition, we searched each plot once between 2100 and 2400 hours in the spring and fall to sample nocturnal species. In the fall, we were able to survey the 1-m² plots only twice in the 1800–2100 hours time interval because it was dark by 1900. In the spring, one 1-m² plot was searched only 11 times, and in the fall, one 1-m² plot was searched only 10 times. This gave us a total of 259 searches of 1-m² plots in the spring [(3 searches in the first four time periods×20 1-m² plots×4 time periods)+(20 searches in the final time period-one 1-m² plot that was searched only once)]. In the fall, we searched all the 1-m² plots 239 times [(3 searches in the first three time periods×20 1-m² plots)+(2 searches in the fourth time period×20 1-m² plots)+(1 search in the final time period×20 1-m² plots)-(2 1-m² plots that were searched only once)]. To minimize variation among days during the fall survey, we divided the 20 1-m² plots into groups of 8 and 12, and searched each plot in each group on the same day.

To compare the numbers of species detected by the 1-m² samples and overview samples in the 12-ha region of oak woodland, we used a *t*-test paired by hectare. However, one of the hectares was not surveyed in the overview method. Therefore, our analysis used only the 11 hectares which were surveyed by both methods.

Overlap of distributions

Using the overview sampling data, we examined the null hypothesis that species identity is independent of overlap with *L. humile*. During the May 1993, September 1993, May 1995, and May 1996 surveys, native ant taxa were not identified to genus or species. We therefore excluded those surveys from this analysis. We calculated the expected number of sample plots in which each native taxon was detected in all of our overview sampling by determining the average proportion of sampling plots in which we detected that taxon; call this value x_n , where n is native taxon n . We similarly calculated an expected value for *L. humile*; call this value a . Then, to calculate the expected proportion of sampling plots in which the distribution of native taxon n overlapped with the distribution of *L. humile*, we multiplied x_n and a . We compared expected and observed values using a 2×2 chi-squared test.

Seasonal effects on distributions

From May 1993 to September 1999, there were 135 overview sample plots that were surveyed in each spring and fall. We used only the data from those sample plots. We tested for seasonal effects on ant distributions in several ways.

First, for data from 1993–1999, we used *t*-tests paired by year to compare the numbers of overview sample plots in which *L. humile* was observed in the spring, to the numbers of overview sample plots in which it was observed in the fall. We also used paired *t*-tests to compare the numbers of sample plots in which we detected any native taxa in the spring to the numbers of sample plots in which we detected any native taxa in the fall.

Second, we examined the effect of season on each native ant taxon using the numbers of total overview sample plots in which we detected that taxon in each survey period. We used data from the 135 sample plots common to all survey periods and excluded the May 1993, September 1993, May 1995, and May 1996 surveys, when native ant taxa were not identified to genus or species. We compared the mean numbers of overview sample plots for each species in the spring to those in the fall using one-tailed *t*-tests.

We also tested for the effects of season using data from our 1-m² samples. For each of the 1-m² plots, we calculated the difference between the spring and fall in the proportion of observations in which native ant taxa and *L. humile* were observed. Differences between seasons in the proportion of *L. humile* were analyzed with a Wilcoxon signed-ranks test because 85% of plots had non-zero differences. Because the proportion of native ants had non-zero differences between seasons in only 60% of the 1-m² plots, they were analyzed with a permutation test as follows: (1) For each 1-m² plot, we calculated the difference between the incidence of native taxa in the two seasons; (2) we found the sum of all differences of the same sign, resulting in a negative and positive sum; (3) we calculated the number of possible permutations as 2^n with n =the number of non-zero differences; (4) we determined the number of permutations (x) with summed differences more extreme than either the positive or negative sum (step 2); and (5) two-tailed significance was calculated at $\alpha=0.05$ as $2x/2^n$.

Invasion rate

To determine the rate at which *L. humile* increased its range in JRBP, we measured the changes from one survey to another in the numbers of overview sample plots in which *L. humile* was seen. In this analysis, we used only the data from 135 sample plots that were surveyed in all 14 surveys from May 1993 to September 1999. For each survey period, we calculated two measures: (1) the number of overview sample plots where *L. humile* moved in: *L. humile* was observed in a given survey (time t) but not in the previous survey (time $t-1$), and (2) the number of overview sample plots where *L. humile* moved out: *L. humile* was not observed in a given survey (time t) but was present at the plot in the previous survey (time $t-1$). The difference between these two numbers is the total number of overview sample plots by which the range size of *L. humile* changed between any two surveys. This number will be negative when *L. humile* moved out of more overview sample plots than it moved into. *L. humile* was often detected at an overview sample plot at time t , not detected at time $t+1$, and then detected at time $t+2$. Thus, some plots are counted more than once. For example, if at a sample plot we detected *L. humile* at time t , did not detect it at time $t+1$, and then detected it at time $t+2$, that plot would be scored as “moved out of” at time $t+1$ and “moved into” at time $t+2$. To calculate the mean rate of invasion for a period of n years, we divided the change in *L. humile*’s range size during that period by n . We tested for seasonal effects on the rate of invasion by comparing the mean rate of invasion in the spring and fall using a *t*-test paired by year.

Results

Our overview surveys detected 20 species at Jasper Ridge Biological Preserve, 13 of which are detected frequently (Table 1). Our overview sampling and 1-m² sampling techniques detected the same numbers of species in both the spring ($t=0.58$, $df=10$, $P=0.57$) and fall ($t=1.49$, $df=10$, $P=0.17$), but the identities of species detected were often different (Table 2). In the spring, the two methods showed the same species in only 4 of the 11 plots. In the fall survey, the two methods showed the

Table 2 Comparison of 1-m² and overview sampling methods. The 1-m² sampling plots occupied 11 of the hectare-scale overview sampling plots

Hectare	1-m ² samples	Overview samples
Spring		
1	<i>Linepithema humile</i> , <i>Prenolepis imparis</i>	<i>L. humile</i> , <i>P. imparis</i>
2	<i>L. humile</i> , <i>P. imparis</i> , <i>Formica moki</i>	<i>L. humile</i>
3	<i>L. humile</i>	<i>L. humile</i> , <i>P. imparis</i> , <i>Camponotus semitestaceus</i> , <i>Lept. nevadensis</i>
4	<i>L. humile</i> , <i>P. imparis</i>	<i>P. imparis</i>
5	<i>L. humile</i>	<i>L. humile</i>
6	<i>L. humile</i> , <i>P. imparis</i>	<i>L. humile</i>
7	<i>L. humile</i> , <i>P. imparis</i> , <i>F. moki</i> , <i>Solenopsis molesta</i>	<i>L. humile</i> , <i>P. imparis</i> , <i>C. semitestaceus</i> , <i>Lept. nevadensis</i>
8	<i>L. humile</i> , <i>Leptothorax nevadensis</i> , <i>Lept. andrei</i> , <i>F. moki</i>	<i>P. imparis</i>
9	<i>L. humile</i>	<i>Tapinoma sessile</i> , <i>P. imparis</i>
10	<i>L. humile</i>	<i>L. humile</i>
11	<i>L. humile</i>	<i>L. humile</i>
Fall		
1	<i>L. humile</i>	<i>L. humile</i>
2	<i>L. humile</i> , <i>P. imparis</i>	<i>L. humile</i>
3	<i>L. humile</i>	<i>L. humile</i>
4	<i>L. humile</i>	<i>L. humile</i>
5	<i>L. humile</i>	<i>L. humile</i>
6	<i>L. humile</i> , <i>P. imparis</i>	<i>L. humile</i>
7	<i>L. humile</i> , <i>F. moki</i>	<i>L. humile</i>
8	<i>Lept. nevadensis</i>	<i>L. humile</i>
9	<i>L. humile</i> , <i>P. imparis</i> , <i>Lept. nevadensis</i>	<i>L. humile</i>
10	<i>L. humile</i>	<i>L. humile</i>
11	<i>L. humile</i>	<i>L. humile</i> , <i>Crematogaster coarctata</i>

same species in 6 of the 11 plots. In 4 of the 5 remaining plots in the fall, the 1-m² samples detected native taxa while the overview sampling detected only *L. humile*.

Overlap of distributions

The distributions of *Formica* spp. ($\chi^2=16.0$, $df=1$, $P<0.001$), *Camponotus* spp. ($\chi^2=7.3$, $df=1$, $P<0.01$), *Crematogaster coarctata* ($\chi^2=4.34$, $df=1$, $P<0.05$), *Messor andrei* ($\chi^2=12.2$, $df=1$, $P<0.001$), and *Prenolepis imparis* ($\chi^2=10.3$, $df=1$, $P<0.005$) were nonrandom with regard to *L. humile*. For all five native taxa, observed values of numbers present when *L. humile* was present were less than expected values from the chi-squared analysis. The distributions of *Pheidole californica* ($\chi^2=0.6$, $df=1$, $P>0.10$), *Liometopum occidentale* ($\chi^2=0.3$, $df=1$, $P>0.50$), *Tapinoma sessile* ($\chi^2=2.6$, $df=1$, $P>0.10$), *Leptothorax* spp. ($\chi^2=0.3$, $df=1$, $P>0.50$), *Solenopsis molesta* ($\chi^2=0.1$, $df=1$, $P>0.50$), and *Stenamma* spp. ($\chi^2=0.4$, $df=1$, $P>0.50$) were statistically independent of the distribution of *Linepithema humile*. Subsequent analyses revealed that our chi-squared analysis may have lacked the power to detect an association between the distributions of *L. humile* and native taxa, so we interpret these results with caution.

Seasonal effects on distributions

There were seasonal effects on the distributions of *L. humile* and native taxa at JRBP (Fig. 1). *L. humile* was sig-

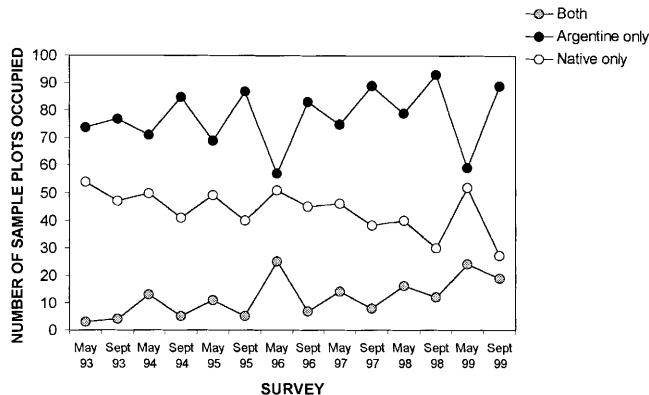


Fig. 1 Seasonal fluctuations in the range expansion of *Linepithema humile*. Data are from 135 overview sample plots surveyed twice yearly from May 1993 to September 1998

nificantly more broadly distributed in the fall than in the spring ($t=5.30$, $df=6$, $P=0.002$) (Fig. 2a), and native taxa were significantly more broadly distributed in the spring than in the fall ($t=5.18$, $df=6$, $P=0.002$) (Fig. 2b). There was also a significant effect of season on the overlap of the distributions of *L. humile* and native taxa; the distributions of *L. humile* and native taxa overlapped significantly more in the spring than in the fall ($t=3.38$, $df=6$, $P=0.01$) (Fig. 2c).

The effects of season on the distribution of each native taxon varied considerably. *Formica* spp., *Prenolepis imparis*, and *Leptothorax* spp. had significantly greater

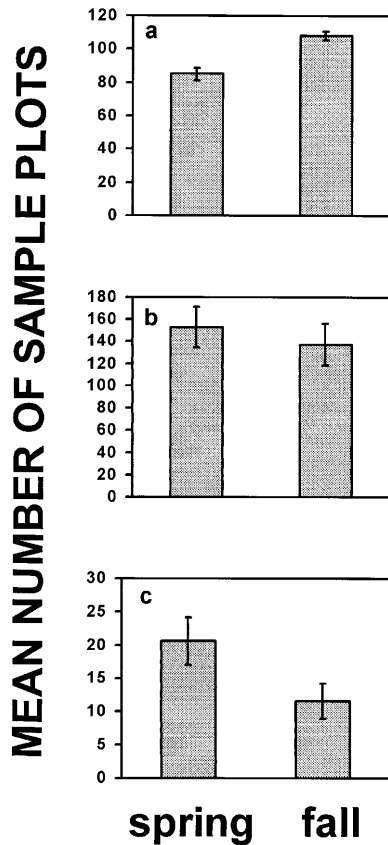


Fig. 2a-c Mean number (\pm SE) of overview sample plots in which we detected each taxon in the spring and fall surveys. **a** The distribution of *L. humile*, **b** the distribution of all native taxa grouped together, and **c** the overlap of *L. humile* and native taxa

distributions in the spring than in the fall. There was no effect of season on any other taxon (Table 3). For taxa that were rarely detected, our analyses may have lacked power to detect an effect of season. Therefore, cautiously interpret the effect of season on rare taxa.

In the 1-m² sampling plots, *Linepithema humile* was detected with equal frequency in the spring and fall (Wilcoxon signed-ranks test, $t=62$, $df=16$, $P>0.05$), but

native taxa were detected in significantly more 1-m² sampling plots in the spring than in the fall (permutation test, $df=11$, $P=0.02$). *Prenolepis imparis*, the most frequently observed native taxon, was detected significantly more frequently in the spring than in the fall (Wilcoxon signed-ranks test, $t=4$, $df=8$, $P<0.05$).

Invasion rate

From May 1993 to September 1999, *L. humile* increased its range by 31 overview sample plots at JRBP (Table 4) for an average annual rate of increase of about 5 sample plots year⁻¹. There was year-to-year variation in the range expansion of *L. humile* at JRBP (Table 5). From one September to the next, it increased its range at JRBP every year but one (September 1995–1996). However, in some years, distribution of *L. humile* at JRBP decreased (May 1994–1995, May 1998–1999, September 1995–1996). Between 1994 and 1995, for both the May and September surveys, there was little change in the range of *L. humile* at JRBP. Comparing one May to the next, *L. humile* moved into from 5 (May 1993–1994) to 17 (May 1998–1999) overview sample plots and out of 6 (May 1993–1994) to 17 (May 1998–1999) overview sample plots. However, comparing one September to the next, *L. humile* moved into from 7 (September 1994–1995) to 16 (September 1993–1994, and September 1996–1997) overview sample plots and out of from 5 (September 1994–1995, and September 1997–1998) to 10 (September 1995–1996) overview sample plots. Generally, *L. humile* increased its range size more between successive September surveys than between May surveys.

There was also a significant effect of season on range expansion. The mean range expansion from May to September (from Table 4) (10.4 overview sample plots \pm 2.6 SEM) was significantly greater than the range expansion from September to May (-7.0 overview sample plots \pm 3.7) ($t=3.87$, $df=9$, $P=0.004$).

Table 3 The effect of season on the distribution of each taxon. Values are the mean number (\pm SEM) of overview sampling plots out of 135 common to each survey from 1993 to 1999

Native taxa	Spring	Fall	df	t	P
<i>Formica</i>	18.3 \pm 1.7	13.3 \pm 1.9	8	1.95	0.04*
<i>Camponotus</i>	9.5 \pm 2.5	8.0 \pm 1.9	6	0.48	0.33
<i>Crematogaster coarctata</i>	6.3 \pm 1.4	3.5 \pm 1.4	7	1.42	0.10
<i>Messor andrei</i>	15.5 \pm 2.2	15.8 \pm 1.9	7	0.12	0.46
<i>Pheidole californica</i>	0.5 \pm 0.3	0.5 \pm 0.2	6	0	0.50
<i>Liometopum occidentale</i>	0.3 \pm 0.3	0.2 \pm 0.2	6	0.28	0.40
<i>Tapinoma sessile</i>	3.0 \pm 1.7	2.3 \pm 0.8	4	0.35	0.37
<i>Prenolepis imparis</i>	29.5 \pm 5.3	12.7 \pm 2.1	4	2.94	0.02*
<i>Leptothorax</i>	3.5 \pm 1.2	0.3 \pm 0.2	3	2.62	0.04*
<i>Solenopsis molesta</i>	0 \pm 0	0.3 \pm 0.2	5	1.58	0.09
<i>Stenamma</i>	0 \pm 0	0.5 \pm 0.3	5	1.46	0.10

* $P\leq 0.05$

Table 4 Seasonal range expansion of *L. humile* at JRBP. Shown are numbers of overview sample plots gained and lost by *L. humile*, out of 135 overview sample plots surveyed twice yearly from May 1993 to September 1999. The first column is the time period. The difference between the second and third columns, shown in the fourth column, is change in the distribution of *L. humile* for the indicated time interval

Time interval	<i>L. humile</i>		
	Moved into	Moved out of	Change
May 1993 to Sept 1993	11	7	4
Sept 1993 to May 1994	12	9	3
May 1994 to Sept 1994	10	4	6
Sept 1994 to May 1995	4	14	-10
May 1995 to Sept 1995	16	4	12
Sept 1995 to May 1996	9	19	-10
May 1996 to Sept 1996	17	9	8
Sept 1996 to May 1997	8	9	-1
May 1997 to Sept 1997	10	2	8
Sept 1997 to May 1998	7	9	-2
May 1998 to Sept 1998	13	3	10
Sept 1998 to May 1999	4	26	-22
May 1999 to Sept 1999	28	3	25
May 1993 to Sept 1999	32	1	31

Table 5 Annual range expansion of *L. humile* at JRBP. Shown are numbers of overview sample plots gained and lost by *L. humile*, out of 135 overview sample plots surveyed twice yearly from May 1993 to September 1999. The difference between the second and third columns, shown in the fourth column, is the change in the distribution of *L. humile* for the indicated time interval

Time interval	<i>L. humile</i>		
	Moved into	Moved out of	Change
May 1993 to May 1994	13	6	7
May 1994 to May 1995	6	10	-4
May 1995 to May 1996	16	14	2
May 1996 to May 1997	16	9	7
May 1997 to May 1998	13	7	6
May 1998 to May 1999	5	17	-12
May 1993 to May 1999	16	10	6
Sept 1993 to Sept 1994	16	7	9
Sept 1994 to Sept 1995	7	5	2
Sept 1995 to Sept 1996	8	10	-2
Sept 1996 to Sept 1997	16	9	7
Sept 1997 to Sept 1998	13	5	8
Sept 1998 to Sept 1999	12	9	3
Sept 1993 to Sept 1999	28	1	27

Discussion

Our long-term investigation of an invasion in progress shows that the invasive Argentine ant, *L. humile*, is increasing its range size at JRBP largely at the expense of native taxa (Fig. 1). However, there is seasonal and annual variation in the rate of its range expansion, and not all native taxa are equally affected.

The comparison of the overview and 1-m² sampling techniques confirms that our overview sampling tech-

nique informs us about changes in the distributions of *L. humile* and epigeic native taxa at Jasper Ridge. Both methods showed the same pattern of seasonal oscillations in the distributions of native taxa and *L. humile*: the distribution of *L. humile* was greater in the fall than in the spring, and the distribution of native taxa was greater in the spring than in the fall. However, our overview method does not detect the presence of hypogeic species, which forage below the leaf litter. Other studies have shown that *L. humile* may not have a negative effect on hypogeic ant species (Ward 1987; Holway 1998; Suarez et al. 1998), though further work is necessary to investigate this.

Patterns in the distributions of several ant species are not random at JRBP. We found that the distributions of most epigeic species overlap much less frequently than expected with the distribution of *L. humile*. These patterns arise for at least two reasons. First, many species are found only in particular habitats. For example, the harvester ant *Messor andrei* is typically found only in serpentine grassland and chaparral communities at JRBP (Brown and Human 1997; Brown and Gordon 2000). To date, *L. humile* has rarely been encountered either in serpentine grassland or chaparral communities at JRBP (N.J. Sanders, unpublished work). Second, Argentine ants influence the distribution of other ant species. Several species, including *Prenolepis imparis*, *Camponotus semitestaceus*, *Formica moki*, *Leptothorax nevadensis* and *Lept. rugatulus* are associated with oak woodlands and riparian zones at JRBP. However, we rarely found any of these species at a sample plot with *Linepithema humile*, though *L. humile* was often detected in similar habitats. Work at JRBP has shown that *L. humile* reduces ant species richness where it invades because of its superior competitive ability (Human and Gordon 1996, 1997). We do not know if competitive interactions with *L. humile* forced native species to emigrate from the sample plot or instead led to the local extinction of native species. We doubt that interactions with *L. humile* forced epigeic species to forage under leaf litter where our overview method might not detect them, because many sampling plots are not covered by leaf litter or plant matter, so native species, if present, would be readily detected.

Several researchers suggest that the activity of ant colonies is correlated with mean temperature (Markin et al. 1974; Sanders 1972; but see Whitford 1978), rainfall (Whitford and Ettershank 1975), resource availability (Whitford and Ettershank 1975; Whitford 1978), or a combination of these factors. Jasper Ridge is located in a Mediterranean climate zone and is subject to cool, wet winters and hot, dry summers. The apparent seasonal oscillations in the distribution of *L. humile* at Jasper Ridge may be due to an interaction of average temperature, rainfall, and competition for resources. When the weather is cool and wet, *L. humile* is not active, but a native ant, *Prenolepis imparis*, is most active under these conditions (Talbot 1943; Lynch et al. 1980; Tschinkel 1987; Ward 1987; Suarez et al. 1998). This species accounts

for a substantial amount of the increase in the total area occupied by native taxa in the spring surveys. Human et al. (1998) found the temperature-humidity envelope of *L. humile* to be wider than those of *C. semitestaceus*, *Formica subpolita*, and *Pheidole californica*. This may allow *L. humile* to be active when temperatures are too high for native taxa, and during this time, *L. humile* may spread into new areas, establish nests, and monopolize resources. When abiotic conditions again become favorable for native taxa to forage, the behavioral dominance of firmly established *L. humile* colonies may lead to the competitive displacement of native taxa.

The intensity of competition for resources probably varies between the spring and fall. Several native ant taxa at Jasper Ridge collect homopteran honeydew and scavenge for insects. The availability of honeydew decreases from spring to fall (Bristow 1991), and the abundance of other arthropods probably decreases as well. When these resources become limited in the fall, competition with *L. humile* may lead either to the emigration or the local extinction of native taxa. At least two studies in California have shown that the activity of *L. humile* in ant communities can vary over the course of 1 year (Suarez et al. 1998; Holway 1999). Studies are needed to examine seasonal or yearly variation in the mechanisms of competition between *L. humile* and native ant taxa.

Between 1993 and 1999 *L. humile* has increased its range by 31 ha at Jasper Ridge, for an average of approximately 5 ha/yr, usually occupying more sample plots in the fall surveys than in the spring surveys (Figs. 1, 2). Although not directly comparable to other estimates of the rate of spread of *L. humile*, the rate of spread in 2 dimensions at JRBP is approximately 50,000 m² year⁻¹, while other studies from California report rates of spread in 1 dimension as anywhere from 0 to 300 m year⁻¹ (Erickson 1971; Holway 1995, 1998; Human and Gordon 1996). From year to year and season to season, the distribution of the invasive Argentine ant varies considerably. The mechanisms by which *L. humile* displaces native taxa may vary temporally as well.

Colonies of most ant species reproduce by sending out winged reproductives once a year. Argentine ant colonies, in contrast, reproduce by budding, and should spread slowly compared to other invasive social insect species (Moller 1996; Holway 1998). Holway (1998) found the rate of spread of *L. humile* near Davis, California to be approximately 16 m year⁻¹. Our results on rate of spread suggest that *L. humile*'s rate of spread can be much quicker (100–500 m per year). Our data also suggest that this rate can vary from season to season, year to year, and perhaps habitat to habitat, though we did not explicitly test this hypothesis.

Despite the tremendous ecological and economic importance of the Argentine ant, there have been no attempts to predict its spread. Our work at Jasper Ridge poses at least two problems in predicting the rate of spread of the Argentine ant. Most models designed to predict rate of spread are derivations of the reaction-diffusion model of Skellam (1951) such that rate of spread, V , is approxi-

mately equal to $2(rD)^{1/2}$, where D is the diffusion coefficient (mean squared displacement per unit time), and r is the intrinsic rate of population increase. Since our results suggest that D can vary temporally and perhaps spatially, and r is also dependent on season for *L. humile* (Markin 1970), caution should be used in attempts to apply Skellam's model to Argentine ant invasions. Approaches similar to the travelling periodic wave models of Shigesada and Kawasaki (1997) are likely to be necessary to predict accurately the Argentine ant's range expansion.

The spread of invasive species is likely to transform species assemblages in many ecosystems throughout the world. In many cases, invasive species devastate the native fauna in their introduced range. In our 7-year study, there has been considerable variation in the spread of *L. humile* and its effects on native taxa. Studies of invasions in progress, such as this one, may help us predict an invader's spread and impact on native ecosystems.

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References

- Andersen AN (1991) Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. *Aust J Ecol* 16:273–279
- Bond W, Slingsby P (1984) Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology* 65:1031–1037
- Bristow CM (1991) Are ant-aphid associations a tritrophic interaction? Oleander aphids and Argentine ants. *Oecologia* 87:514–521
- Brown MJF, Gordon DM (2000) How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. *Behav Ecol Sociobiol* 47:195–203
- Brown MJF, Human KG (1997) Effects of harvester ants on plant species distribution and abundance in a serpentine grassland. *Oecologia* 112:237–243
- Cole FR, Medeiros AC, Loope LL, Zuehlke WW (1992) Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* 73:1313–1322
- Crowell KL (1968) Rates of competitive exclusion by the Argentine ant in Bermuda. *Ecology* 49:551–555
- Drake JA, Mooney HA, Castri FD, Groves RH, Kruger FJ, Rejmanek M, Williamson M (eds) (1989) *Biological invasions: a global perspective*. Wiley, Chichester
- Erickson JM (1971) The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* 78:257–266
- Gordon DM (1995) The expandable network of ant exploration. *Anim Behav* 50:995–1007
- Haskins CP, Haskins EF (1965) *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda – equilibrium or slow replacement? *Ecology* 46:736–740

- Hölldobler B, Wilson EO (1990) The ants. Belknap, Cambridge
- Holway DA (1995) Distribution of the Argentine ant (*Linepithema humile*) in northern California. *Conserv Biol* 9:1634–1637
- Holway DA (1998) Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia* 116:252–258
- Holway DA (1999) Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80:238–251
- Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* 105:405–412
- Human KG, Gordon DM (1997) Effects of Argentine ants on invertebrate diversity in northern California. *Conserv Biol* 11:1242–1248
- Human KG, Gordon DM (1999) Behavioral interactions of the invasive Argentine ant with native ant species. *Insectes Soc* 46:159–163
- Human KG, Weiss S, Weiss A, Sandler B, Gordon DM (1998) The effect of abiotic factors on the local distribution of the invasive Argentine ant (*Linepithema humile*) and native ant species. *Environ Entomol* 27:822–833
- Lynch JF, Balinsky EC, Vail SG (1980) Foraging patterns in three sympatric forest ant species, *Prenolepis imparis*, *Paratrechina melanderi* and *Aphaenogaster rudis*. *Ecol Entomol* 5:353–371
- Markin GP (1970) The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in Southern California. *Ann Entomol Soc Am* 63:1238–1242
- Markin GP, O'Neal J, Dillier JH, Collins HL (1974) Regional variation in seasonal activity of imported fire ant, *Solenopsis saevissima richteri*. *Environ Entomol* 3:446–452
- Moller H (1996) Lessons for invasion theory from social insects. *Biol Conserv* 78:125–142
- Mooney HA, Drake JA (eds) (1986) Ecology of the biological invasions of North America and Hawaii. Springer, Berlin Heidelberg New York
- Sanders CJ (1972) Seasonal and daily activity patterns of carpenter ants (*Camponotus* spp.) in northwestern Ontario (Hymenoptera: Formicidae). *Can Entomol* 104:1861–1867
- Shigesada N, Kawasaki K (1997) Biological invasions: theory and practice. Oxford University Press, Oxford
- Simberloff D, Schmitz DC, Brown TC (eds) (1997) Strangers in paradise: impact and management of nonindigenous species in Florida. Island, Washington, DC
- Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38:196–218
- Suarez AV, Bolger DT, Case TJ (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology* 79:2041–2056
- Talbot M (1943) Response of the ant *Prenolepis imparis* Say to temperature and humidity changes. *Ecology* 24:345–352
- Tremper BS (1976) Distribution of the Argentine ant, *Iridomyrmex humilis* Mayr, in relation to certain native ants of California: ecological, physiological, and behavioral aspects. PhD dissertation, University of California, Berkeley
- Tschinkel WR (1987) Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. *Insectes Soc* 34:143–164
- Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. *Am Sci* 84:468–478
- Ward PS (1987) Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia* 55:1–16
- Wheeler WM (1910) Ants. Columbia University Press, New York
- Whitford WG (1978) Structure and seasonal activity of Chihuahuan desert ant communities. *Insectes Soc* 23:79–88
- Whitford WG, Ettershank G (1975) Factors affecting foraging activity in Chihuahuan desert harvester ants. *Environ Entomol* 4:689–696
- Williamson MH (1996) Biological invasions. Chapman and Hall, London