EFFECTS OF FRAGMENTATION AND INVASION ON NATIVE ANT COMMUNITIES IN COASTAL SOUTHERN CALIFORNIA

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Abstract. We investigated the roles of habitat fragmentation and the invasion of an exotic species on the structure of ground-foraging ant communities in 40 scrub habitat fragments in coastal southern California. In particular, we asked: how do fragment age, fragment size, amount of urban edge, percentage of native vegetation, degree of isolation, and the relative abundance of an exotic species, the Argentine ant (*Linepithema humile*) affect native ants? Within these fragments, Argentine ants were more abundant near developed edges and in areas dominated by exotic vegetation. The number of native ground-foraging ant species at any point declined from an average of >7 to <2 species in the presence of the Argentine ant. Among fragments, a stepwise multiple regression revealed that the abundance of Argentine ants, the size of the fragment, and the number of years since it was isolated from larger continuous areas of scrub habitat best predict the number of remaining native ant species. The Argentine ant was found in every fragment surveyed as well as around the edges of larger unfragmented areas. Fragments had fewer native ant species than similar-sized plots within large unfragmented areas, and fragments with Argentine ant-free refugia had more native ant species than those without refugia. The relative vulnerability of native ants to habitat fragmentation and the subsequent presence of Argentine ants vary among species. The most sensitive species include army ants (*Neivamyrmex* spp.) and harvester ants (genera *Messor* and *Pogonomyrmex*), both of which are important to ecosystem-level processes. Our surveys suggest that the Argentine ant is widespread in fragmented coastal scrub habitats in southern California and strongly affects native ant communities.

Key words: ant communities; Argentine ant; biodiversity; biological invasions; conservation; edge effects; extinction; Formicidae; habitat fragmentation; Linepithema humile.

INTRODUCTION

When changes in a community occur, either through habitat modification or the introduction of foreign species, local declines and even extinctions of native species may occur (Pimm 1986). The effects of fragmentation on species loss are now becoming well known (Cody 1993). Other studies have documented detrimental effects on native biota by exotic invaders (see Carey et al. 1996). However, few studies have looked at the effects of fragmentation on the success of invaders as well as the subsequent effect of the invaders on native species resident in fragments.

Habitat fragmentation can affect species richness in a number of ways. When a portion of a larger area is isolated, that portion may only contain a subset of the available species pool due simply to sampling error or spatial heterogeneity (Preston 1962, MacArthur and Wilson 1967). Alternatively, species within the selected area may become extinct after isolation (Bolger et al. 1991). Extinction after isolation can occur by a number of processes. The habitat fragment may not be large enough to support viable subpopulations of some species. These populations may go extinct due to insufficient resources, environmental stochasticity (Shaffer 1981), demographic stochasticity (Shaffer 1981, Gilpin and Soulé 1986, Goodman 1987), loss of allelic diversity (Frankel and Soulé 1981, Gilpin and Soulé 1986, Lande and Barrowclough 1987), an increase in detrimental edge effects (Wilcove 1985, Yahner 1988, Suarez et al. 1997), or the loss of landscape level processes necessary for the survival of populations (Leach and Givnish 1996). The loss of these subpopulations may then have a cascading effect on other species in the community (see Paine 1966, Parrish and Saila 1970).

Habitat fragmentation can also facilitate the introduction of exotics, which either directly compete with, prey upon, parasitize, or otherwise indirectly affect native species. In the last half of this century, many studies and reviews have been published relating to introductions of exotic species (Elton 1958, Diamond and Case 1986, Groves and Burdon 1986, Holdgate 1986, Mooney and Drake 1986, Drake et al. 1989, di Castri et al. 1990, Carlton and Geller 1993, Lodge 1993, Case 1996). Before an exotic species can become estab-

lished, it must first find suitable habitat. Successful invaders are often anthrophilic species that occupy human-modified habitats and are easily dispersed by humans. Successful invaders are also often habitat generalists and therefore not restricted by specific habitat requirements. However, the invading species must still contend with a community of potential competitors that have evolved within that habitat. Many hypotheses have been proposed that describe the characteristics of habitats susceptible to invasion, including simplified or species-poor communities, poorly adapted native species, absence of predators, empty niches, and new niche opportunities generated by disturbance (Elton 1958, Orians 1986, Fox and Fox 1986, Swincer 1986, Petren and Case 1996).

Exotic ants have been inadvertently introduced by humans to nearly every continent and island in the world (Williams 1994). One species, the Argentine ant (*Linepithema humile*), has become established worldwide (Majer 1994, Passera 1994). As with most exotic species, there is evidence that the rapid spread of the Argentine ant is associated with human disturbance (Erickson 1971, Ducote 1977, Ward 1987, De Kock and Giliomee 1989, Knight and Rust 1990), however, there is growing evidence for the Argentine ant's ability to invade undisturbed habitat (Cole et al. 1992, Human and Gordon 1996, Holway, *in press*). In areas where it has been introduced, the Argentine ant has displaced native ant species (Erickson 1971, Tremper 1976, Ward 1987, De Kock 1990, Holway 1995, Cammell et al. 1996, Human and Gordon 1996), and even previous ant invaders (Haskins and Haskins 1965, Crowell 1968, Fluker and Beardsley 1970, Lieberburg et al. 1975, Cole et al. 1992). There is also evidence that the Argentine ant can change or reduce the native nonant arthropod community (Cole et al. 1992) as has been documented for *Solenopsis invicta* in the southeastern United States (Porter and Savignano 1990).

In this paper, we investigate the interaction of habitat fragmentation and invasion of Argentine ants in structuring the native epigeic (aboveground foraging) ant community in scrub habitat in coastal southern California. The ground-foraging ant communities were surveyed in 40 isolated fragments and one large continuous area of scrub habitat in San Diego County. Fragments of different ages and sizes associated with the urbanization of San Diego County provide us with an ideal "natural" experiment to investigate the effects of fragmentation and the invasion of Argentine ants on the structure of native ant communities. Previous work on this system of fragments (Soulé et al. 1988, 1992, Bolger et al. 1991, 1997) found indirect evidence for local extinctions of birds and small mammals, but the causes of extinction in these studies are not clear. Specifically, we investigated how fragment characteristics facilitate the invasion of an exotic ant species and how their interaction results in the loss of native species.

METHODS

The Argentine ant (Linepithema humile)

The Argentine ant first appeared in the United States around 1891 in New Orleans (Foster 1908, Newell 1908). Its spread throughout California is thought to have begun near Ontario in western San Bernadino County (Woodworth 1908). The ant spread rapidly throughout citrus groves in southern California and the San Francisco Bay area. The life history of the Argentine ant is similar to other successful ant invaders. It has a generalized diet that includes nectar, insects, seeds, carrion, and honeydew secreted by Homopterans (Woodworth 1908, Horton 1918, Mallis 1942, Flanders 1943, Creighton 1950, Markin 1970a). Colonies have multiple queens, which disperse by budding when queens, along with a large group of workers, split off to form a separate colony. Queens are inseminated within the nest prior to dispersal and do not undergo nuptial flights (Markin 1970b, Bartells 1983).

The Argentine ant has been shown to displace native ant species in an old field near San Diego (Erickson 1971) and in riparian areas in northern California (Tremper 1976, Ward 1987) where, over a 20-yr period, it continued to expand into additional areas (Holway 1995). Argentine ant colonies show almost no intercolonial hostility (Markin 1968, 1970b; A. V. Suarez and T. J. Case, *unpublished data*). Argentine ants typically have polydomous colonies interconnected by foraging trails. Brood is frequently exchanged between colonies and workers will care for any queen encountered (Newell and Barber 1913, Mallis 1942). Colonies are very mobile and will frequently change location throughout the year in response to environmental changes such as an increase or decrease in moisture (Barber 1916). These characteristics, specifically the lack of intercolonial aggression, may contribute to the Argentine ant's superior competitive ability over native ants, which often compete both inter- and intraspecifically for resources with other colonies (e.g., Ryti and Case 1988).

Selection and measurement of habitat fragments

The upland coastal habitats of San Diego County, California, consist of shrub land typical of Mediterranean-climate regions (Westman 1981). The scrub habitats common to coastal southern California can be separated into three vegetation types: "coastal sage scrub," dominated by California sagebrush (*Artemisia californica*), black sage (*Salvia mellifera*), white sage (*Salvia apiana*), and buckwheat (*Eriogonum fasciculatum*); "chamise-chaparral," dominated by thick stands of chamise (*Adenstoma fasciculatum*); and "maritime succulent scrub," similar to coastal sage scrub with an abundance of cacti (*Opuntia* spp.) (Mooney 1977, Bradbury 1978, Westman 1981, Beauchamp 1986).

Habitat fragments were created throughout the last

100 yr as urban and suburban development in San Diego County isolated portions of native scrub land from the surrounding continuous vegetation. The habitat fragments used in this study were selected a priori to span: (1) the variation in the size of the habitat fragment, (2) the number of years since it was isolated from the surrounding continuous vegetation, (3) the remaining percentage of native vegetation, (4) the degree of isolation and, (5) the relative amount of urban edge surrounding the fragment. Because most of the development in San Diego has occurred on the mesa tops and in large drainage systems, the remaining native habitat is restricted to relatively narrow canyons with steep slopes not suitable for development. Many of these patches are the same as those used in previous work on birds, mammals and plants (Soulé et al. 1988, 1992, Bolger et al. 1991, 1997, Alberts et al. 1993). They range latitudinally throughout coastal San Diego County but are restricted to within 15 km of the coast (Fig. 1). A total of 40 fragments were sampled for this study (Table 1).

The area and urban edge length of the habitat fragments were measured using digitized images of scaled aerial photographs taken in 1995. The fragment age is defined as the number of years since isolation from continuous vegetation and was obtained from County records (Soulé et al. 1988). The total percent cover of native vegetation remaining in the fragments was estimated visually from aerial photographs by two independent observers who also walked the length of the habitat fragments. For within-fragment comparisons, this was complemented by vegetation surveys conducted every 100 m along the longest axis of the habitat fragment. At each point, the percent cover of exotic vegetation and the distance to the nearest urban edge was determined. The percent cover of exotic vegetation was placed into five categories: $1 = 0–1\%$ cover; $2 = 2–25\%$ cover; $3 = 26–50\%$ cover; $4 = 51–75\%$ cover; and $5 = 76–100\%$ cover. These points coincide with pitfall sampling.

Because the amount of edge is correlated with fragment area, an irregularity index was computed for each fragment by dividing the actual amount of edge by the circumference of a circle (the geometric shape with the smallest amount of edge per area) of the same area as the fragment. This value represents the amount of urban edge specific to a selected fragment relative to the fragment size.

The degree of isolation was calculated by measuring the distance from each habitat fragment to the nearest core area that contained native ant species. Core areas (Miramar Naval Air Station, Proctor Valley, Otay Valley, Cabrillo National Monument, and Carmel Mountain; Fig. 1) were visited at least once, and visual surveys were conducted to ensure that native ant species were abundant. Distances were measured to the nearest 200 m on the aerial photographs.

The unfragmented control area sampled is located within and adjacent to the Elliot Chaparral Reserve, part of the University of California's Natural Reserve System. The reserve is nested within a larger area of undeveloped scrub land (9254.5 ha) that makes up Miramar Naval Air Station. Plots sampled within the unfragmented control area were chosen to represent areas similar in topography and vegetation to the isolated fragments mentioned above. All plots surveyed were located at least 400 m from the nearest developed edge and 50 m apart. A total of six plots were surveyed representing areas of 1, 4, 10, 20, 30, and 50 ha. Additional sampling, consisting of 12 pitfall trap arrays scattered throughout the 88-ha Elliot reserve, was used to estimate the ant fauna for the entire reserve. While the six plots are all independent of each other, the species list for the reserve includes the data from the plots as well as the additional sampling.

Ant sampling

Sampling consisted of placing an array of five pitfall traps every 100 m along a transect corresponding to the longest axis of the habitat fragment or plot within the continuous area. The number of arrays varied with the size of the fragment or plot and ranged from 1 (fragment number 40) to 11 (fragment number 4) (Table 1). The pitfall traps consisted of 60 mm wide (internal diameter at the mouth), 250-mL (8-oz) glass jars. The jars were placed in a pattern resembling the five on a die with the corner jars being 20 m apart. The traps were filled halfway with a 50:50 water : Sierra brand antifreeze mix. Sierra brand antifreeze (Safe Brands, Omaha, Nebraska, USA) was used because it is nontoxic and works as an excellent preservative of insects. The jars were dug into the ground so the lip of the jar was flush with the surface. The jars were collected after 5 d and all ants counted and identified (Table 2). Pitfall traps are an effective method for sampling ant communities (Andersen 1995, 1997) and provide an estimate of ant activity for each species by counting the number of workers falling into the jars for each 5-d sample period. This measure of activity may be biased due to differences in foraging patterns, colony densities, and size among species (Andersen 1997), however, it is relatively unbiased for comparison among areas within species. Pitfall trapping was repeated up to three times, with sample periods in the fall (August–November 1995), winter (November–February 1995–1996) and spring/summer (April–July 1996). Within each period, the order in which the fragments were sampled was chosen randomly.

In addition to pitfall sampling, extensive visual surveys were conducted in each fragment and control plot. Surveys consisted of walking throughout the area, overturning objects, and aspirating samples of all ants seen. Visual surveys were concentrated in areas between the pitfall sample points to ensure that we were detecting all of the ground-foraging ants within the fragment and not simply constructing species lists for
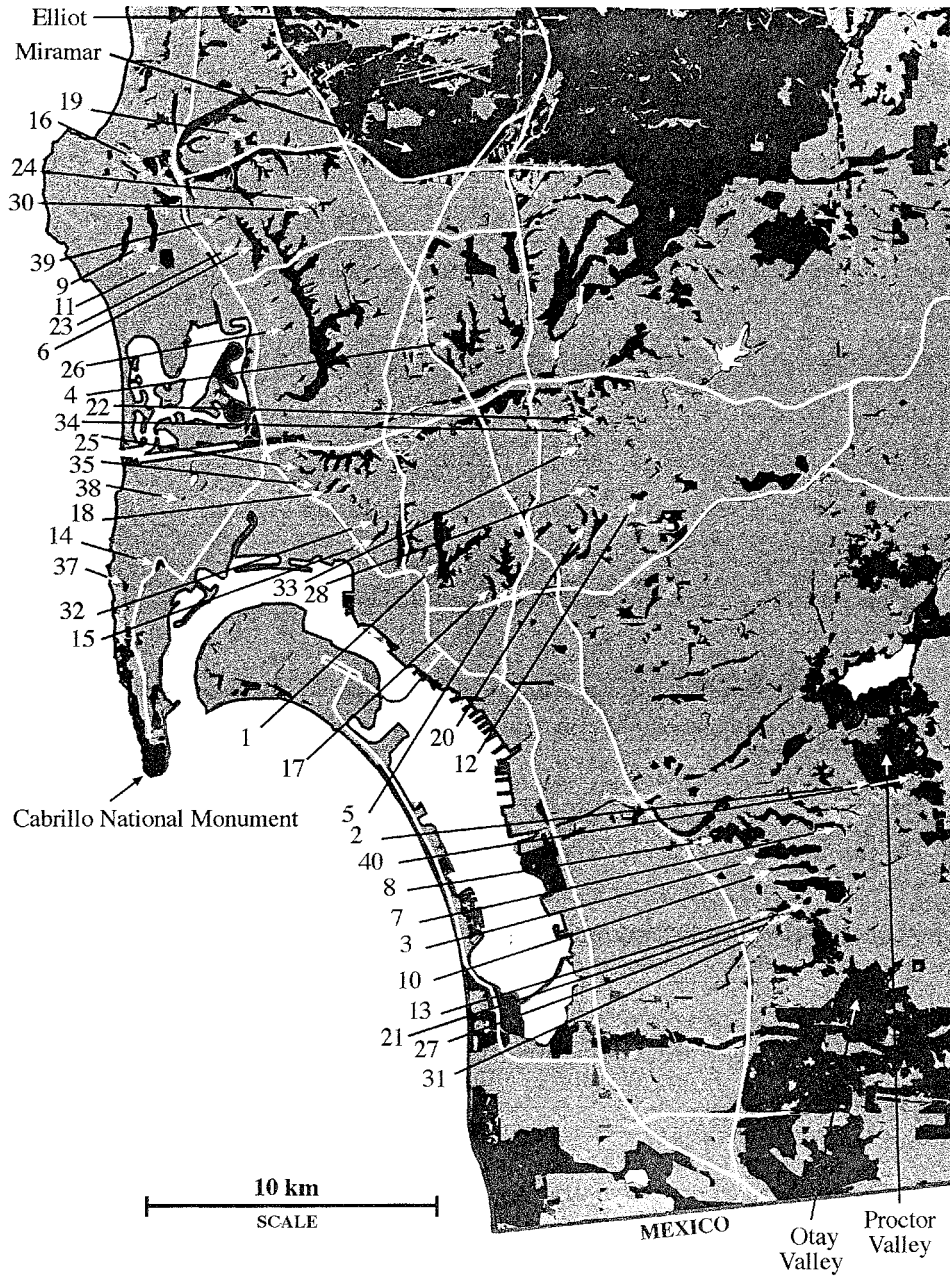
FIG. 1. Map of San Diego County, California, indicating locations of the core areas used to determine isolation distances and 38 of 40 fragments surveyed. The two fragments not shown, Oakcrest (number 29) and Montanosa (number 36), and Carmel Mountain are located within 5 km of the coast ~10 km north of the map area in Encinitas, San Diego County. White lines indicate highways, light gray "background" indicates urbanized areas and open space (non-native vegetation), and black indicates areas with predominately native vegetation.

points within the fragments. Each fragment was visited and inspected visually for ants six times at varying times of day. Occasionally, belowground foraging (hypogeic or cryptobiotic) ants (*Hypoponera* spp., *Stenamma* spp., *Brachymyrmex depilis, Leptothorax nitens*) and arboreal ants (*Pseudomyrmex apache*) were captured or seen during these surveys. These ants do not belong to the guild of ground-foraging ants (Ward

1987, Andersen 1997), are not adequately sampled by pitfall trapping and visual surveys (P. Ward, *personal communication*), and therefore were not included in the analysis. Winged queens and males that were captured in pitfall samples were also not included in the analysis because they may have originated from outside the patch or fragment in which they were found. To ensure that all epigeic ant species were detected and that total

TABLE 1. List of habitat fragments surveyed, including a summary of the measured variables associated with their isolation from continuous scrubland.

Fragment	Fragment number	Total area (ha)	Years since isolation	Remaining native vegetation (%)	Irregularity index	Distance to nearest core area (km)
Florida	1	101.61	59	70	0.400	11.0
Chula Vista Edge	2	100.81	3	90	0.515	0.2
Rice Canyon	3	78.19	3	85	0.545	2.8
Sandmark	4	72.24	29	45	0.579	4.0
34th Street	5	63.9	43	75	0.253	11.8
Balboa Terrace	6	56.36	43	65	0.343	4.2
Bonita Long	7	44.06	8	75	0.581	1.0
Terra Nova	8	44.45	10	90	0.783	4.6
Alta La Jolla	9	34.13	23	50	0.528	7.0
Home Depot	10	31.75	4	85	0.407	3.2
Kate Sessions	11	30.96	25	85	0.753	6.6
Zena	12	14.69	45	30	0.481	6.4
Sage View	13	12.7	19	70	0.439	3.4
Canon	14	11.51	67	20	0.457	1.8
Laural	15	10.16	88	5	0.608	12.0
Pottery	16	9.53	23	50	0.477	4.8
32nd Street	17	9.53	65	15	0.637	12.6
Washington	18	9.39	83	25	0.494	12.0
Syracuse	19	8.73	27	70	0.692	2.6
47th Street	20	8.33	41	40	0.446	10.6
Paseo Del Rey	21	7.94	20	75	0.687	3.6
Baja	22	7.94	40	50	0.435	5.0
Raffee	23	7.94	28	50	0.484	5.2
Acuna	24	7.14	31	30	0.455	1.8
Juan	25	6.75	32	50	0.570	12.2
Edison	26	6.75	17	80	0.596	7.4
Telegraph	27	6.35	19	45	0.377	3.4
Chollas	28	6.35	45	25	0.649	7.4
Oak Crest	29	5.56	15	90	0.828	5.8
Chateau	30	5.56	29	55	0.394	2.6
Sundown	31	5.16	8	40	0.525	3.2
Spruce	32	3.97	95	10	0.578	11.8
60th Street	33	3.97	46	35	0.635	6.0
54th Street	34	3.97	29	50	0.523	5.8
Titus	35	3.18	86	10	0.601	12.2
Montanosa	36	2.78	11	80	0.667	5.0
El Mac	37	2.38	41	60	0.553	1.2
Pointsetta	38	2.38	59	25	0.620	4.2
Camino Coralino	39	1.63	29	20	0.866	4.4
Tarplant	40	0.4	3	85	0.702	0.2

species number for the larger fragments was not biased by sample effort, species accumulation curves were constructed for each fragment. Sample effort for the curves was determined by the cumulative number of pitfall traps and search days within each fragment. Each person search day was given the value of one pitfall trap.

Baits were not used to sample ants because of the Argentine ant's ability to locate and monopolize them (Human and Gordon 1996, Holway, *in press*). Using baits could potentially bias the results towards an increased measure of Argentine ant presence.

Statistical treatments

Two different geographic scales are examined; within- and among-fragment differences in the number of native ants. To examine within-fragment differences, the average number of Argentine ant workers per jar and native ant species per array were calculated for each five-jar pitfall array. The number of native ant species was pooled across sample periods for each array, and the number of Argentine ants per jar was averaged across sample periods for each array. This average was then compared to the amount of exotic vegetation and the distance to the edge of the fragment for each array. All arrays, regardless of the fragment in which they occurred, were considered independently for these analyses. For these analyses, arrays within the control area at and adjacent to the Elliot reserve were not used. A Mann-Whitney U test was used to test for significant differences in ant species richness between categories of Argentine ant activity (0, 1–5, 6–10, 11–20, 21–30, 31–50, and 51–100 ants per jar).

For between-fragment comparisons, an average number of Argentine ants per jar was determined for each fragment by pooling the information from each pitfall array in the fragment for all sampling dates. Linear and stepwise regressions were used to examine correlations between the number of native ant species remaining in a fragment and various independent vari-

TABLE 2. List of ant species detected with our surveys in the 40 isolated habitat fragments and seven control plots, listed by hectare per plot, at the Elliot reserve. Species marked with an asterisk are not aboveground foraging species and were not included in the analyses. Exotic species are in boldface type.

Family Formicidae	Canyon number	Elliot plot
Subfamily Ponerinae		
Hypoponera punctatissima	28	
Hypoponera opacior*	4, 6, 17, 19, 20	
Subfamily Dorylinae		
Neivamyrmex californicus	2, 3, 8, 10	88, 50, 30, 20, 10, 4, 1
Neivamyrmex c.f. *leonardi*		88, 50
Neivamyrmex nigrescens	2	88, 50, 30, 20, 10, 4
Neivamyrmex opacithorax		88, 10
Subfamily Pseudomyrmecinae		
Pseudomyrmex apache*	7, 8	88, 50, 30, 4, 1
Subfamily Dolichoderinae		
Linepithema humile	1–40	88
Tapinoma sessile	2, 3, 7, 8, 10	88, 50, 30, 20, 10, 4, 1
Dorymyrmex insanus	1, 2, 3, 5, 7, 8, 10, 11, 13, 16, 21, 27	88, 50, 30, 20, 10, 4
Dorymyrmex bicolor	1, 2, 3, 10, 21	
Forelius maccooki	2, 3, 7, 8, 10, 21	88, 50, 30, 20, 10, 4, 1
Subfamily Formicinae		
Camponotus dumetorum	16, 24	88, 50, 30
Camponotus yogi	1, 2, 12	88
Camponotus festinatus	2, 7, 11	88, 10
Camponotus vicinus	24	88
Camponotus anthrax		88, 50
Camponotus hyatti	7, 8, 10	88, 10, 4
Camponotus clarithorax	3	
Formica moki	24	88, 50, 30, 20
Formica francoeuri	8	
Myrmecocystus colei	3, 10, 11	88, 50, 20, 10
Myrmecocystus testaceus	11	
Prenolepis imparis	1–12, 14–18, 20, 21, 25, 30–32, 34, 37	88, 50, 30, 20
Brachymyrmex depilis*	1, 16, 18, 22, 25, 28, 37	
Paratrechina cf. *terricola*	3, 10	
Subfamily Myrmicinae		
Cardiocondyla ectopia	5, 14, 18	
Pogonomyrmex subnitidus	14, 29	
Pogonomyrmex californica	1	
Messor andrei	2, 8, 10, 11, 21	88, 50, 30, 20, 10, 4, 1
Pheidole vistana	2, 3, 7, 8, 10, 11	88, 50, 30, 20, 10, 4, 1
Pheidole hyatti	2, 3, 7, 8, 10	
Pheidole californica	2, 3, 7, 10, 27	88
Pheidole tusconica	21, 27	
Pheidole clementensis	2	
Pheidole rugulosa	1, 2	
Pheidole pacifica	1	
Crematogaster californica	1, 2, 3, 7, 8, 10, 11	88, 50, 30, 20, 10, 4, 1
Solenopsis xyloni	1, 2, 3, 7, 8, 10, 11	88, 50, 30, 20, 10, 4, 1
Solenopsis molesta	1–6, 8, 10–29, 32–34, 36–38, 40	88, 50, 30, 20, 10, 4, 1
Solenopsis amblychila	2	
Cyphomyrmex wheeleri	6	
Leptothorax andrei	1–14, 16–19, 21, 23–27, 29–31, 35–38, 40	88, 50, 30, 20, 10, 4, 1
Leptothorax nevadensis	11, 16	88, 50
Leptothorax nitens*		88
Tetramorium spinosum	7, 40	
Stenamma diecki*	5, 7, 12, 29	88, 4, 1
Stenamma californicum*	15, 17, 32	88
Strumigenys silvestrii	5, 28	

ables of the fragment, including the total area, the standardized index of urban edge, the age since the fragment was isolated from the surrounding continuous vegetation, the remaining amount of native vegetation within the fragment, the degree of isolation, and the average Argentine ant activity within the fragment. Non-normal variables were normalized with a log transformation, including the area of the habitat fragment, the age since it was isolated, and Argentine ant

activity. The number of native species within a canyon was (log + 1)-transformed because one canyon had no native species.

The vulnerability of native ant species to fragmentation and Argentine ants was explored with logistic regressions. We used presence/absence rather than abundance because abundance, as measured by number of ants per jar, may be biased by the species foraging method or size. Additionally, a few of the records for
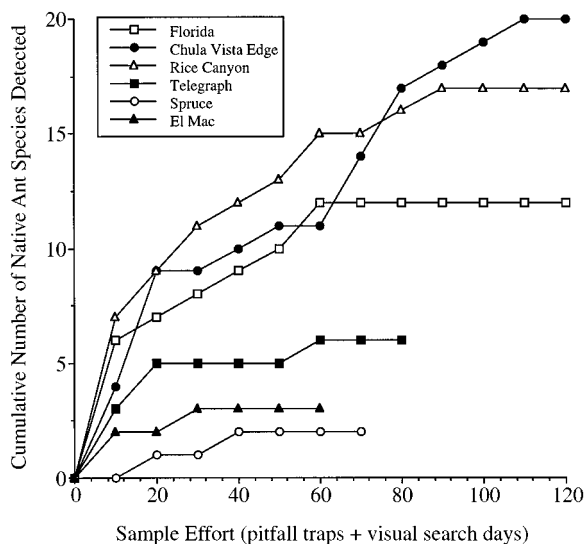
FIG. 2. Species accumulation curves for six representative fragments of various sizes: Florida (101.61 ha), Chula Vista Edge (100.81 ha), Rice (78.19 ha), Telegraph (6.35), Spruce (3.97 ha), and El Mac (2.38 ha). Only native, ground-foraging ants are included in the cumulative number of ant species.
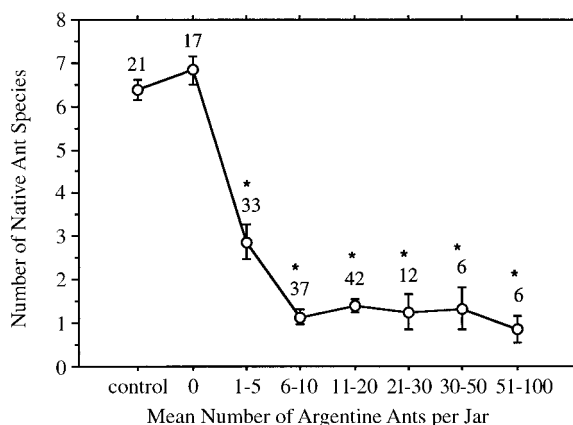

FIG. 3. Relationship between the number of native ant species detected at any given array and the mean number of Argentine ants per pitfall trap at that array. Numbers in the plot indicate the sample size for each category. Control pools sampled arrays from plots at the Elliot reserve where the Argentine ant is absent. Subsequent categories include all points sampled within the 40 habitat fragments. Error bars indicate ± 1 SE. A star above the sample size of a category denotes a significant difference ($P < 0.001$, Mann-Whitney U).

species within the fragments were obtained visually (not from pitfall traps) so it would not be possible to report a value of abundance for those species. The species common enough to include in the analyses were *Solenopsis molesta, Leptothorax andrei, Prenolepis imparis,* and *Dorymyrmex insanus.* Two species, *Solenopsis xyloni* and *Crematogaster californica* were always detected together in the fragments when they occurred so they are represented together in the analyses. Some uncommon species were lumped into generic groups in order to increase the power of the tests. These include the genera *Camponotus, Pheidole,* and *Neivamyrmex.* The genera *Messor* and *Pogonomyrmex* are both commonly referred to as harvester ants because of their diets and behaviors (Davidson 1977*a, b,* Holldobler and Wilson 1990). For this reason, and their importance as food for ant predators such as horned lizards (Pianka and Parker 1975), they were lumped into one group, the harvester ants. The seasonal sampling allows us to look for temporal segregation in activity patterns between the Argentine ant and native ant species.

RESULTS

A total of 46 native ant species and four exotic species [*Linepithema humile* (Mayr), *Cardiocondyla ectopia* (Snelling), *Hypoponera punctatissima* (Roger), and *Strumigenys silvestrii* (Emery)] were found in our surveys (Table 2). Argentine ants were found in every fragment surveyed and along the edges of larger continuous areas of native vegetation. The variables measured for each fragment are summarized in Table 1. Species accumulation curves for all fragments showed

asymptotes in species number and only the second largest fragment did not show a plateau (fragment number 2). Sample curves for three large (numbers 1, 2, and 3) and three smaller fragments (numbers 27, 32, and 37) are shown in Fig. 2.

Between-array comparisons

Considering all the pitfall trap arrays within the fragments, the presence of the Argentine ant correlates with a significant decline in the number of native ant species (Fig. 3). In the presence of the Argentine ant, the average number of native ant species decreases from seven to three. As the average number of Argentine ants increases to >5 workers per jar, <2 species of native ants, on average, continue to coexist with the Argentine ant.

Argentine ant activity was negatively correlated with the distance to the nearest urban edge and positively correlated with the amount of exotic vegetation (Fig 4A, B). On average, Argentine ant activity was high (>5 workers per jar) for all arrays within 100 m from the nearest urban edge. Only at arrays >100 m from the nearest urban edge were Argentine ants found at activity levels <5 workers per jar. The number of native ant species at any array was positively correlated with the distance to the nearest urban edge and negatively correlated with the amount of exotic vegetation (Fig. 4C, D). The amount of exotic vegetation decreases with distance from an urban edge (Fig. 5).

Rice Canyon (fragment number 3) illustrates the roles of urbanization and Argentine ant presence in modifying the native ant community. It was isolated ~3 yr ago (1993) from a larger area of continuous scrub
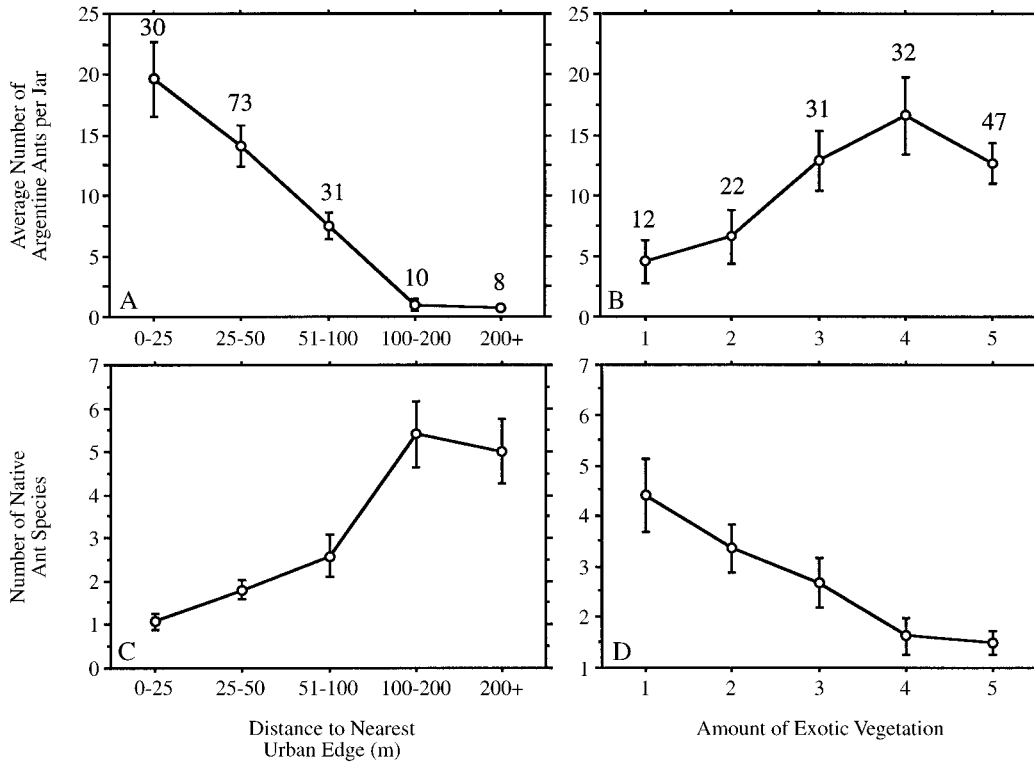
Fig. 4. Associations between Argentine ant activity (average number of workers detected per jar) at any sample array and distance to the nearest urban edge (A) and categories of percent cover of exotic vegetation (B). Association between the number of native ant species detected at any sample array and distance to the nearest urban edge (C) and amount of exotic vegetation (D). The numbers above the points indicate the sample size for each category for all points sampled within the 40 habitat fragments. Error bars indicate ±1 SE. (B, D) 1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–100%.

habitat. Urbanization began at the east and south ends of the canyon and has continued until the present, slowly working its way westward. This has resulted in a gradient of disturbance from the east to west end of

Fig. 5. Correlations between categories of percent cover of exotic vegetation and distance to the nearest urban edge for all sample points within fragments pooled together for all points sampled within the 40 habitat fragments. The numbers above the points indicate the sample size for each category. Error bars indicate ±1 SE.

the fragment. Native ants are still abundant in the west end of the fragment, but the east end is dominated by Argentine ants. The transition between the decline in native ant species and the number of Argentine ants corresponds spatially with the onset of development (Fig. 6).

Among-fragment differences

In bivariate regressions, area ($R^2 = 0.441$, $P < 0.0001$) and percentage native vegetation ($R^2 = 0.349$, $P < 0.0001$) were significantly positively correlated, while age ($R^2 = 0.152$, $P < 0.02$) and Argentine ant activity ($R^2 = 0.483$, $P < 0.0001$) were significantly negatively correlated with the number of native ants species within a canyon. Many of these variables are correlated however (Table 3). The results of a stepwise multiple regression revealed that only area ($P < 0.0001$), age ($P < 0.0005$), and Argentine ant activity ($P < 0.0002$) significantly explained the variance in the number of native ant species among the canyons (Table 4A).

The above analyses were repeated using Argentine ant activity as the dependent variable. The stepwise multiple regression revealed area as the only significant
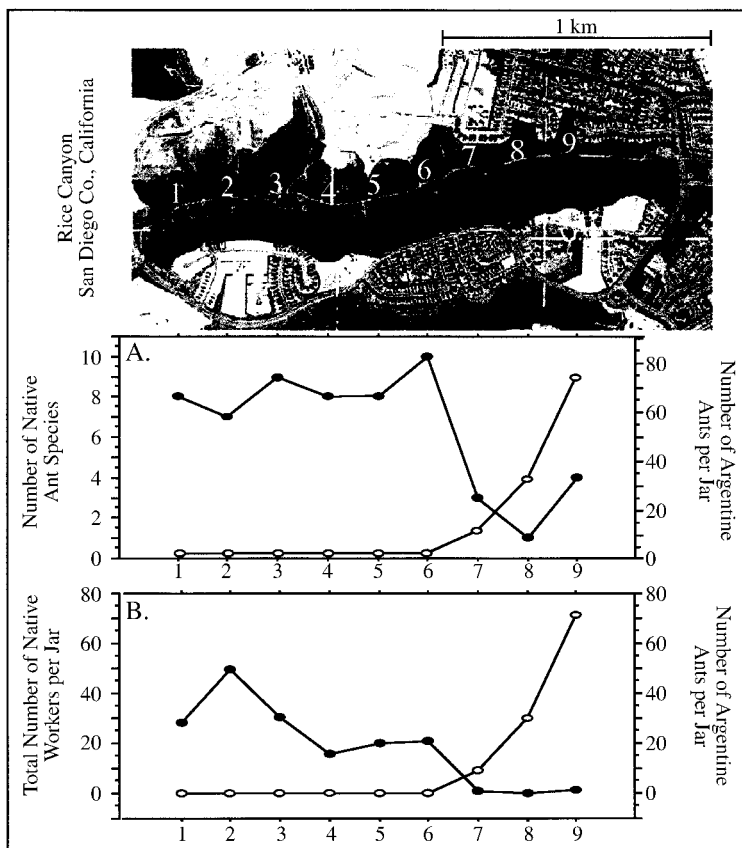
FIG. 6. Photograph of Rice Canyon (number 3 of Table 1) and a transect of sampling points, which runs the length of the canyon. The developed area on the north edge of the canyon begins at point 7 and continues east through point 9. (A) The number of native ant species (●) detected at each sample array along with the number of Argentine ants (○) per jar at each sample array; (B) the average number of native ant workers for all species combined (●) per jar along with the number of Argentine ants (○) per jar at each array.

predictor of log Argentine ant activity ($P < 0.005$) (Table 4B).

Plots within continuous habitat

A total of 28 native species of ants were detected throughout the Elliot reserve, 24 of which were epigeic and included in the analysis (Table 2). The Argentine ant was abundant along the north and east edges of the reserve where a large grove of exotic eucalyptus trees outlines the edges of the reserve. Two fronts of Argentine ants were identified, one penetrating over 400 m into the reserve, but no Argentine ants were found in any of our control plots. The regression slope of

native ant species on area was significantly lower in plots within continuous vegetation than in isolated fragments ($t = 2.52$; df = 40; $P < 0.01$) (Fig. 7).

A dichotomy in total number of native ant species is apparent among the largest of the isolated fragments (>30 ha) (Fig. 7). Six of the fragments lay above the regression line, while four lay below. This separation in total species number among the largest fragments is best explained by Argentine ant presence within these fragments. All six fragments that lie above the regression line contain a mean of <5 Argentine ants per jar while the fragments below the regression line contain a mean of >10 Argentine ants per jar. The age, per-

TABLE 3. Correlation matrix for the variables associated with fragmentation presented in Table 1.

	Log area	Log age	Native veg. (%)	Irregularity	Isolation distance
Log area	1.000	−0.153	0.347	−0.373	0.039
Log age		1.000	−0.766*	−0.143	0.632*
Native veg. (%)			1.000	0.047	−0.455*
Irregularity				1.000	−0.056
Isolation distance					1.000

* Indicates significance (df = 38, $P < 0.05$) using the sequential Bonferroni test (Rice 1989).

TABLE 4. Stepwise regression models using the parameters in Table 1 to account for variation across fragments in the number of ground-foraging native ant species (A) and the average Argentine ant activity (workers per jar) found within those fragments (B).

Variable	Coefficient	SE	F to remove
A) Dependent variable: log native ant species + 1†			
Intercept	1.000	0.124	65.254
Log area	0.244	0.052	21.646
Log age	−0.254	0.066	14.979
Log Argentine ant activity	−0.256	0.063	16.544
B) Dependent variable: log Argentine ant activity‡			
Intercept	1.336	0.144	86.079
Log area	−0.382	−0.422	9.232

† Total df = 36; R^2 = 0.747; $P < 0.001$. Variables not significant in model: percentage remaining native vegetation, irregularity index, isolation distance.

‡ Total df = 38; R^2 = 0.195; $P < 0.005$. Variables not significant in model: log age, percentage remaining vegetation, irregularity index, isolation distance.

centage remaining vegetation, edge index, or isolation distance of these fragments did not separate into these same two groups, suggesting that the penetration of Argentine ants into large fragments reduces the effectiveness of large areas in preserving the total number of native ant species.

Species vulnerability

Three of the measured variables associated with the fragments (age, area, and Argentine ant activity) explained a significant amount of the variation in total native species number (Table 4). Logistic regressions were used to estimate the incidence of various species and species groups as a function of these three variables.

Logistic regressions of presence/absence data for the fragments revealed that the same species or species groups significantly associated with Argentine ant activity (Fig. 8) were also associated with fragment area (Fig. 9). *Prenolepis imparis* is the least vulnerable species and *Neivamyrmex* spp. are the most sensitive. The presence/absence of only five species or species groups were significantly predicted by a logistic regression on age of the habitat fragment (Fig. 10). The genus *Neivamyrmex* was again the most sensitive group.

Solenopsis molesta and *Leptothorax andrei* occur in most habitat fragments sampled, 34 and 32 of 40 fragments, respectively, and were not significantly associated with age, area, or the presence of the Argentine ant.

Ward (1987) suggested that *Prenolepis imparis* was not as sensitive to the presence of Argentine ants due to a segregation in seasonal peak activity periods. To test this we plotted percentage of total seasonal activity by month for *Prenolepis imparis* and the Argentine ant, as estimated from the number of workers captured in pitfall traps for all fragments that contained both species (Fig. 11). There is a seasonal segregation in peak activity period. This pattern was not seen for any other native ant species.

DISCUSSION

Within-fragment patterns.—Our study suggests that the native epigeic ant communities in the scrub habitats of coastal southern California are severely reduced in areas occupied by Argentine ants (Fig. 3). Spatial patterns of Argentine ant abundance suggest that they are invading native habitats from adjacent developed areas. Within fragments, Argentine ants were most abundant along edges and their densities decreased with distance from the edge (Fig. 4A). Areas sampled >200 m from an urban edge contained few (<1 ant per jar on average) or no Argentine ants. Native ant species were more abundant away from edges and in areas with predominately native vegetation (Fig. 4). These patterns suggest that edge effects post fragmentation reduce the ability of fragments to retain native species.

Support for the loss of native ant species as a result of edge effects associated with development and the subsequent presence of Argentine ant comes from Rice
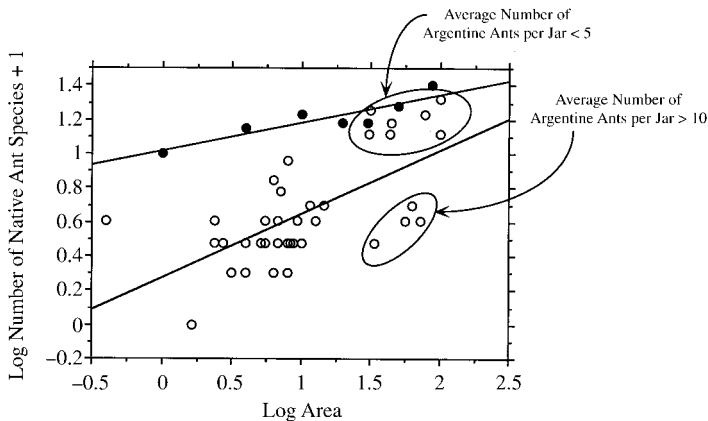

FIG. 7. Regression of the log number of native ant species + 1 detected within a fragment vs. the log area in hectares of that fragment (○) ($y = 0.271 + 0.372x$; $R^2 = 0.441$). The circled fragments above the regression line all contain an average of <5 Argentine ants per jar. The circled fragments below the regression line all contain an average of >10 Argentine ants per jar. Regression of the log number of native ant species + 1 detected within a plot at the UC Elliot reserve vs. the area in hectares of that plot (●) ($y = 1.013 + 0.164x$; $R^2 = 0.806$).
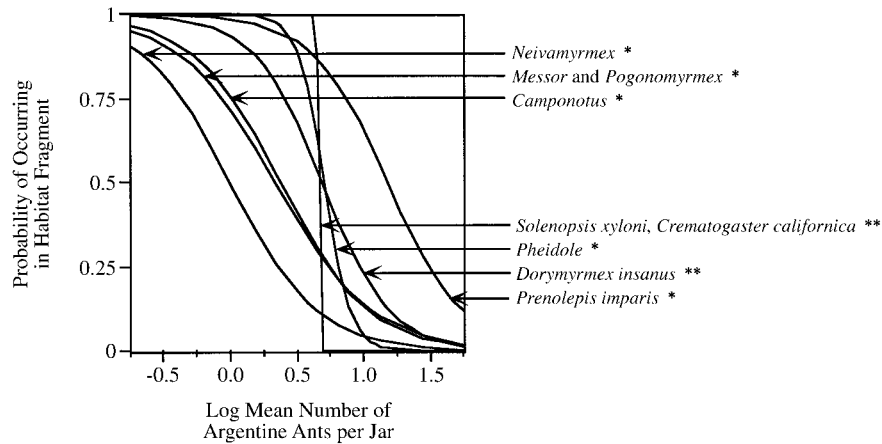
FIG. 8. Logistic regressions of presence/absence data for native ant species and species groups within a fragment vs. the log mean number of Argentine ants per jar (* $P < 0.05$; ** $P < 0.01$). See *Methods: Statistical treatments* for explanation of the species grouping.

Canyon (Fig. 6). These graphs suggest that the presence of the Argentine ant may be dependent on human-mediated disturbance, i.e., water runoff from developed areas. The combination of this disturbance and the presence of the Argentine ant result in a decline in the number of native ant species even before exotic plant species invade. The four native ant species remaining in areas occupied by the Argentine ant within Rice Canyon, albeit in low abundances, are *Solenopsis molesta, Leptothorax andrei, Prenolepis imparis,* and *Dorymyrmex insanus* (of which only one worker was detected). These are the same four species found to be the least vulnerable to both habitat loss and the presence of Argentine ants among fragments (Table 2, Figs. 8 and 9).

Habitat degradation associated with the fragmentation of these canyons can cause a decline in the number of native ant species if they are dependent on the native vegetation for existence. The percentage of remaining native vegetation is highly correlated with the age of the habitat fragment (Table 3) and the distance to the nearest edge (Fig. 5), suggesting that the vegetation changes may be the causal factor responsible for edge effects and the negative effect of age on native species number. However, the results of the stepwise multiple regression suggest that the remaining amount of native vegetation within a fragment did not significantly explain any of the variation in the number of native ant species. In Rice Canyon (Fig. 6) the Argentine ant has penetrated into the fragment from urban development at the east end and displaced native ants. The vegetation, however, is still undisturbed (A. V. Suarez, *personal observation*). At the University of California's Elliot Reserve, Argentine ants have displaced native ants over 400 m into the reserve, and at Torry Pines State Park Argentine ants have penetrated over 1 km into the park (J. King, *unpublished data*), both in areas with predominately native vegetation. In ant surveys of South African fynbos shrubland, De Kock and Giliomee (1989) only found the Argentine ant at disturbed sites near residential areas. Argentine ant penetration into natural areas was dependent on road access, par-
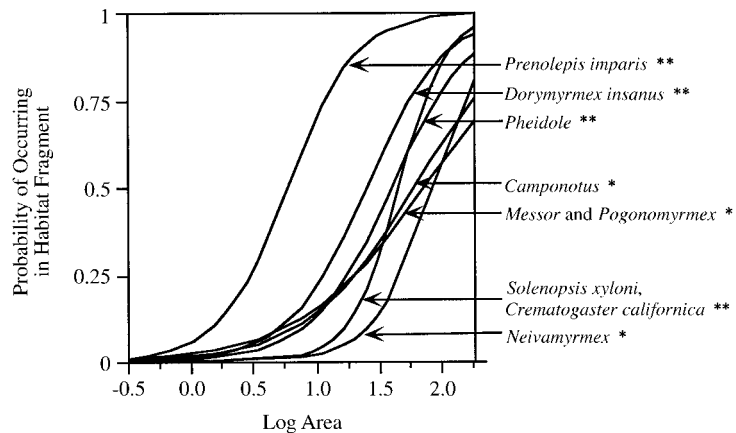
FIG. 9. Logistic regressions of presence/absence data for native ant species and species groups within a fragment vs. the log area in hectares of the fragment (* $P < 0.05$; ** $P < 0.01$). See *Methods: Statistical treatments* for explanation of the species grouping.
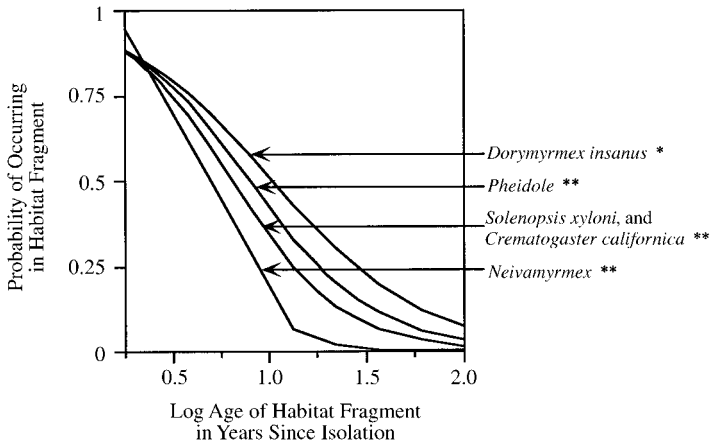
Fig. 10. Logistic regressions of presence/absence data for native ant species and species groups within a fragment vs. the log number of years since the fragment was isolated from continuous scrub land (* $P < 0.05$; ** $P < 0.01$). See *Methods*: *Statistical treatments* for explanation of the species grouping.

ticularly tarred roads, and Argentine ant presence was not correlated with the presence of invasive plants. This evidence suggests that Argentine ants are able to penetrate into areas regardless of the presence of exotic vegetation. The distance they can invade into natural habitat varies among sites and is correlated with human-mediated disturbance. Factors that contribute to the spread of the Argentine ant are probably held in common with those that facilitate the spread of exotic vegetation.

Among-fragment patterns.—Not surprisingly, habitat area best predicted the number of native ant species (Table 4A). Some of this effect may be due to chance sampling of rare species such as *Solenopsis amblychila* and *Cyphomyrmex wheeleri* (Table 2). However, our results suggest that the lower species richness in small fragments is not entirely due to a sampling effect, but rather due to the loss of species following fragmentation.

The negative relationship between native ant species number and time since fragment isolation (Table 4A) implies that local extinctions have occurred in habitat fragments and recolonizations have been rare or absent. The best evidence of prefragmentation species richness comes from the control plots (1–50 ha) within contin-

uous habitat, which contain 16.4 ± 4.6 (mean ± SD) native ant species. In contrast, isolated fragments (1–100 ha) contain only 5.9 ± 4.9 native ant species. This implies that those species have been lost since isolation of the habitat.

Argentine ant abundance decreases with increasing fragment size (Table 4B). This may be a direct result of the association of higher abundances of Argentine ants with urban edges (Fig. 4A). Smaller fragments do not include areas of habitat >100–200 m from an edge. Thus, even in the interior of a smaller fragment, Argentine ants will be abundant. In larger fragments, more area is available distant from urban edges, where Argentine ant activity is low or absent. The effect of fragment area on native species number may directly result from the presence of Argentine ant-free refugia found only in the largest fragments with habitat >200 m from the nearest urban edge.

Argentine ants invade rapidly into areas after urbanization as evidenced by the lack of an effect of fragment age on Argentine ant activity (Table 4B). This is also illustrated in Rice Canyon where Argentine ants have already taken over the eastern third of the canyon within 3 yr of development (Fig. 6). The lack of a lag time for invasion suggests that appropriate measures need
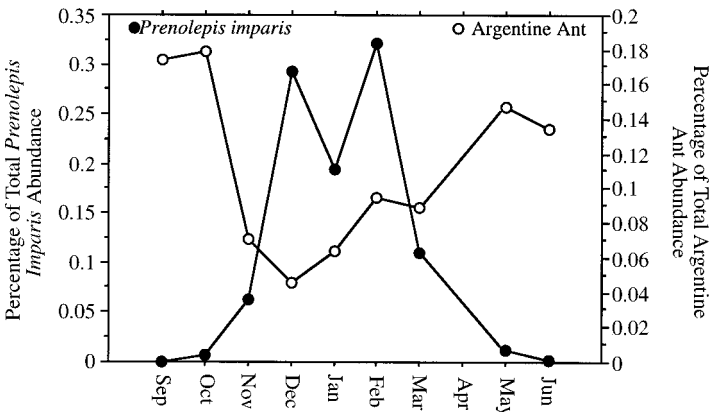

Fig. 11. Seasonal activity patterns of Argentine ants and *Prenolepis imparis*. The percentage of total abundance was calculated by averaging numbers of individuals captured per jar for all canyons combined for each month and dividing by the total number of individuals captured.

to be taken immediately after isolation if a habitat fragment is to be protected against invasion from the Argentine ant.

Argentine ants.—Previous work on this system of fragments in San Diego county with chaparral-dependent birds implies that extinction is occurring post fragmentation, although the causal factors contributing to extinction are still unknown (Soulé et al. 1988, Bolger et al. 1991). In our study, we have implicated a causal agent of local extinction for native ants, the exotic Argentine ant.

The Argentine ant's success in displacing native ants derives from their ability to aggressively monopolize resources (exploitative competition) and prey upon native ants (interference competition) (Tremper 1976, Human and Gordon 1996; Holway, *in press*). In our surveys, we frequently witnessed Argentine ants aggressively attacking native ant colonies. The Argentine ants would overcome native ant colonies by sheer numbers, frequently combining their attacks on the larger native ant species such as the harvester ants (A. V. Suarez, *personal observation*). Previous work has also shown that Argentine ants will find baits faster and recruit more workers to baits than native ants (Human and Gordon 1996; Holway, *in press*).

Argentine ants appear to be most successful near urban edges (Figs. 4 and 6). Their success may be facilitated by human-mediated disturbances, such as the presence of exotic vegetation, changes in soil conditions, and an increase in moisture associated with developed areas. What limits their invasion is unclear, although they appear to dependent on moisture (Hertzer 1930) and are subsequently unsuccessful in arid environments (Smith 1936). The remaining native habitat in coastal southern California consists primarily of canyons surrounded by urban developments (Soulé et al. 1988). The water runoff from these developments accumulates in the canyons, which may result in favorable conditions for Argentine ants.

Species vulnerability.—Some native ant species are more resistant to extinction due to fragmentation and invasion than others. *Solenopsis molesta, Leptothorax andrei,* and *Prenolepis imparis* occurred in nearly every fragment surveyed (Table 2). *Prenolepis imparis* has previously been shown to persist in areas with Argentine ants in other studies (Ward 1987, Human and Gordon 1996). Unlike most native epigeic species, *P. imparis* is most active in the winter months (Tschinkel 1987), the opposite of the highest activity periods of Argentine ants (Fig. 11). Temporal niche partitioning may allow long-term coexistence between these two species (Ward 1987).

Solenopsis molesta was the least vulnerable of all ant species to fragmentation and invasion, occurring in 34 of 40 fragments (Table 2). It has been reported to forage only up to 10 m from the nest (Human and Gordon 1996) and may not need large areas to support large populations. *Solenopsis molesta* has also been reported to be a kleptoparasite of other ant species (Wheeler and Wheeler 1973, Snelling and George 1979). This parasitic association is common between *S. molesta* and the Argentine ant in at least one of the fragments surveyed (A. V. Suarez and T. J. Case, *unpublished data*).

Leptothorax andrei occurred in 32 of 40 fragments. *Leptothorax andrei* workers are very small, averaging ~2.0 mm in length and are often categorized as hypogeic or belowground foraging (Ward 1987). It is possible that the small size and cryptobiotic nature of *L. andrei* reduces competition for resources such as nesting space and food with the larger, aboveground-foraging Argentine ant (2.5–3.0 mm).

The genus *Neivamyrmex* (army ants) include the most vulnerable species (Figs. 8, 9, and 10). These ants were only found in the largest fragments and in areas without any Argentine ants. Ants in the genus *Neivamyrmex* are very specialized foragers. Their colonies are mobile and set up temporary bivouacs between periods of nomadism. Queens within the genus *Neivamyrmex* are wingless and do not undergo nuptial flights, limiting their dispersal and colonization abilities (Gotwald 1995). These characters, i.e., the high degree of nomadism and lack of winged dispersal, make this genus very susceptible to fragmentation.

Harvester ants were also vulnerable to the presence of Argentine ants (Fig. 8). Their importance as seed predators/dispersers and as a food source for ant specialists such as horned lizards (*Phrynosoma coronatum*) suggests that their disappearance from an area could affect other trophic levels within coastal scrub ecosystems. In South African fynbos shrublands, at least one plant species whose seeds are dispersed by ants suffered reduced seedling emergence in areas infested with the exotic Argentine ant (Bond and Slingsby 1984). The indirect effects of Argentine ants on other aspects of the community due to the loss of species such as harvester ants still need to be measured and may be extremely detrimental.

Many ant communities have been shown to be structured based on competition within foraging guilds (Hansen 1978, Lynch et al. 1980, Cole 1983, Davidson 1977a, b, Rosengren 1986, Fellers 1987, Savolainen and Vespsalainen 1988, Ryti and Case 1988, 1992, Andersen and Patel 1994). This may make them particularly sensitive to community perturbations, especially the introduction of another competitor. Some communities may be more vulnerable to invasive species than others. The United States may be particularly prone to exotic ant invasions (Andersen 1997), as demonstrated by the Argentine ant (Smith 1936, Tremper 1976, Human and Gordon 1996), and the red imported fire ant, *Solenopsis invicta* (Tschinkel 1988, Porter and Savignano 1990, Vinson 1994). Like the Argentine ant, *Solenopsis invicta* is associated with human disturbance (Tschinkel 1988), has been demonstrated to displace most native ant species (Stein and Thorvilson

1989, Porter and Savignano 1990), selected arthropods (Hooper 1976, Porter and Savignano 1990), and has even been shown to have detrimental impacts on vertebrate populations (Vinson 1994, Allen et al. 1995). The invasibility of ant communities in the United States may result from the lack of behaviorally dominant species, such as the *Iridomyrmex* spp. of Australia (Andersen and Patel 1994, Andersen 1997), as well as from being relatively species poor (Elton 1958, Andersen 1997).

Conclusions

Our data suggest that local extinctions of native ant species occur in habitat fragments in coastal southern California. Most theory regarding species loss following fragmentation predicts an increase in extinction probability due to stochastic factors, either demographic or environmental, as a result of small population sizes associated with a decrease in total area. However, the importance of deterministic factors, such as detrimental edge effects, are thought to be secondary causes of extinction and are often overlooked. In our study we have implicated a causal agent of local extinction of native ants, the exotic Argentine ant. Our data suggest that in coastal southern California, smaller fragments lack refugia from Argentine ants, and this increases the chance of local extinction of native ants in these fragments.

Native ant species diversity is negatively correlated with the presence of the Argentine ant and the number of years since fragment isolation (age), and positively correlated with fragment area. A small part of the species–area relationship may be due to the sampling effect exerted by the fragment at the time of isolation for some rare species, but we conclude that it is primarily due to the extinction of common native species occurring post fragmentation, due to invasion by Argentine ants.

Argentine ants are abundant in coastal scrub habitats in southern California and were found in all 40 fragments surveyed as well as around the edge of larger, unfragmented habitats. The Argentine ant can spread into an area immediately after isolation from surrounding urban edges where they are most abundant. The association between Argentine ant activity and distance to the nearest urban edge suggests that urban reserves in coastal southern California will only be effective at maintaining natural populations of native ants at distances >200 m from an edge. Argentine ants can follow roads deep into reserves (De Kock and Giliomee 1989) and in larger fragments, internal edges may be as detrimental as external boundary edges.

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