Landscape-level patterns of occurrence of the invasive Argentine ant (*Linepithema humile*) and associated impacts on the native ant community in coastal southern California

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ABSTRACT: Ants are valuable indicators of ecosystem health and key ecological components of most terrestrial communities. In southern California and other Mediterranean ecosystems worldwide the invasive Argentine ant (*Linepithema humile*) represents a major threat to native ant communities in areas of co-occurrence. We described native ant community structure and spatial distribution of Argentine ants in coastal southern California. We investigated the relationship between Argentine ants and distance to urban/agricultural edges and watercourses, and measured changes in the native ant community when in the presence of Argentine ants. We sampled 172 sites distributed across 20 geographic areas located in Los Angeles, San Bernardino, and Orange counties from 1999 through 2003. We identified 53 native ant species (in 24 genera) and 3 exotic ant species. Argentine ants were more likely encountered within 200 meters of urban and agricultural edges. Native ant community richness was substantially reduced when Argentine ants were present. For 37,000 acres of protected conservation lands in the region, 24% of the total land area fell within 200m of urban/agricultural areas in 1992. Following complete build out of areas surrounding conservation lands, the value increased to 44%. In areas identified as vulnerable to Argentine ant invasion, the native ant community is threatened with displacement and many basic ecological processes are likely to be disrupted.

Keywords: edge effects, *Linepithema humile*, biological invasion, Argentine ants, southern California ant community

Introduction

Ants are surface and subterranean predators of small arthropods, generalist scavengers, granivores, detritivores, leaf-cutters that farm fungus, and tenders of aphids and scale insects (Hölldobler and Wilson 1990). Ants perform a variety of ecological functions in terrestrial ecosystems, including cycling of nutrients and organic matter, turning over of soil, dispersal of seeds, and predation and scavenging of small animals (Hölldobler and Wilson 1990, Folgarti 1998, MacMahon et al. 2000). Ants sheer number and great diversity make them significant ecological components in most terrestrial communities worldwide (Hölldobler and Wilson 1990).

In California, the ant fauna shows considerable diversity and regional endemism. In total, 281 species in 44 genera have been identified in the state with 39 of the species, or 15% of the total native ant fauna, considered to be endemic (Ward 2005). Within this fauna, introduced species are also present. In total, 26 introduced species have been identified within the state although most are largely confined to disturbed sites at low elevations (Ward 2005).

One of the most ecologically important introduced ant species in California is the Argentine ant (*Linepithema humile*). Native to northern Argentina (Wild 2004), *L. humile* has invaded areas with suitable climates, especially Mediterranean-type ecosystems, worldwide (Suarez et al. 2001, Tsutsui et al. 2001). In invaded landscapes Argentine ants are restricted primarily to disturbed areas, but have shown the ability to invade natural areas (Suarez et al. 1998, Suarez et al. 2001). Where Argentine ants are present, the above ground native ant fauna and local arthropod community is often displaced (Erickson 1971, Tremper 1976, Ward 1987, Holway 1995, Cammel et al. 1996, Human and Gordon 1996, Holway 1998b, Suarez et al. 1998). This displacement is presumed to lead to the disruption of a number of key ecological processes within invaded terrestrial communities (Holway et al. 2002, Holway and Suarez 2006).

Because of the significant ecological threat that Argentine ants present to native ecological systems, the spatial patterns of occurrence and potential for Argentine ant invasion should be of great interest to conservation biologists, land managers, and land planners designing and managing terrestrial nature reserves in regions where Argentine ants are known to occur. With Argentine ants typically invading natural landscapes through the wildland-urban interface (Suarez et al. 1998), vulnerability of conservation lands to invasion depends largely on both the spatial arrangement of the urban/agricultural edge and distance from these edges across which Argentine ants are able to successfully invade.

In this paper, we describe the structure of the native ant community and distribution of the Argentine ant within coastal lowland areas of southern California, a region presently experiencing rapid rates of land-use change. We ask at what distances are urban/agricultural edges and watercourses important in explaining Argentine ant presence at the landscape-scale and explore how the native ant community changes in the presence of Argentine ants. In addition, based on recovered spatial patterns of Argentine ant invasion, we measure current and projected vulnerability of conservation lands in Orange County, California to invasion.

Methods and materials

From October 1999 through January 2003, we sampled 172 sites distributed across 20 geographic areas in coastal sage scrub dominated foothills and lowlands of coastal southern California (table 1; fig.1). The 20 geographic areas were concentrated in Los Angeles and Orange Counties with individual sites stratified across a range of distances from urban and agricultural edges and embedded in both isolated and large contiguous natural landscapes. Site locations were selected in association with coastal locations of pitfall arrays sampled as part of a USGS monitoring project designed to collect baseline data on the distribution of reptiles and amphibians across southern California (Fisher and Case 2000). Sites were typically sampled every several months throughout the study, with each site sampled on a minimum of 5 and maximum of 14 occasions. At a site, we placed five pitfall traps (50mL tubes) in a pattern resembling the five on a die with the corner traps being 20m apart. We dug traps into the ground so the lip of each tube was flush with the surface, filled them with antifreeze (???), and left them open to capture and preserve ants during each collection period. A single collection period, or sample occasion, lasted for ten consecutive days. In total, compiled data represents 1,161 sample occasions or 58,050 individual trap nights.

To compare the distribution of native ant species across sample sites, we constructed likelihood-based models of site occupancy for the top 12 most frequently detected native ant species using the program PRESENCE (MacKenzie et al. 2002). We included the presence/absence of *L. humile* as a site covariate in the 12 models to assess the importance of Argentine ants in explaining occupancy patterns of individual species. We also constructed site occupancy models for *L. humile*. In the Argentine ant models we included site covariates to assess the importance of landscape-level patterns in explaining species presence and absence. Using GIS (California Department of Forestry and Fire Protection; Fire and Resource Assessment Program 2002 – Statewide Composite of Digital Vegetation and Habitat Data) we characterized sites by their distance from urban/agricultural edges and watercourses. We defined four distance variables (<100m, <200m, <300m, and <500m) from urban/agricultural edges and a single distance variable (W<50m) that differentiated sites located less than and greater than 50m from mapped watercourses. The candidate set of models were ranked according to AIC criteria (Akaike 1973) and parameter estimates (i.e. site occupancy, local extinction, and detection probability) model-averaged using Akaike weights to derive a weighted average.

Using the Mann-Whitney test, we checked for difference in the density of native ants between sites grouped by distance to urban/agricultural edges and sites with and without Argentine ants. We tested for the relationship between increases in the proportion of sites occupied by Argentine ants and mean native species richness across geographic areas using least-squares linear regression. At sites where Argentine ants were detected, we used a one-way ANOVA to compare differences in species richness by Argentine ant activity levels. Lastly, using GIS and the results from the occupancy modeling, we estimate the total acreage of conservation lands in central and coastal Orange County vulnerable to Argentine ant invasion by buffering urban and agricultural areas by the values of the distance variables found in the highest ranking occupancy model and overlay the results across present-day reserve boundaries.

Results

A total of 53 native ant species (in 24 genera) and 3 exotic species (*Linepithema humile*, *Cardiocondyla ectopia*, and *Monomorium pharaonis*) were found during the surveys (table 2). The number of native ant species detected represents 21% of the total native ant species and 55% of the genera recognized to occur within California.

The distribution of different ant species varied widely across the study area. For the top twelve captured native species, individual distributions ranged from 16 to 83% of the total number of sampled sites (fig. 2a). Naïve estimates of occupancy, for most species included in the modeling process, closely matched model estimates (fig. 2a). This is not surprising given naïve estimates were derived from an exceptionally large number of sample occasions (1,161). It is interesting naïve estimate of site occupancy for three of the most commonly captured species, *Temnothorax andrei* (LEAN), *Neivamyrmex californicus* (NECA), and *Neivamyrmex nigrescens* (NENI), were much lower than modeled estimates of occupancy. Although sample sizes were large, the low rates of detection suffered by each of these species (mean probability of detection ± SE: 11 ± 4%; fig. 2b) relative to the other most commonly captured species (40 ± 5%) apparently lead to a discrepancy in the estimates, not a uncommon result in studies where species rates of detection are much less than one (MacKenzie et al. 2005).

The Argentine ant was detected in 17 of 20 geographic areas (86%) and 58 of 172 surveyed sites (naïve estimate of occupancy: 34%). Highest ranking occupancy model included only the site covariate: <200m from urban/agricultural areas (table 3). According to the highest ranking model there was a 75% chance that sites falling within 200m of an urban or agricultural area were occupied by Argentine ants. Outside of 200m, the model indicates that the probability of site occupancy drops to 10%. Whether or not perennial or ephemeral watercourses were present within 50m of survey sites was not important when included as the sole site covariate in the model or when distance to urban/agriculture was already included in the model (i.e. AIC score increased when W<50m to watercourses was included in either model). Model-averaged estimate of annual site occupancy for the species was 29 ± 1% (± 1 SE), annual extinction rate (partially offset by an uncalculated colonization rate) was 9 ± 3%, and probability of detection was 76 ± 2%.

Across geographic areas and between sites, the presence of Argentine ants was correlated with a diminished native ant community. In line with the spatial patterns exhibited by Argentine ants, we discovered large differences in the number of native ant species detected between sites located within (Mean ± 1 SE: 5.4 ± 0.6, $n = 44$) and beyond (8.8 ± 0.3, $n = 128$) 200m of urban and agricultural areas (Mann -Whitney test: $U = 4351$, $P < 0.001$, $n = 172$). Across geographic areas the average number of native ant species detected declined as the proportion of sites within each geographic area with Argentine ants increased ($t = -4.948$, $R^2 = 0.58$, $P < 0.001$, $n = 20$; fig. 3). Across sites the richness of the native ant community was also much reduced in the presence of Argentine ants (fig. 4). The density of native species at sites with *Linepithema humile* was significantly lower than sites without *L. humile* ($U = 5272.5$, $P < 0.001$, $n = 172$; mean, median, and SE of native ant species at 58 sites with *L. humile*: 4.9, 3.5, and 0.5; at 114 sites without *L. humile*: 8.9, 9.0, and 0.3).

At sites where Argentine ants were present, the native ant community appeared sensitive to the level of Argentine ant activity (i.e. Argentine ant abundance). Measuring the average number of Argentine ants collected per 10-day sample period, we defined three different levels of Argentine ant activity (Level 1: < 1 Argentine ant collected per 10-day sample period; Level 2: ≥ 1 and < 10; and Level 3: ≥ 10). Comparing the mean number of native ant species detected between levels, we found a significant decline in the number of native ant species present as Argentine ant activity increased ($F_2 = 7.137$, $P < 0.01$, $n = 58$; Mean [± 1 SE] native ant species richness by Argentine activity level 1: 7.2 ± 0.9, $n = 22$; level 2: 3.8 ± 0.7, $n = 26$; and level 3: 2.7 ± 0.8, $n = 10$).

Interestingly, sensitivity to the presence of Argentine ants was not consistent across native species. Of the top 12 distributed native ants of the genus *Neivamyrmex* (army ants), and the species *Tapinoma sessile* (maloderous house ant), *Crematogaster californica*, and *Pheidole hyatti* were the most sensitive to the presence of Argentine ants, while *Temnothorax Andrei*, *Solenopsis molesta* (thief ant), *Prenolepis imparis* (winter ant), and *Dorymyrmex insanus* (crazy ant) were the least sensitive (fig. 2c).

Lastly, using 200m from urban and agricultural edges as the distance variable that best explains Argentine ant presence at the landscape level, we calculated the total acreage of conservation lands protected under regional federal and state habitat plans in central and coastal Orange County (see http://www.naturereserveoc.org/) susceptible to Argentine ant invasion. Surprisingly, we found a large proportion of the total mapped conservation areas to be vulnerable. Presently, the total acreage of conservation lands, as mapped by County of Orange, Resources and Development Management Department (http://www.ocplanning.net/), is 36,923 acres. In 1992, 8,889 acres (or 24%) of the total acreage of the reserve fell within 200m of mapped urban and agricultural areas. With complete build-out of lands surrounding the reserve, 16,283 acres (or 44%) of the total reserve area will be located within 200m of urban and/or agricultural areas.

Discussion

In describing native ant community structure, landscape-level patterns of Argentine ant invasion, and displacement of native ant species in the presence of Argentine ants in coastal lowland areas of southern California, we demonstrated the significance of the Argentine ant invasion for ant diversity in southern California and quantified the vulnerability of protected conservation lands in Orange County to invasion. Our results show across large geographic areas of coastal southern California, scrublands located within 200 meters of urban and agricultural areas are highly vulnerable to invasion by Argentine ants. At sites invaded by Argentine ants, the native ant community is often displaced with median species richness declining on average by more than 60% relative to non-invaded sites. Buffering mapped urban and agricultural areas in Orange County by 200 meters showed the total acreage of reserve lands identified as vulnerable to invasion ranged from 24 to 44% of total reserve area, with the actual value dependent on current development status of the open-space surrounding reserve boundaries.

In agreement with our results, previous studies of Argentine ant invasions in coastal southern California have also identified 200m as the distance from the urban-scrub interface across which Argentine ants successfully invade natural areas. Within isolated habitat fragments in urbanized areas of San Diego County, approximately 130 km south of our study sites, Argentine ants showed a sharp decline in abundance/presence with increasing distance from the urban-scrub interface. Within the habitat fragments, Argentine ants were rarely detected beyond 200 meters from the wildland-urban interface (Suarez et al. 1998, Bolger et al. 2000). The consistency in measures between the studies is interesting because the studies are measuring the effects of urbanization and habitat fragmentation on Argentine ant invasion success at different spatial scales. In both Suarez et al. (1998) and Bolger et al. (2000) sample locations were largely limited to habitat fragments less than 100 ha in size. In our study, approximately 90% of our 172 sample sites were embedded in large contiguous natural landscapes >15,000 ha in size and stratified across a range of distances from the urban-wildland interface. The similarity across studies in the patterns of invasion suggests that invasion is truly an edge effect and not solely an artifact of the insularization of natural areas in heavily urbanized landscapes.

The absence of watercourses as a site covariate in the highest ranking occupancy model is of interest given the positive association between riparian areas and Argentine ant abundance identified in earlier studies (Holway 2005; Holway and Suarez et al. 2006). In these studies, the authors describe a sharp drop off in argentine ant abundance and soil moisture level when sampling outside of the riparian corridor and thus by 50m argentine ants might be uncommon enough for watercourses to fail as a good predictor of occurrence at the landscape-scale. In addition, mapped watercourses in our study included both perennial and seasonal streams. The inclusion of ephemeral streams in the analysis might explain why we did not find a strong relationship between argentine ants and riparian areas, as moisture levels associated with these systems would be expected to be much lower than streams with perennial flows.

In addition to documenting landscape-level patterns of *L. humile* occurrence, our results show local scale displacement of the native ant community in the presence of Argentine ants, well documented across a number of field sites in California (Ward 1987, Suarez et al. 1998, Holway and Suarez 2006), is being repeated throughout the coastal southern California region. In agreement with previous studies (Ward 1987, Suarez et al. 1998, Holway 1998a, Holway et al. 2002), we found the epigeic, or above ground native ant community, is largely being displaced at invaded sites, with ecologically similar (e.g. *Tapinoma sessile*) and dispersal-limited species *Neivamyrmex spp.* appearing to be the most sensitive. Also consistent with other studies, the four least sensitive species identified in our study and those thought to compete the least with *L. humile*, *Prenolepis imparis, Dorymyrmex insanus, Temnothorax andrei,* and *Solenopsis molesta,* are the same species that persisted the longest in invaded natural habitats in San Diego (Suarez et al. 1998), and for *P. imparis* and *D. insanus*, in others areas of California (Tremper 1976, Ward 1987, Holway 1998a).

The displacement of native ants, largely through the combined effects of interference and exploitative competition (Human and Gordon 1996) and the direct raiding of nests (Ward 1987; unpublished observation by M.J. Mitrovich), is suggested to result in large ecological consequences for invaded landscapes (see review by Holway et al 2002). In southern California, declines in terrestrial mammal (Laakkonen et al. 2001) and reptile (Fisher et al. 2002) species, reduced abundance of invertebrate populations (Bolger et al. 2000), and disruption of key ecological processes (Holway and Suarez 2006), have been linked to *L. humile* invasion.

Consequences of invasion become meaningful to conservation biologists, land planners, and land managers if large amounts of protected lands are found to be vulnerable to invasion. This is what we have shown with respect to the conservation lands in central and coastal Orange County. In Orange County the linear and fragmented design of the reserve system contributed much to its high measure of vulnerability. Because Argentine ants are difficult to control and nearly impossible to eradicate once established (Holway et al. 2002; Holway and Suarez 2006), the importance of reserve design in minimizing the occurrence of Argentine ants on reserve lands is highlighted. Unfortunately, in other areas of coastal southern California established and proposed land reserves appear to be also substantially fragmented and linear in design (see http://www.dfg.ca.gov/nccp/), thus the likelihood of ecological processes being disrupted on these lands is equally high.

In conclusion, given that (1) native ants are considered to be critical components of most terrestrial ecosystems, (2) native ants are readily displaced in the presence of Argentine ants, and (3) regional conservation areas are likely to be vulnerable to invasion due to their often linear and fragmented design, we can identify *L. humile* as a significant threat to the ecological integrity of protected lands within coastal southern California and predict that within invaded landscapes many basic ecological processes will be disrupted.

References

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Cazakil, editors. Proceedings of the second international symposium information theory. Akademiai Kidao, Budapest, Hungary.

Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case. 2000. Arthropods in urban fragments in southern California: area, age and edge effects. Ecological Applications 10:1230-1248.

Cammell, M. E., M. J. Way, and M. R. Paiva. 1996. Diversity and structure of ant communities associated with oak, pine, eucalyptus and arable habitats in Portugal. Insect Society 43: 37-46.

Erickson, J. M. 1971. The displacement of native ant species by the introduced Argentine ant, Iridomyrmex humilis Mayr. Psyche 78: 257-266.

Fisher, R. N., and T. J. Case. 2000. Distribution of the herpetofauna of coastal southern California with reference to elevation effects, pp. 137-143 In J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham (eds.), 2nd Interface between ecology and land development in California. U.S. Geological Survey Open-File Report 00-62, Sacramento, California.

Fisher, R. N., A. V. Suarez, and T. J. Case. 2002. Spatial patterns in the abundance of the Coastal Horned Lizard. Conservation Biology 16: 205-215.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7: 1221-1244.

Hölldobler, B., and E. O. Wilson. 1990. The Ants. Cambridge, Massachusetts: Belknap.

Holway, D.A. 1995. Distribution of the Argentine ant (Linepithema humile) in northern California. Conservation Biology 9: 1634 – 1637.

Holway, D.A. 1998a. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. Oecologia 116: 252-258.

Holway, D.A. 1998b. Factors governing rate of invasions: a natural experiment using Argentine ants. Oecologia 115: 206-212.

Holway, D. A. 2005. Edge effects of an invasive species across a natural ecological boundary. Biological Conservation 121: 561-567.

Holway, D. A., and T. J. Case. 2001. Effects of colony level variation on competitive ability in the invasive Argentine ant. Animal Behavior 61: 1181-1192.

Holway, D.A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002. The causes and consequences of ant invasions. Annual Review of Ecology and Systematics 33: 181-233.

Holway, D. A., and A. V. Suarez. 2006. Homogenization of ant communities in mediterranean California: the effects of urbanization and invasion. Biological Conservation 127: 319-326.

Human, K. G. and D. M. Gordon. 1996. Exploitation and interference competition between the invasive Argentine ant, Linepithema humile, and native ant species. Oecologia 105: 405-412.

Laakkonen, J., R. N. Fisher, and T. J. Case. 2001. Effect of land cover, habitat fragmentation and ant colonies on the distribution of and abundance of shrews in southern California. Journal of Animal Ecology 70: 776-788.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

MacKenzie, D. I., J. D. Nichols, N. Sutton, K. Kawanishi, and L. L. Bailey. 2005. Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101-1113.

MacMahon, J. A., J. F. Mull., and T. O. Crist. 2000. Harvester ants (Pogonomyrmex spp.): their community and ecosystem influences. Annual Review of Ecology and Systematics 31: 265-291.

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.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79: 2041-2056.

Suarez, A. V., D. A. Holway, and T. J. Case. 2001. Paterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proceedings National Academy of Sciences USA 98: 1095-1100.

Tremper, B. S. 1976. Distribution of the Argentine ant, Iridomyrmex humilis Mayr, in relation to certain native ants of California: ecological, physiological, and behavioral aspects. PhD thesis. University of California, at Berkeley.

Tsutsui, N. D., A. V. Suarez, D. A. Holway, and T. J. Case. 2001. Relationships among native and introduced populations of the Argentine ant (Linepithema humile) and the source of introduced populations. Molecular Ecology 10: 2151-2161.

Ward, P.S. 1987. Distribution of the introduced Argentine ant (Iridomyrmex humilis) in natural habitats of the lower Sacramento Valley and its effect on the indigenous ant fauna. Hilgardia 55: 1-16.

Ward, P. 2005. A synoptic review of the ants of California (Hymenoptera: Formicidae). Zootaxa 936: 1-63.

Wild, A. L. 2004. Taxonomy and distribution of the Argentine ant, Linepithema humile (Hymenoptera: Formicidae). Annals of the Entomological Society of America 97: 1204-1215.

Table 1. Locality information, number of sites, proportion of sites with Argentine ant (*Linepithema humile*) detected, and average native ant species richness for each surveyed geographic area.

Area No.	Area ID	County	# Sites	Proportion of sites with *L. humile*	Native ant species richness (Mean ± 1 SE)
1	Puente Hills 1	Los Angeles	8	0.63	4.9 ± 1.0
2	Puente Hills 2	Los Angeles	4	0.75	5.5 ± 1.2
3	Puente Hills 3	Los Angeles	3	1.00	5.0 ± 0.6
4	Puente Hills 4	Orange	4	1.00	2.3 ± 1.6
5	Chino Hills State Park 1	Orange	3	0.00	11.3 ± 1.9
6	Unocal	Orange	3	1.00	1.0 ± 0.0
7	Chino Hills State Park 2	Orange	13	0.08	6.3 ± 0.7
8	Chino Hills State Park 3	San Bernardino	9	0.11	6.0 ± 1.0
9	Coal Canyon	Orange	7	0.22	6.1 ± 1.7
10	Weir Canyon	Orange	12	0.00	11.5 ± 0.7
11	Orange Hills	Orange	5	1.00	2.4 ± 0.5
12	Peters Canyon Regional Park	Orange	5	1.00	9.6 ± 2.5
13	Rattlesnake Reservoir	Orange	5	1.00	3.4 ± 0.9
14	Limestone Canyon	Orange	19	0.16	10.0 ± 0.9
15	Agua Chinon	Orange	7	0.29	7.1 ± 1.5
16	UC Irvine Ecological Preserve	Orange	5	1.00	2.2 ± 0.8
17	Southern California Edison Parcel	Orange	5	0.00	14.2 ± 1.4
18	San Joaquin Hills	Orange	21	0.33	8.2 ± 0.7
19	Audubon Starr Ranch Sanctuary	Orange	17	0.06	10.0 ± 0.7
20	Aliso & Wood Canyons Wilderness Park	Orange	17	0.29	7.1 ± 0.5

Table 2. List of ant species detected within the 20 geographic areas across the 172 sites. Asterisk indicates exotic species. Numbers describing geographic areas where species were detected refer to table 1.

Family Formicidae	Geographic Area
Subfamily Ecitoninae	
Neivamyrmex californicus	5, 7, 10, 12, 13, 14, 17, 18, 19, 20
Neivamyrmex nigrescens	5, 7, 8, 9, 10, 14, 15, 17, 18, 19
Neivamyrmex opacithorax	19
Subfamily Pseudomyrmecinae	
Pseudomyrmex apache	7, 17
Subfamily Dolichoderinae	
Dorymyrmex bicolor	7, 8, 9, 10, 12, 13, 14, 15, 17, 18, 19
Dorymyrmex insanus	1, 5, 6, 7, 8, 9, 10, 12, 14, 15, 17, 18, 19, 20
Forelius foetidus	7, 8, 9, 10, 13, 14, 17, 19
Forelius pruinosus	7, 8, 10, 11, 12, 13, 14, 17, 19, 20
*Linepithema humile**	1, 2, 3, 4, 6, 7, 8, 9, 11, 12, 13, 14, 15, 16, 18, 19, 20
Liometopum occidentale	8, 10, 19, 20
Tapinoma sessile	1, 2, 5, 7, 8, 9, 10, 14, 15, 16, 17, 18, 19, 20
Subfamily Formicinae	
Brachymyrmex depilis	18
Camponotus sayi	12, 14, 17, 20
Camponotus semitestaceus	11, 20
Camponotus spp. CA-01	9, 10
Camponotus vicinus	1
Formica francoeuri	8, 9, 15, 20
Formica moki	1, 2, 7, 8, 9, 10, 12, 14, 15, 16, 17, 18, 19, 20
Formica xerophila	19
Myrmecocystus kennedyi	1, 7, 8, 10, 15, 17
Myrmecocystus mexicanus	9, 12
Myrmecocystus mimicus	1, 7, 8, 9, 10, 12, 14, 15, 17, 18, 19, 20
Myrmecocystus semirufus	12, 20
Myrmecocystus testaceus	5, 7, 8, 9, 10, 12, 14, 15, 17, 18
Paratrechina c.f. terricola	1, 2, 7, 10, 12, 14, 15
Polyergus breviceps	17
Prenolepis imparis	1, 2, 3, 5, 6, 8, 9, 10, 12, 14, 16, 18, 19, 20
Subfamily Myrmicinae	
*Cardiocondyla ectopia**	14, 20
Crematogaster californica	1, 2, 5, 7, 8, 9, 10, 12, 13, 14, 15, 16, 17, 18, 19, 20
Crematogaster coarctata	7, 10, 12, 14, 17, 18, 19, 20
Crematogaster hespera	2, 5, 7, 9, 10, 12, 14, 17, 18, 19
Crematogaster mormonum	7, 14, 18, 19, 20
Cyphomyrmex wheeleri	10, 14
Temnothorax andrei	1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20

Temnothorax nevadensis	20
Temnothorax nitens	19
Temnothorax sp CA-06	9
Messor andrei	10, 12, 14, 17, 18, 19
Messor stoddardi	5, 10,
Monomorium ergatogyna	4, 5, 7, 8, 10, 12, 14, 17, 18, 19, 20
Monomorium minimum	4, 10, 17, 18, 19
*Monomorium pharaonis**	16
Myrmecina americana	10, 18
Pheidole cerebrosior	3, 4, 8, 9, 12
Pheidole clementensis	2, 5, 7, 8, 14
Pheidole hyatti	1, 2, 3, 4, 5, 7, 8, 9, 10, 11, 12, 13, 14, 15, 17, 18, 19, 20
Pheidole vistana	2, 10, 11, 12, 14, 15, 19
Pogonomyrmex californicus	3, 5, 8, 9, 12, 14, 15, 20
Pogonomyrmex rugosus	10, 14, 18, 19
Pogonomyrmex subnitidus	3, 5, 7, 9, 10, 14
Solenopsis amblychila	5, 7, 8, 10, 13, 14, 15, 19
Solenopsis aurea	3, 4, 5, 7, 10, 11, 12, 14, 15, 17, 19, 20
Solenopsis molesta	1, 2, 3, 4, 5, 7, 8, 9, 13, 14, 16, 17, 18, 19, 20
Solenopsis xyloni	1, 4, 5, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20

Table 3. Summary of model selection procedure for the Argentine ant (*Linepithema humile*). Difference in AIC values between each model and the low-AIC model (ΔAIC); AIC model weights (w), number of parameters in the model (K); overall estimate of the fraction of sites occupied (ψ), annual extinction rate (ε), probability of detection (P), and associated standard error (in parentheses).

Model	ΔAIC	w_i	K	Ψ	ε	P
$\psi(<200\text{m})\varepsilon(\cdot)p(\cdot)$	0.00	0.69	4	0.29 (0.01)	0.09 (0.03)	0.76 (0.02)
$\psi(<200\text{m, W}<50\text{m})\varepsilon(\cdot)p(\cdot)$	1.64	0.31	5	0.29 (0.01)	0.09 (0.03)	0.76 (0.02)
$\psi(<300\text{m})\varepsilon(\cdot)p(\cdot)$	17.06	0.00	4	0.29 (0.01)	0.08 (0.02)	0.76 (0.02)
$\psi(<400\text{m})\varepsilon(\cdot)p(\cdot)$	17.33	0.00	4	0.29 (0.01)	0.08 (0.02)	0.76 (0.02)
$\psi(<500\text{m})\varepsilon(\cdot)p(\cdot)$	27.10	0.00	4	0.29 (0.01)	0.08 (0.02)	0.76 (0.02)
$\psi(<100\text{m})\varepsilon(\cdot)p(\cdot)$	50.23	0.00	4	0.29 (0.03)	0.08 (0.02)	0.76 (0.02)
$\psi(\cdot)\varepsilon(\cdot)p(\cdot)$	83.84	0.00	3	0.29 (0.03)	0.08 (0.02)	0.76 (0.02)
$\psi(\text{W}<50\text{m})\varepsilon(\cdot)p(\cdot)$	87.19	0.00	4	0.29 (0.05)	0.08 (0.02)	0.76 (0.02)
$\psi(\cdot)p(\cdot)$	196.16	0.00	2	0.17 (0.02)	0.00 (0.00)	0.78 (0.02)
Model-averaged estimates				0.29 (0.01)	0.09 (0.03)	0.76 (0.02)

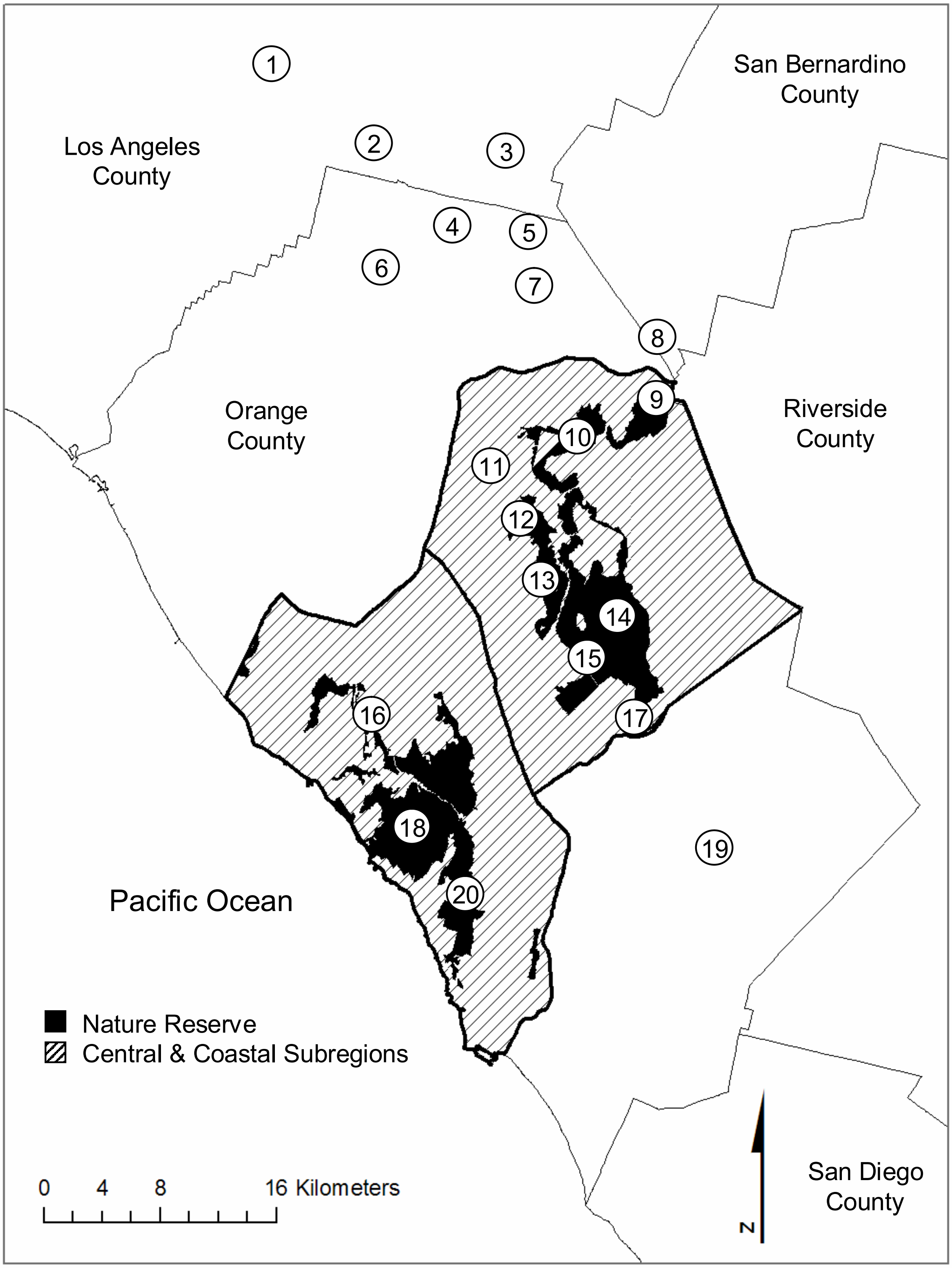
Figures

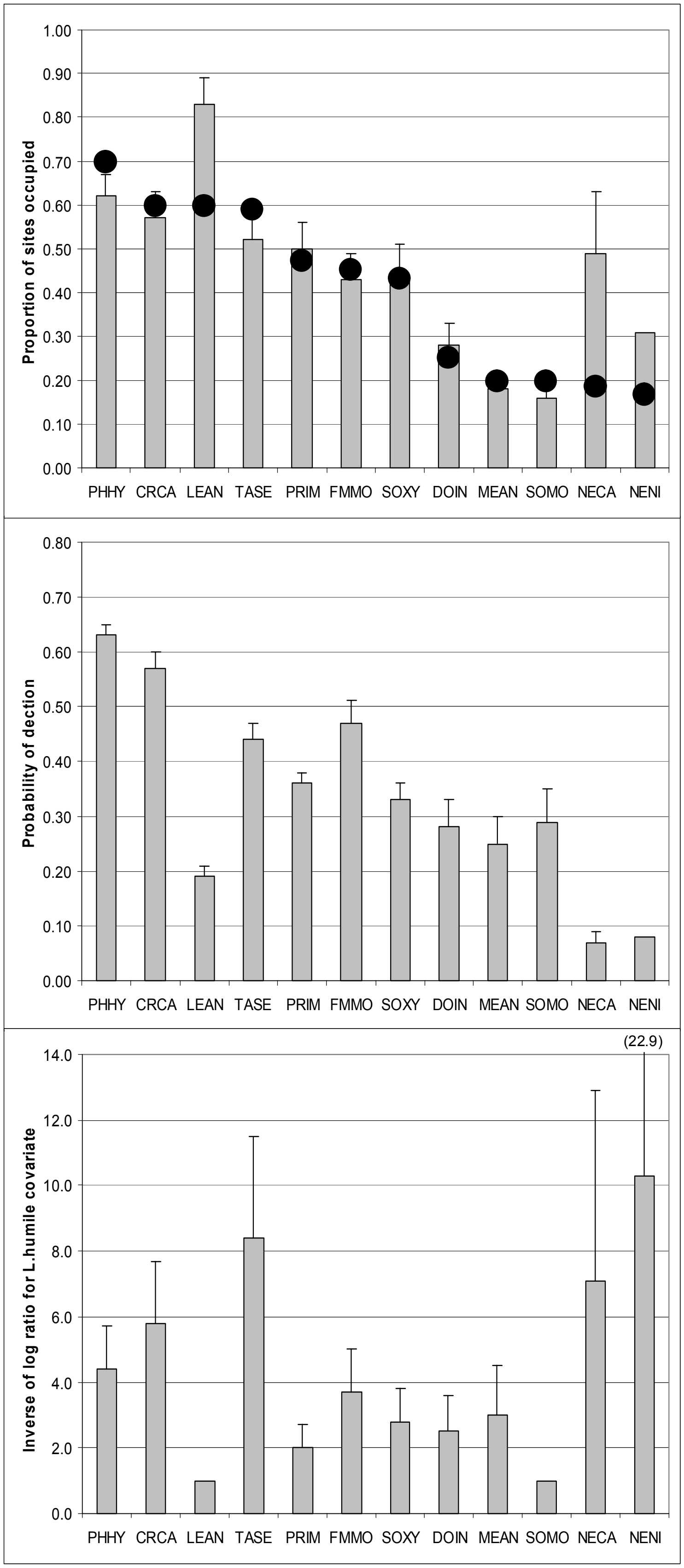
1. Geographic areas (numbered circles) sampled in coastal southern California. Dark polygons indicate distribution of conservation lands in coastal and central subregions (hatched areas) of Orange County, CA evaluated for susceptibility to invasion by Argentine ants.

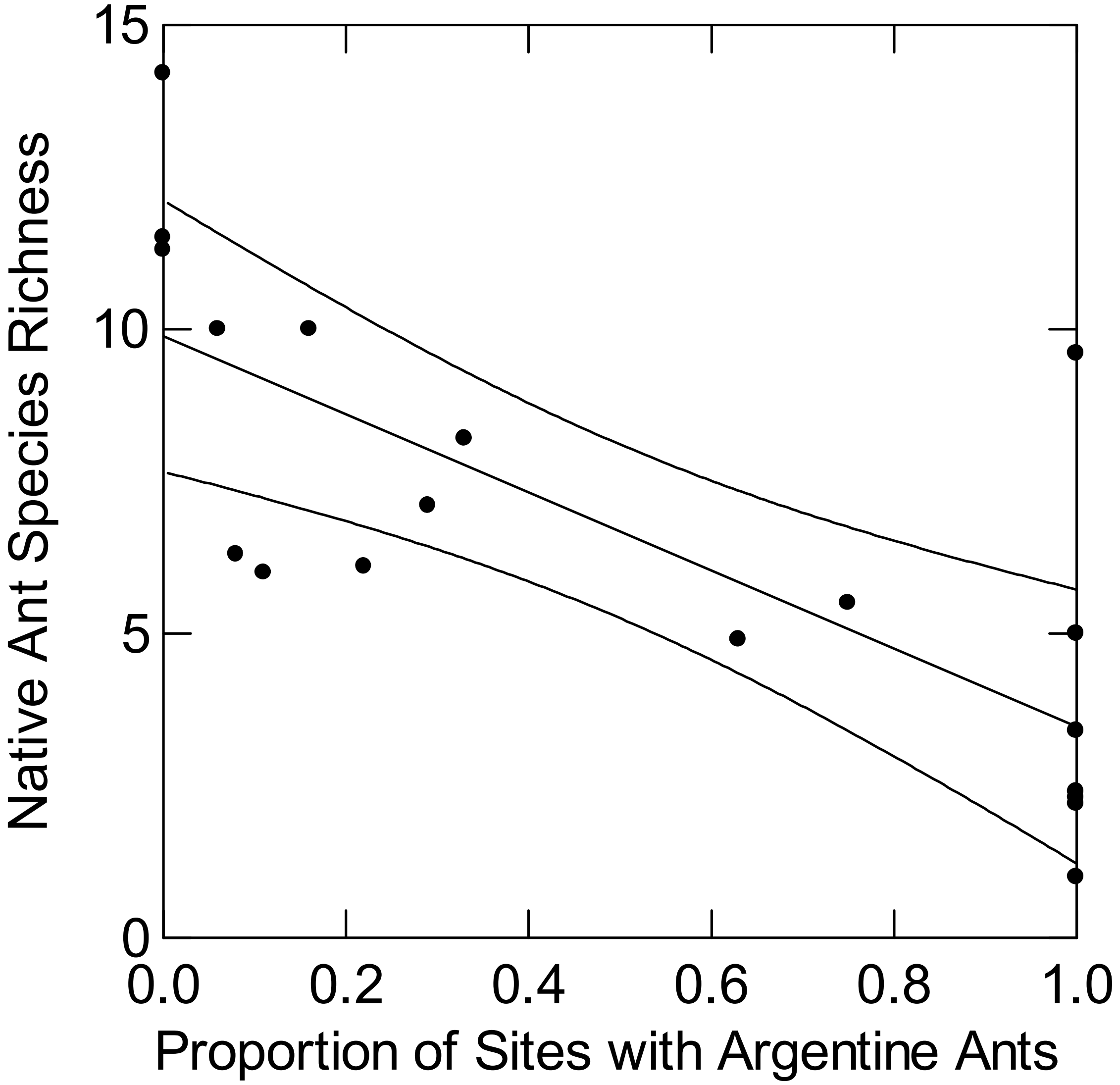
2. Top graph: Naïve estimates (dark circles) and site occupancy estimates of site occupancy (gray bars with error bar equaling +1 SE) for 12 most widely detected native ant species. Middle graph: probability of detection (+1 SE) for same 12 species as estimated by program PRESENCE. Bottom graph: Species-specific sensitivity to the presence of Argentine ants as indicated by the inverse of the log-ratio (+1 SE) for the covariate "L.humile" calculated by program PRESENCE. Note, a value of 1.0 indicates no observed sensitivity to *L. humile* (i.e. model with the presence/absence of *L. humile* included as a site covariate did not rank higher than models that did not take into account the distribution of *L. humile*), a value of 10.0 indicates that a species is 10 times less likely to be present at sites where *L. humile* was detected versus sites where *L. humile* was not detected. PHHY = *Pheidole hyatti*; CRCA = *Crematogaster californica*; LEAN = *Temnothorax andrei*; TASE = *Tapinoma sessile*; PRIM = *Prenolepis impairs*; FMMO = *Formica moki*; SOXY = *Solenopsis xyloni*; DOIN= *Dorymyrmex insanus*; MEAN = *Messor andrei*; SOMO = *Solenopsis molesta*; NECA = *Neivamyrmex californicus*; and NENI = *Neivamyrmex nigrescens*.

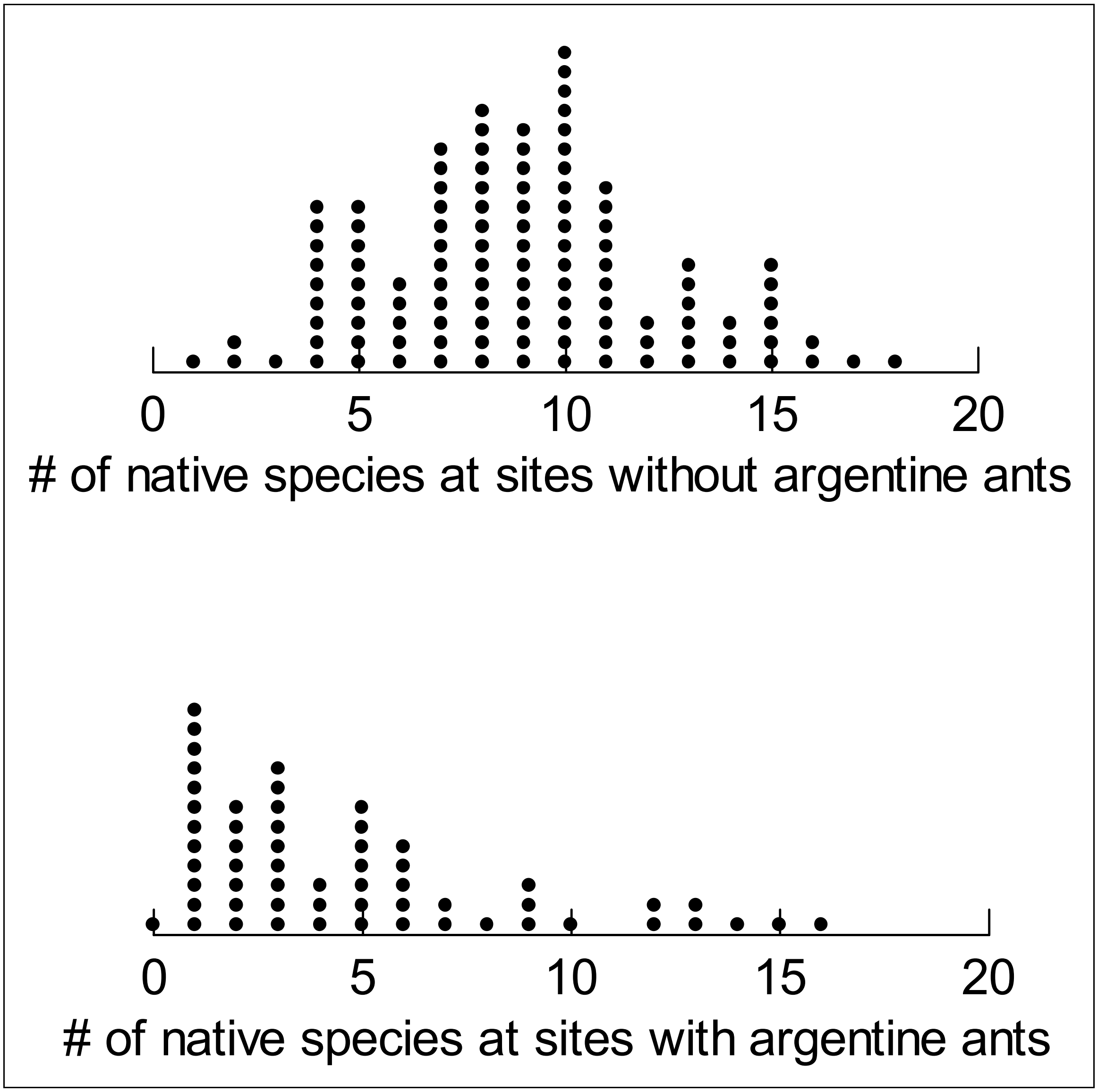
3. Regression (with 95% confidence interval) of the average number of native ant species per site versus the proportion of sites within a sampled geographic area occupied by Argentine ants.

4. Differences in the density of native ant species at sites with and without Argentine ants.


San Bernardino County
1
Los Angeles County
2
3
4
5
6
7
8
9
Orange County
Riverside County
10
11
12
13
14
15
16
17
18
19
20
Pacific Ocean
■ Nature Reserve
▨ Central & Coastal Subregions
0 4 8 16 Kilometers
N
San Diego County


Proportion of sites occupied
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
PHHY CRCA LEAN TASE PRIM FMMO SOXY DOIN MEAN SOMO NECA NENI
Probability of dection
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
PHHY CRCA LEAN TASE PRIM FMMO SOXY DOIN MEAN SOMO NECA NENI
Inverse of log ratio for L.humile covariate
(22.9)
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
PHHY CRCA LEAN TASE PRIM FMMO SOXY DOIN MEAN SOMO NECA NENI


15
10
5
0
0.0
0.2
0.4
0.6
0.8
1.0
Native Ant Species Richness
Proportion of Sites with Argentine Ants


0
5
10
15
20
# of native species at sites without argentine ants
0
5
10
15
20
# of native species at sites with argentine ants