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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Predicting Argentine Ant (*Linepithema humile*) Invasions at Multiple Spatial Scales: The  
Relative Importance of Abiotic and Biotic Factors

A Dissertation submitted in partial satisfaction of the requirements for the degree

Doctor of Philosophy

in

Biology

by

Sean B. Menke

Committee in charge:

Professor David Holway, Chair  
Professor Paul Dayton  
Professor Walter Jetz  
Professor Russell Lande  
Professor Kaustuv Roy  
Professor Philip Ward

2007

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The Dissertation of Sean B. Menke is approved, and it is acceptable in quality and form for publication on microfilm:

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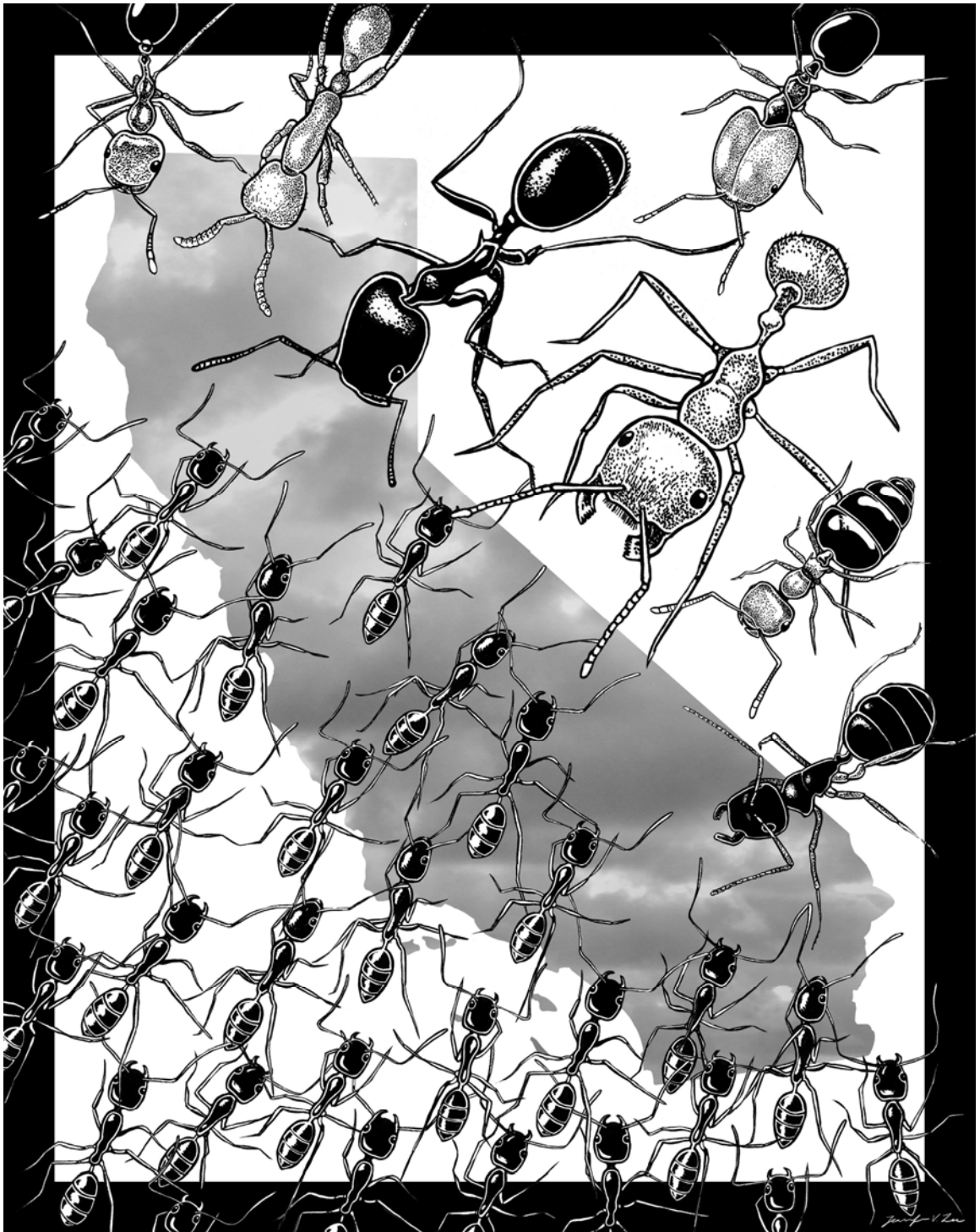
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Chair

University of California, San Diego

2007



Preliminary Illustration: The Creeping Horde, created by Jennifer Zee 2007.

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The dissertation author is the primary researcher and primary author for all chapters. The co-authors aided in experimental design, data collection, or manuscript preparation.

The text of Chapter 1, in full, is a reprint of the material as it appears in Menke, S.B. and D.A. Holway. 2006. Abiotic factors control invasion by Argentine ants at the community scale. *Journal of Animal Ecology*, 75: 368-376.

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## VITA

- 1999 Bachelor of Arts with High Distinction, University of Minnesota – Morris  
Drs. Peter M. Whelan & David M. Hoppe, undergraduate advisors
- 2002 Master of Science in Zoology, University of Oklahoma  
Dr. Laurie J. Vitt, thesis advisor
- 2007 Doctor of Philosophy in Biology, University of California, San Diego  
Dr. David A. Holway, dissertation advisor

## PUBLICATIONS

- Menke, S.B., R.N. Fisher, W. Jetz, D.A. Holway. *In Press*. Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. *Ecology*.
- Menke, S.B. and D.A. Holway. 2006. Abiotic factors control invasion by Argentine ants at the community scale. *Journal of Animal Ecology*, 75:368-376.
- Munroe, T.A. and S.B. Menke. 2004. Two new soleid flatfishes (Pleuronectiformes: Soleidae: *Soleichthys*) from Australian waters, with a re-description of *Soleichthys microcephalus* (Günther). *Records of the Australian Museum*, 56:247-258.
- Menke, S.B. 2003. Lizard community structure across a grassland/creosote shrubland ecotone in the Chihuahuan Desert. *Canadian Journal of Zoology*, 81:1829-1838.
- Anderson, D.R., A.E. Carlson, H.G. Friedrich, M.C. Funk, F. Hammergren, P.A. Joyce III, J.A. Klicka, D.T. Marsden, S.B. Menke, D.W. Preuss, T. Raphael, R.A. Schmidt, and R.M. Zink. 1998. Predation on artificial ground nests at Itasca State Park. *The Loon*, 69:176-183.

ABSTRACT OF THE DISSERTATION

Predicting Argentine Ant (*Linepithema humile*) Invasions at Multiple Spatial Scales: The  
Relative Importance of Abiotic and Biotic Factors

by

Sean B. Menke

Doctor of Philosophy in Biology

University of California, San Diego, 2007

Professor David Holway, Chair

A prominent and unresolved question in ecology concerns why communities differ in their susceptibility to invasion. A complete knowledge of this issue will only result from an understanding of how biotic interactions and abiotic suitability interact with one another and change in importance across spatial scales. Factors important in determining the spread of invasive species at the community scale, such as local environmental conditions and biotic resistance, may be completely different from the factors that determine occurrence at the regional or global scale.

Argentine ants (*Linepithema humile*) are an ecologically and economically damaging species that have been spread globally. Strongly competitive species such as this, are predicted to be more limited by abiotic than by biotic factors, but this prediction has rarely been tested. In Chapter 1 I use manipulative field experiments to demonstrate that abiotic factors (elevated soil moisture levels) increased both the abundance of Argentine ants and their ability to invade native ant communities. Using a factorial field experiment, in Chapter 2 I show that biotic resistance from native ants was unimportant and abiotic factors were preeminent in determining invasion success. Interestingly, an analysis of similar variables at the landscape scale revealed that Argentine ant occurrence was not correlated with precipitation. Through the application of predictive distribution models for Argentine ants across southern California, I demonstrate in Chapter 3 that insufficient sampling of environmental parameters leads to incorrect predictions of their distribution. Also, in multiple variable models, environmental variables differed in their relative importance across regions and spatial grain.

The results of this dissertation are of general 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, this research illustrates surprising complexities with respect to how the abiotic factors limiting invasion success change in importance with spatial scale. Lastly, my results suggest that it is essential to account for the sufficiency of sampling when creating predictive distribution models and that it is important to use variables that are meaningful with respect to the spatial resolution of the data being analyzed.

## Chapter 1

Abiotic factors control invasion by Argentine ants at the community scale

# Abiotic factors control invasion by Argentine ants at the community scale

SEAN B. MENKE<sup>1</sup> and DAVID A. HOLWAY

*Division of Biological Sciences, 9500 Gilman Drive, MC 0116, University of California at San Diego, La Jolla, CA 92093–0116, USA*

## 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).

Correspondence: Sean B. Menke, Section of Ecology, Behaviour and Evolution, Division of Biological Sciences, 9500 Gilman Drive, MC 0116, University of California at San Diego, La Jolla, CA 92093–0116, USA. Tel: (858) 822 6590; Fax: (858) 534 7108; E-mail: smenke@biomail.ucsd.edu

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  $3 \times 30$  m. Drip irrigation delivered approximately equal amounts of water uniformly along the length of each treatment transect and ran for  $4 \text{ h day}^{-1}$ , 3 days  $\text{week}^{-1}$  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  $\alpha$  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



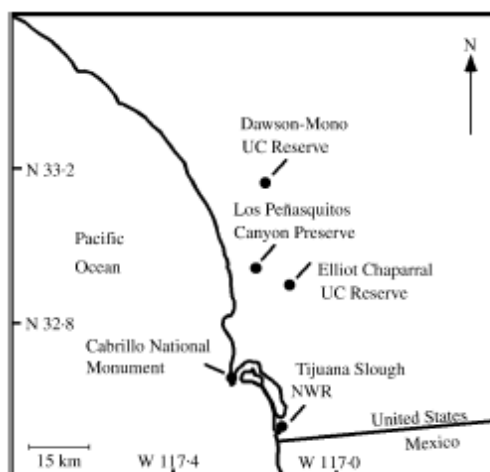


Fig. 1. Map of south-western San Diego County, CA. Filled circles show locations of study sites used in experiment 2.

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  $3 \times 100$  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<sup>2</sup> 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  $\alpha$  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:  $t_{16} = 0.138$ ,  $P = 0.89$ ).

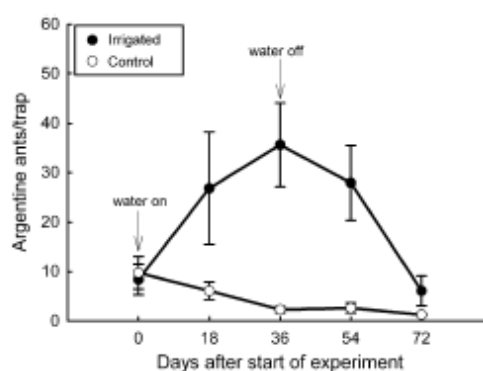


Fig. 2. Results of experiment 1. Mean ( $\pm 1$  SE) number of Argentine ants in pitfall traps along control ( $n = 5$ ) and irrigated ( $n = 5$ ) transects over the course of 72 days. Control transects received no irrigation.

## 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 ( $3.0 \pm 0.4$  bricks plot<sup>-1</sup>)], 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.

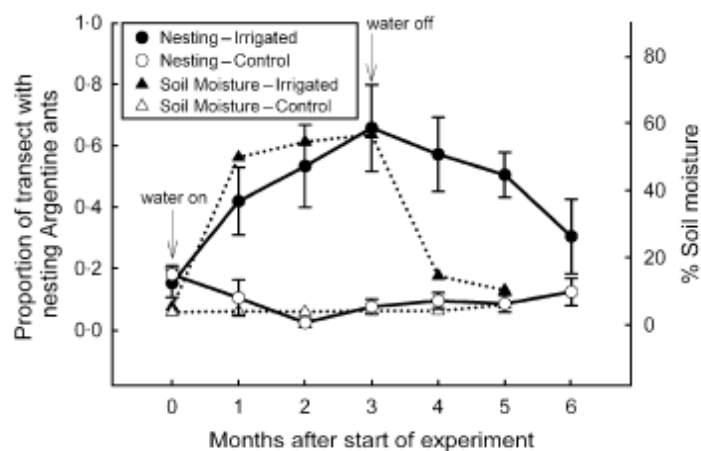


Fig. 3. Results of experiment 2. Mean ( $\pm 1$  SE) proportion of each control ( $n = 5$ ) and irrigated ( $n = 5$ ) transect that supported nesting Argentine ants over a 6-month period. Also shown are mean measurements of percentage of soil moisture in control and irrigated transects. Control transects 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>Formica moki</i>		X			
<i>Messor andrei</i>			X		
<i>Myrmecocystus testaceus</i>	X				
<i>Pheidole hyatti</i>	X				
<i>Pheidole vistanana</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 ( $\pm 1$  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):  $F_{3,16} = 0.78$ ,  $P = 0.52$ ;  $2.3 \pm 0.3$  ants trap<sup>-1</sup> – 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% ( $1.0 \pm 0.0$  bricks plot<sup>-1</sup>) in plots that received herbicide to 47% ( $1.4 \pm 0.2$  bricks plot<sup>-1</sup>) 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 km<sup>2</sup>). 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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## Chapter 2

Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales

**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, 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.

### **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 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) 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).

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 UC Elliot Chaparral Reserve (<http://elliott.ucnrs.org/>). 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. 2-1). Each plot measured 10 x 10 m with a 7 m buffer; 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.

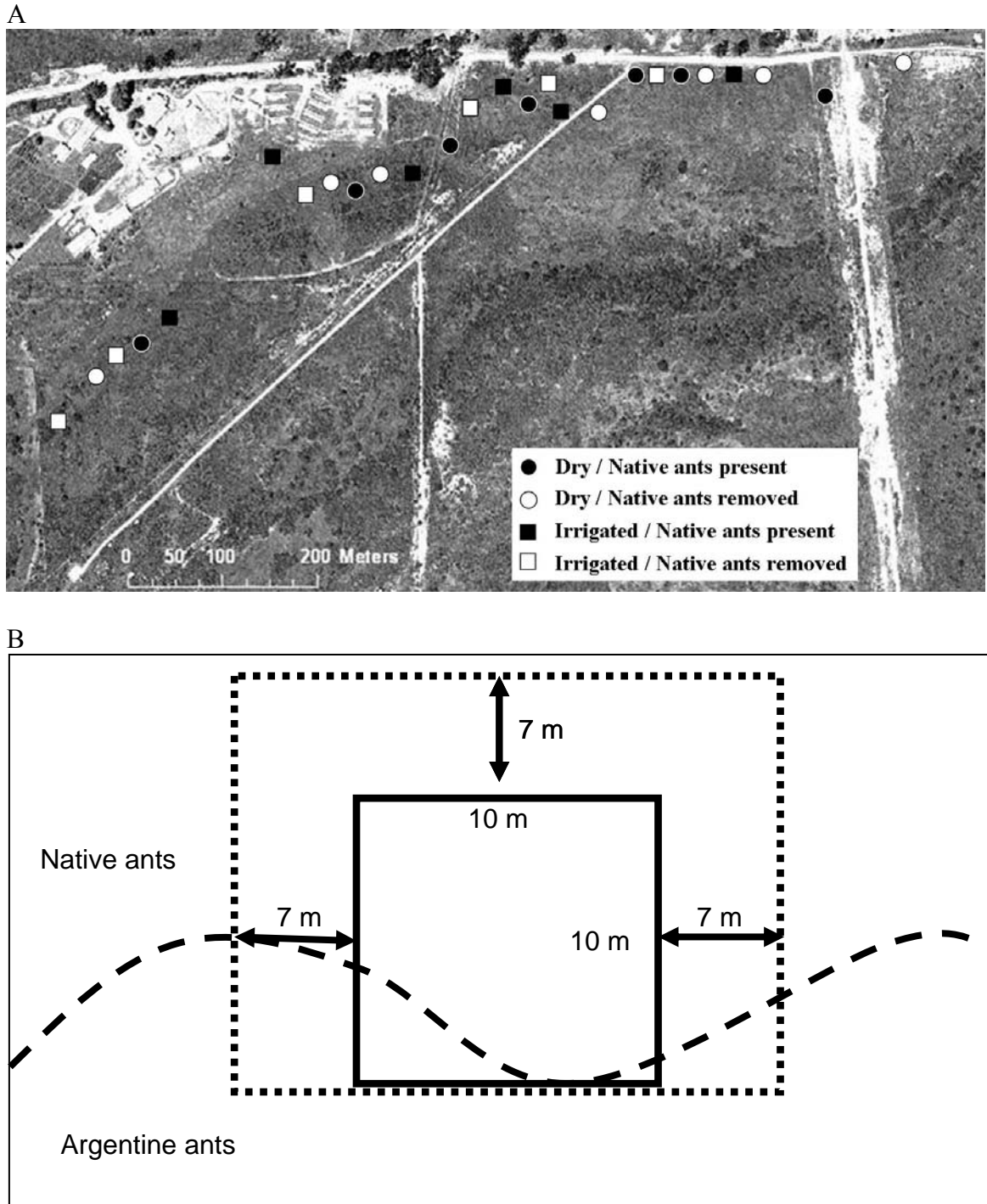


Figure 2 – 1: Design of field experiment I (A) Aerial view showing the location of all 28 plots at the UC Elliot Chaparral Reserve. (B) Configuration of a typical plot, its buffer, and the location of the invasion front.

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 lists for each plot. After we located and marked native ant colonies, we placed Maxforce<sup>®</sup> granular ant bait, 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 not dissolve in water, and degrade within 48 h (Krushelnycky et al. 2004).

To minimize the risk of non-target 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 (non-toxic) 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% at 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 and 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<sup>®</sup>, 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 5 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.

#### *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 UC Elliot Chaparral Reserve. We established 5 pairs of 12 x 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 dataset of 393 sites distributed throughout southern California (Fig. 2-2); 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 4 times, including both summer and winter

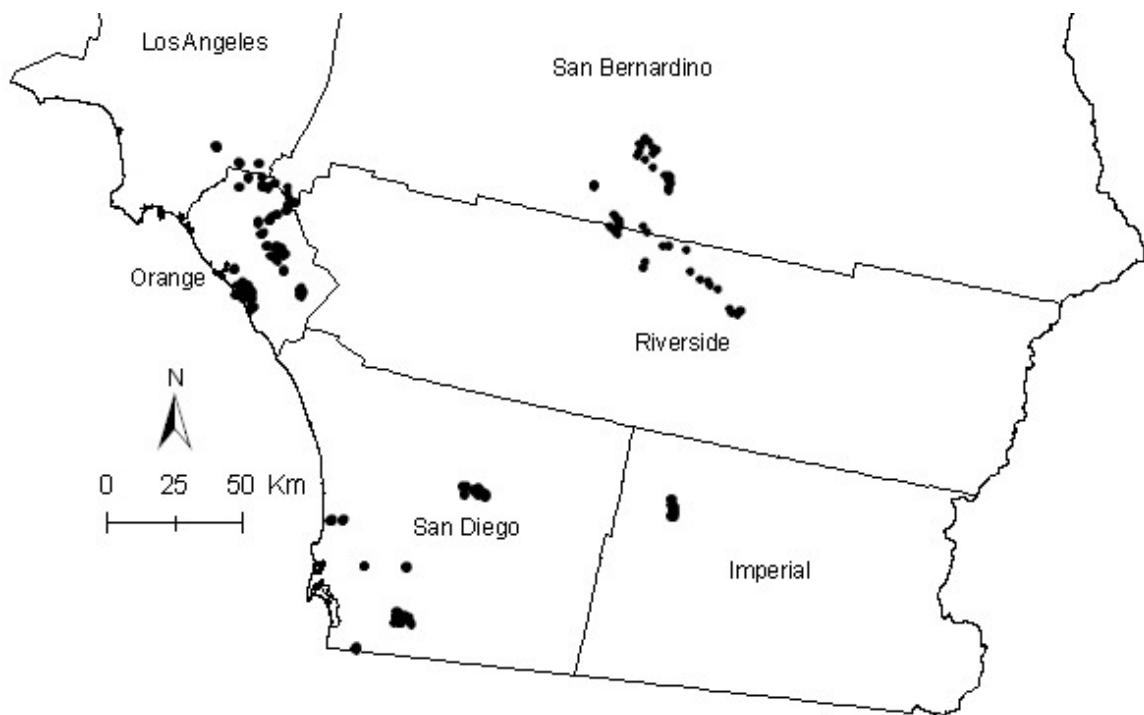


Figure 2 – 2: Locations of pitfall trap arrays (n = 393) in six southern California counties.

sampling in each of 2 years between 1999 and 2005. To standardize sampling effort among sites, we used data for only the first 2 summer and 2 winter sampling periods.

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 inter-correlated) 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 1966-1995 at 1000 m resolution and are described in detail in Franklin et al. (2001). NDVI was averaged from 16 day composites (July 28 – August 12) taken between 2000-2002 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 1998b, Holway 1998a). Therefore, we restricted the native ant portion of our analysis to the 324 sites lacking 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.

## 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 3 months (two-way MANOVA: Wilk's  $\lambda = 0.25$ ,  $p < 0.0001$ ) (Fig. 2-3AB). 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 interaction term was non-significant ( $F_{2, 21} = 2.27$ ,  $p = 0.13$ ), the importance of native ant removal was evident only in irrigated plots (Fig. 2-3AB). 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. 2-3AB) (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

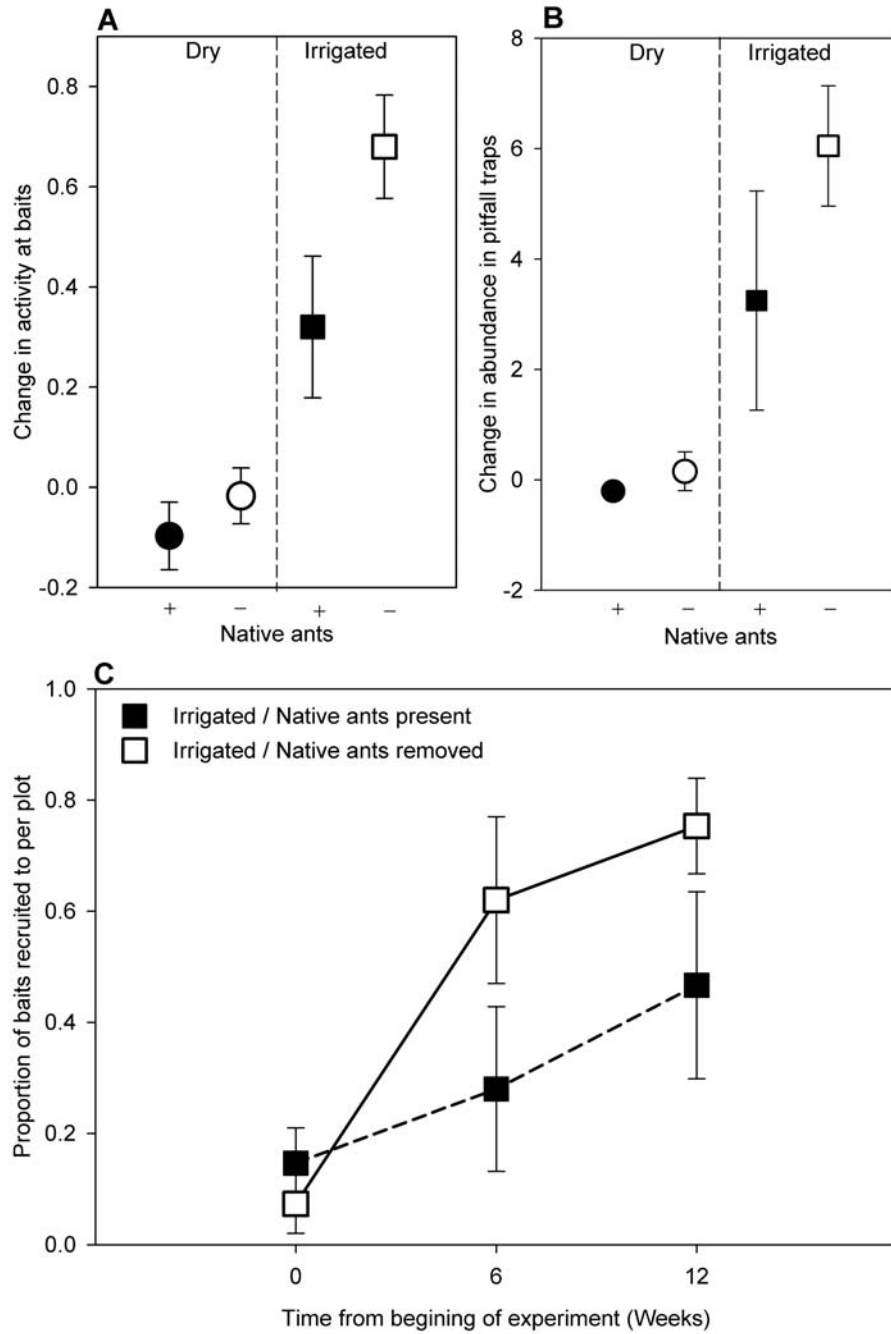


Figure 2 – 3: Results of field experiment I. **(A)** Mean ( $\pm$  SE) change in Argentine ant activity as measured by the proportion of baits recruited to at the beginning and end of the experiment. **(B)** Mean ( $\pm$  SE) change in Argentine ant abundance in pitfall traps at the beginning and end of the experiment. **(C)** Mean ( $\pm$  SE) proportion of baits recruited to by Argentine ants in irrigated plots.

(repeated-measures MANOVA: time  $F_{2,9} = 17.98$ ,  $p < 0.001$ ; time x removal  $F_{2,9} = 4.88$ ,  $p < 0.05$ ) (Fig. 2-3C). Pesticides appeared to have no unintended effects. Argentine ants showed the strongest increases in irrigated plots in which we used Maxforce<sup>®</sup> to remove native ants (Fig. 2-3).

#### *Field experiment II: Native ant response to irrigation*

Native ants exhibited divergent responses to irrigation (Fig. 2-4). *Solenopsis xyloni* increased in abundance nearly 100 fold in pitfall traps after 6 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 2-1). 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 2-1, Fig. 2-5).

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

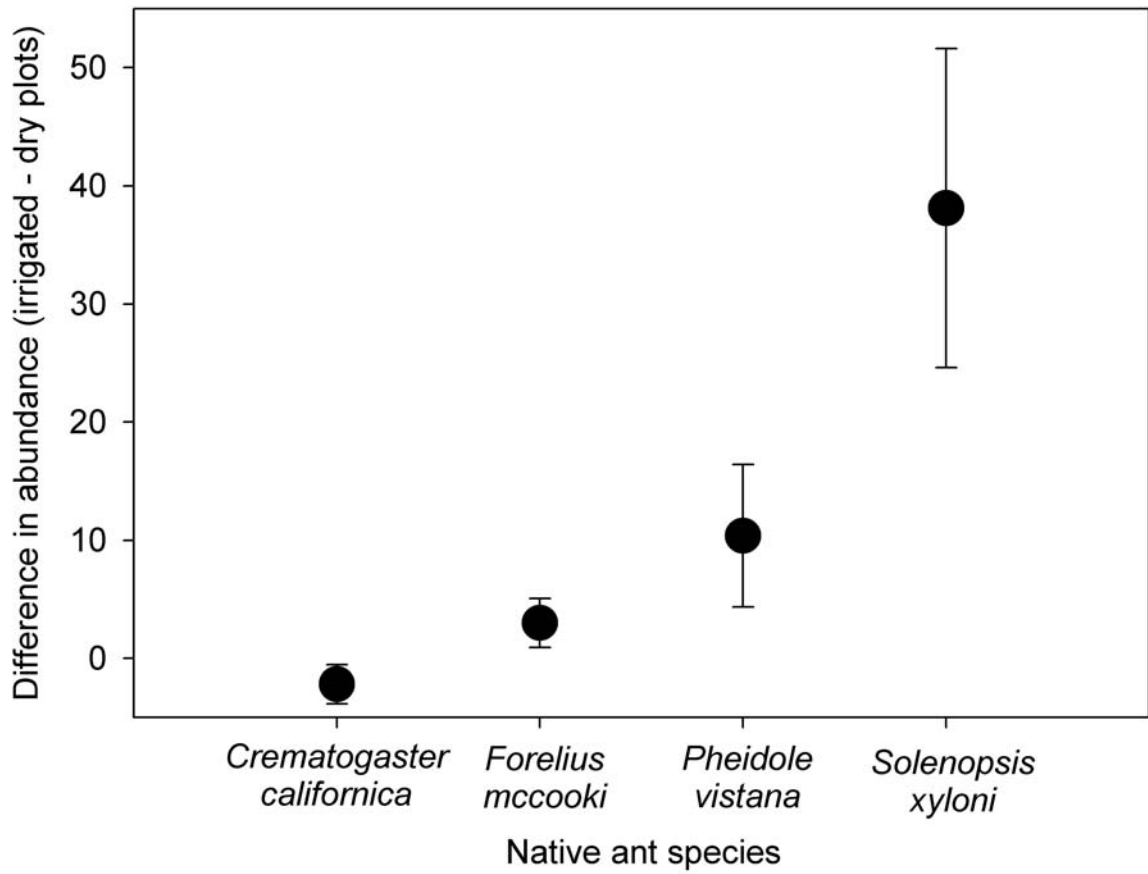


Figure 2 – 4: Results of field experiment II. Mean ( $\pm$  SE) difference in native ant abundance in pitfall traps (irrigated - dry plots) after 6 months of irrigation. Plots used for this experiment all lacked Argentine ants.



Table 2 – 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. In each analysis the two best-fitting one-predictor models (judged by lowest AIC) are highlighted in bold.

Variable	Argentine ant occurrence			Number of native ant species		
	slope	z-value	$\Delta$ AIC	slope	z-value	$\Delta$ AIC
Null			85.62			78.8
Maximum temperature	-0.264	-4.803 ****	52.45	-0.034	-7.107 ****	23.4
Minimum temperature	<b>1.087</b>	<b>5.212 ****</b>	<b>5.21</b>	-0.015	-2.141 **	72.4
NDVI	0.217	4.267 ****	67.47	<b>0.005</b>	<b>7.980 ****</b>	<b>17.4</b>
Precipitation	0.029	2.505 *	81.15	<b>0.014</b>	<b>9.011 ****</b>	<b>0.0</b>
Distance to perennial stream	-0.324	-3.848 ****	72.79	-0.002	-0.162	80.8
Distance to urban area	<b>-0.941</b>	<b>-7.881 ****</b>	<b>0.00</b>	-0.022	-1.380	78.9

$\Delta$ AIC is the difference of each model from the strongest model in the analysis. Significance of regression models is marked with asterisks (\* < 0.05, \*\* < 0.01, \*\*\* < 0.001, \*\*\*\* < 0.0001).

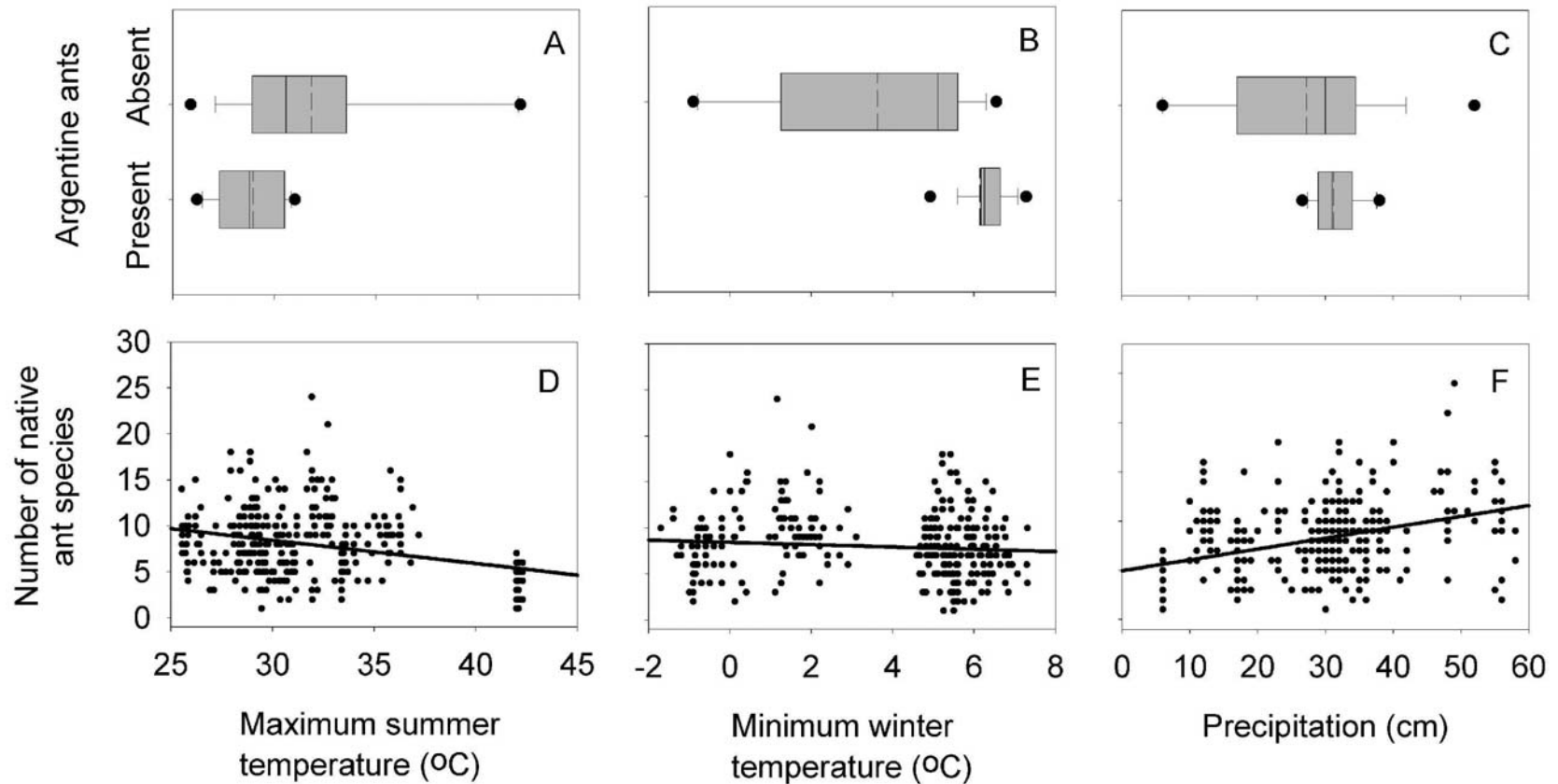


Figure 2 – 5: Results of landscape-level analyses showing how Argentine ant presence and native ant diversity relate to maximum summer temperature, minimum winter temperature, and precipitation. (**A – C**) Argentine ant presence and absence at 394 sites. Standard box plots show the 25th, median, and 75th percentiles (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 2-1.

increasing NDVI (a measure of the greenness of vegetation) (Table 2-1, Fig. 2-5). High maximum summer temperatures significantly depressed the number of native ant species. Areas with higher minimum winter temperatures had fewer native ant species (Fig. 2-5), in contrast to Argentine ants, which require warm winter temperatures. Proximity to urban environments had no detectable effect on the number of native ant species (Table 2-1).

#### *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 & 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 & 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

Table 2 – 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. Biotic factors were not included at the landscape scale because as Argentine ants spread, they displace native ants.

	<b>Community scale</b>		<b>Landscape scale</b>		
	Abiotic factors	Biotic factors	Abiotic factors		
	<u>Soil moisture</u>	<u>Competition from ants</u>	<u>Max temp</u>	<u>Min temp</u>	<u>Precip</u>
Argentine ants	+	0	-	+	0
Native ants	0 / +	-	-	0	+

+ = positive response, - = negative response, 0 = no response.

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. 2-3AB). At irrigated sites, in contrast, interspecific competition from native ants slowed but did not prevent the spread of Argentine ants (Fig. 2-3C). 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. 2-4). Interestingly, *S. xyloni*, like the Argentine ant, can act like a behaviorally dominant species (*pers. obs.*), 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. 2-4) presumably reflects species-level differences in physiological tolerances (Schilman et al. 2005, 2007). While Menke & 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 2-2). Interestingly, precipitation, which best predicted the number of native ant species, did not explain patterns of Argentine ant 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. 2-5). 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 2-2). 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 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. 2-3C). 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 (Table 2-1, 2-2).

### *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 (Table 2-1) - variables often used to delimit large-scale patterns of distribution (Peterson 2003). 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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## Chapter 3

Effects of sampling, regional comparisons, and scale on the accuracy and correlates of species distribution models: a test with Argentine ants

**Abstract.** Predictive modeling of species distributions is a rapidly proliferating research area, especially in studies relating to climate change and the spread of introduced species. Although these modeling approaches have clear merit, important pitfalls exist that can bias predictions. These problems include the following: models that use presence only data, insufficient or unrepresentative sampling of environmental parameter space, models that are not tested with independent data sets or that predict distributions beyond known parameter space, and the use of variables at the incorrect spatial resolution. To quantify the extent to which these problems can potentially bias model predictions, we use actual presence and absence data for Argentine ants (*Linepithema humile*) independently collected in two adjacent regions of southern California to examine 1) effects of insufficient sampling of environmental variables, 2) the generality of landscape-scale models created in different regions, and 3) the importance of predictive variables across different levels of spatial resolution. First, we demonstrate that insufficient sampling of environmental parameter space incorrectly predicts species distributions when models are applied to adjacent regions. Second, despite extensive sampling and the geographical proximity of the two regions in our study, prominent differences existed with respect to the univariate predictors of Argentine ant occurrence. Models using data that sufficiently sampled the environmental parameter space resulted in the best and most general models. Lastly, in multiple variable models, environmental variables differed in their relative importance across spatial grain. For example, the best models at the finest spatial grain did not overlap with those at the coarsest spatial grain. Taken together, our results suggest that it is essential to account for the sufficiency of sampling when creating predictive distribution models and that care should be used when projecting these models into novel

environments. Finally, it is important to use variables that are meaningful with respect to the spatial resolution of the data being analyzed.

### **Introduction**

Predictive models of species distributions will increasingly be used as a forecasting tool as climate change and species introductions continue to rearrange the earth's biota. Although efforts to predict distributional changes in the face of climate change and other sources of environmental variation are now common (Guisan and Zimmermann 2000, Peterson 2003, Elith et al. 2006), current predictive modeling approaches are subject to a number of limitations (Fielding and Bell 1997, Pearson and Dawson 2003). One such limitation concerns the inability to test model predictions with independent data sets (Araujo and Rahbek 2006, Hawkins et al. 2007). Moreover, predictive models cannot account for the creation of novel climates nor do they consider how species will respond to the loss of existing climates (Williams et al. 2007). Lastly, biotic interactions may mitigate the effects of environmental change on patterns of species occurrence (Suttle et al. 2007).

A current focus of species distribution models (SDMs) centers on predicting the occurrence of species introduced into new environments by humans (Peterson 2003). Two challenges exist in modeling the distribution of introduced species. First, biotic interactions may influence where species will invade (Levine and D'Antonio 1999, Guisan and Zimmermann 2000, Peterson 2003, Bruno et al. 2004). Second, obtaining accurate absence data for species that are actively expanding their ranges remains problematic (Guisan and Thuiller 2005). However, modeling efforts that involve introduced species have the advantage that multiple invaded regions and the native range

can all be used to independently test model predictions (Fitzpatrick et al. 2006, Roura-Pascual et al. 2006). Efforts to model the distribution of introduced species are conducted on a wide range of organisms and a over a diversity of spatial scales (Korzukhin et al. 2001, Morrison et al. 2004, Rew et al. 2005, Munoz and Real 2006).

Accurate predictions of species distributions hinge on adequately sampling environmental variation. Because geographical regions differ in both their range of environmental variation and how this variation is distributed, unrealistic extrapolations may result when the environmental profile of the region into which predictions are made does not match that of the sampling region (Fig. 3-1A). Problems may also arise when the distribution of environmental variation is insufficiently sampled. Sampling may be incomplete when intervals of environmental variation are not included in the sampled distribution (Fig. 3-1B) - for example, as a result of small sample size. Biased sampling may occur when particular ranges of environmental variation are either under or over sampled relative to their frequency (Fig. 3-1B). With respect to issues of sampling, most studies investigate how sample size affects model accuracy (Stockwell and Peterson 2002, McPherson et al. 2004), rather than the sampling pitfalls summarized in Figure 3-1A&B (but see Kadmon et al. 2003). Another sampling problem concerns environmental data that are collected at one spatial scale and then used to predict species occurrence at a different spatial scale (McPherson et al. 2006). Prediction errors may also result when environmental variables change in importance at different spatial grains (Luoto et al. 2007, Whittingham et al. 2007).

To quantify the extent to which these problems may bias predictions of SDMs, we use actual presence and absence data for Argentine ants (*Linepithema humile*) to examine

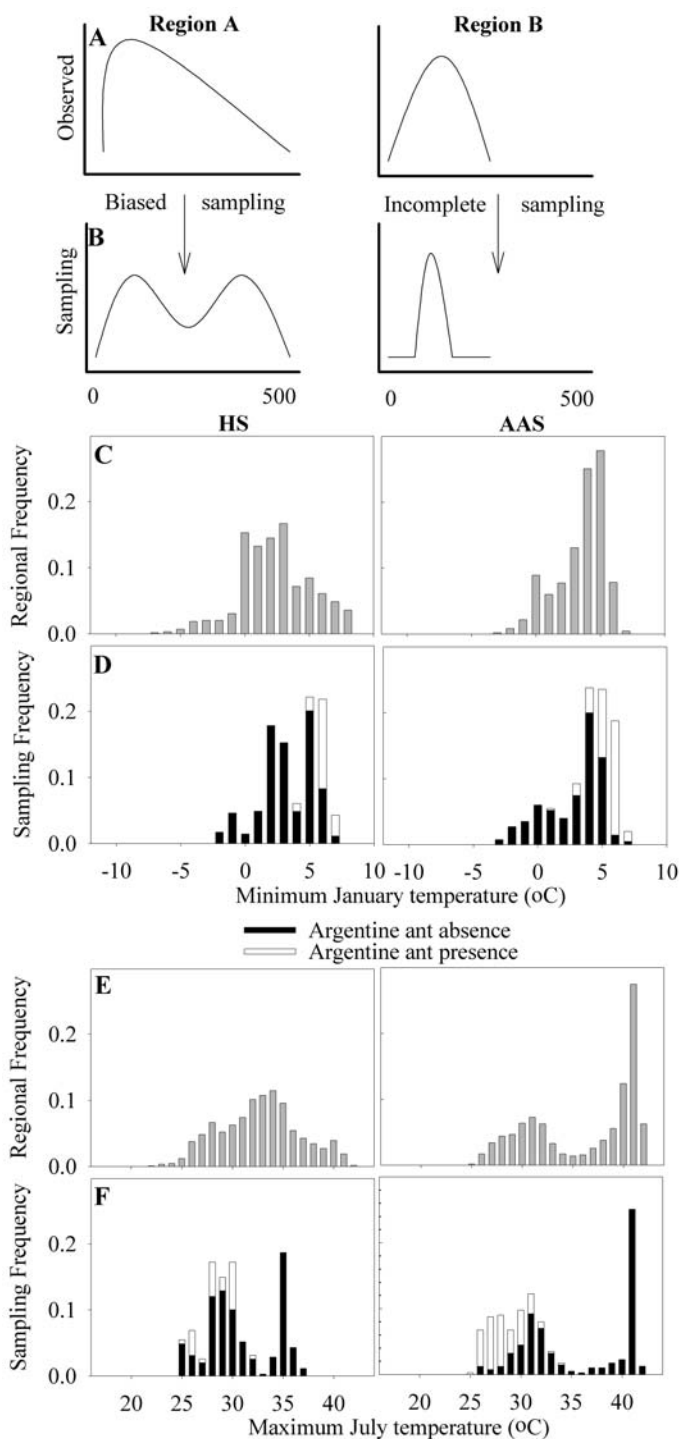


Figure 3 – 1: Conceptual diagram of hypothetical issues that result from (A) disparities in environmental variation between regions, and (B) insufficient sampling. Empirical distributions of (C) region wide values and (D) sample points for minimum January temperature (°C). Empirical distributions of (E) region wide values and (F) sample points for maximum July temperature (°C).

the following: 1) the effect of insufficient sampling of environmental variation on model predictions, 2) the generality of landscape-scale models created in different regions, and 3) how the importance of specific predictive variables changes across different levels of spatial resolution. Other studies have addressed related questions including performance comparisons of different modeling techniques (Elith et al. 2006), the role of sample size (Stockwell and Peterson 2002, McPherson et al. 2004), and the effect of spatial grain (McPherson et al. 2006, Guisan et al. 2007). These studies are often constrained by the use of presence only data (Kadmon et al. 2003) or the use of pseudo-absence data (Fitzpatrick et al. 2006, Roura-Pascual et al. 2006). Unlike these previous studies we use true absence data to simultaneously and comprehensively analyze how sampling, scale, and regional disparities affect the predictions of species distribution models for a widespread invader. Our study is unique in its simultaneous treatment of these three factors. An additional advantage of our system is that biotic resistance from native species appears to be of weak importance in influencing where introduced populations of Argentine ants occur (Holway 1998b, Menke et al. *In Press*). Taken together, our analyses illustrate how violations in model assumptions can lead to serious biases in predicted species distributions.

## **Methods**

### *Study system*

The Argentine ant is a widespread, abundant, and ecologically damaging invasive species (Holway et al. 2002a). Native to northern Argentina and surrounding regions (Tsumsui 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). Although common in urban and agricultural environments, *L. humile* readily invades natural habitats (Suarez et al. 2001), where it displaces above ground foraging native ant species (Ward 1987, Human and Gordon 1996, Holway 1998a, Suarez et al. 1998). 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). In seasonally dry California, Argentine ants have been present for approximately a century (Woodworth 1908), but are restricted to areas with suitable levels of soil moisture, especially riparian corridors and human-modified environments (Ward 1987, Holway 2005, Menke and Holway 2006).

Attempts to predict the distribution of Argentine ants have been the focus of several recent studies. Roura-Pascual et al. (2004) used ecological niche modeling to predict the global distribution of *L. humile*. Using native range presence data, these authors applied the Genetic Algorithm for Rule-set Prediction (GARP) to generate predictions about where Argentine ants would occur under different climate change scenarios. Building on the results of their 2004 study, Roura-Pascual and colleagues again used GARP to assess model generality in different invaded regions (Roura-Pascual et al. 2006). Hartley et al. (2006) adopted a more mechanistic approach in that they used physiological tolerances of the Argentine ant to develop a bioclimatic envelope model. Although their predicted global distribution of *L. humile* overlapped with that of Roura-Pascual et al. (2004), the model produced by Hartley and colleagues yielded a broader potential distribution on every major continent. Hartley and Lester (2003) and

Krushelnycky et al. (2005) created predictive models at a regional scale based on temperature-dependent colony growth in New Zealand and Hawaii respectively. In this study, we use actual presence and absence data collected in two different regions to build on this body of previous work.

### *Sampling regions*

We focus our efforts on the three bioregions of southern California (Fig. 3-2A). The south coast bioregion has a mediterranean climate and a large urban population. Inland from the south coast bioregion, the Mojave and Colorado desert bioregions differ from one another primarily with respect to the Colorado desert's hotter summer temperatures, milder winter temperatures, and larger areas devoted to agriculture. To assess how differences in sampling effort affect model generality, we analyzed two independent datasets collected in adjacent regions of southern California (Fig. 3-2A). The first dataset was collected in the herpetological survey region (HS); this region is 25,550 km<sup>2</sup> and includes all of Orange County, and parts of Los Angeles, Riverside, and San Bernardino Counties (Fig. 3-2B). This sampling effort was initially designed by the US Geological Survey (USGS) to monitor reptiles and amphibians in natural areas with differing levels of fragmentation throughout southern California (Fisher et al. 2002); an ant sampling protocol was later added to these existing sites (Laakkonen et al. 2001). The second dataset was collected in the Argentine ant survey region (AAS), which is 22,584 km<sup>2</sup> and includes all of San Diego and Imperial Counties (Fig. 3-2C). This dataset was tailored specifically to known patterns of Argentine ant distribution in southern California.



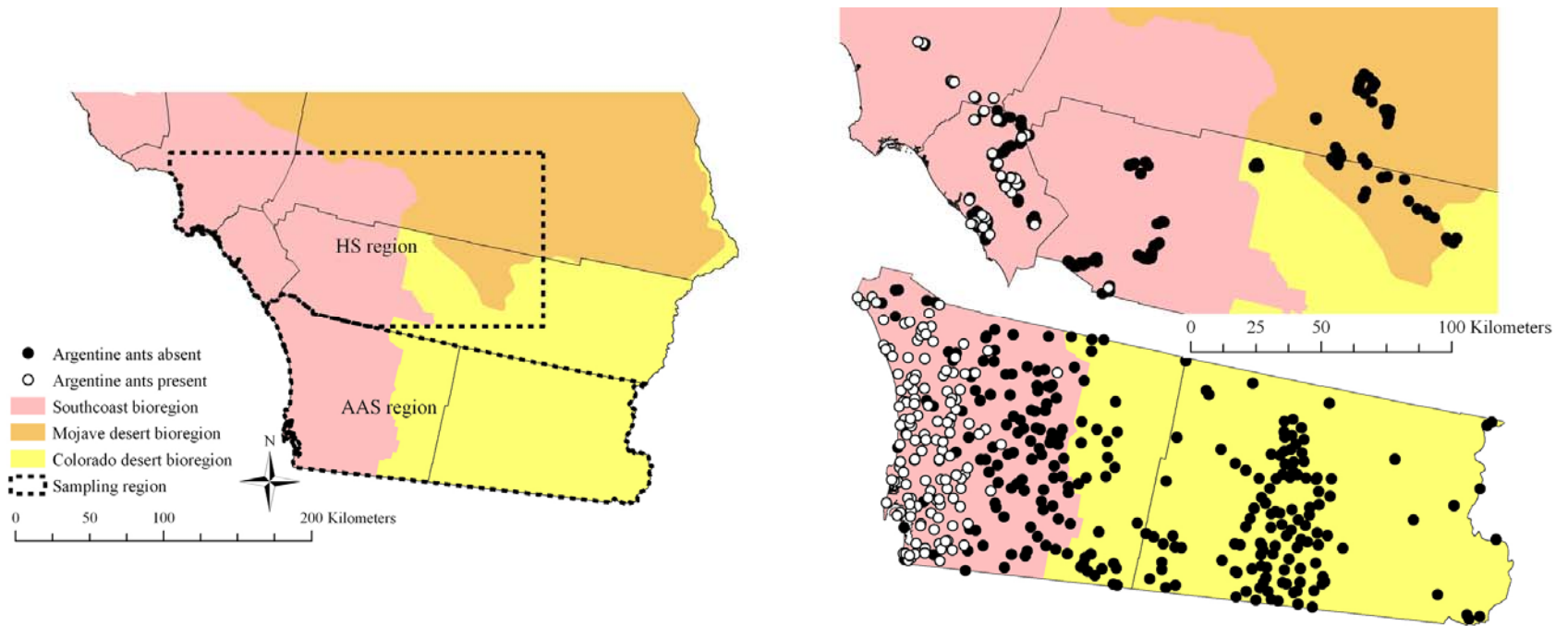


Figure 3 – 2: (A) Map of southern California showing our two study regions (HS and AAS). Presence and absence locations of Argentine ants in (B) the HS region and (C) the AAS region.

Ants were sampled differently in the two regions, but both sampling protocols yield accurate presence / absence data for *L. humile*. The HS region included 348 sites; 69 of which were invaded by Argentine ants (Fig. 3-2B). At each HS site, ants were sampled using five pitfall traps placed in the ground in the configuration of the five on a die, with corner traps separated by 40 m. All HS sites that were classified as *L. humile* absences were sampled a minimum of 4 times, including both summer and winter sampling in each of two years between 1999 and 2005.

The AAS region included 399 sites, 139 of which were invaded by Argentine ants. Sampling points in this region were randomly assigned to 8 land-cover classifications (Agriculture, Barren, Conifer, Desert, Hardwood, Herbaceous, Shrub, and Urban). The number of sampling locations in each land-cover area was based on the extent of each land-cover type and by the probability of *L. humile* occurrence. These probabilities were empirically derived from patterns of Argentine ant occurrence in each land-cover type from the pitfall trap results in the HS region. Land-cover types were then subdivided into 30 vegetation categories, and sampling points were assigned based on the proportion of the land-cover type occupied by each vegetation category. Sampling points were then randomly assigned locations using Hawth's Analysis Tools for ArcGIS™. This distribution of sampling points was specifically designed to sample the full habitat and climate heterogeneity of the AAS region. To determine whether or not Argentine ants were present at a site, we used tuna baits placed every 5 m along two 50 m transects in the shape of a cross and visual surveys (e.g., inspection of tree trunks, open bare ground, potential nesting sites). Each site was baited and searched for 45 minutes or until Argentine ants were positively identified; surveys took place in the spring and early

summer during times of the day when *L. humile* is known to be active. Because Argentine ants forage diurnally throughout the year and displace nearly all above ground foraging native ant species, it is possible to unambiguously determine whether or not *L. humile* is present (Ward 1987, Holway 1995).

#### *Environmental predictor layers*

Potential predictor variables of Argentine ant occurrence include a set of 13 environmental layers. Climate variables included aspect, elevation, maximum July temperature (maxT), minimum January temperature (minT), average annual rainfall (ppt), and normalized difference vegetation index (NDVI). Aspect and elevation were derived from the 30 m California digital elevation model (DEM). MaxT, minT, and ppt are averages from 1966-1995 at 1000 m resolution and are described in detail in Franklin et al. (2001). NDVI was averaged from 16 day composites (July 28 – August 12) recorded between 2000-2002 by the National Oceanic and Atmospheric Administration's advanced high resolution radiometer satellite series (resolution: 250 m). Habitat variables included land-cover type (veg), soil hydrogroup (soil), distance to intermittent water body (Iwater), and distance to perennial water body (Pwater). Veg is based on the life\_form category in the Multi-source Land Cover Data (v02\_2) (resolution: 100 m) compiled by the California Department of Forestry and Fire Protection. Soil is based on the U.S. Department of Agriculture, Soil Conservation Service (STATSGO) at 2.5 km resolution. Iwater and Pwater were derived from high resolution datasets in the National Hydrographic Database. Human impact variables are distance to agricultural area, distance to highways, and distance to urban area. Distance to agriculture and urban areas were determined using the Multi-source Land Cover Data (v02\_2), and distance to

highways calculated using the US Census Bureau Tiger 2k (version: June 7, 2002) data layer. Distance to nearest highway or urban area was combined into one variable to approximate human alterations to the environment (human). These environmental layers were selected from a range of possible (and often inter-correlated) variables because of their common usage in bioclimate and niche models and their putative importance in influencing Argentine ant occurrence (Holway 1998b, Hartley et al. 2006, Menke and Holway 2006, Roura-Pascual et al. 2006, Menke et al. *In Press*). All variables were resampled from their native resolution to 100 m resolution and natural log + 1 transformed except for minT which was natural log + 10 transformed for analyses. Aspect, elevation, and soil were excluded from the final analyses due to their poor predictive ability or co-linearity with other predictors.

#### *Univariate models*

We first identified the important predictors of Argentine ant occurrence in the HS and AAS regions as in Menke et al. (*In Press*). For each of the nine environmental predictors we performed univariate logistic regression (GLM, binary with logit link). For every environmental predictor we randomly selected two thirds of the presences and absences as training data. The predictive ability of each univariate model in each region was then quantified with the remaining third of the data points using the area under the curve (AUC) of receiver operating characteristic (ROC) plots (Cumming 2000). This analysis was iterated 30 times and the average results are reported. ROC plots assess model performance by plotting sensitivity (proportion of presences correctly predicted) versus 1 – specificity (proportion of absences correctly predicted). AUC is a threshold-independent measure of model accuracy ranging in value from 0 to 1, with values larger

than 0.5 indicating performance better than random (Swets 1988). Univariate models with AUC values above 0.75 were considered to be strong predictors of Argentine ant occurrence, and those environmental predictors were used in further analyses.

#### *Model generality across regions*

Using the univariate GLM approach, it was unclear whether the predictors that explain *L. humile* occurrence are the same in each region and how they should be combined to create the best overall model. This uncertainty results from predictors possessing similar degrees of explanatory power and inter-correlations among predictors. We therefore used an additional, alternative approach to test how the relative fits of models containing all possible combinations of predictors varied between the two regions. To do this we used a model averaging technique described by Burnham & Anderson (2002). This approach compares the relative fits of a suite of candidate models using Akaike's Information Criterion (AIC) (Stephens et al. 2005). The absolute size of the AIC is unimportant; instead differences in AIC values among models indicate the relative support for the different models. We calculated an "Akaike weight",  $w_i$ , for each model. For a set of models, the  $w_i$  sum to 1 and have a probabilistic interpretation: of these models,  $w_i$  is the probability that model  $i$  would be selected as the best fitting model if the data were collected again under identical circumstances. Our confidence set is the smallest subset of candidate models for which the  $w_i$  sum to 0.95. This set represents a set of models for which there is 95% probability that the set would contain the best approximating model to the true model were the data collected again under the same circumstances.

To determine how well distributional data collected in one region predict occurrence elsewhere, we created 95% confidence sets using a modeling approach that compares the relative fits of models containing all combinations of predictors for each region. We calculated separate confidence sets for the HS and AAS regions. We included seven environmental predictors that had either an AUC value greater than 0.75 in at least one region or that was a predictor commonly used in bioclimatic models. Interaction terms were not included in the creation of the confidence sets because all of the variables were log transformed; this transformation improved linearity of the predictors. The performance of the best two models from the confidence set for each region was tested in the opposite region using AUC.

#### *Model generality across spatial grain*

To determine how the coarseness of environmental layers affects their importance as predictor variables, we re-sampled the seven environmental layers (100 m resolution) used in the regional analysis at three increasingly coarser resolutions (1 km, 5 km, 10 km). All analyses were conducted on a dataset that combined the two regional datasets. At coarser spatial grains, cells with multiple samples were assigned a “present” value if any of the sub-samples included a presence. The importance of individual environmental variables at each spatial grain was calculated using AUC on the univariate logistic regressions. Confidence sets were then created for each spatial grain using all combinations of the seven environmental predictors.

## **Results**

### *Environmental variation and sufficiency of sampling*

Although the two regions in this study are adjacent and extend from the coast to inland deserts, their environmental distributions differ. Compared to the AAS region, the HS region has colder winter temperatures (Fig. 3-1C). The distributions of maximum summer temperatures also appear to differ between the two regions. While the range of summer temperatures is approximately similar, the AAS region exhibits strong bimodality with the desert portions of this region frequently experiencing maximum summer temperatures greater than 40°C (Fig. 3-1E).

The thoroughness of data collection can magnify prediction errors concerning the limits of species ranges, especially when regions differ in their distributions of climate variables (Fig. 3-1D, F). Based on the sampled environmental variation in the two regions in our study, insufficient sampling may be a concern in the HS region. For example, with respect to minT, the sampling distribution differed from the environmental distribution in the HS region (Kolmogorov-Smirnov test:  $D = 0.47$ ,  $p = 0.03$ ) but not the AAS region (K-S test:  $D = 0.11$ ,  $p > 0.5$ ). This difference appears to result in large part from the HS sample failing to include extreme temperature values (Fig. 3-1C&D). A similar trend appears evident with respect to maxT. The sampling regime in the HS region failed to sample temperatures above 37°C, while the sampling in the AAS region was conducted across the full extent of maxT (Fig. 3-1E& F). While the sampling distributions were not significantly different from the environmental distribution, the AAS data (K-S test:  $D = 0.17$ ,  $p > 0.5$ ) appeared to sample the environmental variation better compared to the HS data (K-S test:  $D = 0.31$ ,  $p = 0.12$ ).

Differences in the distributions and sampling of environmental variables between regions, as discussed above, can lead to large errors in predicted ranges (Fig. 3-3). For

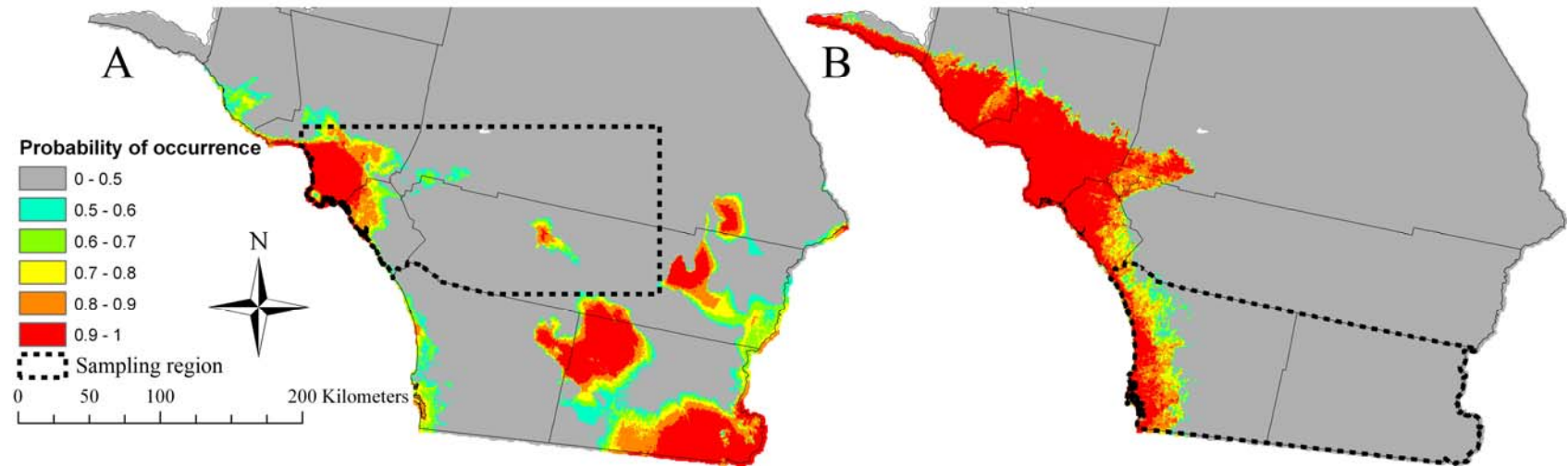


Figure 3 – 3: Predicted probability of Argentine ant occurrence based a climate envelope model ( $y \sim \max T + \min T + \text{NDVI} + \text{ppt}$ ) using (A) the HS and (B) AAS data.



example, a bioclimate model for southern California that is based on the HS data and that is composed of four commonly used climate variables (maxT, minT, NDVI, & ppt) both over and under predicts *L. humile* occurrence. The model predicts Argentine ant occurrence in multiple desert locations where they do not occur (Fig. 3-2B&C, Fig. 3-3A) but fails to predict their presence along much of the coast where *L. humile* is widespread and abundant (Fig. 3-2B&C, Fig. 3-3A). In contrast, when the same model was created with the AAS data, the resulting predictions closely match the known distribution of Argentine ants in southern California (Fig. 3-2B&C, Fig. 3-3B).

#### *Univariate models*

Despite extensive sampling and despite the geographical proximity of the HS and AAS regions, the univariate predictors of Argentine ant occurrence differed between regions (Table 3-1). Although minT, veg, and human were all useful univariate predictors in both regions, each region also included univariate predictors unique to that region. While maxT was the best predictor in the AAS region (AUC = 0.91), it failed to predict Argentine ant occurrence in the HS region (AUC = 0.69). Conversely, Pwater was a strong predictor in the HS region (AUC = 0.77), but performed not much better than random in the AAS region (AUC = 0.58). Even though veg was important in both regions, parameter estimates for two land-cover categories (hardwood trees and herbaceous) shifted in sign depending on which region they were in (Table 3-1). Proximity to nearest agricultural area, NDVI, and ppt were all unimportant univariate predictors in both regions.

Table 3 – 1. Single predictor effects of nine environmental variables on Argentine ant occurrence from univariate logistic regression. The best explanatory variables (AUC > 0.75) are highlighted in bold and the correlation coefficients that switched signs in each region are italicized.

Variable	Region					
	HS			AAS		
	AUC	$\Delta$ AIC	Parameter Estimates	AUC	$\Delta$ AIC	Parameter Estimates
Maximum summer temperature	0.69	74.3	-8.15	<b>0.91</b>	0.0	-22.28
Minimum winter temperature	<b>0.91</b>	0.0	26.62	<b>0.90</b>	30.0	22.46
NDVI	0.67	74.8	3.93	0.46	164.7	0.09
Precipitation	0.64	77.7	3.76	0.57	143.4	0.97
Land-cover	<b>0.80</b>	52.1	Cat.	<b>0.85</b>	51.4	Cat.
Distance to intermittent water	0.51	84.4	-0.19	0.70	150.0	-0.45
Distance to perennial water	<b>0.77</b>	59.6	<b>-0.91</b>	0.58	156.3	<b>0.22</b>
Distance to agricultural zone	0.56	80.7	<b>-0.26</b>	0.55	156.7	<b>0.10</b>
Distance to human modified area	<b>0.82</b>	45.7	-0.91	<b>0.88</b>	42.3	-0.51
<b>Land-cover</b>						
Agriculture			-0.12			-1.56
Barren						-0.53
Conifer			-18.45			-16.00
Desert			-18.45			-16.00
Hardwood			<i>-1.82</i>			<i>0.63</i>
Herbaceous			<i>-1.28</i>			<i>0.74</i>
Shrub			-1.84			-0.39
Urban			2.69			3.33

*Model generality across regions*

Though there was a great deal of overlap in model confidence sets between the two regions, two lines of evidence suggest that models created from the AAS data exhibited greater generality. First, the models shared between the two regions have a 62% probability of being the best model according to AIC in the AAS region, but only a 23% probability of being the best model in the HS region (Fig. 3-4C). Second, models created using the AAS data perform better in the HS region compared to how well models created using the HS data perform in the AAS region. For example, the top two models from the AAS region ( $y \sim \text{minT} + \text{NDVI} + \text{ppt} + \text{veg} + \text{Pwater}$ : AIC  $w_i = 0.14$ ;  $y \sim \text{minT} + \text{ppt} + \text{veg} + \text{Pwater}$ : AIC  $w_i = 0.14$ ) tested using the data from the HS region yield AUCs of 0.927 and 0.925 respectively (Table 3 – 2). Conversely the top two models from the HS region ( $y \sim \text{minT} + \text{veg} + \text{Pwater} + \text{Human}$ : AIC  $w_i = 0.14$ ;  $y \sim \text{minT} + \text{veg} + \text{Pwater}$ : AIC  $w_i = 0.13$ ) tested using the data from the AAS region yield lower AUCs of 0.897 and 0.864 respectively (Table 3 – 2).

Results of the model averaging analysis (Fig. 3-4A) reveal surprising differences when compared to the results from the univariate models (Table 3-1). The importance of individual univariate predictors does not necessarily correspond to how often they appear in the model confidence sets. For instance, human appears in only 55% of the models in the HS region and 43% of the models in the AAS region (Fig. 3-4A), even though it was a universally strong univariate predictor (Table 3-1). Similarly, maxT was the most important univariate predictor in the AAS region (Table 3-1), but does not occur in any of the top five models in the AAS confidence set (Table 3 – 2). Conversely, ppt is an

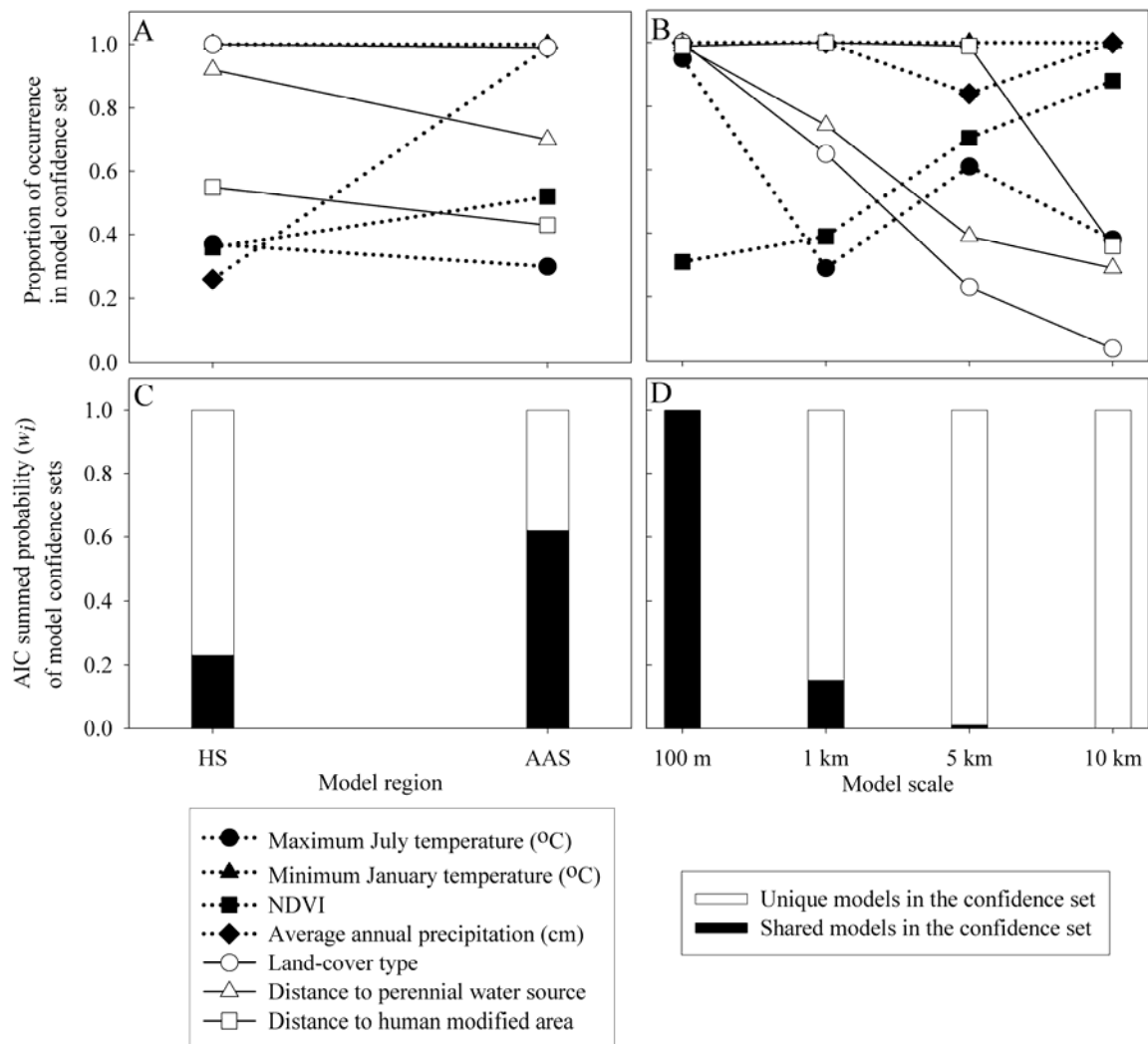


Figure 3 – 4: Model differences across region and scale. The proportion of models in confidence sets that contained each predictor (A) between regions, and (B) across spatial grains. Amount of the AIC summed probability ( $w_i$ ) explained by the models (C) when comparing each region, and (D) when comparing the confidence sets of each spatial grain to the 100 m spatial grain.

Table 3 – 2. Model averaging analysis of the regional confidence sets. Confidence sets were generated by finding the set of best-fitting models that yielded an AIC summed probability ( $w_i$ ) of 0.95, separately for the HS and AAS regions.

HS region									AAS region								
maxT	minT	NDVI	ppt	veg	Pwater	human	AIC	$w_i$	maxT	minT	NDVI	ppt	veg	Pwater	human	AIC	$w_i$
Five best models									Five best models								
	x			x	x	x	171.03	0.14	x	x	x	x	x	x		134.82	0.14
	x			x	x		171.09	0.13	x			x	x	x		134.82	0.14
	x	x		x	x	x	171.93	0.09	x	x	x	x	x	x	x	135.33	0.11
x	x			x	x	x	171.95	0.09	x			x	x	x	x	135.45	0.10
x	x			x	x		172.04	0.08	x			x	x			136.45	0.06
<b>0.52</b>									<b>0.55</b>								
All models in common with AAS region									All models in common with HS region								
	x		x	x	x	x	173.15	0.05	x	x	x	x	x	x		134.82	0.14
	x		x	x	x		173.20	0.05	x			x	x	x		134.82	0.14
x	x		x	x	x	x	173.92	0.03	x	x	x	x	x	x	x	135.33	0.11
	x	x	x	x	x	x	174.06	0.03	x			x	x	x	x	135.45	0.10
x	x		x	x	x		174.14	0.03	x	x		x	x	x		136.76	0.05
	x	x	x	x	x		174.42	0.02	x	x	x	x	x	x	x	137.05	0.05
x	x	x	x	x	x	x	175.05	0.02	x	x		x	x	x	x	137.43	0.04
<b>0.23</b>									<b>0.62</b>								
... 5 other models									... 7 other models								
<b>0.20</b>									<b>0.28</b>								

Abbreviations: maxT-maximum July temperature (°C); minT-minimum January temperature (°C); ppt-precipitation (cm); veg-land-cover type; Pwater-distance to nearest perennial water source (m); human-distance to nearest human modified area (m).

unimportant univariate predictor in both regions (Table 3-1) but appears in 99% of the models in the confidence set for the AAS region (Fig. 3-4A).

*Model generality across spatial grain*

Our analyses of model averaging revealed that model composition changed dramatically with relatively small changes in spatial grain (Fig. 3-4B). The extent to which model confidence sets overlapped with the confidence set at the 100 m scale diminished with increasingly coarse spatial resolution to the point that by 10 km no models were shared (Fig. 3-4D). This loss in model overlap results in large part from habitat variables decreasing in importance at coarser spatial grains (Fig. 3-4B). For example, at the 100 m scale, the confidence set is comprised of three models, each with at least 6 out of 7 predictor variables, while at the 10 km scale, the confidence set included 15 models with only three predictor variables of overwhelming importance (Table 3-3).

In the model averaging results, most predictors became less common in model confidence sets with coarsening spatial grain, but other predictors became more common or displayed variable patterns (Fig. 3-4B). For example, NDVI appeared in a greater percentage of models at coarser spatial scales, whereas veg and Pwater became less common (Fig. 3-4B). Human remained in at least 99% of all models until the 10 km spatial grain where it only occurred in 36% of the models and also became an unimportant univariate predictor (Fig. 3-4B, Table 3-4). Unlike the model averaging results, no other univariate predictors aside from Human changed in importance at coarser spatial resolutions (Table 3-4).

The best AIC model for each region and spatial grain all performed similarly and well, but important discrepancies existed (Fig. 3-5). Differences between models



Table 3 – 4. Single predictor effects of seven environmental variables on Argentine ant occurrence at four different spatial grains using logistic regression (100m = 747 points: 208 pres, 539 abs; 1km = 588 points: 176 pres, 412 abs; 5km = 374 points: 117 pres, 257 abs; 10km = 191 points: 64 pres, 127 abs). In each analysis the best explanatory variables (variables with AUC > 0.75) are highlighted in bold.

Variable	100m			1km			5km			10km		
	AUC	ΔAIC	Parameter Estimates	AUC	ΔAIC	Parameter Estimates	AUC	ΔAIC	Parameter Estimates	AUC	ΔAIC	Parameter Estimates
Maximum summer temperature	<b>0.81</b>	74.4	-12.67	<b>0.85</b>	41.8	-14.30	<b>0.91</b>	0.0	-20.05	<b>0.91</b>	0.0	-20.94
Minimum winter temperature	<b>0.88</b>	0.0	20.03	<b>0.88</b>	0.0	20.88	<b>0.90</b>	2.4	21.92	<b>0.88</b>	16.8	16.43
NDVI	0.55	208.3	1.07	0.53	180.9	0.71	0.56	123.9	1.06	0.65	63.3	2.43
Precipitation	0.51	190.7	0.96	0.54	156.7	1.09	0.61	103.7	1.20	0.71	53.0	1.61
Land-cover	<b>0.83</b>	13.8	Cat.	<b>0.82</b>	44.9	Cat.	<b>0.84</b>	32.5	Cat.	<b>0.89</b>	5.8	Cat.
Distance to perennial water	0.57	211.3	-0.05	0.46	183.7	0.03	0.52	127.5	0.10	0.55	73.1	-0.14
Distance to human modified area	<b>0.88</b>	40.5	-0.54	<b>0.89</b>	14.5	-0.53	<b>0.86</b>	38.5	-0.47	0.47	73.8	-0.03
<b>Land-cover</b>												
Agriculture			-1.45			-2.60			-2.22			-2.26
Barren			-0.79			1.29			NA			NA
Conifer			-17.12			-15.97			-16.34			NA
Desert			-17.12			-15.97			-16.34			-16.96
Hardwood			-0.07			1.31			1.33			NA
Herbaceous			0.32			1.27			2.22			2.17
Shrub			-0.51			1.55			1.35			1.92
Urban			3.30			3.96			3.70			4.60



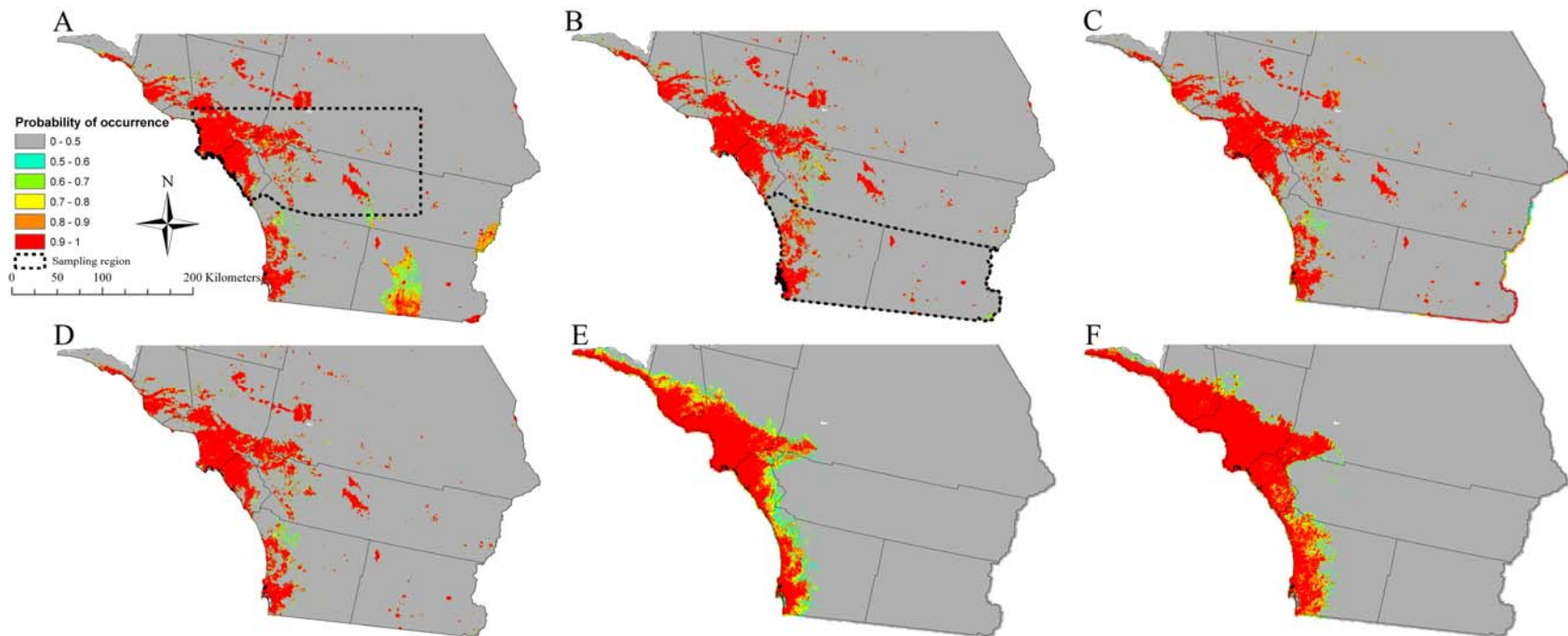


Figure 3 – 5: Predicted probability of Argentine ant occurrence in southern California based on the best AIC models for the following: **(A)** the HS data ( $y \sim \text{mint} + \text{veg} + \text{Pwater} + \text{human}$ ), **(B)** the AAS data ( $y \sim \text{mint} + \text{NDVI} + \text{ppt} + \text{veg} + \text{Pwater}$ ), **(C)** the combined 100 m dataset ( $y \sim \text{maxT} + \text{minT} + \text{ppt} + \text{veg} + \text{Pwater} + \text{human}$ ), **(D)** the 1 km dataset ( $y \sim \text{minT} + \text{ppt} + \text{veg} + \text{Pwater} + \text{human}$ ), **(E)** the 5 km dataset ( $y \sim \text{maxT} + \text{mint} + \text{NDVI} + \text{ppt} + \text{human}$ ), and **(F)** the 10 km dataset ( $y \sim \text{minT} + \text{NDVI} + \text{ppt}$ ).

created from the regional datasets were mostly due to the importance given to proximity to nearest perennial water source and precipitation (Table 3-1). The HS model predicted Argentine ant occurrence of be highly probable in the agricultural areas of the Colorado desert (Fig. 3-5A), which receives little rainfall, but contains numerous irrigation canals and has a large inland sea. In contrast, the AAS model predicted that *L. humile* does not occur in these areas (Fig. 3-5B). Both regional models predicted that Argentine ants should occur in urban environments at lower elevations irrespective of whether or not they are in deserts (Fig. 3-5A&B). The models created from the combined datasets at 100 m and 1 km closely resemble the model created for the AAS region (Fig. 3-5C&D). Models at the coarsest two spatial grains only predicted *L. humile* occurrence in the coastal areas west of the coastal mountain ranges (Fig. 3-5E&F). As the spatial grain was coarsened, predictions of Argentine ant occurrence became broader with the ranges extending further inland and consolidating along the coast in un-urbanized environments (Fig. 3-5C-F).

## Discussion

Efforts to model species distributions increasingly attempt 1) to identify factors that determine current range limits, and 2) to predict potential ranges of introduced species and range shifts resulting from climate change. In this study, we systematically analyzed how the accuracy of model predictions hinges on sufficient sampling, independently collected data from different regions, and the spatial grain of environmental predictor variables. First, we demonstrate that insufficient sampling of environmental parameter space (Fig. 3-1) incorrectly predicted species distributions when models were applied to independent data sets in adjacent regions (Fig. 3-3). Second,

despite extensive sampling in two geographically adjacent regions in our study (Fig. 3-2), differences existed with respect to the univariate predictors of occurrence (Table 3-1). Models using data that sufficiently sampled the environmental parameter space resulted in the most general models (Fig. 3-4C). Lastly, in models with multiple variables, environmental factors changed in their relative importance across spatial grain (Fig. 3-4B) and there was no overlap in model confidence sets between the finest and coarsest spatial grains (Fig. 3-4D). The findings of this study illustrate that caution is warranted when making biological inferences from species distribution models, especially in cases where predictions are being made across time and space.

The first important result concerns how insufficient sampling (Fig. 3-1) can compromise model accuracy (Fig. 3-3). Even though we fully sampled across the environmental tolerances of *L. humile* in the HS region (Fig. 3-1D&F, Fig. 3-2B), our sampling did not fully encompass the known parameter space for this region and in part as a consequence resulted in incorrect model predictions when using a multi-variable model (Fig. 3-3). This finding provides an example of how it is not only important to sample outside the environmental tolerances of the focal species but also to sufficiently sample the multivariate environmental space of the region. When using presence only data, however, Kadmon et al. (2003) demonstrated that model performance decreased when sampling extended across the full range of the species distribution. This discrepancy may in large part be due to issues relating to the change in model prediction error from omission to commission based on the increasing ratio of presence-to-absence points in a sample (McPherson et al. 2004). Because widely distributed species may often have higher presence-to-absence ratios compared to locally distributed species,

interspecific comparisons of model parameters are problematic (McPherson et al. 2004). Furthermore, in presence only models, locally distributed species will have better model performance compared to widely distributed species (Elith et al. 2006). Most current work on species distribution models uses presence only data because species occurrence data sets seldom includes absences (Peterson 2003, Elith et al. 2006).

Independent regions that were in close geographic proximity (Fig. 3-2) and were sampled with different levels of thoroughness (Fig. 3-1) produced multivariable models that differed in their composition (Fig. 3-4) and ability to accurately predict species occurrence patterns. These findings illustrate that it is essential to use independently collected data to assess model accuracy (Fielding and Bell 1997). For example, one important issue concerns the ability of models to accurately predict patterns of distribution outside the original study area (Hawkins et al. 2007). But the accuracy of most models is tested with data collected from the same region or with a subset of the data that were withheld from model creation (Kadmon et al. 2003, Elith et al. 2006).

When independent data are used to assess model accuracy, two potential pitfalls may commonly result. First, a variety of errors can occur if the resolution of the testing data set differs from that of the predictive model (McPherson et al. 2006, Guisan et al. 2007). Second, when the model is not parameterized for the environmental gradient in the predicted area, large errors in predicted species distribution may occur (Fig. 3-3). Studies attempting to predict the spread of introduced species are often faced with these problems because they consider independent regions, which often have novel environments, differ in the resolution of their environmental data layers, or differ in the resolution at which occurrence data are recorded (Fitzpatrick et al. 2006, Roura-Pascual et al. 2006). These

problems are further compounded in studies that attempt to predict range shifts caused by climate change because current predictions call for the appearance of environments with no present analog (Pearson and Dawson 2003, Williams et al. 2007).

In addition to issues relating to sufficient sampling and independently collected data, model accuracy may also be affected by environmental factors that change in relative importance across spatial grain (Fig. 3-4B). In general, coarsening the spatial grain of data tends to decrease model performance (Guisan et al. 2007). In our analyses, for example, this loss of accuracy appears to result from an increase in the over-prediction of occurrences, which is caused in large part by the diminishing importance of habitat variables (e.g. land-cover, distance to perennial water, distance to human modified area) with increasing scale (Fig. 3-4, Fig. 3-5). A number of recent studies have also noted that habitat variables as well as variables influenced by anthropogenic activity decrease in explanatory power at coarser spatial grains (Luoto et al. 2007, Pautasso 2007, Whittingham et al. 2007). This form of scale dependence may be related to the size of species ranges; narrowly ranging or specialist species are presumably more strongly associated with fine grain variables than more wide ranging or generalist species (McPherson et al. 2004, Menendez et al. 2007). With respect to Argentine ants, a species strongly limited by its physiological tolerances, patterns of occurrence at the community scale in southern California are strongly dependent on fine-scale differences in soil moisture (Holway 2005, Menke and Holway 2006, Menke et al. *In Press*). This association weakens at coarser spatial scales where climatic factors become more important (Fig. 3-4B). Taken together, these findings illustrate that care should be

exercised to match the spatial resolution of predictions to the environmental correlates used to create the models (Karl et al. 2000, McPherson et al. 2006).

### *Conclusions*

The primary goal of this study was to quantitatively assess how the performance of species distribution models is affected by the following: sampling of the environmental envelope, testing with independently collected data from different regions, and manipulating the spatial resolution of environmental predictor variables. Model accuracy is strongly influenced by the sufficiency of sampling of the species' distribution as well as the environmental parameter space in which predictions are going to be made. Moreover, we found that variables change dramatically in importance at different spatial resolutions; climatic factors become more important at coarser resolutions, and habitat variables become less important. In light of these findings, we recommend that efforts to model species distributions take into consideration 1) inclusion of both presence and absence data, 2) sufficient sampling of the species' environmental range, 3) sufficient sampling of the environmental parameter space of the region into which predictions will be made, 4) testing model predictions in a distinct region with independently collected data, 5) using variables at the appropriate spatial grain, and 6) making model predictions at the same resolution as model parameterization. Exercising appropriate levels of caution in efforts to model species distributions will increase the likelihood that predictions are biologically meaningful.

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