ROLE OF ABIOTIC FACTORS IN GOVERNING SUSCEPTIBILITY TO INVASION: A TEST WITH ARGENTINE ANTS

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Abstract. Hypotheses concerning community-level vulnerability to invasion often emphasize biotic interactions but fail to consider fine-scale variation in the physical environment. In this study, the interplay between interspecific competition and abiotic factors is examined with respect to whether scrub habitats in southern California become invaded by the Argentine ant (*Linepithema humile*). Argentine ants penetrate further into and attain higher abundances in mesic scrub fragments than they do in xeric scrub fragments. Probably as a result, native ant richness is lower in small (<30 ha), mesic fragments than in either small, xeric fragments or in small plots in unfragmented areas. Compared to six species of native ants, Argentine ants ranked lowest in their ability to tolerate high temperatures in the laboratory with 100% of field-collected workers dying after 60 min of exposure to temperatures ≥46°C. Field data corroborate these results; mean temperatures at which colonies of Argentine ants attained maximum abundance at baits (34.0°C) and abandoned baits (41.6°C) were both lower than for the native ant *Dorymyrmex insanus*. Laboratory studies further revealed that low levels of soil moisture depress mean worker survival in experimental colonies of Argentine ants. In a factorial laboratory experiment that varied both physical conditions and interspecific competition, Argentine ants exhibited greater worker activity and survival under warm, moist conditions than under hot, dry conditions, whereas the presence of a competitor, *Forelius mccooki*, had no significant effect. Experimental colonies of *F. mccooki*, in contrast, were more active under hot, dry conditions than under warm, moist conditions and exhibited reduced activity in the presence of *L. humile* irrespective of physical conditions. Taken together, these experimental data demonstrate how the abiotic environment impinges on both colony-level activity and colony growth in the Argentine ant and provide a general explanation for the patterns observed at the community level. A key consequence of the condition-specific nature of the competitive asymmetry between Argentine ants and native ants is that community-level vulnerability to invasion appears to depend primarily on the suitability of the physical environment from the perspective of *L. humile*.

Key words: abiotic factors; biological invasions; competitive exclusion; condition-specific competition; habitat fragmentation; interspecific competition; Linepithema humile.

INTRODUCTION

A major challenge of invasion biology lies in identifying factors that make communities vulnerable to invasion. Elton (1958) proposed that a community's resistance to invasion is proportional to its diversity. Elton's idea, often referred to as "biotic resistance," is a central theme in invasion biology and is buttressed both by theoretical (Case 1990) and empirical studies (Tilman 1997, Stachowicz et al. 1999, Levine 2000, Naeem et al. 2000). Although biotic resistance influences invasion success in some systems, its importance in others may be outweighed by factors that covary with or are unrelated to species richness (Simberloff

1989, Moyle and Light 1996, Levine and D'Antonio 1999). For example, the suitability of the physical environment from the perspective of an invader can in some cases eclipse species richness as a determinant of community-level vulnerability to invasion (Moyle and Light 1996, Harrison 1999, Fausch et al. 2001).

Understanding the relative importance of biotic vs. abiotic factors in determining local patterns of species diversity is also of interest from the perspective of community ecology. For example, the outcome of interspecific competition is contingent on features of the physical environment (Park 1954, Connell 1961*a, b*, Dunson and Travis 1991), with competitively dominant species, by definition, commonly limited in their abundance and distribution more by abiotic factors than by interspecific competition (Connell 1961*a, b*, Dunham 1980). Species-level differences in competitive ability and tolerance to physical conditions may commonly promote species coexistence, thereby influencing species diversity at a local scale (Chesson 1986, Tilman

and Pacala 1993). Despite the history of interest on this topic, there remain relatively few experimental studies on animals that have documented the mechanisms underlying condition-specific competition (Kingsolver 1989, Dunson and Travis 1991, Warner et al. 1993, Taniguchi and Nakano 2000).

In this study, we examine how the physical environment influences competitive impacts of the Argentine ant (*Linepithema humile*). This widespread species displaces native ants throughout its introduced range (Newell and Barber 1913, Hölldobler and Wilson 1990, Williams 1994). The strong competitive asymmetry between Argentine ants and native ants stems from *L. humile*'s ability to excel at both exploitative and interference competition (Human and Gordon 1996, 1999, Holway 1999). Although competitively dominant as an invader, the Argentine ant's success appears contingent on abiotic factors. For example, in California, USA, Argentine ants are absent from both cold-temperate and xeric environments and as a result are largely confined to the coast and to low-elevation mesic areas in the interior, such as riparian woodlands and urban areas (Markin 1970, Tremper 1976, Ward 1987, Holway 1995, Human et al. 1998, Suarez et al. 1998). Even within apparently suitable habitat, Argentine ants spread faster in areas with higher levels of soil moisture (Holway 1998) and attain maximum abundance along habitat edges that border irrigated urban areas (Human et al. 1998, Suarez et al. 1998, Bolger et al. 2000).

Here we employ a diversity of approaches at three separate spatial scales to test the extent to which the physical environment limits post-establishment invasion success in Argentine ants. At the community level, we compare patterns of native ant richness and Argentine ant abundance between xeric and mesic chaparral and coastal sage scrub fragments to test the hypothesis that Argentine ants invade mesic fragments to a greater extent than xeric fragments. At the colony level, we first determine the physiological tolerances of Argentine ants and those of different native ants and then use these results in a laboratory-based factorial experiment to test how abiotic factors (soil moisture and temperature) and interference competition ($\pm$) influence foraging activity and worker survival in colonies of Argentine ants and in colonies of the native ant *Forelius mccooki*. We also conduct a field experiment at multiple contact zones to test how soil temperature variation affects foraging activity of established colonies of Argentine ants and those of the native ant *Dorymyrmex insanus*.

METHODS

Field sampling

To test whether abiotic factors govern the extent to which Argentine ants invade natural ecosystems, we sampled ants from chaparral and coastal sage scrub habitats in San Diego and Riverside Counties, California, USA, that differed from one another with respect to their topography and degree of fragmentation. Within the San Diego metropolitan area, chaparral and coastal sage scrub now exist primarily in isolated fragments surrounded by urban development (Soulé et al. 1988, Suarez et al. 1998). Because mesa tops and broad coastal valleys are selectively targeted for development, the remaining undeveloped land in San Diego mostly consists of narrow, steep-sided canyons. Such fragments, in addition to containing natural drainages, concentrate runoff and irrigation from urban and agricultural areas, creating locally mesic environments (Soulé et al. 1988, Alberts et al. 1993). For example, a typical household in San Diego uses an average of 1220 mm/yr of water (per unit area) for outdoor use (San Diego County Water Authority, *personal communication*), whereas precipitation in coastal San Diego County averages only ~240 mm/yr. In contrast to the canyon fragments, a minority of fragments can be classified as either hilltops or small plateaus; these areas fail to collect runoff. Because of the putative disparity in moisture accumulation between canyon and hilltop habitat patches, we refer to such sites as mesic and xeric fragments, respectively.

We sampled ants from a total of 37 canyon (mesic) and 11 hilltop (xeric) fragments ranging in size from 0.4 to 110 ha. Forty of these fragments are the same as those used in a previous study (Suarez et al. 1998). In addition, we also sampled plots within five urban areas and three large (>100 km) unfragmented areas of mixed chaparral and coastal sage scrub chosen for their geographic proximity to the habitat fragments. Within two of the unfragmented areas, we sampled multiple plots similar in topography and vegetation to the isolated fragments mentioned above. All plots surveyed within unfragmented areas were located at least 400 m from the nearest developed edge. We sampled seven plots (ranging in size from 1 to 50 ha) within the University of California Elliot Chaparral Reserve (San Diego County), six plots (1–52 ha) within the Metropolitan Water District Southwest Riverside County Multispecies Reserve (Riverside County), and one plot (99.3 ha) at the Sweetwater Reserve (San Diego County). Additional sampling scattered throughout the 88-ha Elliot Reserve and 400-ha Metropolitan Water District Reserve was used to estimate the ant fauna for the entire reserves.

The number of ant species at each site was estimated using pitfall traps and visual surveys following the protocol in Suarez et al. (1998). At three different sampling periods (fall, winter, spring/summer), we placed an array of five traps every 100 m along a transect corresponding to the longest axis of the fragment or plot within an unfragmented area (see Suarez et al. 1998 for a complete description of methods). In urban areas, we did not sample relative to the size of urban development but instead placed two arrays 100 m apart. Ant richness for each fragment was determined by pooling

samples among arrays and seasons; hypogeic ants and alates were excluded from all analyses. The number of Argentine ants per trap at each array was averaged across seasons. Pitfall trap arrays in urban areas and habitat fragments were categorized by the distance from the center of the array to the nearest urban edge and placed into the following categories: urban, 0–25 m, 26–50 m, 51–100 m, and >100 m. When a fragment had more than one array at any given distance category, we averaged the number of Argentine ants per jar among arrays from the same distance category to get a single value per fragment. In addition to pitfall sampling, we conducted extensive visual surveys ($n = 4$–6 visits per site or plot) to complete species lists for each fragment or unfragmented plot. To ensure that sampling was sufficient at each site, species accumulation curves were constructed for each fragment (see Suarez et al. 1998). These curves attained asymptotes for all but the largest fragments and plots within unfragmented areas.

Laboratory experiments

Laboratory experiment 1: thermal tolerance.—We exposed groups of workers of six different ant species to a 12°C-range of temperatures to determine their tolerances to high temperatures. We used the following native ant species: *Crematogaster californica*, *Solenopsis xyloni*, *Pogonomyrmex subnitidus*, *Dorymyrmex insanus*, *Forelius mccooki*, and the exotic *Linepithema humile*. The five native ant species chosen are among the most common and widespread ants in chaparral and coastal sage scrub in coastal southern California and are all displaced by Argentine ants in these habitats (Suarez et al. 1998). All ants were collected from the field in San Diego County and tested in the laboratory within 12 h. We tested temperature tolerance at intervals of 2°C from 42° to 54°C. For each temperature, we placed 10 workers of each species in glass test tubes (16 × 150 mm) plugged with moistened cotton and then placed tubes in an incubator (Fisher Scientific Isotemp Incubator Model 630D; Fisher Scientific, Pittsburgh, Pennsylvania, USA). After 60 min, we tallied the number of living workers in each test tube. We used five replicates for each species and temperature.

Laboratory experiment 2: soil-moisture tolerance.—We tested how soil moisture influences worker mortality in experimental colonies of *L. humile* and *F. mccooki*. We chose *F. mccooki* to match against *L. humile* in laboratory experiments 2 and 3 in part because *Linepithema* and *Forelius* are sister genera (Chiotis et al. 2000) and tend to be proficient competitors that form large polygynous colonies (Newell and Barber 1913, Hölldobler 1982, Van Zee et al. 1997). In this experiment (and also in laboratory experiment 3), we collected source material for experimental colonies from supercolonies of *L. humile* located in La Jolla, San Diego County, and from colonies of *F. mccooki* located at the University of California Elliot Chaparral Reserve. After removal from the field, we divided colony fragments into experimental colonies and housed these in plastic containers (30 × 14 × 8 cm) lined with Fluon (Northern Products, Woonsocket, Rhode Island, USA) and Tanglefoot (Tanglefoot, Grand Rapids, Michigan, USA) to prevent ants from escaping. Experimental colonies were maintained in the laboratory for 1–2 wk prior to the start of each experiment.

We tested how soil moisture affects worker mortality in experimental colonies as follows. Thirty colonies of each species were reared in nest containers filled with sand (30 × 14 × 8 cm). Using 1 cm diameter balls of clay, we affixed a single glass test tube (16 × 150 mm) to the floor of each nest container to serve as a nest chamber. We then placed a 5-cm length of curved plastic tubing in the mouth of the test tube with the tubing curved upwards; the tubing was held in place with a cotton plug. We then covered the nest chamber with a uniform, 10-cm layer of fine washed quartz sand, keeping the end of the plastic tubing above the surface of the sand. After nest containers were set up, we introduced three queens and ~400 workers to each container. We then randomly assigned colonies to one of six experimental groups, each of which received a different amount of water: 0, 5, 10, 15, 20, and 25 mL/d. For the next 6 wk, we added water to each nest container every day (except every seventh day). To add water, we used a 10-mL pipette and dribbled the proscribed volume for each colony in the sand within a 5 cm radius of where the plastic tubing rose above the sand's surface. We fed colonies a 20% solution of sucrose in water (sugar water) daily and sources of protein (crickets and scrambled eggs) at least twice per week. All experimental colonies were placed on shelves and reared in a single temperature-controlled room at 24°C; colonies were spatially interspersed with respect to treatment. After 6 wk, we carefully removed all of the ants from each container and counted the number that survived and the number that died. For each species, we used a one-way ANOVA to compare the proportion of surviving workers (number of alive/number of alive + number of dead) across soil moisture categories; dependent variables were arcsine transformed prior to analysis.

Laboratory experiment 3: condition-specific competition.—We tested how variation in physical conditions (temperature and soil moisture) and the presence or absence of interspecific competition affect activity and mortality in experimental colonies of *L. humile* and *F. mccooki*. We used a fully crossed, two-way factorial design; each factorial combination had five replicates. For each species, we established 20 experimental colonies, each with three queens and ~400 workers. We randomly assigned colonies to one of three experimental groups: an interspecific competition group (each replicate composed of one *L. humile* colony paired with one *F. mccooki* colony), an *L. humile* group (each replicate composed of one *L. humile* colony), and an *F. mccooki* group (each replicate composed of one *F.*

mccooki colony). For colonies in the interspecific competition group, we used 3-m lengths of plastic tubing to connect colonies together via a shared foraging container (a plastic container the size of the nest containers). For replicates without competitors, we used 3-m lengths of plastic tubing to connect individual colonies to their own foraging container. After setting up nest containers as in laboratory experiment 2, we divided each of the three groups in half and randomly assigned colonies to one of two groups: a warm, moist treatment and a hot, dry treatment. For the warm, moist treatment, we reared colonies at 23–25°C and added 20 mL of water to each nest container daily. For the hot, dry treatment, we also reared colonies at 23–25°C, but added only 5 mL of water to each nest container daily and kept the surface of the sand in the foraging containers at 42–44°C using heat lamps (one lamp with a 75-W bulb above each foraging container) left on throughout the 12-h daily cycle. All experimental colonies were placed on shelves and reared in a single temperature-controlled room at 24°C; colonies were spatially interspersed with respect to treatment. We fed colonies 20% sugar water daily and sources of protein (crickets or scrambled eggs) at least twice per week. In addition, every day we placed a weigh boat containing 0.25 mL of water in the nest container of each colony.

For the first 4 wk of the experiment, we let *F. mccooki* colonies forage in foraging containers, but prevented *L. humile* from doing so by blocking the plastic tubing leading from each *L. humile* nest container to the foraging container. In this phase of the experiment, we placed food both in the nest containers and in the foraging containers. Four weeks after the start of the experiment, we provided *L. humile* with access to the foraging containers and placed food only there and only during the day. Therefore, colonies in the 43°C, 5 mL/d water treatment had to forage while heat lamps were on. Once Argentine ants had access to the foraging containers, we measured foraging activity on five separate days by counting the number of workers in each foraging container 1 h after feeding (sugar water and cricket) and at least 4 h after the heat lamps turned on. For data analysis, we used each colony's mean activity. We concluded the experiment 2 wk after Argentine ants were first provided with access to the foraging containers. We then counted the number of living and dead workers in each replicate and calculated the proportion of surviving workers as in laboratory experiment 2; these values were arcsine transformed prior to statistical analysis. For each species, we used separate two-way ANOVAs to analyze the results of this experiment with physical conditions (43°C, 5 mL/d water and 24°C, 20 mL/d water) and interspecific competition ($\pm$) treated as fixed factors.

Short-term removal experiment

In this field experiment, we conducted a series of short-term removals across a thermal gradient to test how recruitment to baits by *L. humile* and the native *Dorymyrmex insanus* depends on soil temperature. We identified seven contact zones (each $\geq$500 m apart), areas where Argentine ants met native ants, in areas of mixed chaparral and coastal sage scrub that bordered urban development in La Jolla and Del Mar, San Diego County, and studied recruitment behavior among established colonies in situ. At each site, *L. humile* was penetrating into the natural vegetation from the irrigated urban edge. *D. insanus* was typically the only species of native ant still present at these sites, although two sites still had active colonies of *Pogonomyrmex subnitidus*. Although studying competition at active contact zones does not permit the same degree of statistical replication achievable by other experimental means, by using established colonies, this approach provides a complement to the laboratory experiments described above.

We conducted this experiment from mid-June to late July 2000. Both Argentine ants and native ants are highly active in coastal San Diego during the summer months, but worker activity often ceases in the middle of the day due to high temperatures. At each of the seven sites, we located between two and four points ($\geq$5 m apart) where we observed both *L. humile* and *D. insanus* workers foraging on the ground within 10 cm of one another. Points were selected during morning hours when both species were foraging actively (soil surface temperatures 20–25°C). At each site, we conducted a removal experiment over two consecutive days. On the first day, we removed (by aspiration) either *D. insanus* or *L. humile* (order determined randomly for each point) from within 0.25 m of baits placed at each point. On the second day, we performed the complement removal at each point. Each bait consisted of ~1 mL of 20% sugar water placed in a single drop in the center of a circular plastic disc (3.5 cm diameter); baits were replenished as needed. For each point, we recorded soil temperature (5 mm below the surface) and the number of workers at the bait every 15 min. We conducted removals over approximately the same span of times (0800–1300) and soil temperatures (27–52°C) at each site. Although interference competition between these two species is not addressed here, a previous study (Holway 1999) found that *D. insanus* abandoned baits in the presence of *L. humile* at soil surface temperatures between 18° and 25°C. Dependent variables for this experiment included the temperature at which each species attained its maximum abundance at baits and the maximum temperature at which each species was present at baits. For data analysis, we averaged values within sites for each of the two species.

Results

Field sampling

Species–area relationships for the three types of sites sampled in this study, xeric fragments, mesic frag-
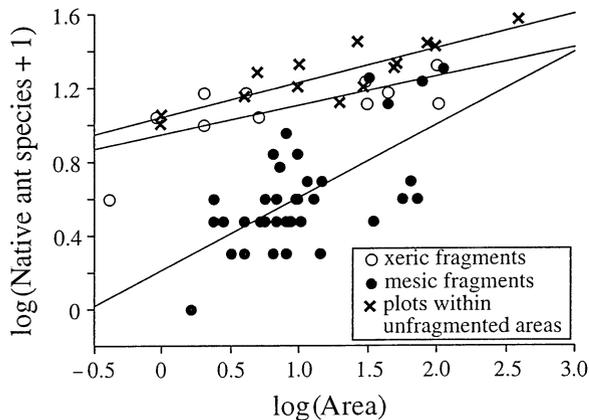
FIG. 1. Species–area relationships for the three types of chaparral/coastal sage scrub sites sampled in San Diego and Riverside Counties, California, USA. Plots are within unfragmented areas, xeric fragments, and mesic fragments. For plots within unfragmented areas, log(native ant spp. + 1) = 1.038 + 0.187(log [area]) (simple linear regression: $F_{1,12}$ = 33.043, P < 0.001, R^2 = 0.739). For xeric fragments, log(native ant spp. + 1) = 0.947 + 0.156(log [area]) (simple linear regression: $F_{1,9}$ = 8.874, P = 0.016, R^2 = 0.496). For mesic fragments, log(native ant spp. + 1) = 0.214 + 0.393(log [area]) (simple linear regression: $F_{1,35}$ = 24.591, P < 0.001, R^2 = 0.413). See *Methods* for details about sampling.

ments, and plots within unfragmented areas, are shown in Fig. 1. Species–area relationships for xeric fragments and for plots within unfragmented areas have slopes that are not significantly different (two-sample t test: t = 0.79, df = 21, P > 0.2). The species–area relationship for mesic fragments, in contrast, has a significantly steeper slope: mesic vs. xeric (two-sample t test: t = 3.15, df = 44, P < 0.005) and mesic vs. plots within unfragmented areas (two-sample t test: t = 3.26, df = 47, P < 0.005). The steeper slope for the mesic fragment regression results from the low species richness of small (≤30 ha), mesic fragments. Although mesic areas could have fewer species of native ants compared to xeric areas generally, data from the unfragmented areas suggest otherwise. When pitfall trap arrays from the three unfragmented areas are divided into mesic sites (e.g., drainages) and xeric sites (e.g., hilltops and mesas), average species richness for each habitat type per site did not statistically differ: arrays within drainages had 6.4 ± 0.6 species (means ± 1 SE), whereas arrays on mesas and hilltops had 6.7 ± 0.7 species (two-sample t test: t = 0.828, df = 4, P = 0.454).

Argentine ants fail to penetrate into xeric fragments as deeply as they do into mesic fragments (Fig. 2). While there was no significant difference in the abundance of Argentine ants in xeric and mesic fragments between 0 and 25 m from urban edges (two-sample t test: t = 2.361, df = 21, P = 0.285), in xeric fragments, Argentine ants were scarce to absent at distances exceeding 25 m from edges. In mesic fragments, *L. humile* was significantly more abundant than in xeric frag-

ments in the 26–50 m (two-sample t test: t = 3.575, df = 30, P = 0.012) and 51–100 m (two-sample t test: t = 3.93, df = 13, P = 0.0017) distance categories. In the sites sampled here, Argentine ants had a limited ability to penetrate into natural vegetation >100 m beyond urban edges in both xeric and mesic fragments (Fig. 2). Moreover, Argentine ant abundance ranked highest in the urban sites sampled (Fig. 2). The only native ant species coexisting with Argentine ants in these urban areas are the same hypogeic species shown to persist in natural habitat invaded by Argentine ants (e.g., *Solenopsis molesta*, *Leptothorax andrei*, and *Hypoponera* spp.; Ward 1987, Holway 1998, Suarez et al. 1998).

Laboratory experiments

Laboratory experiment 1: thermal tolerance.—For all six species of ants tested, worker survival was strongly dependent on temperature after 60 min of exposure (Fig. 3). Relative to native ants, Argentine ant workers ranked lowest in their ability to withstand hot temperatures, with 50% mortality occurring at ~45°C and 100% mortality occurring at temperatures ≥46°C (Fig. 3). *Forelius mccooki* workers, in contrast, were able to tolerate the highest temperatures, with 50% mortality occurring at ~51°C and 100% mortality occurring at temperatures ≥52°C (Fig. 3). Workers of the
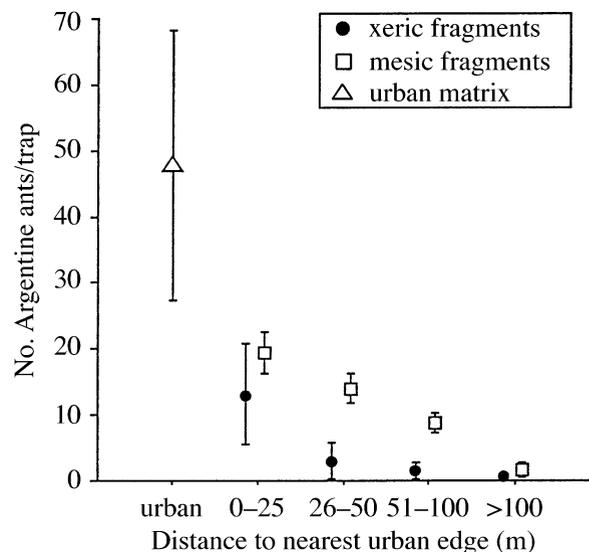

FIG. 2. Number of Argentine ants per pitfall trap (means ± 1 SE) as a function of distance in meters to the nearest urban edge. The number of Argentine ants per trap at each array was averaged across seasons (fall, winter, spring/summer). For fragments with more than one set of pitfall traps within a distance category, a mean value was calculated for that category; this value was used in the analysis. Sample sizes are as follows: sites in the urban matrix (n = 5), xeric sites (0–25 m, n = 7; 26–50 m, n = 4; 51–100 m, n = 4; >100 m, n = 8), and mesic sites ((0–25 m, n = 16; 26–50 m, n = 28; 51–100 m, n = 11; >100 m, n = 3). See *Methods* for details about sampling.
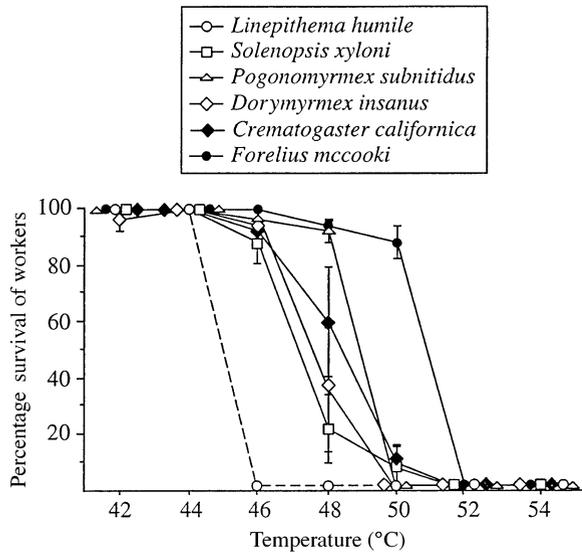
FIG. 3. Results of laboratory experiment 1 (thermal tolerance). Percentage survival of workers of five native ant species (*Crematogaster californica*, *Solenopsis xyloni*, *Pogonomyrmex subnitidus*, *Dorymyrmex insanus*, and *Forelius mccooki*) and the Argentine ant (*Linepithema humile*) after 60 min as a function of temperature (means $\pm$ 1 SE). Each replicate consisted of 10 workers held in a 150-mL test tube plugged with cotton to prevent ants from escaping. $N = 5$ for each factorial combination. See *Methods* for additional details.

four other native species were intermediate in their ability to tolerate high temperatures (Fig. 3); these species experienced 50% mortality between 47° and 49°C.

Laboratory experiment 2: soil-moisture tolerance.— For experimental colonies of both *L. humile* and *F. mccooki*, worker survival after 6 wk depended strongly on soil moisture, but the observed responses differed between the two species. All colonies suffered 100% mortality in treatments that received no water (Fig. 4). In treatments that did receive water, survival of *L. humile* workers depended strongly on soil moisture (Fig. 4; one-way ANOVA: $F_{4,20} = 6.022$, $P = 0.0024$). For *L. humile* colonies, worker survival failed to surpass 80% until $\geq$15 mL of water were added daily (Fig. 4). In contrast, survival of *F. mccooki* workers in treatments with added water uniformly exceeded 80% and was independent of soil moisture (Fig. 4; one-way ANOVA: $F_{4,20} = 0.0937$, $P = 0.4626$).

Laboratory experiment 3: condition-specific competition.—Interspecific competition and the physical environment affected *L. humile* and *F. mccooki* in different ways. For *L. humile*, worker activity in the 24°C, 20 mL/d water treatment (16 ± 2 workers; means $\pm$ 1 SE) significantly exceeded that in the 43°C, 5 mL/d water treatment (2 ± 1 workers; Fig. 5A; two-way ANOVA: $F_{1,16} = 70.381$, $P < 0.001$), whereas the presence or absence of *F. mccooki* had no significant effect (Fig. 5A; two-way ANOVA: $F_{1,16} = 1.647$, $P > 0.05$). Worker survival showed a qualitatively similar pattern.

Experimental colonies of *L. humile* experienced significantly higher percentage of worker survival in the 24°C, 20 mL/d water treatment ($85 \pm 3\%$) than in the 43°C, 5 mL/d water treatment ($58 \pm 6\%$; Fig. 5B; two-way ANOVA: $F_{1,16} = 20.678$, $P < 0.001$), but the presence or absence of *F. mccooki* had no significant effect (Fig. 5B; two-way ANOVA: $F_{1,16} = 3.160$, $P > 0.05$).

In contrast, workers in *F. mccooki* colonies were most active under hot, dry conditions but foraged less, irrespective of conditions, in the presence of *L. humile*. In the absence of Argentine ants, *F. mccooki* colonies were significantly more active in the 43°C, 5 mL/d water treatment than in the 24°C, 20 mL/d water treatment (Fig. 5C; two-sample t test: $t_8 = 3.299$, $P = 0.011$). The presence of Argentine ants, however, significantly depressed *F. mccooki* activity both in the 43°C, 5 mL/d water treatment (Fig. 5C; two-sample t test: $t_8 = 2.539$, $P = 0.035$) and in the 24°C, 20 mL/d water treatment (Fig. 5C; Mann-Whitney U test: $U = 2.500$, $P = 0.018$). Although the foraging activity of *F. mccooki* was strongly affected by both interspecific competition and the physical environment, worker survival was independent of both of these variables (Fig. 5D).

Short-term removal experiment

The short-term removal experiment demonstrated that, compared to *Dormyrmex insanus*, *L. humile* tends to exploit food resources under lower soil temperatures. Argentine ants attained maximum abundance at baits at a significantly lower temperature (34.0 ± 1.21°C; mean $\pm$ 1 SE) than did *D. insanus* (39.4 ± 0.79°C; paired t test: $t_6 = 4.371$, $P = 0.0047$). Argentine ants abandoned baits at 41.6 ± 0.88°C, just 2°C less than the temperature at which Argentine ant workers suf-
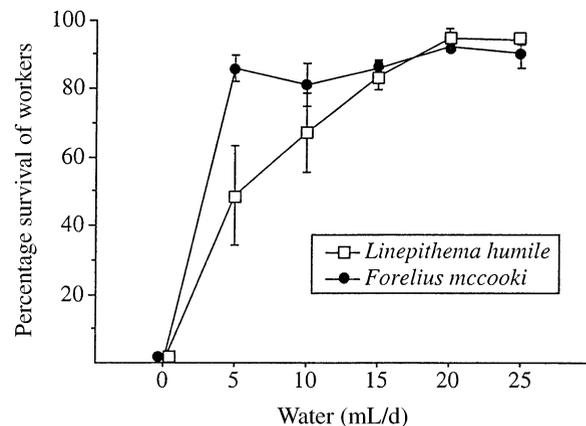

FIG. 4. Results of laboratory experiment 2 (soil-moisture tolerance). Percentage survival of workers in experimental colonies of *Linepithema humile* and *Forelius mccooki* as a function of amount of water added to nest containers daily (means $\pm$ 1 SE). Colonies contained ~400 workers and three queens at the start of the experiment and were reared in plastic containers half-filled with sand. $N = 5$ for each factorial combination. See *Methods* for additional details.
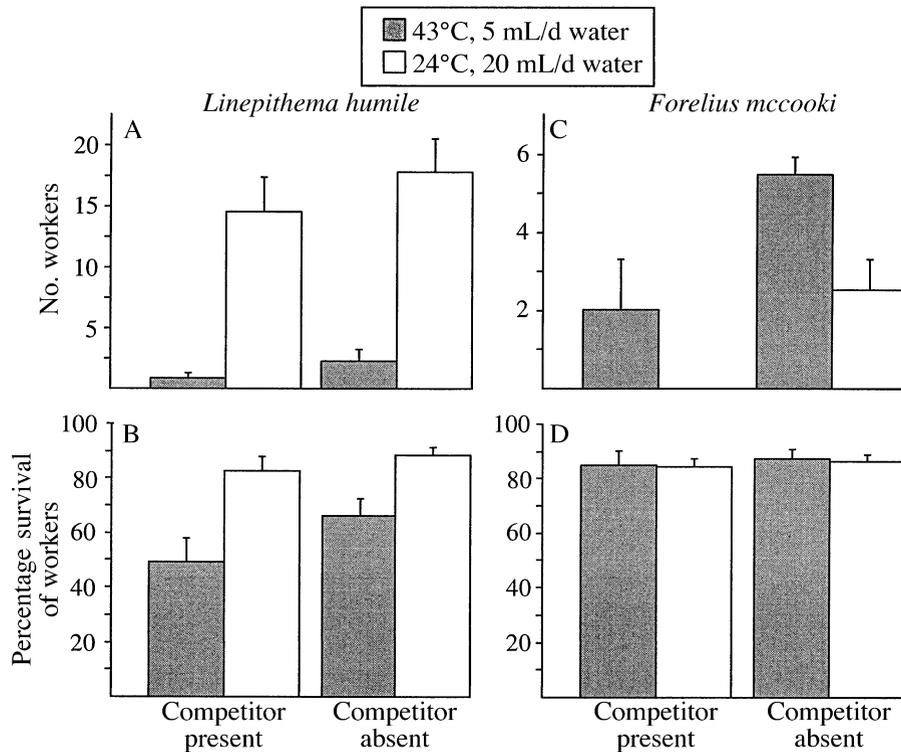
FIG. 5. Results of laboratory experiment 3 (condition-specific competition). (A) Number of *Linepithema humile* workers present in foraging containers 1 h after feeding (means + 1 SE) and (B) percentage survival of workers in experimental colonies of *L. humile* as a function of physical conditions (43°C, 5 mL/d water vs. 24°C, 20 mL/d water) and interspecific competition (±). (C) Number of *Forelius mccooki* workers present in foraging containers 1 h after feeding and (D) percentage survival of workers in experimental colonies of *F. mccooki* as a function of physical conditions (43°C, 5 mL/d water vs. 24°C, 20 mL/d water) and interspecific competition (±). N = 5 for each factorial combination. See *Methods* for additional details.

fered 100% mortality after 60 min of exposure in the laboratory (Fig. 3). By comparison, *D. insanus* showed a significantly greater tolerance of high temperatures, remaining at baits until soil temperatures reached 47.0 ± 0.53°C (paired *t* test: $t_6 = 4.975$, $P = 0.0025$). As for *L. humile*, the mean temperature at which *D. insanus* abandoned baits was just a few degrees less than that at which workers of this species suffered 100% mortality after 60 min of exposure in the laboratory (Fig. 3).

DISCUSSION

The results of this study provide experimental support for the hypothesis that variation in the extent to which communities are invaded by Argentine ants in southern California depends primarily on features of the physical environment. At the community level, field sampling in scrub fragments revealed that, on average, Argentine ants penetrate further into and attain higher abundances in mesic fragments than in xeric fragments. Probably as a direct result, native ant richness is lower in small (<30 ha), mesic fragments than in small, xeric fragments. The low richness of small, mesic fragments is unlikely to be caused by differences in diversity prior

to habitat fragmentation since plots differing in their topography within unfragmented areas supported similar numbers of native ant species. Moreover, the low diversity typical of small, mesic fragments is unlikely to be the cause of the Argentine ant's success in those areas since other studies conducted in California found that rate of invasion is independent of native ant richness (Holway 1998).

At the colony level, our laboratory and field experiments documented that Argentine ants, compared to native ants, are less tolerant of both high temperatures and low levels of soil moisture. Moreover, in a factorial laboratory experiment that varied both physical conditions and the presence of interspecific competition, Argentine ant colonies foraged more actively and experienced less mortality when reared under warm, moist conditions than under hot, dry conditions, whereas the presence of an interspecific competitor, *F. mccooki*, had no effect. Experimental colonies of *F. mccooki*, in contrast, were more active under hot, dry conditions than under warm, moist conditions and exhibited reduced activity in the presence of *L. humile* irrespective of the physical conditions. The presence of *L. humile* may have failed to depress worker survival

in *F. mccooki* colonies because these colonies remained underground in their nests during the final 2 wk of the experiment. Had this experiment run longer, *F. mccooki* probably would have suffered reduced worker survival because, at least in the warm, moist treatment, the presence of *L. humile* completely prevented *F. mccooki* workers from foraging for food.

The experimental data reported here on the physiological limitations of the Argentine ant are corroborated by other studies. For example, Tremper (1976) conducted detailed physiological studies of Argentine ants and native ants in northern California. Consistent with our results, Tremper (1976) reported that Argentine ants had a critical thermal maximum (50% worker mortality) between 45° and 46°C. At a hot, dry inland site (Livermore, Alameda County), the thermal critical maximum for *L. humile* workers ranked lowest relative to six species of native ants (Tremper 1976). In contrast, at cooler coastal sites (e.g., La Honda and Jasper Ridge Biological Preserve, San Mateo County), Argentine ants were intermediate in their ability, relative to native ants, to tolerate high temperatures (Tremper 1976, Human et al. 1998). Also in agreement with our results are the findings of Witt and Giliomee (1999) who reported that in the fynbos of South Africa, Argentine ants attain a maximum activity at lower soil surface temperatures than do four species of native ants and cease foraging at soil surface temperatures between 40° and 44°C. Our laboratory and field estimates of thermal tolerance are also consistent with one another. For example, both our estimate of the maximum temperature at which Argentine ants remain at baits in the field (41.6°C) and the similar estimate by Witt and Giliomee (1999) fall just a few degrees shy of the critical thermal maxima reported by Tremper (1976).

Although previous studies have documented the physiological limitations of *L. humile*, ours is the first to examine experimentally the interplay between abiotic factors and interspecific competition and to suggest a mechanism for the limited ability of the Argentine ant to penetrate into dry environments. In particular, we argue that the results of the colony-level experiments described here scale up to the community level and provide the best explanation for the depressed native ant richness of small, mesic scrub fragments. For example, our laboratory experiments suggest that in mesic areas with the right combination of high soil moisture and reduced ground-level insolation, Argentine ant colonies would forage more actively and experience less worker mortality than they would in more xeric environments. Because the competitive prowess of the Argentine ant hinges on numerical advantages (Holway 1999, Holway and Case 2001), in relatively mesic environments, Argentine ants are more likely to maintain the large, active worker forces required to displace native ants. By comparison, in xeric environments, with their drier soils and greater soil-surface insolation (due to sparse vegetative cover), we would expect Argentine ants to be less active and present at low enough densities so that native ants remain largely unaffected. This hypothesis is further supported by the findings of other studies. First, in a 4-yr study conducted at 20 riparian sites in northern California, the Argentine ant's rate of spread was independent of anthropogenic disturbance and native ant richness but was strongly influenced by abiotic suitability: Argentine ants spread at moist sites (perennial streams) but not at dry sites (intermittent streams; Holway 1998). Second, numerous authors have concluded that soil moisture is the main factor in governing the success of the Argentine ant in mediterranean portions of California (Markin 1970, Tremper 1976, Ward 1987, Gulmahamad and Martinez 1999) and in other areas with similar climates (Witt and Giliomee 1999).

Our study provides an experimental demonstration of how the post-establishment invasion success of a competitively dominant invader hinges upon variation in the physical environment. The key role of abiotic factors in Argentine ant invasions reflects their central importance in determining community-level patterns in ants generally (Hölldobler and Wilson 1990, Andersen 1992, Cerda et al. 1997, Bestelmeyer 2000, Kaspari et al. 2000, Johnson 2001). The condition-specific nature of the competition between Argentine ants and native ants resembles that observed in other animal communities in which differences exist with respect to competitive ability and tolerance of extreme physical conditions (Connell 1961*a, b*, Dunham 1980). As pointed out by Ricklefs (1990), asymmetry in competitive ability often reflects asymmetry in ecology. As *L. humile* is native to mesic, subtropical environments in northern Argentina (Tsutsui et al. 2001), it is perhaps not surprising that Argentine ants appear ill-suited for conditions under which ants native to coastal southern California, many of them desert species, attain peak activity. Our results suggest that anthropogenic modifications to the physical environment are preeminent in determining the extent to which mediterranean scrub communities in southern California are susceptible to invasion by Argentine ants. An analogous case was described by Moyle and Light (1996) who argued that the majority of fish species introduced to freshwater habitats in California are poorly adapted to the seasonally erratic flow regimes typical of this region and as a consequence can only invade areas where water flows are made less variable by humans.

collected during this project have been deposited at the Bohart Museum of Entomology at the University of California, Davis, under the collection numbers AVS 1-500 and AVS 1000-1300.

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