BIOTIC AND ABIOTIC CONTROLS OF ARGENTINE ANT INVASION SUCCESS AT LOCAL AND LANDSCAPE SCALES

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Abstract. Although the ecological success of introduced species hinges on biotic interactions and physical conditions, few experimental studies—especially on animals—have simultaneously investigated the relative importance of both types of factors. The lack of such research may stem from the common assumption that native and introduced species exhibit similar environmental tolerances. Here we combine experimental and spatial modeling approaches (1) to determine the relative importance of biotic and abiotic controls of Argentine ant (*Linepithema humile*) invasion success, (2) to examine how the importance of these factors changes with spatial scale in southern California (USA), and (3) to assess how Argentine ants differ from native ants in their environmental tolerances. A factorial field experiment that combined native ant removal with irrigation revealed that Argentine ants failed to invade any dry plots (even those lacking native ants) but readily invaded all moist plots. Native ants slowed the spread of Argentine ants into irrigated plots but did not prevent invasion. In areas without Argentine ants, native ant species showed variable responses to irrigation. At the landscape scale, Argentine ant occurrence was positively correlated with minimum winter temperature (but not precipitation), whereas native ant diversity increased with precipitation and was negatively correlated with minimum winter temperature. These results are of interest for several reasons. First, they demonstrate that fine-scale differences in the physical environment can eclipse biotic resistance from native competitors in determining community susceptibility to invasion. Second, our results illustrate surprising complexities with respect to how the abiotic factors limiting invasion can change with spatial scale, and third, how native and invasive species can differ in their responses to the physical environment. Idiosyncratic and scale-dependent processes complicate attempts to forecast where introduced species will occur and how their range limits may shift as a result of climate change.

Key words: abiotic factors; ant; biotic resistance; GIS; invasion; Linepithema humile; scale.

INTRODUCTION

A central goal of invasion biology is to predict where introduced species will occur. Progress towards this goal requires an understanding of what factors limit invasion success and how they change in importance with spatial scale. As with range limits in general, two broad categories of factors affect where introduced species will occur: the physical environment (Moyle and Light 1996, Blackburn and Duncan 2001, Gabriel et al. 2001) and species interactions (Simberloff and Von Holle 1999, Stachowicz et al. 1999, Torchin et al. 2003). Because the outcomes of species interactions hinge on the environment in which they occur, it is essential to quantify how biotic and abiotic factors interact to influence spread and establishment of introduced species. Surprisingly, few experimental studies have tested the relative importance of species interactions and physical conditions in determining the distribution of introduced species (but see D'Antonio 1993, Byers 2002, Dethier and Hacker 2005).

A second major challenge in invasion biology, as in ecology generally, lies in understanding how factors that control species distribution change in importance with spatial scale (Levin 1992, Levine and D'Antonio 1999). For example, correlations between native and introduced species diversity may commonly reverse in sign with increasing spatial scale. Negative relationships between diversity and invasibility are often predicted at the community scale, while positive relationships are often reported at larger spatial scales (Shea and Chesson 2002). Both relationships are predicated on the assumption that native and introduced species closely resemble one another with respect to their resource requirements and environmental tolerances (Levine and D'Antonio 1999). But what about cases where invaders and natives differ? The existence of such differences may commonly result from the fact that invasive species originate in regions often unlike those where they are introduced. For example, introduced species that are strong

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competitors may, by definition, be more limited by physical conditions than by interspecific competition from native species (Moyle and Light 1996, Holway et al. 2002b). If such introduced species also differ from natives in their environmental tolerances, then the factors that control native diversity may not be the same as those that determine invader abundance, and the relationship between diversity and invasibility may be weak irrespective of scale. Such cases are highly important: strongly competitive invasive species would be expected to cause large effects on the communities they invade.

Given present concerns about introduced species and controversies surrounding why they are successful, studies that test the relative importance of species interactions and abiotic factors across different spatial scales are needed to further our understanding of controls on introduced species occurrence. It is also important to assess the extent to which the factors that determine occurrence of introduced species are the same as those that influence native diversity. Here we use a combination of experimental and analytical approaches to test the relative importance of biotic and abiotic factors in determining the local and regional occurrence of Argentine ants (Linepithema humile). At the community scale, we conduct a series of field manipulations (1) to gauge the relative importance of interspecific competition from native ants and the abiotic environment in determining invasion success and (2) to determine if native ants and Argentine ants respond similarly to key physical conditions. To complement these community-level experiments, we use GIS-based approaches to examine patterns of occurrence at the landscape-scale: (1) to test if the environmental variables that determine invader occurrence at the community scale are also important at the landscape scale, and (2) to test if the environmental correlates of native species diversity are the same as those that determine introduced species occurrence. As recent reviews attest (Herben et al. 2004, Levine et al. 2004), most empirical studies in this area of research involve plants with few manipulative experiments that address animal invasions (but see Petren and Case 1998, Byers 2002). For these reasons, our study represents a novel test of hypotheses concerning community susceptibility to invasion.

METHODS

Study system

The Argentine ant is a widespread, abundant, and ecologically damaging invasive species (Holway et al. 2002a). Although common in urban and agricultural environments, L. humile readily invades natural habitats (Suarez et al. 2001), where it displaces many native ants (Ward 1987, Human and Gordon 1996, Holway 1998a, Suarez et al. 1998). Local extinctions of native ant species resulting from Argentine ant invasions may negatively affect species that interact strongly with native ants (Bolger et al. 2000, Laakkonen et al. 2001,

Fisher et al. 2002, Carney et al. 2003). Argentine ants are easily introduced into new areas because they often associate with humans, exhibit general nesting and dietary requirements, and maintain colonies with numerous queens (Newell and Barber 1913). In part because of these characteristics, human-mediated introductions are the predominate mode of spread in this species (Suarez et al. 2001; see Plate 1).

Native to northern Argentina and surrounding regions (Tsutsui et al. 2001, Wild 2004), L. humile now occurs worldwide in areas with suitable climates and is particularly successful in mediterranean-type ecosystems (Suarez et al. 2001). At a global scale, this species appears to be limited by cold winter and high summer temperatures (Roura-Pascual et al. 2004, Hartley et al. 2006). Temperature and precipitation determine the temperature-humidity envelope influencing the surface activity of ants at small spatial scales. Accordingly, the environmental tolerances of the Argentine ant (Schilman et al. 2005) restrict its local distribution to areas with appropriate physical conditions. In seasonally dry southern California, for example, Argentine ants are restricted to areas with suitable levels of soil moisture (Ward 1987, Holway 1995, Menke and Holway 2006).

Field experiment I: Argentine ant response to irrigation and native ant removal

We conducted a factorial experiment that combined native ant removal with soil moisture manipulation at the University of California Elliot Chaparral Reserve. This site contains a long (>1.5 km) contact zone between L. humile and native ants that has been stable for at least the last decade (Holway and Suarez 2004). Argentine ants occupy a large Eucalyptus grove that borders the reserve's northern edge but do not penetrate more than 50 m into adjacent chaparral. We established 28 plots along this contact zone (Fig. 1). Each plot measured 10 × 10 m with a 7-m buffer; the distance between buffers was at least 20 m. Active colonies of Argentine ants and native ants were present inside each plot at the start of the experiment. We assigned seven plots to each of four experimental groups: irrigation + native ant removal, irrigation + native ants present, dry + native ant removal, dry + native ants present.

Removal treatments were randomly assigned to plots prior to the onset of the experiment. Irrigated plots were alternated or separated from one another by a minimum of 75 m. To locate native ant colonies, we used a grid of 25 evenly spaced baits placed every 2 m inside each plot and every 2 m in the buffer zone outside each plot. We used baits together with standardized visual surveys to build a species list for each plot. After we located and marked native ant colonies, we placed Maxforce granular ant bait (Bayer Environmental Science, Montvale, New Jersey, USA), fire ant bait, and ant gel just outside the nest entrances of native ants in all removal plots and their buffer zones. These baits are non-toxic to birds and mammals, are not assimilated by plants, do
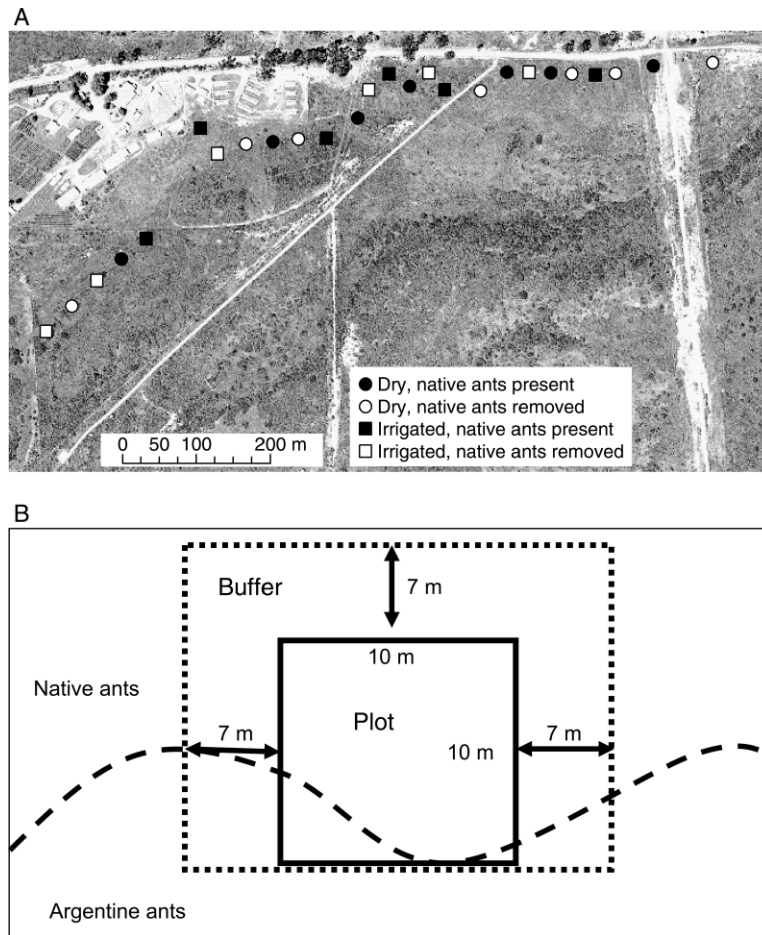
FIG. 1. Design of field experiment I. (A) Aerial view showing the location of all 28 plots at the University of California Elliot Chaparral Reserve. (B) Configuration of a typical 10 × 10 m plot, its 7-m buffer, and the location of the invasion front (dashed line).

not dissolve in water, and degrade within 48 hours (Krushelnycky et al. 2004).

To minimize the risk of nontarget effects, we continuously monitored toxicant-containing baits to confirm that native ants were the only arthropods present and that Argentine ants were never present. Native ant activity in the vicinity of all treated nests ceased after two consecutive days of treatment with poison baits. Every two weeks, we used baits (nontoxic) and visual surveys to confirm the absence of native ants in removal plots, and we retreated removal plots as needed throughout the experiment. Toxicants greatly reduced native ant presence in removal plots. At the end of the experiment, for example, native ants were almost entirely absent in both pitfall traps and at baits in treated dry plots versus untreated dry plots (1 ant/trap vs. 10 ants/trap, two-sample t test, $t_{12} = 2.47$, $P < 0.05$; 8% vs. 55% of baits, $t_{12} = 7.42$, $P < 0.0001$).

To elevate soil moisture levels, we used a drip irrigation system similar to that described in Menke and Holway (2006). In each plot we placed five 10 m long irrigation hoses parallel to and equidistant from one another such that the entire plot was watered uniformly for one hour per day. Irrigation lines were also placed in the same configuration in dry plots, but these hoses delivered no water. Drip irrigation increased soil moisture levels to an extent achieved in other manipulative experiments; these levels were roughly equivalent to those typical of natural riparian corridors, urban lawns, and agricultural fields (Holway and Suarez 2006, Menke and Holway 2006). During the course of the experiment soil moisture levels in non-irrigated plots remained very low. Changes in soil moisture levels alter the temperature–humidity envelope important to worker activity and survival (Hölldobler and Wilson 1990).

We began irrigation in July 2005, within two weeks of the first application of Maxforce, and stopped irrigation in September 2005. We used pitfall traps to estimate *L. humile* abundance at the beginning and end of the experiment. In each plot, we placed five traps in the pattern of the five on a die and left traps in the ground for five days. Pitfall trapping occurred only before and

after the experiment to avoid altering ant density while the experiment was in progress. Each month, we used a grid of 25 baits placed in each plot to quantify the extent to which Argentine ants were nesting.

We used a two-way MANOVA to test how the two treatments influenced the ability of Argentine ants to spread in experimental plots. In this MANOVA, the two response variables were measures of ant activity from the pitfall trap and bait surveys. For both response variables we calculated the difference in Argentine ant abundance between the beginning and end of the experiment and used these differences as data points in the analysis. Pitfall trap data were log-transformed and bait data (which consisted of proportions) were arcsine-square-root transformed prior to analysis. To examine temporal changes in *L. humile* presence in irrigated plots, we used a repeated-measures MANOVA. This analysis used data from the three monthly baiting surveys; these data were arcsine square root transformed. All statistics were performed using JMP 5.1 (SAS Institute, Cary, North Carolina, USA).

Field experiment II: Native ant response to irrigation

We conducted a second field experiment to assess the response of native ants to irrigation. This experiment was also conducted at the University of California Elliot Chaparral Reserve. We established five pairs of 12 × 12 m plots in areas away from those occupied by *L. humile*. Each pair of plots consisted of an irrigated plot and a dry plot. Irrigated plots were watered by sprinkler from April to September 2003. We used pitfall traps to monitor native ant activity in each plot. The dependant variable in this analysis was the difference in ant abundance in pitfall traps for each pair of irrigated and dry plots at the end of the experiment. We then used one sample *t* tests to compare these differences from zero for each of four common above ground foraging native ants (*Crematogaster californica, Forelius mccooki, Pheidole vistana,* and *Solenopsis xyloni*). These species are common and widespread in coastal San Diego County (Suarez et al. 1998, Holway 2005). Pitfall trap data were log transformed and all statistics were performed using JMP 5.1.

Patterns at the landscape scale

To complement the community-level experiments, we also examined landscape-level patterns of Argentine ant occurrence and native ant diversity. This analysis used a data set of 393 sites distributed throughout southern California (Fig. 2); 69 of these sites had Argentine ants. At each site, we placed five traps in the ground in the pattern of the five on a die, with corner traps separated by 40 m. Pitfall traps were left open for 10 days. All sites were sampled a minimum of four times, including both summer and winter sampling in each of 2 years between 1999 and 2005. To standardize sampling effort among sites, we used data for only the first two summer and two winter sampling periods.
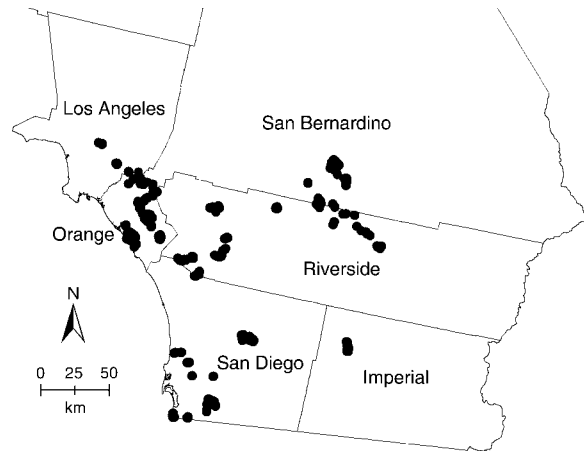

Fig. 2.   Locations of pitfall trap arrays (*n* = 393 sites) in six southern California counties.

We selected the following environmental variables as potential predictors of Argentine ant occurrence and native ant diversity: maximum July temperature, minimum January temperature, average rainfall, normalized difference vegetation index (NDVI), distance to nearest urban area, and distance to nearest perennial stream. These predictors were selected from a range of possible (often intercorrelated) variables because of their putative importance in influencing both Argentine ants (Holway 1998b, Holway et al. 2002b, Hartley et al. 2006, Holway and Suarez 2006) and native ants (Hölldobler and Wilson 1990, Kaspari et al. 2000). The three climate variables—maximum July temperature, minimum January temperature, and average rainfall—are averages from 1966 to 1995 at 1000-m resolution and are described in detail in Franklin et al. (2001). NDVI was averaged from 16 day composites (28 July–12 August) taken between 2000 and 2002 by the National Oceanic and Atmospheric Administration's advanced high resolution radiometer satellite series (resolution: 250 m). Distance to nearest urban area was calculated using the Multi-source Land Cover Data (v02_2) (resolution: 100 m) compiled by the California Department of Forestry and Fire Protection. Distance to nearest perennial stream was derived from high resolution datasets in the National Hydrographic Database.

We used a generalized linear modeling approach (logistic regression; GLM, binary with logit link) to fit each environmental variable with the landscape-level pattern of Argentine ant occurrence. We used the same general approach (Poisson regression; GLM, Poisson with log-link) to identify the environmental correlates of the number of native ant species. We refrained from a direct test of the relationship between the number of native ant species and Argentine ant presence, because *L. humile* displaces above ground foraging native ants in California (Ward 1987, Human and Gordon 1996, Holway 1998a, b). Therefore, we restricted the native ant portion of our analysis to the 324 sites lacking
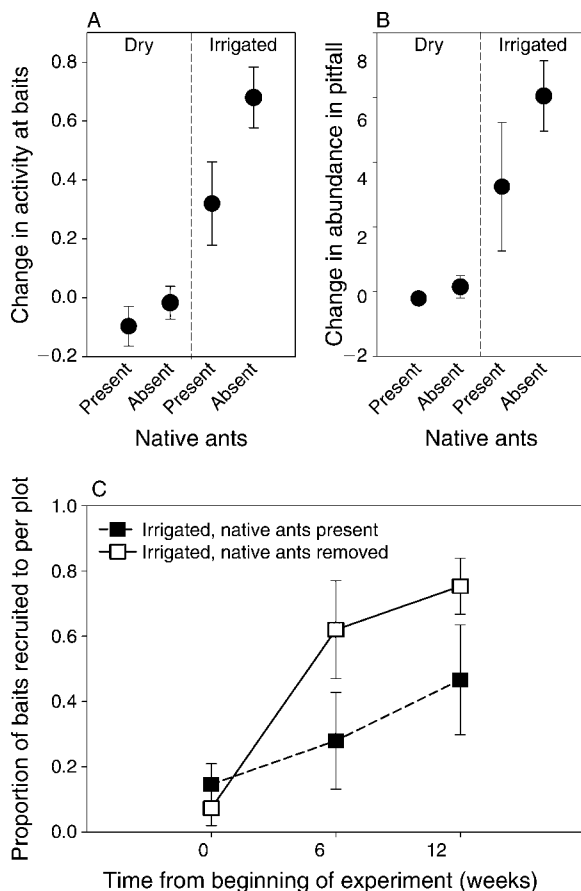
FIG. 3. Results of field experiment I. (A) Change in Argentine ant activity (mean ± SE) as measured by the proportion of baits recruited to at the beginning and end of the experiment. (B) Change in Argentine ant abundance (mean ± SE) in pitfall traps at the beginning and end of the experiment. (C) Proportion of baits (mean ± SE) recruited to by Argentine ants in irrigated plots.

Argentine ants. To gauge the importance of each variable, we assessed its ability to reduce the Akaike information criterion (AIC), a widely used and largely unbiased measure of model fit (Swets 1988, McPherson et al. 2004). All statistics were performed using R 2.3.0 (*available online*).[4]

RESULTS

Field experiment I: Argentine ant response to irrigation and native ant removal

Both irrigation and native ant removal led to increased abundance of Argentine ants in experimental plots after three months (two-way MANOVA: Wilks' λ = 0.25, $P < 0.0001$; Fig. 3A, B). Argentine ants responded positively and strongly to irrigation ($F_{2,21}$ = 23.52, $P < 0.0001$). There was also a positive effect of native ant removal ($F_{2,21} = 5.27$, $P < 0.05$). While the

[4] ⟨http://www.r-project.org/⟩

interaction term was nonsignificant ($F_{2,21} = 2.27$, $P = 0.13$), the importance of native ant removal was evident only in irrigated plots (Fig. 3A, B). In dry plots without native ants, Argentine ants did not change in abundance (one-sample t tests: bait surveys $t_6 = -0.32$, $P > 0.05$; pitfall traps $t_6 = 0.20$, $P > 0.05$), whereas in irrigated plots without native ants, Argentine ants increased in abundance at least 10-fold over the course of the experiment both at baits and in pitfall traps (Fig. 3A, B; one-sample t tests: bait surveys $t_5 = 5.68$, $P < 0.01$; pitfall traps $t_5 = 11.34$, $P < 0.0001$). Although the presence of native ants was a significant factor, bait surveys revealed that native ants merely slowed the spread of Argentine ants in the early stages of the experiment and did not prevent *L. humile* from invading as the experiment progressed (repeated-measures MAN-OVA: time $F_{2,9} = 17.98$, $P < 0.001$; time × removal $F_{2,9} = 4.88$, $P < 0.05$; Fig. 3C). Pesticides appeared to have no unintended effects. Argentine ants showed the strongest increases in irrigated plots in which we used Maxforce to remove native ants (Fig. 3).

Field experiment II: Native ant response to irrigation

Native ants exhibited divergent responses to irrigation (Fig. 4). *Solenopsis xyloni* increased in abundance nearly 100-fold in pitfall traps after six months of irrigation (one-sample t test: $t_4 = 4.63$, $P < 0.01$), whereas *Forelius mccooki* ($t_4 = 2.15$, $P > 0.05$) and *Crematogaster californica* ($t_4 = -1.43$, $P > 0.05$) did not appear to respond to irrigation. *Pheidole vistana* appeared to respond to an intermediate degree ($t_4 = 2.65$, $0.05 < P < 0.10$).

Patterns at the landscape scale

At the landscape scale Argentine ants and native ants responded differently to environmental variables known to determine ant activity and occurrence. The presence of *L. humile* was best explained by its positive association with urban areas (Table 1). The second most important correlate was minimum winter temperature: the colder the temperature, the less likely Argentine ants were to be present. High temperatures also decreased the likelihood of *L. humile* occurrence, but like precipitation, maximum summer temperature was a relatively poor predictor, yielding only a small reduction in AIC (Table 1, Fig. 5).

Compared to environmental correlates of Argentine ant occurrence, the number of native ant species exhibited a nearly opposite pattern. Native ants increased in species number with increasing precipitation (the best predictor variable) and, less strongly, with increasing NDVI (a measure of the greenness of vegetation) (Table 1, Fig. 5). High maximum summer temperatures significantly depressed the number of native ant species. Areas with higher minimum winter temperatures had fewer native ant species (Fig. 5), whereas Argentine ants require warmer winter temperatures. Proximity to urban environments had no
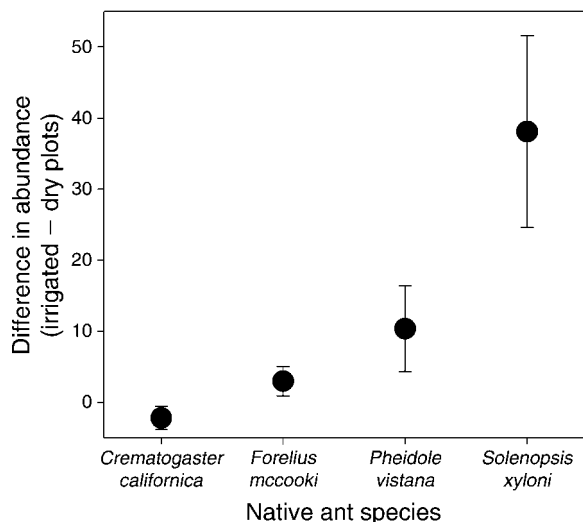
Fig. 4. Results of field experiment II. Difference in native ant abundance in pitfall traps (irrigated − dry plots) after six months of irrigation. Plots used for this experiment all lacked Argentine ants. Values are mean ± SE.

detectable effect on the number of native ant species (Table 1).

Cross-scale comparison of ant responses

Argentine ants and native ants differed in their responses to environmental factors at the landscape and community scales. Although our field experiments identified soil moisture as the preeminent factor limiting Argentine ants, at the landscape scale, variables that strongly influence soil moisture (e.g., maximum summer temperature and precipitation) appear unimportant in determining *L. humile* occurrence (Tables 1 and 2). In contrast, native ants exhibited variable responses to elevated soil moisture at the community scale with only one of four species strongly increasing in activity. At the landscape scale, the number of native ant species responded variably to environmental conditions known to influence ant activity; diversity increased with

precipitation but decreased with maximum summer temperature (Tables 1 and 2).

Discussion

Our field experiments build on previous work that demonstrates the importance of soil moisture in controlling the spread of Argentine ants in seasonally dry environments (Holway 1998b, Holway et al. 2002b, Menke and Holway 2006). The present study, however, tests two novel hypotheses. First, we examined the relative importance of interspecific competition and physical conditions in limiting the local spread of *L. humile*. When the abiotic environment was unsuitable for Argentine ants, they failed to spread in experimental plots regardless of presence or absence of native ants (Fig. 3A, B). At irrigated sites, in contrast, interspecific competition from native ants slowed but did not prevent the spread of Argentine ants (Fig. 3C). Second, our field experiments allowed us to test the assumption that native ants respond in a similar manner to the same environmental variation that encourages the spread of Argentine ants. No native ant species decreased its activity in response to irrigation, and only one species, *S. xyloni*, appeared to benefit (Fig. 4). Interestingly, *S. xyloni*, like the Argentine ant, can act like a behaviorally dominant species (S. B. Menke, *personal observation*), but unlike *L. humile*, *S. xyloni* can occupy extremely arid environments. The variation observed among the native ant species in response to elevated levels of soil moisture (Fig. 4) presumably reflects species-level differences in physiological tolerances (Schilman et al. 2005, 2007). While Menke and Holway (2006) noted that native ant activity increased with irrigation, the results of the present study are the first to demonstrate species-specific disparities in how altered physical conditions affect activity.

The abiotic factors controlling ant activity and abundance at the community scale were dissimilar to those correlated with invader occurrence and native diversity at the landscape scale (Table 2). Interestingly, precipitation, which best predicted the number of native ant species, did not explain patterns of Argentine ant

TABLE 1. Single-predictor effects of six environmental variables on Argentine ant occurrence (393 sites; logistic regression) and the number of native ant species at sites where Argentine ants were absent (324 sites; Poisson regression) across southern California.

	Argentine ant occurrence			No. native ant species		
Variable	Slope	z	ΔAIC	Slope	z	ΔAIC
Null			85.62			78.8
Maximum temperature	−0.264	−4.803****	52.45	−0.034	−7.107****	23.4
Minimum temperature	**1.087**	**5.212******	**5.21**	−0.015	−2.141**	72.4
NDVI	0.217	4.267****	67.47	**0.005**	**7.980******	**17.4**
Precipitation	0.029	2.505*	81.15	**0.014**	**9.011******	**0.0**
Distance to perennial stream	−0.324	−3.848****	72.79	−0.002	−0.162	80.8
Distance to urban area	**−0.941**	**−7.881******	**0.00**	−0.022	−1.380	78.9

Notes: In each analysis, the two best-fitting one-predictor models (judged by lowest AIC) are presented in boldface type. NDVI is the normalized difference vegetation index. ΔAIC is the difference of each model from the strongest model in the analysis. Significance of regression models is indicated with asterisks (* $P < 0.05$, ** $P < 0.01$, **** $P < 0.0001$). Results from the Wald test are shown (z).
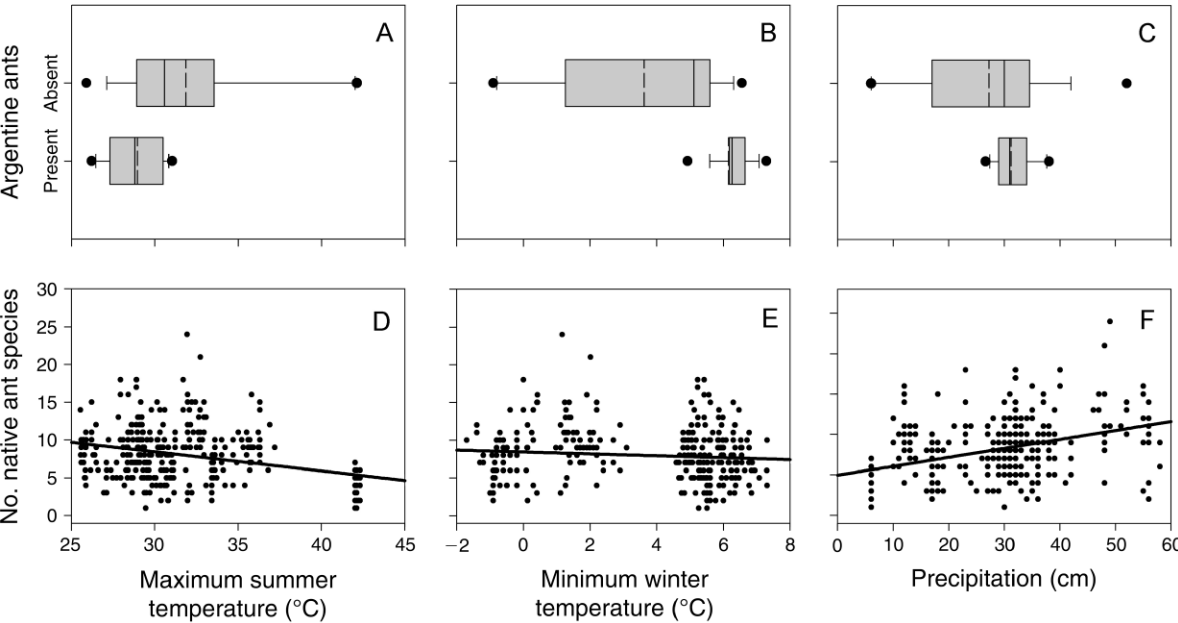
FIG. 5. Results of landscape-level analyses showing how Argentine ant presence and native ant diversity relate to maximum summer temperature, minimum winter temperature, and precipitation. (A–C) Argentine ant presence and absence at 394 sites. Standard box plots show the 25th percentile, median, and 75th percentile (solid lines), means (dashed lines), the 10th and 90th percentiles (whiskers), and 95% confidence limits (circles). (D–F) The number of native ant species at 324 sites that all lacked Argentine ants. Regression lines are based on GLM; these regression lines do not qualitatively differ from those of the Poisson regressions in Table 1.

occurrence, suggesting that local levels of soil moisture are to some extent decoupled from landscape-level patterns of precipitation. The most important environmental determinant of Argentine ant presence at the landscape scale was minimum winter temperature; low temperatures decreased the probability of *L. humile* occurrence, reflecting the fact that Argentine ants do not occur in environments with prolonged freezing temperatures (Suarez et al. 2001, Krushelnycky et al. 2005, Hartley et al. 2006). In the same cold winter environments of southern California in which *L. humile* do not occur, native ants exhibit their highest diversity (Fig. 5). Argentine ant occurrence was strongly predicted by proximity to urban areas. This positive association presumably results from the Argentine ant's inherent dispersal limitations, an increased frequency of human-

mediated introductions (i.e., propagule pressure), the status of urban areas as source habitats, and anthropogenic modifications to the physical environment that favor Argentine ants (e.g., elevated soil moisture).

Taken together our results suggest a mismatch between the factors that determine Argentine ant occurrence and those that control native ant activity and diversity across multiple spatial scales (Table 2). Although introduced and native species may often respond similarly to environmental factors independent of spatial scale (Levine and D'Antonio 1999, Stohlgren et al. 1999, Naeem et al. 2000), our results demonstrate a case where an ecologically and economically destructive invasive species responds to the environment differently compared to natives. At the community-scale Argentine ants and most native ants respond divergently to

TABLE 2. A summary of the responses of Argentine ants and native ants to abiotic and biotic factors from experiments at the community scale and predictive models at the landscape scale.

	Community scale		Landscape scale		
Ant group	Soil moisture†	Competition from ants‡	Maximum temperature†	Minimum temperature†	Precipitation†
Argentine	+	0	−	+	0
Native	0/+	−	−	0	+

Notes: Biotic factors were not included at the landscape scale because as Argentine ants spread, they displace native ants. Symbols indicate: +, positive response; −, negative response; 0, no response.
† Abiotic factor.
‡ Biotic factor.

PLATE 1.   Coastal sage scrub in Los Peñasquitos Canyon Preserve, California, USA. Human alterations to the abiotic environment from irrigation and urban runoff contribute to the spread of Argentine ants into seasonally dry scrub habitats throughout southern California. Alterations to the abiotic environment that determine spread at the local scale are disassociated from the climate variables that predict occurrence at the landscape scale. Photo credit: S. B. Menke.

elevated levels of soil moisture. This result may help explain why competition from native ants slowed but did not stop the spread of Argentine ants in experimental plots (Fig. 3C). While Holway (1998b) reported no relationship between the rate of spread of Argentine ants and the number of native ant species, the current study illustrates that the presence of native ants can slow the invasion of Argentine ants under certain environmental conditions (e.g., in wet environments). Disparities in how native and introduced ants respond to the physical environment were also observed at the landscape scale. The number of native ant species and the occurrence of Argentine ants were associated with distinctly different environmental variables (Tables 1 and 2).

General significance

With the proliferation of global environmental datasets and heightened concerns about climate change, ecologists are increasingly relying on predictive models that use coarse environmental data to forecast the spread and distribution of introduced species (Levin 1992, Neubert and Caswell 2000, Peterson 2003, Hastings et al. 2005). For this reason, it is important to develop a more quantitative understanding of how factors associated with species occurrence change in importance across contrasting spatial scales. As is the case for other organisms (Rosenzweig 1995), the factors influencing ant diversity and patterns of occurrence dramatically change with spatial scale (Kaspari et al. 2000, 2003). In the present study, the environmental factors associated with invader occurrence also exhibited strong scale dependency. Factors explaining occurrence at the community scale, such as soil moisture, appeared largely independent of factors operating at the landscape scale, such as temperature and precipitation (variables often used to delimit large-scale patterns of distribution [Peterson 2003]) (see Table 1). Efforts to model ranges of native and introduced species that rely on coarse environmental data may often exclude factors that determine occurrence at the community scale (McPherson et al. 2006).

Scale-dependent factors limiting the occurrence of invasive species, such as those discussed above, also relate to the potential distribution and persistence of native species (Sax and Gaines 2003, Melbourne et al. 2007). Although native populations may persist in the presence of strongly competitive introduced species, invasions may nonetheless increase the risk of extinction for native taxa. In addition to direct displacement, effects of invasions on native species include secondary

effects such as reductions in the size, quality, or connectivity of suitable habitat (Mack et al. 2000). In the Argentine ant system, for example, the direct displacement of native ants may work in concert with the modification, destruction, and fragmentation of habitat to restrict the area over which native ant species can occur (Suarez et al. 1998). Human modifications to the environment that expand areas suitable to invasive species will in turn increase the fragmentation and isolation of native populations, factors known to increase extinction risk. Increased isolation and fragmentation of native populations will further elevate future extinction risk under scenarios of global climate change (Warren et al. 2001).

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