

Abiotic factors control invasion by Argentine ants at the community scale

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Summary

1. A prominent and unresolved question in ecology concerns why communities differ in their susceptibility to invasion. While studies often emphasize biotic resistance, it is less widely appreciated how the physical environment affects community vulnerability to invasion.

2. In this study we performed field experiments to test how abiotic variation directly and indirectly influences the extent to which *Linepithema humile* Mayr (Argentine ants) invade seasonally dry environments in southern California.

3. In controlled and replicated experiments involving drip irrigation, we demonstrate (i) that elevated levels of soil moisture increased both the abundance of Argentine ants and their ability to invade native ant communities and (ii) that cessation of irrigation caused declines in the abundance of Argentine ants and led to their withdrawal from previously occupied areas.

4. Because drip irrigation stimulated plant growth, in an additional experiment we manipulated both soil moisture and plant cover to assess the direct vs. indirect effects of added water on the abundance of *L. humile*.

5. Local abundance of Argentine ants increased in irrigated plots but was 38% higher in irrigated plots with plants compared to irrigated plots where plant growth was suppressed. The results of this experiment thus argue for a direct role of soil moisture in influencing Argentine ant abundance but suggest that the indirect effects of added water may also be important.

6. Our study illustrates more generally that fine-scale variation in the physical environment can control whether communities become invaded by non-native species and suggests that an understanding of community susceptibility to invasion will be improved by a better appreciation of interactions between the biotic and abiotic environment.

Key-words: Argentine ants, biological invasion, physical conditions, soil moisture.

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Introduction

An important goal of ecology lies in understanding why some communities are readily invaded, whereas others appear closed to the addition of new species. While many recent studies focus on how diversity may influence susceptibility to invasion (Levine & D'Antonio 1999; Stachowicz, Whitlatch & Osman 1999; Levine 2000; Kennedy *et al.* 2002), much less

attention, in comparison, is given to the importance of abiotic suitability. When physical conditions do receive consideration, their importance is usually emphasized for large spatial scales: for example, how climate controls the establishment of introduced species in new regions (Blackburn & Duncan 2001) or sets distributional limits at a global scale (Morrison *et al.* 2004; Roura-Pascual *et al.* 2004). At smaller spatial scales, abiotic variability seldom receives attention as a factor influencing a community's vulnerability to invasion. This seems surprising, given that abiotic heterogeneity and species-level differences in environmental tolerances are often emphasized as factors promoting coexistence among interspecific competitors (Chesson & Huntly 1997).

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In this study we test the importance of fine-scale variation in the physical environment as a determinant of community susceptibility to invasion by the Argentine ant, a widespread, abundant and ecologically damaging invasive species (Holway *et al.* 2002a). Native to northern Argentina and surrounding regions (Tsutsui *et al.* 2001; Wild 2004), *L. humile* now occurs world-wide in areas with suitable climates and appears particularly successful in Mediterranean-type ecosystems (Suarez, Holway & Case 2001). Although often associated with anthropogenically disturbed habitats (Passera 1994), Argentine ants readily invade natural environments where they displace native ants aggressively in many parts of the world (Tremper 1976; Bond & Slingsby 1984; Ward 1987; Human & Gordon 1996; Way *et al.* 1997; Miyake *et al.* 2002).

Correlational evidence suggests that fine-scale variation in the physical environment may limit the extent to which Argentine ants invade native ant communities. In areas with seasonally dry Mediterranean-type climates, for example, *L. humile* abundance changes dramatically across soil moisture gradients: heavily invaded mesic sites occur in proximity to mainly uninvaded xeric sites (Holway 1998a; Suarez, Bolger & Case 1998; Holway, Suarez & Case 2002b; Holway 2005). Similar associations have been reported for the red imported fire ant (*Solenopsis invicta*) (Tschinkel 1987). Although such observations point to a role for abiotic factors, studies on this topic have not measured, let alone manipulated, soil moisture (Holway 1998b; Human *et al.* 1998; Suarez *et al.* 1998; DiGirolamo & Fox 2006). Because confounding variables cloud the interpretation of these studies, experiments are required to evaluate how abiotic factors contribute to patterns of invasion at the community level. Here, we use a series of experimental approaches to examine the direct and indirect effects of soil moisture in controlling invasion success of Argentine ants. Our focus is timely, given the recognized and growing importance of invasions, the scarcity of comparable experimental studies on animals and the secondary role often assigned to fine-scale variation in the physical environment as a determinant of invasion success.

Materials and methods

EXPERIMENT 1: EFFECTS OF SOIL MOISTURE ON ARGENTINE ANT ABUNDANCE

We first conducted an experiment to test the relationship between soil moisture variation and *L. humile* abundance, because the ability of Argentine ants to displace native ants depends in large part on numerical advantages (Holway 1999; Human & Gordon 1999; Holway & Case 2001). We used drip irrigation to increase soil moisture levels in a 2-ha bare, dry field at the UC San Diego Biology Field Station in August–October 2003. Conspicuous above-ground foraging native ants are absent at this site, but low densities of Argentine

ants occur throughout. We arranged control ($n = 5$) and treatment ($n = 5$) transects in an alternating configuration such that no two transects were closer than 20 m at any point. Each transect measured 3×30 m. Drip irrigation delivered approximately equal amounts of water uniformly along the length of each treatment transect and ran for 4 h day^{-1} , 3 days week^{-1} for 36 days. Control transects were identical to treatment transects, except that irrigation lines carried no water. While irrigation was being used, soil moisture levels along treatment transects ranged from 50% to 80% saturation depending on the time since last watering, whereas control transects averaged $< 5\%$ saturation throughout the experiment. All soil moisture measurements (including those discussed in experiments 2–3) were obtained using an Aquaterr EC-200® soil probe (Aquaterr Instruments Incorporated, Costa Mesa, CA, 93637, USA), which estimates the percentage of saturation of the top 10 cm of soil.

We used two methods to estimate *L. humile* abundance: occurrence in pitfall traps and occupation of experimentally provided nesting sites. We conducted pitfall trap sampling every 18 days for 72 days: 36 days while irrigation was running and for an additional 36 days after irrigation stopped. During each of the five sampling periods, we placed five traps evenly along every transect. Each trap consisted of a 50 mL, plastic centrifuge tube buried with the 2.8 cm rim flush with soil level. All traps contained 30 mL of a dilute saline–detergent solution and were left in the ground for 48 h. To quantify occupation of nesting sites, we partially embedded five bricks ($20.5 \times 9.5 \times 5.5$ cm) in the soil every 5 m along each transect at the start of the study and examined the soil beneath the bricks for nesting activity at 36 days. Nesting sites were considered occupied if queens, brood or both were present in the soil immediately underneath the bricks.

In the analysis of the pitfall trap data we calculated the mean number of ants per trap for each transect and sampling period and used these means as data points. We then used *t*-tests to compare ant abundances between control and treatment transects for three different time-points: the start of the experiment, the end of irrigation (after 36 days) and the end of the experiment (after 72 days). We log-transformed abundance data prior to analysis to correct for unequal variances, and used the Bonferroni correction to adjust α for three comparisons. In the analysis of the nesting site data we used the proportion of sites occupied per transect as data points.

EXPERIMENT 2: ARGENTINE ANT INVASION OF NATIVE ANT COMMUNITIES

To test whether soil moisture limits invasion of Argentine ants into native ant communities, we used drip irrigation to manipulate soil moisture levels across five contact zones between Argentine ants and native ants. Study sites were distributed across a large portion of south-western San Diego County, CA (Fig. 1). The

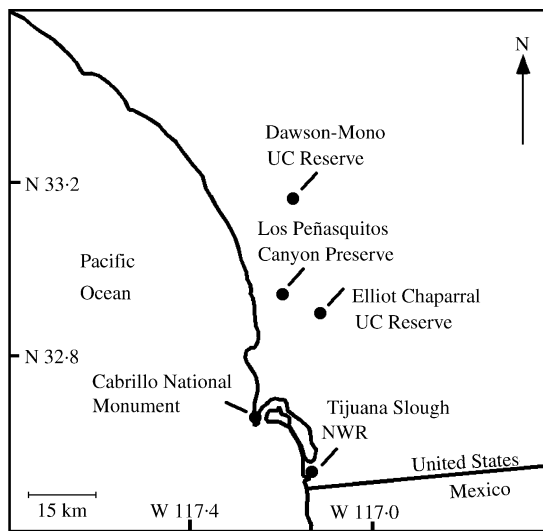


Fig. 1. Map of south-western San Diego County, CA. Filled circles show locations of study sites used in experiment 2.

abrupt contact zones at each site appear to result from pre-existing gradients of soil moisture with Argentine ants occupying relatively moist areas and native ants occurring in drier, exposed areas. Native ants known to be highly susceptible to displacement by Argentine ants (Holway 2005; Ward 1987) were found at or near every contact zone. This pattern indicates that the native ant communities at these sites have not experienced recent invasion by Argentine ants. Sites varied with respect to distance from the coast (Fig. 1) and elevation (10–93 m). Dominant vegetation consisted of a mixture of annual grasses and scrub, with scrub cover ranging from 10% to 60%. At each site we set up single treatment and control transects (each measured 3×100 m), which began in the *L. humile* occupied area and extended 100 m into the area with native ants.

We set the spatial and temporal scale of this experiment to exploit key aspects of the Argentine ant's ecology and the prevailing seasonality of precipitation. Transect length corresponded to empirically determined annual rates of spread for *L. humile* (Holway 1998b). We predicted that spread along irrigated transects would result from spatially continuous budding of colonies established at the base of each transect. Colonies of this species relocate opportunistically the location of nests in response to changing environmental circumstances (Newell & Barber 1913). In addition, all transects intersected multiple colonies of native ants. We monitored transects in May–October 2004; irrigation ran for the first 3 months. This 6-month span includes the seasonal peak in colony growth for Argentine ants in mesic habitats (Markin 1970) as well as the prolonged summer drought in California.

Irrigation and monitoring took place as follows. Along the length of each transect, we extended two parallel drip irrigation lines separated by 1.5 m. As in experiment 1, control lines were identical to treatment lines except that they delivered no water. Treatment

and control transects at each site were separated by at least 50 m. Irrigation lines were joined to a main water line, which was fitted with a timer and flow regulator to ensure that treatment transects received approximately equal amounts of water. We ran irrigation from 0900 to 1000 every day for 3 months. At monthly intervals, we measured the following: (1) the proportion of each transect (divided into 5-m intervals) with nesting Argentine ants; (2) the number of native ant species and their recruitment activity at baits; and (3) soil moisture. We located nests of Argentine ants by following recruitment trails back to nest entrances. We placed paired 1-g tuna baits every 5 m along each transect and recorded the species present after 60 min and whether recruitment (> 10 conspecific workers present) had occurred at each bait. All baiting took place over temperature intervals at which Argentine ants and the common native ant species are known to forage outside their nests (Holway 1999; Holway *et al.* 2002b). We also conducted standardized monthly visual surveys at each transect to detect nesting activity and species that might have been missed during bait transects. Pitfall traps could not be used here because of the risk of excessive mortality resulting from repeated sampling in a spatially restricted area. We measured soil moisture at 20-m intervals along each transect every month. At 3 months, we estimated the percentage of vegetative cover in 1-m^2 quadrats placed at 10-m intervals along each transect.

To compare the extent of net spread by Argentine ants between treatment and control transects, we determined the farthest point at which Argentine ants were nesting along each transect relative to where they nested at the beginning of the study. We used one-sample *t*-tests to determine if differences in net spread between treatment and control transects differed from zero. We made two such comparisons: (1) at 3 months (i.e. at the end of irrigation) and (2) at 6 months (i.e. at the end of the experiment). We used a Bonferroni correction in this analysis to adjust α for two comparisons. We also tested whether native ant activity at baits changed as a result of irrigation. The dependent variable in this analysis was the proportion of baits to which native ants recruited in the uninvaded sections of each transect. For each transect, we averaged native ant activity across all time periods during which irrigation ran and used these time-averaged values as a measure of native ant activity (Holway 1998b). Because data on Argentine ant spread and native ant activity consist of proportions, these data were arcsine square root-transformed prior to analysis.

EXPERIMENT 3: DIRECT VS. INDIRECT EFFECTS OF SOIL MOISTURE

Because irrigation can enhance plant growth, we conducted a third field experiment in which we manipulated both soil moisture and plant cover to test whether hypothesized increases in Argentine ant abundance

resulting from irrigation might be due to elevated soil moisture acting in the absence of plant growth or from some combination of increased soil moisture and augmented plant growth. We conducted this experiment in June–August 2004 at the site used in experiment 1. We established 20 experimental plots (each measuring 5 × 5 m) and assigned individual plots to one of four treatment groups: (1) irrigation and herbicide; (2) irrigation but no herbicide; (3) herbicide but no irrigation; and (4) no irrigation or herbicide. None of the plots had any plant cover when the experiment began. The spatial configuration of treatments was such that no two plots in the same treatment group were adjacent to one another and no two irrigated plots were adjacent to one another. Plots were separated by at least 20 m. As with the previous two experiments, we used drip irrigation to increase soil moisture and placed irrigation lines that delivered no water in dry plots. Soil moisture levels in irrigated and dry plots were similar to those observed in experiment 1. Two weeks after the start of the experiment, when irrigation began to stimulate plant growth, we misted Roundup® (Monsanto) onto half the plots to suppress plant growth. All plots treated with herbicide received a once-only application of 1.1 L of a 2% solution of Roundup® in water.

We used pitfall traps and artificial nesting sites to estimate Argentine ant abundance in each plot. Methods were identical to those used in experiment 1, except as follows. Pitfall trap sampling took place just before irrigation began and again at the end of the experiment (40 days). For these two sampling periods, we placed five traps in each experimental plot in the configuration of the five on a die. At the start of the experiment we placed three bricks in each plot and determined whether these nesting sites were occupied after 40 days. At the end of the experiment, we also estimated the percentage of plant cover in five haphazardly selected 30 × 30 cm quadrats within each plot (avoiding areas where traps or bricks were located). We used plot means as data points for analyses involving plant cover and pitfall trap captures.

Although no harmful effects of Roundup® on ants would be expected (Jackson & Pitre 2004), we conducted a laboratory experiment to examine whether direct exposure to this herbicide induces mortality in Argentine ants. We constructed 18 pairs of experimental colonies; each pair originated from a different location in San Diego County. Collecting sites were all separated by ≥ 5 km. Each experimental colony consisted of three queens and approximately 525 workers. Colonies were reared under standard laboratory conditions (Thomas, Tsutsui & Holway 2005). After 14 days in the laboratory, we misted treatment colonies with 25 mL of a 2% Roundup® solution and misted control colonies with 25 mL of water. Forty days after application of either Roundup® or water, worker survivorship did not differ between treatment (456 ± 12 living workers) (mean ± 1 SE) and control (453 ± 11 living workers) colonies (t -test: $t_{16} = 0.138$, $P = 0.89$).

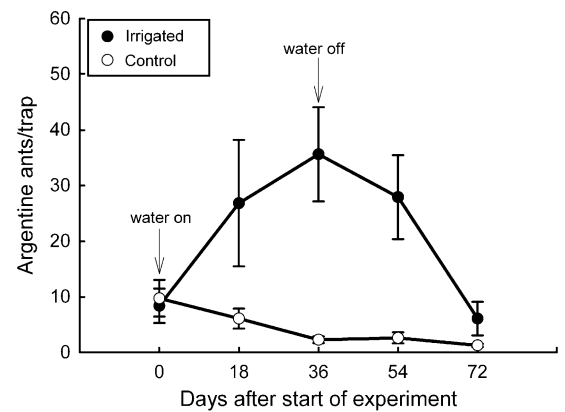


Fig. 2. Results of experiment 1. Mean (± 1 SE) number of Argentine ants in pitfall traps along control ($n = 5$) and irrigated ($n = 5$) transects over the course of 72 days. Control transects received no irrigation.

Results

EXPERIMENT 1: EFFECTS OF SOIL MOISTURE ON ARGENTINE ANT ABUNDANCE

In experimental transects, the local abundance of *L. humile* increased with experimental addition of water and then decreased once irrigation ceased (Fig. 2). Prior to the onset of irrigation, the number of Argentine ants captured in pitfall traps did not differ between control and treatment transects (t -test: $t_8 = 0.378$, $P = 0.72$), but disparities in abundance quickly arose once irrigation started (Fig. 2). Thirty-six days after irrigation began Argentine ants were, on average, 16 times more abundant in pitfall traps along treatment transects than along control transects (t -test: $t_8 = 6.36$, $P < 0.0001$) and had relocated nests extensively along treatment transects [60% of nesting sites occupied (3.0 ± 0.4 bricks plot⁻¹)], whereas no such relocation occurred along control transects (Mann–Whitney U -test: $U = 2.693$, $P < 0.01$). After irrigation stopped, *L. humile* exhibited a symmetrical decrease in abundance, returning to control levels after 72 days (t -test: $t_8 = 2.55$, $P = 0.03$; not significant after Bonferroni correction, $\alpha = 0.017$).

EXPERIMENT 2: ARGENTINE ANT INVASION OF NATIVE ANT COMMUNITIES

Argentine ants invaded native ant communities subject to irrigation, but retreated once irrigation ceased and soil moisture declined (Fig. 3). During the first 3 months of the experiment, *L. humile* advanced steadily along irrigated transects while retreating slightly from control transects. At 3 months, Argentine ants nested in 54% more of each irrigated transect, on average, compared to each control transect (one-sample t -test: $t_4 = 8.01$, $P < 0.01$). During monthly sampling periods at all sites, *L. humile* consistently excluded native ants from baits along sections of transect where it was nesting.

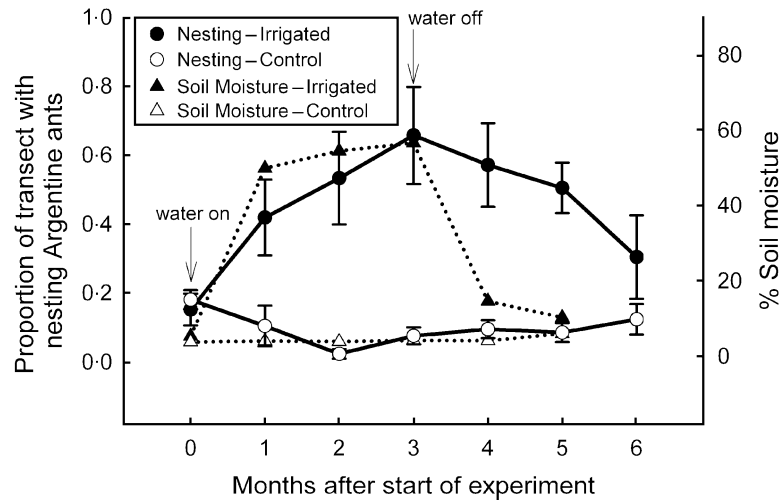


Fig. 3. Results of experiment 2. Mean (± 1 SE) proportion of each control ($n = 5$) and irrigated ($n = 5$) transect that supported nesting Argentine ants over a 6-month period. Also shown are mean measurements of percentage of soil moisture in control and irrigated transects. Control transects received no irrigation.

In the uninvaded sections of transects, irrigation also appeared to stimulate native ant activity. Although native ant activity at baits did not differ between control and treatment transects prior to the onset of irrigation (one-sample t -test: $t_4 = 1.31$, $P = 0.26$), while irrigation was running native ants recruited to more baits along treatment transects than along control transects (one-sample t -test: $t_4 = 2.79$, $P < 0.05$) (see Table 1 for native ant species). Increased native ant activity at baits was insufficient, however, to discourage the spread of Argentine ants (Fig. 3). Once irrigation was shut off, Argentine ant presence on treatment transects declined monotonically. Although the difference between treatment and control transects still exceeded zero at 6 months (one-sample t -test: $t_4 = 6.07$, $P < 0.01$), Argentine ants had abandoned more than half of the transect area that they occupied after 3 months of irrigation (Fig. 3).

Despite heterogeneity in the five study sites with respect to soil type, extent of summer fog, dominant vegetation and degree of exposure, drip irrigation elevated soil moisture to an extent similar to that observed under more homogeneous conditions (e.g. experiment 1). After 3 months of irrigation soil moisture was, on average, an order of magnitude higher along irrigated transects compared to control transects (Fig. 3; $56.6 \pm 4.5\%$ saturation vs. $4.2 \pm 0.6\%$ saturation) (one-sample t -test: $t_4 = 16.8$, $P < 0.0001$). No rain fell during the 6-month experiment, except for one precipitation event in mid-October 2004, just before the end of the study. In part because of this long drought, irrigation stimulated plant growth. Percentage plant cover was almost seven times higher in irrigated transects ($48.5 \pm 11.1\%$) compared to control transects ($7.25 \pm 1.58\%$) (one-sample t -test: $t_4 = 5.55$, $P < 0.01$). Most plant growth consisted of non-woody introduced species (esp.

Table 1. Above-ground foraging native ants observed at baits and during standardized visual surveys at control and treatment transects

	Cabrillo National Monument	Dawson-Mono UC Reserve	Elliot Chaparral UC Reserve	Los Peñasquitos Canyon Preserve	Tijuana Slough National Wildlife Refuge
<i>Camponotus vicinus</i>					X
<i>Crematogaster californica</i>	X		X	X	X
<i>Crematogaster hespera</i>		X			
<i>Dorymyrmex insanus</i>	X	X			X
<i>Forelius mccooki</i>			X		
<i>Formica moki</i>		X			
<i>Messor andrei</i>			X		
<i>Myrmecocystus testaceus</i>	X				
<i>Pheidole hyatti</i>	X				
<i>Pheidole vistana</i>			X	X	
<i>Solenopsis xyloni</i>		X	X	X	X
<i>Tapinoma sessile</i>		X		X	

We deposited voucher specimens in the Bohart Museum of Entomology, University of California, Davis (UCDC).

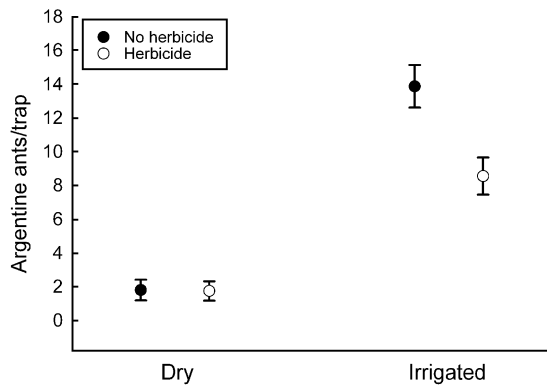


Fig. 4. Results of experiment 3. Mean (± 1 SE) number of Argentine ants in pitfall traps in dry and irrigated experimental plots that were either treated with herbicide or had no herbicide applied; $n = 5$ for each combination of main effects. Argentine ant abundance in pitfalls determined 40 days after start of irrigation.

Carduus sp., *Centaurea solstitialis*, *Chrysanthemum coronarium*).

EXPERIMENT 3: DIRECT VS. INDIRECT EFFECTS OF SOIL MOISTURE

In the factorial experiment in which we manipulated soil moisture and plant cover, irrigation and herbicide affected plant growth in a predictable manner. In irrigated plots the extent of plant growth after 40 days depended strongly on whether plots were treated with herbicide: $78.6 \pm 4.0\%$ cover (no herbicide) vs. $7.8 \pm 4.0\%$ cover (herbicide) (t -test: $t_8 = 9.707$, $P < 0.0001$). Dry plots experienced little plant growth after 40 days: $6.8 \pm 3.1\%$ cover (no herbicide) vs. $0.2 \pm 0.1\%$ cover (herbicide).

Prior to the onset of irrigation, the mean number of Argentine ants captured in pitfall traps did not differ across plots (one-way analysis of variance (ANOVA): $F_{3,16} = 0.78$, $P = 0.52$; 2.3 ± 0.3 ants trap⁻¹ – all plots pooled). After 40 days of irrigation *L. humile* presence depended primarily on whether plots received irrigation, but was also influenced positively by plant growth (Fig. 4). Worker abundance in pitfall traps increased with irrigation (two-way ANOVA: $F_{1,16} = 100.93$, $P < 0.0001$) and decreased with herbicide (two-way ANOVA: $F_{1,16} = 8.22$, $P < 0.05$), but there was a significant interaction between these two factors (two-way ANOVA: $F_{1,16} = 34.54$, $P < 0.05$). Pitfall trap captures were uniformly low in dry plots but were, on average, five to eight times higher in irrigated plots depending on whether herbicide had been applied (Fig. 4). The occupation of experimentally added nesting sites revealed a pattern qualitatively similar to that observed for the pitfall data. In dry plots none of the nesting sites were occupied by Argentine ants after 40 days, whereas in irrigated plots occupation ranged from 33% (1.0 ± 0.0 bricks plot⁻¹) in plots that received herbicide to 47% (1.4 ± 0.2 bricks plot⁻¹) in plots that did not receive herbicide.

Discussion

This study provides a striking experimental demonstration of how community vulnerability to invasion can hinge upon fine-scale variation in environmental conditions. Irrigation led to increases in the local abundance of *L. humile* (Fig. 2) and fuelled the invasion of native ant communities (Fig. 3). Similarly, when we stopped watering Argentine ants declined in abundance (Fig. 2) and retreated from areas that were occupied when added water was present (Fig. 3). The Argentine ant's rapid and strongly positive response to irrigation was probably the combined result of colony reproduction by budding, nest relocation and enhanced colony productivity.

Elevated soil moisture may contribute both directly and indirectly to the spread of *L. humile*. Argentine ant abundance increased in irrigated plots even when plant growth was suppressed (Fig. 4), and there was no indication that Argentine ants were attracted to food resources in these plots. These findings argue for an important and direct role for soil moisture and are consistent with the physiological limitations of *L. humile* (Holway *et al.* 2002b). We stress the importance of soil moisture, but recognize that this variable acts in combination with ground temperature variation to create a 'temperature-humidity envelope' within which workers can remain active without experiencing lethal physiological stress (Hölldobler & Wilson 1990). Indirect effects of soil moisture may also be important and include those caused by plants: further amelioration of the physical environment (e.g. shade) and increased resource availability (e.g. nectar, aggregations of honeydew-producing insects). The latter is of interest, given how strongly Argentine ants respond to the presence of honeydew-producing insects (Newell & Barber 1913). In experiment 3, censuses conducted immediately after we stopped irrigating revealed aphid aggregations in all plots that received added water but no herbicide; we did not detect aphids elsewhere. The presence of aphids provides a probable explanation for why Argentine ant abundance in irrigated plots was 38% higher in plots with plants compared to those treated with herbicide (Fig. 4). Future research might explore further the interactions between added water, plant growth and changes in resource availability resulting from primary production.

A somewhat unexpected result of our study was that native ants also reacted positively to irrigation. As with Argentine ants, native ants may have responded both directly and indirectly to added water. At two sites we recorded the native *Tapinoma sessile* relocating its nests to areas within irrigated transects, perhaps to take advantage of a more favourable physical environment. At another site we observed a harvester ant, *Messor andrei*, forming recruitment trails to irrigated transects, where it fed on seeds produced by weeds that grew in response to the added water. None of the common native ant species observed in our study exhibited

diminished activity in response to irrigation. Despite increased native ant activity, *L. humile* advanced along irrigated transects. Holway (1998b) reported a comparable finding; in that study the rate that Argentine ants spread in riparian corridors correlated positively with native ant presence at baits. These results suggest that competition from native ants may not be a powerful force limiting the spread of *L. humile* in areas that are abiotically suitable from the perspective of this invader.

CONSERVATION IMPLICATIONS

In seasonally dry environments under threat of invasion by Argentine ants, sensible water use practices should be a more prominent consideration of reserve design and management. Our results illustrate, for example, how the interception and diversion of urban run-off could restrict the Argentine ant's spread into natural areas. The common use of drip irrigation in habitat restoration projects should also be evaluated carefully for unintended consequences (e.g. encouraging invasive species). No simple relationship exists between the extent of invasion by Argentine ants and the magnitude of surface water inputs. Our manipulations, however, were modest in terms of volume, duration and spatial scale, yet the abundance of *L. humile* increased or decreased dramatically in response to the presence or absence of added water. These results suggest that even small reductions in urban run-off may act to limit *L. humile* in areas that are otherwise too dry. Although this study focuses on a single invasive species, our results may be of broader practical significance. Because many of the plants and animals that invade mediterranean habitats in southern California require mesic conditions (Alberts *et al.* 1993; Bolger *et al.* 2000), our findings are generally relevant to conservation planning and land management in this biologically rich but compromised region.

RELEVANCE TO LARGE-SCALE MODELLING EFFORTS

As problems caused by invasive species grow in public awareness, ecologists may rely increasingly on geographic information systems (GIS) models and related procedures [e.g. Genetic Algorithm for Rule Set Production (GARP)] to forecast potential range limits of invasive species (Peterson 2003; Arriaga *et al.* 2004; Morrison *et al.* 2004; Roura-Pascual *et al.* 2004). While these approaches have obvious merit, our study highlights the necessity of considering fine-scale environmental heterogeneity. First, we demonstrated that abiotic factors varying over just a few metres can determine the presence or absence of an invasive species in natural communities. Typical GIS models, in contrast, use environmental data that average local variation across much larger spatial scales (e.g. = 1 km²). Moreover, variation in the key abiotic factor from our study was

only partly a function of local climate; both stream flow and urban run-off no doubt contribute importantly to soil moisture variation in our system and are decoupled to varying degrees from local climatic variation. For these reasons, sites that a temperature envelope model might identify as being unsuitable for an invasive species could, none the less, support heavy infestations. Efforts to model potential range limits of invasive species may be improved through a more sophisticated understanding of scaling issues such as those discussed here (Mack 2000).

Conclusions

Our study illustrates how fine-scale variation in the physical environment may act both directly and indirectly to influence community susceptibility to invasion. These results cannot be used to clarify the role of biotic resistance in this system (sites did not differ in the number of native ant species present; Table 1), but results from other studies (Holway 1998b) suggest that the number of native ant species does little to curb the rate at which *L. humile* spreads in natural communities. Given the Argentine ant's extreme competitive dominance, we suspect that if biotic resistance does act in this system, it may be most important in areas where *L. humile* experiences stressful physical conditions. In hot, dry environments, for example, Argentine ants will have reduced foraging activity and high worker mortality, both of which will reduce its competitive strength against native ants better adapted to this range of abiotic variation (Holway *et al.* 2002b). It seems probable that interspecific competition from native ants may combine with abiotic stress to limit the extent to which Argentine ants invade xeric environments (Thomas & Holway 2005). Analogous conclusions have been discussed for plant invasions (Amsberry *et al.* 2000). In a recent meta-analysis, for example, Levine, Adler & Yelenik (2004) found that biotic resistance acted most strongly to reduce the spread of invasive plants in environments that were physiologically stressful to the invader. Taken together, these results generally argue for an improved understanding of how biotic and abiotic factors interact with one another to generate variation in community susceptibility to invasion.

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